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THE EVOLUTION OF COURTSHIP BEHAVIOR IN SALAMANDERS

by

Stevan James Arnold

Volume I

A dissertation submitted in partial fulfillment
of the requirements for the degree of
Doctor of Philosophy
(Zoology)
in The University of Michigan
1972

Doctoral Committee:

Associate Professor Arnold G. Kluge, Co-Chairman
Professor Richard D. Alexander, Co-Chairman
Associate Professor Brian A. Hazlett
Professor John A. Jacquez

Beware of the dull hand of competence in pursuit of a narrow empiricism.

- R. Levins (1966)

Theory like fog on glasses, cloud facts.

- C. Chan (1933)

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This work is dedicated to those naturalists with a sustained curiosity about the courtship of salamanders; Francesco Gasco, Jacob von Bedriaga, Ernst Zeller, G. Kingsley Noble, James O. Organ and Robert Thorn.

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INTRODUCTION

The courtship behavior of salamanders has fascinated naturalists for a long time. This fascination is not surprising for salamander courtship is so complex and elegant that it would delight any choreographer. Much of this extraordinary complexity is a consequence of the peculiar means by which insemination is accomplished in many salamanders. Rather than transferring sperm to the female directly by means of an intromittent organ, many salamander males attach a sperm bearing structure (the spermatophore) to the substrate. The female must then retrieve sperm mass with her vent. Before and during this process, the male runs, swims and leaps about the female and moves his body, limbs and tail in a bewildering variety of ways.

Early interest in salamander courtship behavior focused on the mechanism of insemination. A flurry of interest was created by the startling discovery that fertilization was internal and accomplished by means of spermatophores (see Zeller, 1890 for a fascinating historical survey). Later, workers discovered that fertilization was external in some salamanders (Smith, 1907; Sasaki, 1924).

Dunn (1923), and later Noble (1931), were the first workers to consider courtship behavior valuable indicators of phylogenetic relationships among salamanders. Subsequently many investigators have sought to compare their observations with published accounts and have used Dunn's and particularly Noble's insights to organize their interpretations. Salthe (1967) has recently summarized much of the available literature on salamander courtship behavior and presented a large body of speculation about the adaptive significance and phylogenetic modification of courtship behavior.

Since Salthe's (1967) review much new information has come to light. This new information, together with my own observations, suggests that many evolutionary interpretations of courtship can now be re-evaluated. In addition we now have enough information about courtship behaviour in salamanders to look at the phenomenon from some new perspectives. In particular, "What is the adaptive significance of the temporal organization of courtship behaviour in particular salamander species?". Why should the courtship of some species take so long and be so complex, and be so "straight-forward" in other species? Why should some species terminate courtship after only one spermatophore is deposited when other species continue to court until 40 or more spermatophores are deposited?

The first chapter attempts to answer these questions by focusing on three species. In the second chapter I deal with these questions from a historical perspective. Here I attempt to reconstruct the phylogeny of courtship behaviour in salamanders, suggest what courtship behaviour was like in ancestral salamanders, and speculate about the evolutionary processes which have changed courtship behaviour in evolutionary time.

MATERIALS AND METHODS

The sources of animals used are listed in Appendix II.

Animals were maintained on a natural photoperiod either by housing them in a room with a skylight or by setting the artificial photoperiod in the observation room to coincide with outside photoperiod. Temperatures during maintenance of animals and observations ranged from 55-65 degrees F (exceptions are indicated in the text). Animals were fed every several days. Terrestrial species were fed flies (domestic houseflies or blowflies), crickets or earthworms; and aquatic species were fed earthworms or chopped chicken liver. Individuals which were maintained for two weeks or less (eg. Plethodon and Ambystoma) were sometimes not fed.

In all cases observations are based on spontaneous courtship behaviour. In no case were hormones or drugs administered to induce courtship behaviour. Spontaneous courtship behaviour was obtained by collecting the animals during the natural courtship season and moving them as quickly as possible to the observation room.

In general observations were made on captive animals with only a pair housed together during observations. Pairs of pethodontid salamanders were housed together continuously, while pairs of salamandrids and ambystomatids were placed together only during observation sessions. For these last two families, when observations were not in progress the sexes were segregated either by returning males and females to separate male and female containers or by segregating individuals.

Species in which courtship behaviour is nocturnal (eg. plethodontids) were observed at night with dim, white light illumination.

A special procedure was adopted for some Ambystoma species (A. maculatum, A. tigrinum, A. texanum and A. laterale). Animals were collected as they migrated to breeding ponds. They were then housed in containers with damp leaf litter at 40-45 degrees F. They were placed in water only during observation sessions and then immediately returned to the leaf litter containers when observations were over. Other species which court under water (eg. salamandrids) were housed continuously in water.

A variety of containers were used to observe aquatic courtship but frequently large 30 gallon observation tanks were employed. Terrestrial courtship was observed in containers with only a moist paper towel substrate. Usually plastic shoeboxes (15cm x 29 cm x 8.5 cm high) were used, but sometimes larger (10 or 15 gallon) glass aquaria were used.

Records of courtship behaviour were made by tape recording a verbal description of ongoing activities (with either a Norelco dictaphone or a Uher-Report L tape recorder), by making handwritten notes and sketches, or by still and motion picture photography. Each of these recording devices has its own particular virtues, and whenever possible I recorded observations of courtship in all these ways.

Motion pictures were made with 16mm film (usually Kodak 4X reversal film) at 18 or 22 frames per second. Bolex and Pathe motion picture cameras were used. Relatively long sequences of behaviour (12-15 minutes) were filmed using a 400 ft magazine. Still photographs were made with 35mm film (usually Kodak Panatomic X or Tri-X) using a Pentax Spotmatic camera with a "macrolens".

For species with nocturnal courtship it was necessary to supplement the usual dim illumination during photography sessions. During still photography a very bright electronic flash was employed (1/1000 sec in duration). This brief flash of light never appeared to interrupt or otherwise affect courtship behaviour. During motion picture photography, however, I employed continuous bright light from one or two flood lamps. The onset of continuous bright light tended to interrupt behaviour during preliminary courtship. By either increasing the illumination very gradually or by waiting until courtship had progressed to the context of spermatophore deposition and sperm transfer, I found that nocturnal species would continue to court under bright illumination. I noticed no changes in courtship activities shown under these circumstances compared with activities shown in very dim light.

Courtship accounts for each species were then compiled from tape-recorded observations, handwritten notes and sketches, still photographs and movies.

For each species in which I have observed courtship behaviour, I have presented my observations with the same format. I first define a set of behavioral actions performed by the male, and then discuss how these actions are arranged in time during courtship encounters. In the latter section, for each species, I have concentrated on how changes in male behavior are related to changes in female behavior. The list of male actions constitutes the "vocabulary" of male courtship, and the section on temporal relations is the "grammar" of courtship in that species.

When defining the list of male actions for each species, I frequently had to decide whether to distinguish or lump two male actions. I often employed the following methodological insight (credited to R. D. Alexander by S. Altmann (1965)); two actions were recognized when two actions were recognized by the courting animals. For example in many species I distinguish between two male actions which differ only because in one case a spermatophore is deposited. The distinction is important because a specific cue is required from the female before the male actually completes the action and deposits a spermatophore. The male actually "recognizes" two actions and executes the second action, which includes a spermatophore deposition, only when the female indicates that she is likely to retrieve sperm from a spermatophore.

I do not pretend that the "vocabulary" and "grammar" is completely understood for each species I have observed. Often only a few observation sessions are required to establish the basic "vocabulary" of courtship. But even so, some "words" (eg. spermatophore deposition) are relatively rare. Consequently the "vocabularly" for each species will always be incomplete (see Altmann, 1965 for a discussion of this problem). The "grammar" of courtship is even more elusive. In a few instances I have attempted to elucidate the "grammar" of courtship by tabulation and statistical analysis of the ordering of "words" during courtship. This approach is fruitful in particular instances, but it is impractical to apply these approaches to very many species. For most species I have simply summarized the temporal sequences which occurred during my observations, without any numerical qualifications. Nevertheless these discussions of temporal relations in each species provide a minimum estimate of the complexity that is present in courtship behavior, and suggest many hypotheses about the "casual basis" and adaptive significance of courtship.

In many cases I have used an abbreviated style to refer to the body regions of salamanders. For example, the short-hand notation "dorsal proximal tail" should be taken to mean "the dorsal surface of the proximal portion of the tail". "Midbody" refers to the body region between the insertion of the forelimbs and the insertion of the hindlimbs (i.e. the trunk).

It is very difficult to visualize behavior from just a verbal description. Much of the subtle grace of movement during courtship has been lost in my attempts to portray the variability of courtship sequences in each species. Gasco and Bedriaga succeeded in capturing the elegance of courtship with vivid descriptive language, and their works should be consulted to really visualize courtship behavior. Wherever possible I have provided figures of courting animals from photographs and movies. Sometimes the esthetics of courtship behavior can be appreciated from these figures.

In all cases line drawings were made by tracing photographs or motion picture frames of courting animals.

Most arithmetic calculations, including statistical testing and analysis of information transmission, and some figures were done by computer (IBM 360) at the University of Michigan.

The taxonomy of salamanders that I have employed follows Brame (1967).

CHAPTER I.

COURTSHIP BEHAVIOR AND NATURAL SELECTION

INTRODUCTION

The purpose of this chapter is to discover how and why natural selection modifies courtship behavior. I purposefully chose two species (Ambystoma maculatum and Plethodon jordani) for comparison which differ greatly in several aspects of courtship behavior (eg. in the number of spermatophores deposited by a male per courtship and the rate of spermatophore deposition). Later I included a third species (Ambystoma tigrinum) which appeared intermediate in these respects. I assume that in each of these species courtship behavior has responded to a long history of selection for the reproductive success of individuals. Therefore, differences between these species in courtship behavior represent either alternative solutions to the same selective pressures or solutions to different selective pressures. The problem is then to (1) identify aspects of courtship behavior which bear directly on the reproductive success of individuals, (2) to see whether species differ in these aspects of courtship behavior, and (3) to determine whether the differences are due to differences in the selective pressures experienced by the three species.

During evolution there has been relatively little modification of female sexual behavior in salamanders. In contrast the overt sexual behavior of the male has been modified extensively. For this reason I will deal principally with aspects of male behavior.

The probability that the male will inseminate the female is the single most importantindex of male reproductive success in a courtship encounter. Consequently I have focused on aspects of male behavior which might influence this probability.

Of the three species Ambystoma tigrinum has the widest geographic distribution. It is found from coast to coast in the United States but with some major discontinuities in distribution. Ambystoma maculatum is broadly distributed in eastern United States. Plethodon jordani is restricted to the Appalachian Mountains. Fertilization is internal in all three species. Both Ambystoma species court and lay their eggs under water in ponds, while Plethodon jordani courts and lays eggs on land. Other aspects of the general biology of these species will be discussed in the sections which follow.

MATERIALS AND METHODS

Observations on Ambystoma maculatum are based on animals from two localities; Goss Pond, near Dixboro (S. E. of the intersection of Goss and Earhart Rds.), Washtenaw Co., Michigan, and the Edwin S. George Reserve (University of Michigan, Museum of Zoology), near Pinckney, Livingston Co., Michigan (abbreviated hereafter as E.S.G.R.). Ambystoma tigrinum are from the E.S.G.R., Livingston Co., Michigan. Plethodon jordani are from the south side of Whitetop Mtn., (4200-4800 ft), Grayson Co., Virginia. The courtship description which follows and all experiments with Plethodon jordani are based on animals from this one locality. Figures of courtship activities are based on animals from two other localities (see figures), but I detected no differences in courtship behavior between animals from these three localities.

Laboratory observations and experiments with multiple males courting with a single female are based upon Ambystoma maculatum males courting with females from Goss Pond, but all other observations are based on A. maculatum from Goss Pond. I made separate observations on the number of spermatophores deposited per courtship by males from both of these localities.

Ambystoma maculatum and A. tigrinum were collected as they migrated to breeding ponds in early spring (1969, 1970, 1971) either by patrolling the margins of the pond (at Goss Pond) or by trapping animals with drift fences (on the E.S.G.R. through the courtesy of H. Wilbur). Consequently the males had not yet deposited spermatophores, or courted, and the females had not yet been inseminated that breeding season. All courtship observations were made within 10 days of the date of capture. From soon after the time of capture until observations were made the animals were housed in damp leaf litter in a refrigerator at 40 deg. F. Once a male had deposited spermatophores and once a female had been inseminated, they were returned to their breeding ponds.

Plethodon jordani were collected during the courtship season in July, August and September (1968, 1969, 1970). Observations of courtship were made at night with dim light illumination. A male and a female were housed together in a terrarium with a moist paper towel substrate. They were left together during the few weeks they were held for observations. Air temperatures were 55-60 deg. F.

Observations of courtship behavior in *Ambystoma maculatum* and *A. tigrinum* were made at night in large aquaria with a wooden substrate and a water temperature of 50-60 deg. F.

I observed courtship in approximately 10 pairs of *Ambystoma tigrinum*, 30 pairs of *Ambystoma maculatum* and 50 pairs of *Plethodon jordani*.

Records of courtship behavior were made by filming courtship in *Ambystoma maculatum* and *A. tigrinum* and by describing courtship into a tape recorder in *Plethodon jordani*. Accounts of courtship behavior in each species were compiled from these records.

RESULTS

A. Accounts of courtship behavior

Ambystoma maculatum

Catalog of male actions

A.) NUDGING. The male contacts his lateral snout to the female's lateral body (Fig. 3I).

B.) HEAD-SWINGING. The male swings his head laterally to and fro in short arcs with his mentum or chin in contact with the female's body.

C.) LIFTING. The male lifts his head with the dorsum of his head or snout in contact with the female's ventral body (Fig. 1A, 3K). The male may simultaneously turn his head sharply to one side towards the female (Fig.1B).

D.) VENT-SHUFFLING. The male shuffles the vent laterally in contact with the substrate by swinging the entire posterior body and tail from side to side. This action may be performed with the male stationary or while moving forward slowly (Fig. 1C, G, H, L).

E.) MALE STATIONARY - HINDLIMBS ADPRESSED. While stationary the male adpresses his hindlimbs against his lateral tail base. The hindlimbs are slightly raised from the substrate, and the midbody is arched upwards slightly so that only the sacrum, vent and pectoral region contact the substrate. The tail is level and may be slowly undulated (Fig. 2E).

F.) SPERMATOPHORE DEPOSITION. When spermatophore depositions occur they follow the preceding action (E). The male is stationary with midbody arched upward slightly, and the vent is thus pressed against the substrate. The hindlimbs are adpressed, and the forelimbs are outstretched with the forefeet raised from the substrate. The male may or may not undulate his tail slowly during spermatophore deposition. Spermatophore deposition terminates with the male arching his tail upwards and lifting his vent free of the spermatophore while moving forward (Fig. 2F).

TEMPORAL RELATIONS (Ambystoma maculatum)

Upon contacting a female, a sexually active male moves rapidly along the length of the female while performing nudging, head-swinging and lifting (Fig. 3I, J, K). The male moves anterior to posterior or posterior to anterior along the female while performing these actions.

Frequently the male moves anterior to the female's head while nudging her laterally or swinging his head in contact with her dorsum, and then lifts (Fig. 1A) and turns towards the female under her chin or anterior midbody (Fig. 1B). He may then proceed posteriorly along the opposite side of the female while nudging her. He may then lift under her tail while turning towards her and continue moving forward anteriorly along the female's side. In this way the male may circle around and around the female while continuously contacting her with his head.

The female may repeatedly turn towards the male as he contacts her and nudge the male laterally or rub his dorsum with her chin by swinging her head laterally.

After nudging and rubbing the female, the male moves away from her while shuffling his vent against the substrate (Fig. 1C, 3L). Vent-shuffling is usually initiated after first lifting under the female's chin. The male may then cease vent-shuffling and move back towards the female and reinitiate nudging and head-swinging (Fig. 2H to 3I). Or after vent-shuffling the male may pause and adpress his hindlimbs (Fig. 1C to 2E). He may then either move forward again shuffling his vent, or he may deposit a spermatophore de novo (as in Fig. 2E to 2F).

Spermatophore depositions are of two types. The male may deposit a spermatophore on top of a pre-existing spermatophore, or he may deposit a spermatophore de novo. In the former case, the male squats upon the original spermatophore, inserting it into his cloaca, and deposits a new gelatinous base, which completely covers the original spermatophore and which bears a new sperm mass at its apex. After such a spermatophore deposition the original sperm mass, if still present, is completely inaccessible to the female. Less frequently the new spermatophore base is attached to the original spermatophore below the original sperm mass, so that a multiple structure is produced with more than one accessible sperm mass.

A shorter sequence of cues is required by the male to deposit a secondary spermatophore than to deposit a spermatophore *de novo*. The male will interrupt any courtship activity (nudging, head-swinging, lifting or vent-shuffling) to deposit a secondary spermatophore, if a spermatophore contacts his vent. When a spermatophore contacts the male's lateral or ventral body, he shifts his body laterally while moving forward so that the spermatophore slides posteriorly in contact with his ventral midline towards his vent. If the spermatophore contacts his vent, he shuffles his vent over the top of it, inserts the spermatophore into his vent and deposits a new sperm bearing structure. In contrast, spermatophores are deposited *de novo* only after the male has just contacted the female with his snout (via nudging or head-swinging), has lifted under her chin (or, less frequently, her tail) and moved away from the female shuffling his vent against the substrate.

After a spermatophore deposition the male moves forward and shuffles his vent against the substrate. He may immediately deposit another spermatophore, if a pre-existing spermatophore contacts his vent, without any intervening contact with the female. Otherwise the male moves rapidly back towards the female and resumes nudging and head-swinging (Fig. 2G to 3I).

A sexually active female orients to spermatophores which contact her lateral or ventral body just as the male does. She shifts her body laterally, to and fro, while moving forward so that the spermatophore slides posteriorly in contact with her ventral midline. If the spermatophore then contacts her vent, she shuffles her vent while squatting upon it and inserts the spermatophore into her cloaca. She then pauses motionless over the spermatophore for several seconds in the same posture that the male assumes while depositing a spermatophore. Her hindlimbs are pressed posteriorly towards her tail base, and her body is arched upward very slightly (Fig. 2H, 3I). She does not undulate her tail. The female moves off of the spermatophore by arching her tail base slightly while moving forward. Sometimes the entire sperm mass is removed by the female, sometimes only a portion of it, and frequently the sperm mass of the spermatophore appears just as massive as before the female squatted upon it.

The male process of depositing spermatophores and the female process of finding them are quite independent activities. The female may be engaged in finding or squatting on a spermatophore while the male is nudging her, head-swinging, lifting, vent-shuffling, depositing a spermatophore, or surfacing for air. The female may be finding a spermatophore, squatting on a spermatophore, nudging the male, moving about, or surfacing for air while the male is depositing a spermatophore.

Frequently the female is several inches or more from the male when she finds a spermatophore. The female may nudge the tail or the tail base of the male as he deposits a spermatophore, and then move forward behind him when he moves forward and finds the spermatophore he has just deposited (as in Fig. 2E to 2H); but this is rather exceptional.

Occasionally the nudgings of the sexual partner will push the other animal forward or to one side and dislodge the female from a spermatophore or the male from the site of spermatophore deposition.

When not finding or squatting on a spermatophore and when not contacting the male, the female may move slowly forward while stepping from side to side with the hindlimbs.

When one animal has separated from the other sexual partner, it tends to turn and move back towards the sexual partner. As a consequence the male's spermatophores and the activities of courtship take place within an area 50cm or less in diameter, even in a large container. When an animal surfaces for air during courtship, it tends to turn after gulping air and swim back down to the site of departure with surprising accuracy.

Wright and Allen (1909) observed _A. maculatum_ from New York courting in the laboratory. The male repeatedly nudged the female with his snout and forced his head under her venter and then departed from the female and deposited a spermatophore. The male alternated between rubbing the female and departing to deposit a spermatophore, so that 22 spermatophores were deposited in 45 minutes. During spermatophore deposition the male grasped a stick with his hindlimbs and undulated his tail momentarily before moving off of the spermatophore. During most of this time the female remained quiescent, but 3 times she moved over a spermatophore and paused with her vent upon it. This female apparently made no effort to take the spermatophore into her cloaca.

I find that females usually insert nearly the entire spermatophore into their cloacae, but they may also simply pause with the vent upon it. The position of the male's hindlimbs during spermatophore deposition depends on the substrate available for spermatophore deposition. Both in the laboratory and in the field I have observed males clasping twigs or leaves with the hindlimbs as they deposit a spermatophore, just as Wright and

Allen (1909) noted. Uzzell (1969) has also observed this phenomenon. The male may also clasp a pre-existing spermatophore with his hindlimbs when depositing a secondary spermatophore. When only a level surface is available for spermatophore deposition, as in my observation tanks, the male presses his hindlimbs backwards towards his tail base during spermatophore deposition.

Figure 1. Courtship activities in Ambystoma maculatum.

Fig. A. The male lifts his head under the female's chin while moving forward (0 sec).

Fig. B. The male turns under the female, towards her body, and begins to move forward away from her (1.0 sec).

Fig. C. The male moves away from the female while shuffling his vent against the substrate. The female is now moving forward over the male's tail (3.0 sec).

Fig. D. The male is stationary with his vent pressed to the substrate and is undulating his tail laterally. The female is stationary (7.4 sec).

(Figures 1, 2 and 3 are taken from a 16mm. movie of one continuous sequence of courtship activities. The times, denoted above in seconds, represent the elapsed time from the onset of the sequence at Fig. 1A. These animals are from Goss Pond, Washtenaw Co., Michigan).

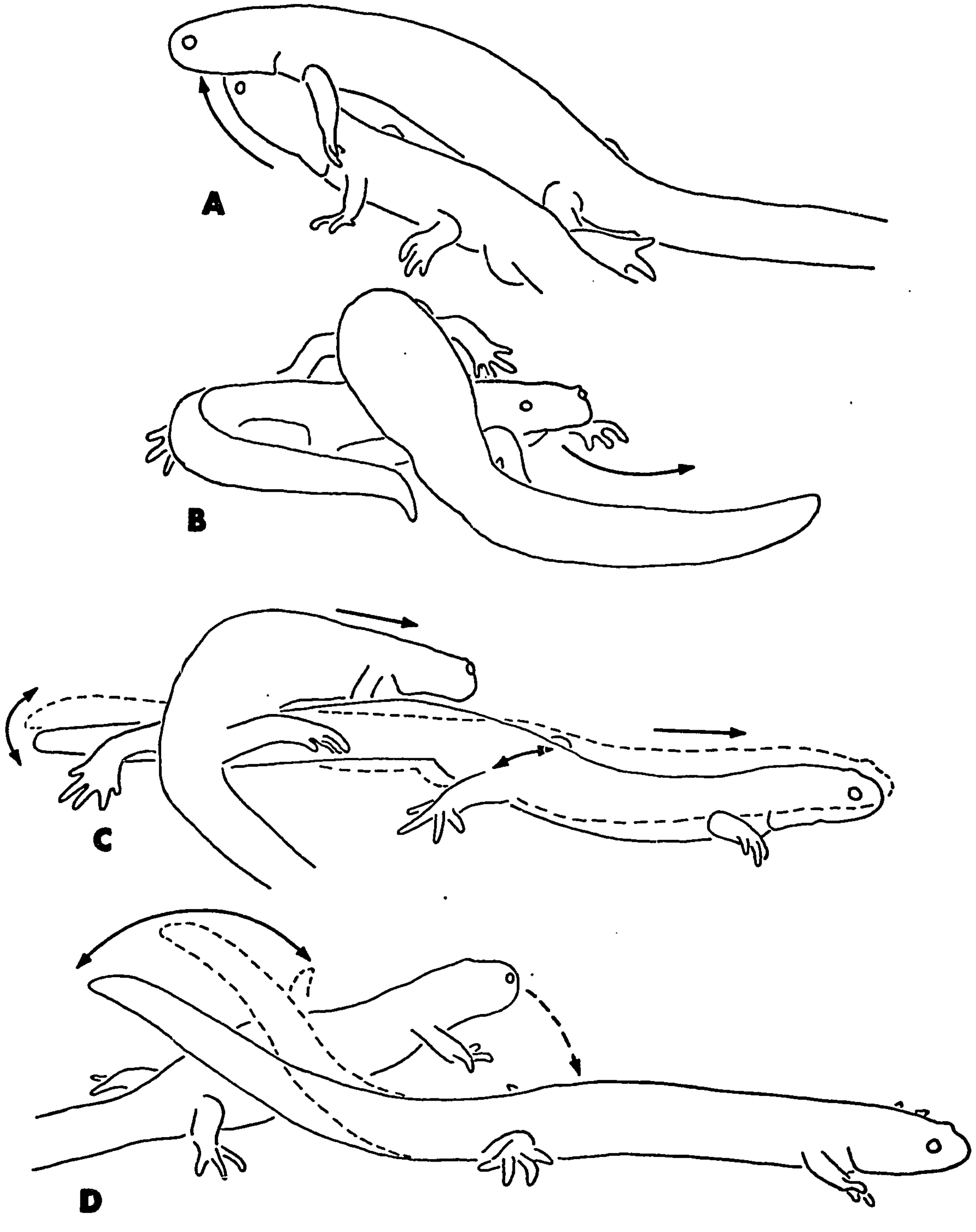

A
B
C
D

Figure 2. Courtship activities in Ambystoma maculatum (continued from Fig. 1). The male is to the right of the female.

Fig. E. The male has initiated spermatophore deposition. The female has turned towards him and is rubbing her snout laterally on his dorsal hindbody (11.4 sec).

Fig. F. The male moves forward off of and away from the spermatophore (indicated with large arrow head). The female is now moving forward along parallel to him (15.7 sec).

Fig. G. The male shuffles his vent laterally against the substrate while moving forward. The female continues moving forward (note position of spermatophore) (18.5 sec).

Fig. H The male continues moving forward and away from the female while shuffling his vent against the substrate. The female has found the spermatophore with her vent, lowered her vent upon, and is pausing with the spermatophore inserted into her cloaca (23.1 sec).

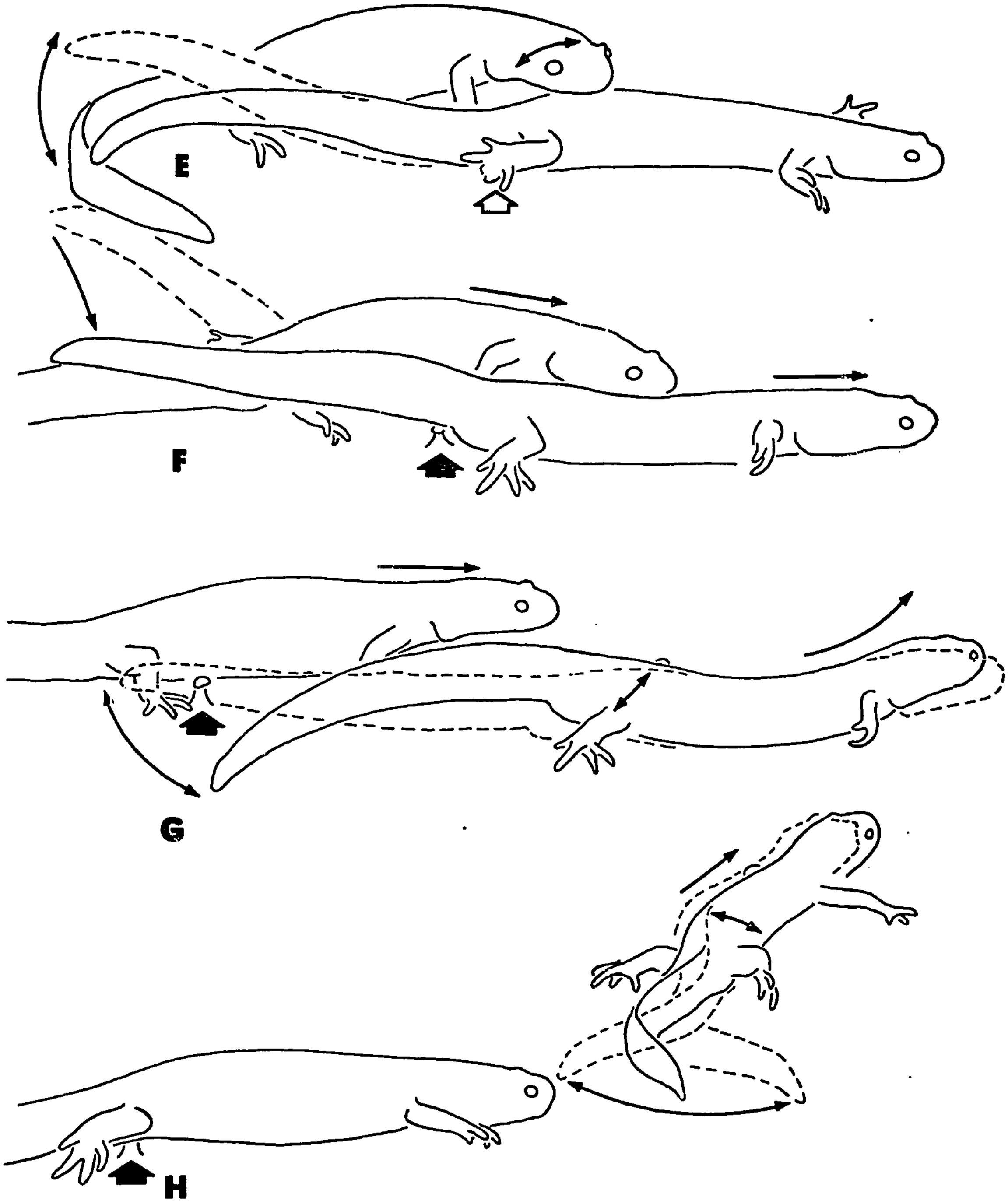

E
F
G
H

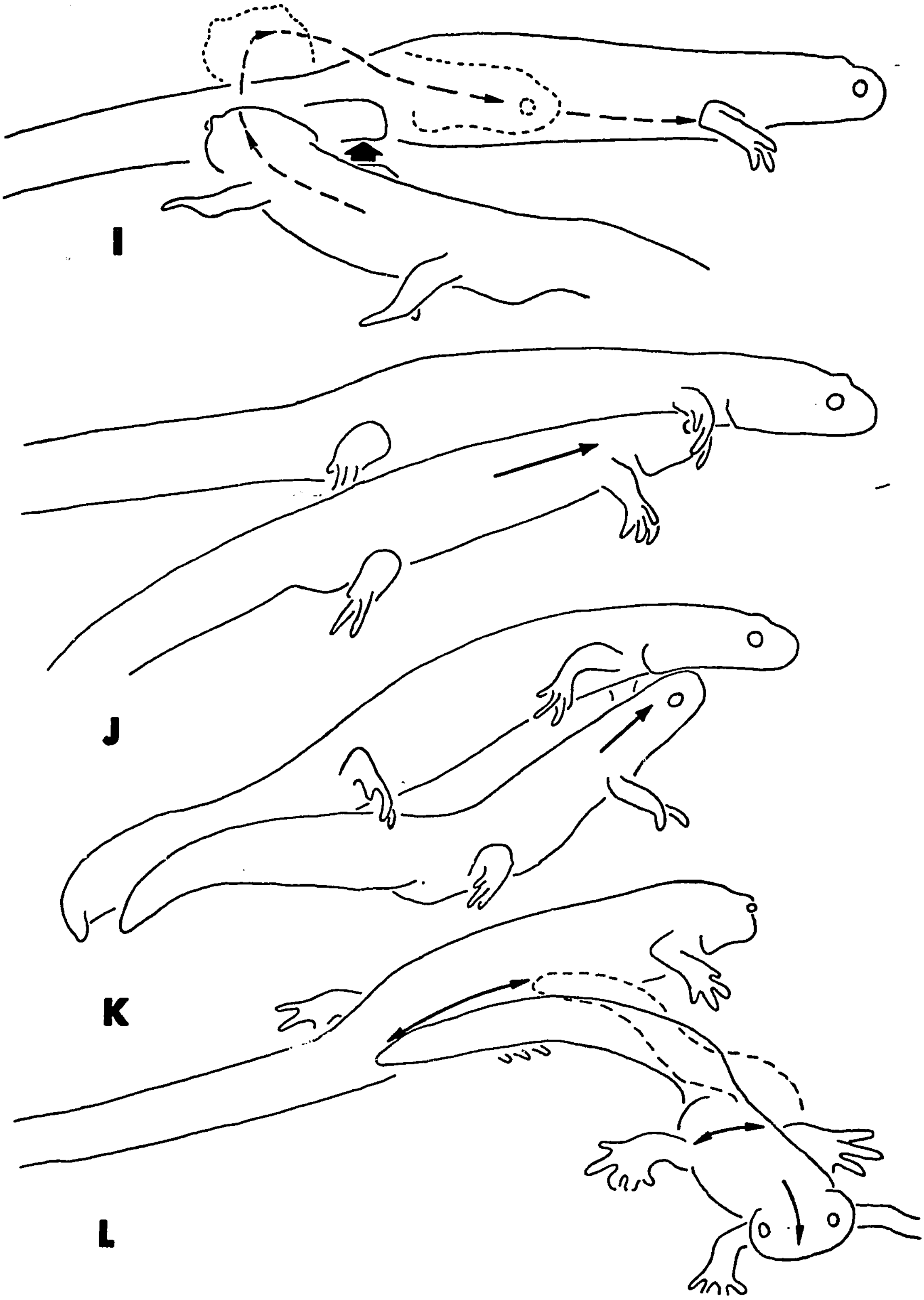
Figure 3. Courtship activities in Ambystoma maculatum, (continued from Fig. 2).

Fig. I. The female is still stationary over the spermatophore with the spermatophore inserted into her cloaca. The male has again approached the female, and now begins moving beside her while nudging her with his snout (39.9 sec).

Fig. J. The male has reached the female's forelimb and is now pushing his head under the female's chest (41.7 sec).

Fig. K. The male lifts under the female's chin and dislodges the female from the spermatophore (43.9 sec).

Fig. L. The male has turned and moved away from the female and is now shuffling his vent against the substrate as he moves forward (47.9 sec).


I
J
K
L

Ambystoma tigrinum

Catalog of male actions

The following actions are performed by the male while facing towards the female.

A.) NUDGING The male contacts his snout or lateral snout to the female's lateral body.

B.) HEAD-SWINGING The male swings his head laterally to and fro with his chin in contact with the female's dorsum.

C.) LIFTING The male lifts his head with the dorsum of his head in contact with the female's venter. The male may simultaneously turn his head to the side towards the female.

D.) SHOVING The male swims vigorously while pushing his snout against the female's lateral or ventral body and consequently shoves the female through the water for a distance of several centimeters to a meter (Fig.4A). Frequently the female's entire body is suspended in the water as the male shoves her rapidly forward and upward (Fig.4B).

The following actions are performed by the male while facing away from the female.

E.) STATIONARY WITH TAIL-TAPPING While stationary with the tail directed straight backwards, the male repeatedly raises and lowers his tail, tapping its ventral surface against the female's body or, less frequently, against the substrate. In addition to the repeated upward and downward motion, the tail is undulated slightly laterally (Fig.4D, 5A).

F.) BACKING UP The male backs up rapidly a few centimeters with the tail level, or nearly so, and directed straight backward.

G.) MOVING FORWARD The male moves forward with the tail directed straight backward, and he may simultaneously raise and lower his tail repeatedly (tail tapping) with slight lateral tail undulation (Fig. 5B, D, F).

H.) STATIONARY WITH HINDLIMBS PRESSED TOWARDS TAIL BASE While stationary the male presses his hindlimbs towards his lateral tail base while arching the midbody upward slightly. The tail is raised 45 to 90 degrees and undulated laterally very rapidly (Fig. 5C).

I.) SPERMATOPHORE DEPOSITION When spermatophore deposition occurs it follows the preceding action (H), with the male continuing in the same posture. The hindlimbs are pressed towards the tail base, the midbody is arched upwards slightly, the tail is raised high and undulated very rapidly, and the forelimbs are out-stretched and raised above the substrate (Fig. 5C). Spermatophore deposition terminates with the male ceasing tail undulations and moving forward while lifting the vent free of the spermatophore.

Temporal relations (*Ambystoma tigrinum*)

When the male contacts a female he moves very rapidly along her length and diagonally over the top of her while performing nudging, head-swinging and lifting. The male may repeatedly circle around and over the female while continuously performing these actions.

If the female moves away from the male, he follows rapidly behind her, intermittently nudging her tail as she moves forward, and then resumes nudging, head-swinging and lifting when she stops.

After performing these actions, the male may vigorously swim while shoving the female through the water, with his body perpendicular to hers and with his snout pressing against her midbody.

After shoving, and sometimes after the actions of nudging, head-swinging and lifting, the male turns and moves away from the female, usually perpendicular to her (Fig. 4C). He pauses with his vent 1/2 to slightly more than one tail length from the female's body and performs tail-tapping with the ventral surface of his tail lightly striking the dorsal surface of the female's body with each downward stroke (Fig. 4D). If his distal tail fails to strike the female's body, or if the female does not move forward and contact his anterior tail or cloaca, the male backs up and resumes tail tapping. If the female still does not contact his anterior tail or cloaca or if she moves off breaking contact with his tail, the male ceases tail tapping, turns and again approaches her, he then resumes nudging, head-swinging and lifting.

If, however, the female moves forward and contacts his tail within two to three vent lengths of his vent (Fig. 5A to B), the male moves forward on a straight course (action 5B) and will continue forward so long as the female continues to nudge his anterior tail, cloaca or the ventral surfaces of his hindlimbs. Whenever such contact ceases, the male pauses and resumes tail tapping. If the female fails to contact his anterior tail or cloaca he may then back up and resume tail tapping. If the female still fails to contact these regions of his body, the male turns and again approaches the female.

If, however, the female continues to nudge the male's anterior tail and cloaca, both animals move forward on a straight course for several centimeters (Fig. 5B), with the male pausing each time the female fails to contact his anterior tail. The male then pauses, and while adpressing his hindlimbs he undulates his tail rapidly with the tail raised 45° to 90° (Fig. 5C). If the female breaks contact with his anterior tail or cloaca, the male ceases the rapid tail undulations and resumes tail tapping. If, however, the female continues to contact his anterior tail or cloaca, the male deposits a spermatophore (Fig. 5C) and moves forward (Fig. 5D). He may then continue forward and deposit additional spermatophores, without recontacting the female with his snout, if the female continues to follow behind him and nudge his anterior tail and cloaca.

Rarely the male will deposit a spermatophore after simply moving away from the female and performing tail tapping, even though the female has not contacted his anterior tail or cloaca.

When moving forward behind the male, the female moves slowly forward and slowly steps from side to side with her hindlimbs. When the male pauses and initiates spermatophore deposition, the female usually stops behind him with her snout in contact with his tail base or cloaca as he vigorously undulates his raised tail.

The female appears to find spermatophores by touch. If the female contacts a spermatophore with her lateral or ventral body, as she follows behind the male, she shifts her body laterally over the top of the spermatophore while moving forward. The spermatophore then slides posteriorly in contact with her ventral midline towards her vent. If the spermatophore contacts her vent, she shuffles her vent laterally over the top of it and then squats upon it, inserting the spermatophore into her cloaca. She then assumes the posture assumed by the male during spermatophore deposition. She presses her hindlimbs against her tail base, arches her body upward slightly and undulates her tail rapidly with her tail raised (Fig. 5C, D). After several seconds she ceases tail undulations, moves forward off of the spermatophore, and nudges the male's tail base or cloaca, if he still lies in front of her (Fig. 5E, F).

Although the female usually finds and squats upon spermatophores while following behind the male, the spermatophore she finds may not be the one just deposited by the male. For example the female may find a spermatophore deposited much earlier by the male, if she passes over it while following the male. The female may also find and squat upon spermatophores as the male performs nudging, head swinging or lifting, but she can not find spermatophores while the male is shoving her.

If the male contacts a spermatophore with his lateral or ventral body while moving forward in front of the female, the male may orient to them just as the female would and deposit a spermatophore on top of a pre-existing one. Such secondary spermatophore depositions render the sperm mass of the original spermatophore inaccessible to the female. The male does not orient to spermatophores and deposit secondary spermatophores while performing the actions of nudging, head-swinging, lifting or shoving.

Kumpf (1934) provides a brief description of behavior in _Ambystoma tigrinum_ from Long Island, New York courting in the laboratory in March. As I did, Kumpf observed the male behaviors of nudging and shoving and the characteristic posture assumed by the male during spermatophore deposition. Kumpf fails to call attention to the marked tendency of the female to find spermatophores while following behind the male. Kumpf also notes that the males deposited relatively few spermatophores. When I placed pairs together which had been collected in the breeding ponds, and hence when the females were likely to have already been inseminated, I found that the females tended not to follow the male, and that males deposited very few spermatophores. Most of my observations were based on animals collected as they moved to breeding ponds. These animas had therefore not yet courted that breeding season. In such pairs the female tends to consistently follow the male during and after spermatophore depositions, and males deposit many more spermatophores. I suspect that Kumpf observed courtship in animals which had already courted, and that the females had already been inseminated.

Male Ambystoma tigrinum have proportionally longer tails than females, but this is not the case in Ambystoma maculatum (see Fig. 6). In addition the male's tail tip is spatulate shaped in lateral outline, and the whole tail is higher and more compressed than female's tails in Ambystoma tigrinum. The longer tail and special tail tip of A. tigrinum males is probably related to the male behavior of monitoring the female's position by tail-tapping just before spermatophore deposition. The lateral compression of the male's tail is probably related to this behavior and also provides a larger surface for rapid swimming during the male action of shoving the female. These special behaviors together with these sexual modifications of the tail are absent in Ambystoma maculatum.

Figure 4. Courtship activities in Ambystoma tigrinum.

Fig. A. The male (left) is shoving the female laterally through the water (0 sec).

Fig. B. The male continues to shove the female and pushes her body upward in the water (0.9 sec).

Fig. C. The male has stopped shoving the female and now slides his snout rapidly over the dorsum of the female (along the path indicated by the dotted line), and then moves away from the female (along the indicated path) (42.3 - 56.2 sec).

Fig. D. The male has paused facing away from the female and repeatedly taps the ventral surface of his tail tip on the female's dorsum (60.6 sec).

(These figures are taken from a 16mm. movie of one continuous sequence of courtship activities lasting 60.6 seconds. The animals are from the E.S.G. Reserve, Livingston C., Michigan).

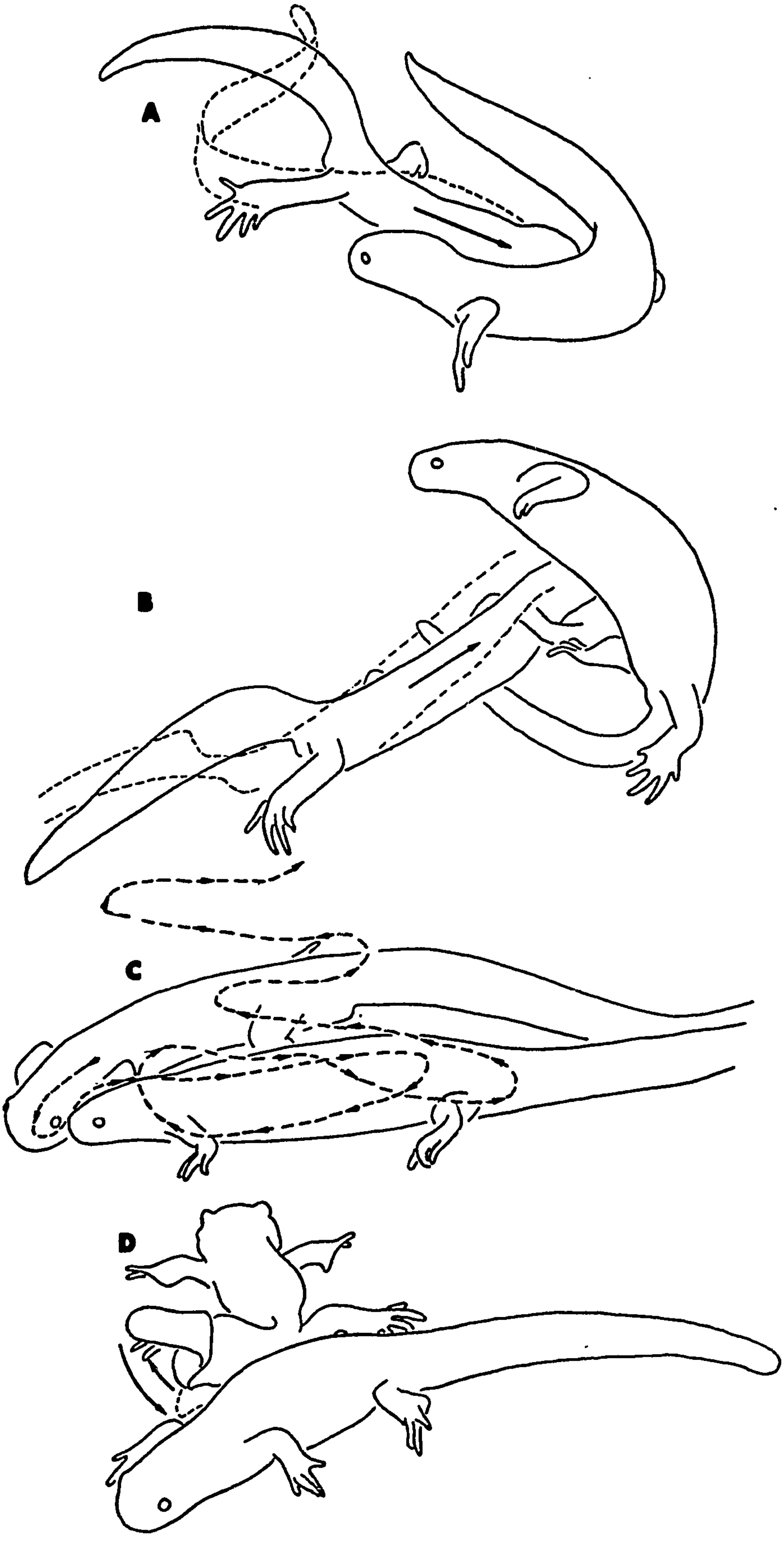

A
B
C
D

Figure 5. Courtship activities in Ambystoma tigrinum. (the male is on the left).

Fig. A. The male is performing tail-tapping while stationary in front of the female. A spermatophore which was deposited earlier by the male lies out of view behind the male's sacrum (indicated by solid arrow head 1). The female is stationary (0 sec).

Fig. B. The female has now moved forward and is nudging the male's lateral tail base with her snout as she moves forward behind the male. The male is now moving forward (2.4 sec).

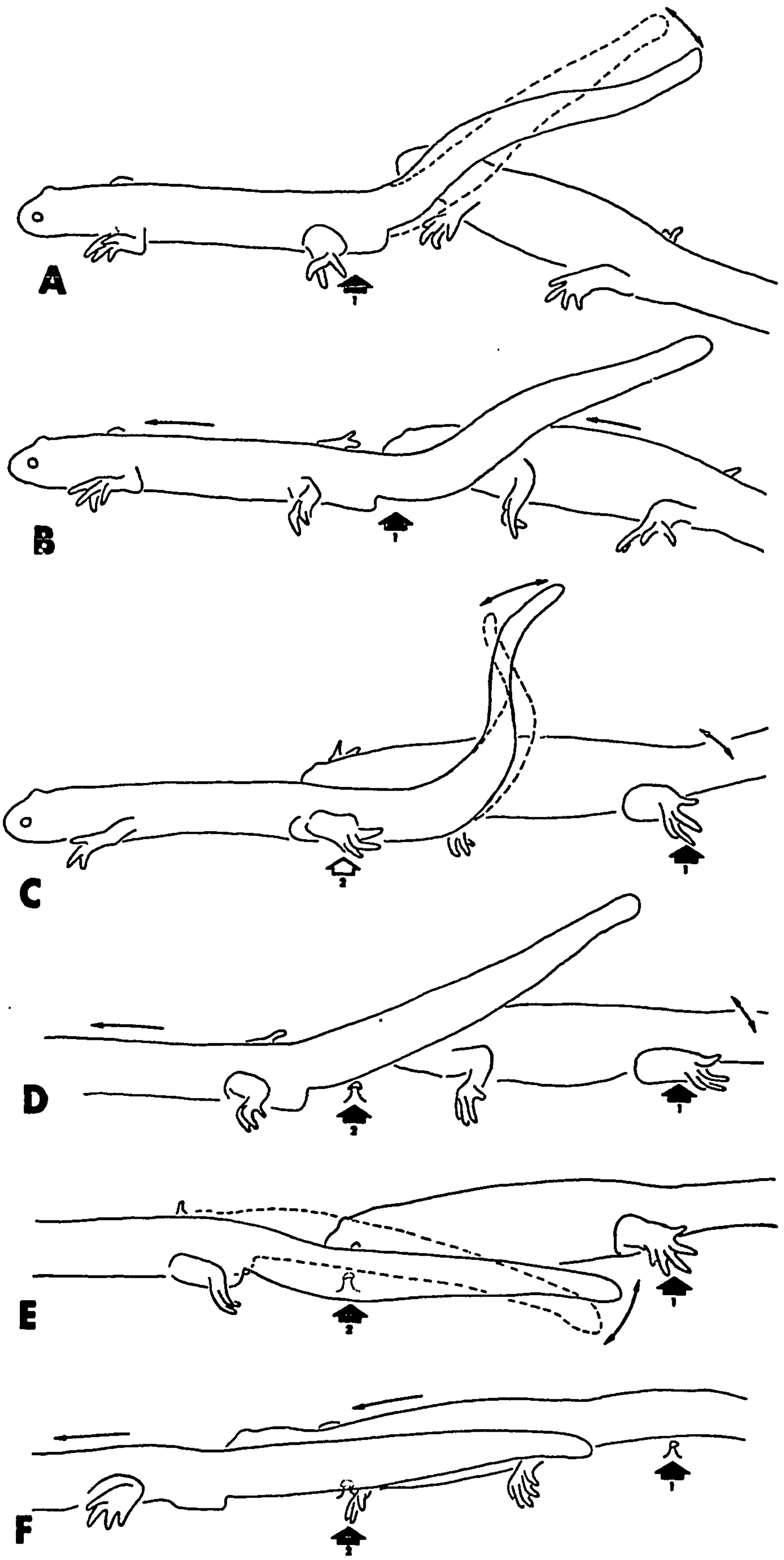
Fig. C. The female has moved over the top of spermatophore 1, found it with her vent, lowered her vent upon, and is now stationary with the spermatophore inserted into her cloaca. She undulates her tail laterally. The male is stationary with his hindlimbs adpressed and has initiated spermatophore deposition. The female's snout contacts his right hindlimb, as the male undulates his tail very rapidly with his tail raised (14.9 sec).

Fig. D. The male is now moving forward away from the spermatophore (2) he has just deposited. The female remains stationary behind him with spermatophore (1) still inserted into her cloaca (22.8 sec).

Fig. E. The female remains stationary over spermatophore 1 and the male pauses in front of her (26.0 sec).

Fig. F. The female has now moved forward off of spermatophore (1) and is contacting her snout to the male's lateral tail base. The male is moving forward in front of her (29.1 sec).

(These figures are taken from a 16mm. movie of one continuous sequence of activities lasting 29.1 seconds. The animals are from the E.S.G. Reserve, Livingston Co., Michigan).


A
1
B
1
C
2
1
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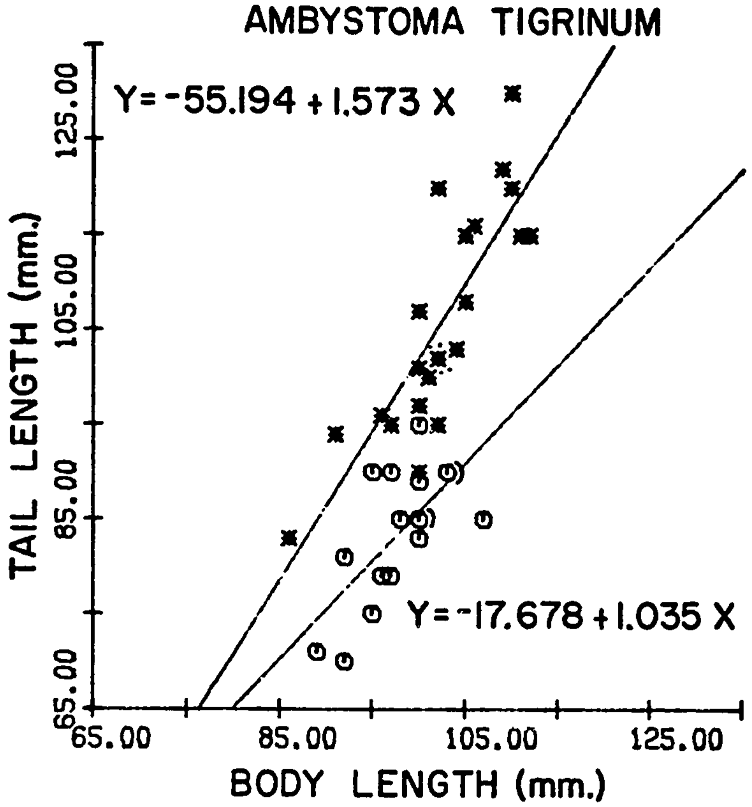
2
1
E
1
2
F
1
2

Figure 6. Sexual dimorphism in tail length in _Ambystoma tigrinum_.

Fig. A. Male _Ambystoma tigrinum_ have proportionally longer tails than females. Tail length is shown as a function of body length (measured from tip of snout to posterior margin of vent), in males (indicated with x's) and in females (indicated with o's). Regressions for males and for females differ in slope. (22 male and 17 female _Ambystoma tigrinum_ from the E.S.G.R., Lviingston Co., Michigan. Measurements are on live animals).

Fig. B. Male _Ambystoma maculatum_ do not have proportionally longer tails than females. Tail length is shown as a function of body length (measured from the tip of the snout to the posterior margin of the vent). Regressions for males and females do not differ in slope and intercept. Males indicated with x's and females indicated with o's. (44 males and 24 females from the E.S.G.R., Livingston Co., Michigan. Measurements are on live animals).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Y=-17.678+1.035 X
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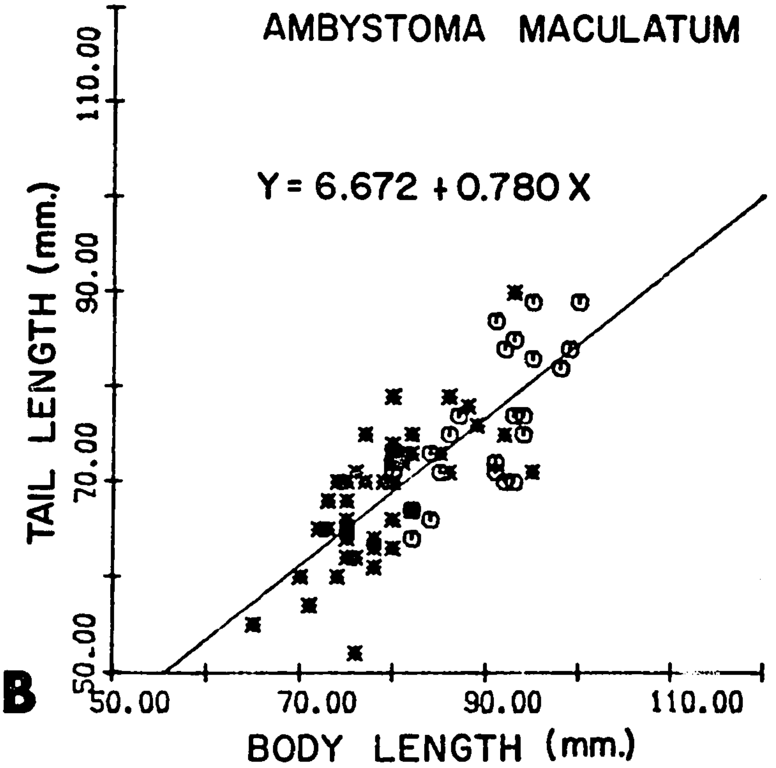
85.00
105.00
125.00
65.00
85.00
105.00
125.00
BODY LENGTH (mm.)

A


AMBYSTOMA MACULATUM
Y = 6.672 + 0.780 X
TAIL LENGTH (mm.)
50.00
70.00
90.00
110.00
50.00
70.00
90.00
110.00
BODY LENGTH (mm.)

B

Plethodon jordani

Catalog of male actions

The following actions are performed by the male while facing towards the female.

A.) TAPPING The male rapidly lowers and raises his head, and consequently his naso labial cirri tap the dorsum of the female or the substrate.

B.) HEAD-SLIDING The male moves forward sliding his mentum in contact with the female's dorsum (Fig. 7).

C.) NUDGING The male contacts his snout or lateral snout to the female's lateral body (Fig. 8A).

D.) FOOT DANCE The male raises and lowers his forelimbs and hindlimbs. Only one limb is raised and lowered at a time. There is no obvious patterning to the sequences of limb movements. The sequence is definitely not the sequence used in locomotion. The patterning of sequences is either very complex, or it is very simple and stochastic, with the probability of raising and lowering a limb independent of previous movements of the other limbs. This action is performed when the animal is stationary or moving forward very slowly.

E.) LIFTING While turning his head towards the female, the male lifts his head and contacts his snout, lateral snout or the dorsum of his head to the female's chin. Lifting is usually performed with the male's body parallel to the female and facing in the same direction (Fig. 8B), but it may also be performed with the male facing the female head-on.

The following actions are performed by the male while facing away from the female.

F.) STATIONARY WITH TAIL ARCHED AND UNDULATING While stationary, the male arches his proximal tail upward and undulates his tail laterally. His midbody and vent are raised above the substrate (Fig. 8E, 9A, 9C). The male may, or may not, perform a foot dance simultaneously.

G.) FORWARD WITH TAIL ARCHED The male moves forward on a straight course while arching his proximal tail upward slightly and with the vent raised above the substrate (see posture in Fig. 9C). The male may, or may not, undulate his tail laterally.

H.) TURNING BACK TOWARDS THE FEMALE This is actually a complex series of actions (see Fig. 71B). With the female's chin resting on the male's arched and undulating proximal tail and with the male facing straight away from the female, the male turns his head and forebody back towards the female's head by slowly stepping to one side with his forelimbs (Fig. 71B, arrow 1). The male then maintains this posture with his body axis in a U-shape, with his head held high (posture shown in Fig. 71B). He accentuates the upward arch of his tail, and the lateral undulations of his tail increase in amplitude. While maintaining this U-shaped posture, the male may pivot forward about a point at the center of the U by stepping forward with both forelimbs and hindlimbs. After maintaining this U-shaped posture, the male gradually turns his head even further towards the female so that, with his head held high, his mentum lies directly above the female's head. The male's body axis now forms a complete circle rather than a U. The male pauses momentarily in this circular posture and then suddenly and rapidly brings his head downward, slapping his mental gland on the dorsum of the female's head or snout. The slapping motion is executed very rapidly, and the male's head is pulled backward as it moves downward (Fig. 71B, arrow 2). The male again pauses momentarily, with his head level now, and then turns slightly away from the female, so that his body axis again forms a U. He now pauses in this posture. Finally the male turns fully away from the female, straightening his body axis (Fig. 71B, arrow 3).

I.) SLIDING VENT AGAINST SUBSTRATE The male moves forward sliding his vent in contact with the substrate. The tail is level and may undulate slightly laterally. The midbody is in contact with the substrate.

J.) STATIONARY WITH VENT IN CONTACT WITH SUBSTRATE The male pauses with vent and midbody in contact with the substrate. The male's tail undulates slightly laterally. Usually the tail is level, but infrequently the male may arch the proximal tail upward.

K.) SPERMATOPHORE DEPOSITION The male pauses with his vent in contact with the substrate. The tail is level, and tail undulations of large amplitude proceed along the entire length of the tail (Fig. 10A). The tail undulations appear to increase in frequency and amplitude during the course of spermatophore deposition. Spermatophore deposition terminates with the male ceasing tail undulations and then lifting his vent free of the spermatophore as he flexes his proximal tail 45° to 90° to one side (Fig. 10B).

L.) FORWARD WITH FLEXED TAIL The male moves forward with his proximal tail flexed 45° - 90° to one side (Fig. 10C). As he moves forward, the male holds his body in a sigmoid lateral flexure (Fig. 10D). His vent is held above the substrate.

M.) STATIONARY WITH FLEXED TAIL The following series of actions is executed by the male as the female stops with her vent near or over the spermatophore. The male stops and extends upward and backward on his hindlimbs and consequently straightens the sigmoid flexure of his body. The male then repeatedly and rhythmically extends and flexes his hindlimbs (Fig. 10F).

Simultaneously he extends backwards on his forelimbs, but does not flex and extend his forelimbs. The male's proximal tail is flexed to one side throughout. Finally the male ceases the rhythmic extentions and flexions of his hindlimbs and remains motionless, extended on his hindlimbs (Fig.71C).

Temporal relations (Plethodon jordani)

Upon initiating, or reinitiating, contact with a female, the male moves along the length of the female's body, either anteriad or posteriad, while performing tapping, nudging or head-sliding. The male may perform foot dance simultaneously with any of these modes of head contact. Usually the male moves along beside the female, but less frequently he may move anteriad or posteriad on top of the female's body and slide his mentum in contact with her dorsum (Fig. 7 shows a male sliding anteriad on top of the female).

If the male reaches the end of the female's tail when moving posteriad, he continues on past the tip of the tail, then taps the substrate, turns, recontacts the end of her tail with his snout and moves anteriad along beside her body.

Whenever the female moves away from the male, as he contacts her with his head, he moves rapidly towards her in bursts each time she moves forward. When the female is stationary, and the male's head is only a few centimeters from her, he approaches her very slowly with his body and head held low to the ground, and he may simultaneously perform a foot dance. Once the male recontacts the female with his snout, he resumes tapping, nudging and head-sliding.

The male may reach the female's head in either of two ways; by moving anteriad along beside (or on top) of her while contacting her with his head, or by moving directly towards her head while crouching low to the ground and without contacting her body.

Once the male reaches the female's head, he may nudge or slide his mental gland along the female's cheek or lateral snout while tilting his head slightly to one side (Fig. 8A). The male then turns his head towards the female, and under her chin, and lifts under her chin (Fig. 8B). He may arhythmically rub the female's chin by sliding his lateral snout, snout or the dorsum of his head forward and backward or laterally. The male then crawls forward under the female's chin (Fig. 8C).

Frequently the female raises her head or turns her head to one side as the male lifts and contacts her chin. She may also depart from the male. If she does, the male turns and again approaches her.

If, however, the female's chin contacts the male's dorsal body as he crawls beneath her chin, he continues forward and does not approach the female (Fig. 8C, 8D). He then arches and undulates his tail, if the female's chin contacts his dorsal, proximal tail (Fig. 8E). If the female's chin fails to contact the dorsum of his proximal tail, the male continues moving posteriad along the side of the female and resumes tapping, nudging and head-sliding and does arch and undulate his tail. Virtually any contact to the dorsum of the male's proximal tail will elicit the response of arching and undulating the tail. The only requirement is that the contact occur while, or shortly after, the male has contacted the female with his snout. Thus the male may suddenly pause and arch and undulate his tail if any region of the female's body or even inanimate objects contact the male's dorsal, proximal tail, as he moves along beside the female.

When the female's chin contacts his dorsal body as he crawls beneath her chin, the male frequently turns away from the female as he moves forward, so that he follows a sigmoid path with the inflexion point beneath the female's chin. The male then pauses facing directly away from the female and on the same line as the axis of her body as he arches and undulates his tail in contact with her chin.

When the male pauses while arching and undulating his tail in contact with the female's chin, the female may give any of three responses. She may depart from the male, she may remain motionless, or she may move forward and step astride the male's tail (Fig. 9B). If the female departs from the male, he ceases tail arching and undulation and turns and approaches her. If the female remains motionless, after several minutes the male lowers his tail, ceases tail undulations and approaches the female. Similarly, inanimate objects, or regions of the female's body other than her chin, will maintain stationary contact with the male's tail or break contact with it and thereby cause the male to approach the female. If, however, the female steps astride the male's tail (Fig. 9A, B) and then slides anteriorly with her chin in contact with it, the male moves forward while arching and undulating his tail, and the pair move forward in a tail-straddling walk (Fig. 9C).

Some females actively approach the male, as he performs nudging or head-sliding, step astride the male's tail and slide forward along the male's tail. In such cases the male immediately moves forward while arching and undulating his tail. In most cases, however, the female simply remains stationary, or departs from the male, whenever the male crawls forward under her chin. The male then alternates, again and again, between moving along beside the female while contacting with his head and crawling under her chin. Eventually the female may step astride the male's tail, as it undulates under her chin, and then move forward in a tail-straddling walk. If the female repeatedly fails to give this response, however, the male eventually moves away from her and terminates courtship without depositing a spermatophore.

The tail-straddling walk is, therefore, an obligatory precursor to spermatophore deposition. The communication processes during the tail-straddling walk will be discussed in detail in a subsequent section. In brief, the male moves forward and continues forward whenever the female's chin contacts his anterior tail. He stops and accentuates the arch of his tail while undulating his tail, whenever the female's chin slips posteriorly along his tail. The tail-straddling walk usually lasts for several minutes, and during this time the pair move forward a few to several centimeters.

In most courtships the male remains on a straight course during the tail-straddling walk. In other courtships the male repeatedly alternates between progress on a straight course and turning back towards the female and in the process slapping his mental gland on the female's head (Fig.71B).

If the female departs from the male at any time during the tail-straddling walk, the male lowers his tail, ceases tail undulations and reapproaches the female. If, however, the female continues to slide forward intermittently along the male's tail, the male lowers his vent and begins sliding his vent in contact with the substrate. The male may then immediately pause and deposit a spermatophore. Alternatively, the male may vacillate between holding the vent in contact with the substrate (either while stationary or while moving forward) and holding the vent above the substrate (either while stationary or while moving forward), and then finally deposit a spermatophore after pausing with the vent in contact with the substrate.

Should the female depart soon after spermatophore deposition begins, the male approaches the female without depositing a spermatophore. If, however, the female departs a few minutes after spermatophore deposition begins, the male continues just as if the female were present. The undulations of his tail increase in frequency and amplitude and then cease abruptly. The male lifts his vent off the spermatophore, and moves away from the spermatophore on a straight course, pausing intermittently, and finally stops with his vent approximately one snout-vent length in front of the spermatophore. He does not flex his tail to one side, however.

Usually the female does remain astride the male's tail as he deposits the spermatophore (Fig. 10A). She remains essentially motionless but may slide anteriorly or posteriorly a few millimeters along his tail. Occasionally the female appears to swing her head in short arcs laterally in a rhythmic fashion over the male's undulating tail. In most instances, however, the female does not move her head actively in this way. The male's tail undulates in contact with the entire length of the female's abdomen, and frequently a film of mucous can be seen between the male's undulating tail and the female's body.

Following spermatophore deposition, the male withdraws his tail from under the female's body (Fig. 10B) and moves forward with his tail flexed to one side. The female follows behind him with her chin resting on his dorsal tail base (Fig. 10C, D). As the female moves forward, the spermatophore contacts her ventral forebody (Fig. 10C) and slides posterior in contact with her ventral body (Fig. 10D). If the spermatophore contacts her vent (Fig. 10E), the female lowers her vent upon it and inserts the entire spermatophore into her cloaca. She undulates her tail base laterally while resting on the spermatophore, but is otherwise completely motionless (Fig. 10F). The male, meanwhile, stops in front of the female and, with tail still flexed to one side, executes the series of actions previously described (see action M). The extentions and flexions of his hindlimbs move the female's head up and down rhythmically as her chin rests on his tail base (Fig. 10F).

The actions which occur next are remarkably variable from courtship to courtship. The female may remain motionless over the spermatophore, or she may suddenly depart from the male and the spermatophore. The male may remain motionless, or he may suddenly swing around back towards the female (Fig. 10G). After swinging around, the male may remain motionless, he may briefly tap or nudge the female, or he may bite the female. Females flee immediately when bitten by the male. After the female has departed, the male may tap the substrate and circle about the side of the spermatophore deposition. If he contacts the spermatophore with his nasolabial cirri, the male usually grasps the spermatophore repeatedly with his mouth and eats part or all of it.

Usually courtship behavior ceases after one spermatophore deposition. The female usually flees and repeatedly moves away from the male whether she has successfully removed the sperm cap or not. If the male does reinitiate head contact with the female after spermatophore deposition, contacts are frequently terminated quickly by the male moving away from the female. Usually within five minutes after spermatophore deposition, the male no longer responds to movement by the female and does not approach her.

Green and Richmond (1944) observed a male and female in a tail-straddling walk in the field in North Carolina. The behavior they observed agrees in all respects with my observations on captive animals. The male moved forward while arching and undulating his tail with the female astride the male's tail and with her chin resting on his dorsal tail base. This behavior continued for 25 minutes, and during this time the pair moved in a circular path about 10 ft. in diameter.

Organ (1958) provided descriptions of courtship behavior of animals in the laboratory together with some field observations. My observations are in good agreement with Organ's descriptions. Above I have given some additional details on the positions assumed during courtship (particularly during the tail-straddling walk, and during and after spermatophore deposition). Organ (1958) also found that the behavior I have called "turning back towards the female" was infrequent. He observed animals in this position (see Fig. 71B) only once in the field.

Despite its rather restricted geographic range, Plethodon jordani shows very marked geographic variation in morphology, particularly in various aspects of coloration (see Highton, 1962). Surprisingly, I was unable to detect any geographic variation in courtship behavior. I observed courtship behavior in Plethodon jordani metcalfi (Whitetop Mtn., Grayson Co., Virginia), P. j. melaventris (Highlands, Macon Co., North Carolina), P. j. shermani (Standing Indian Rec. Area, Macon Co., North Carolina), and P. j. jordani (Swain Co., North Carolina). I could see no differences in the occurence or temporal patterning of courtship actions between these populations of Plethodon jordani.

It is very likely that females are inseminated more than once, and by more than one male, during a courtship season. In captivity females will continue to court, and successfully retrieve sperm caps, after they have been inseminated. When more than one male was housed with a female, the female was sometimes inseminated by more than one male but always on different nights. Organ and Lowenthal (1963) have found that the sperm cap of Plethodon jordani spermatophores is covered with thick capsules. Consequently, once the female is inseminated a few days are required to break down these structures, and during this time the female cannot accomodate additional sperm caps within her cloaca.

On a very few occasions I observed female's performing each of the following "male" actions; foot dance, tail arched and undulating in contact with the male's chin, and turning back towards the male's head (but then not slapping the mentum on the male's head, as a male would with a female). The rare occurence of these behaviors in females suggests that the alleles governing these behaviors are not sex-linked.

Figure 7. Courtship activities in Plethodon *jordani*.

The male is on the left. The male has approached a female and is now sliding his mentum along her dorsal tail (Fig. A), onto her dorsal sarcum (Fig. B), and then onto dorsal hindbody (Fig. C). The female is slowly moving forward and the male performs head sliding. In Fig. D. the male has moved off of the female's dorsum and is sliding his mentum onto the female's dorsal head as she turns away from him. The male's nasolabial cirrus is visible in Fig. B. as a slight projection just below his snout. Notice that the male does not grasp the female's dorsum with his forelimbs, but rather simply crawls along her dorsum.

(These animals are from Standing Indian Recreation Area, Macon Co., North Carolina; *Plethodon jordani shermani*).

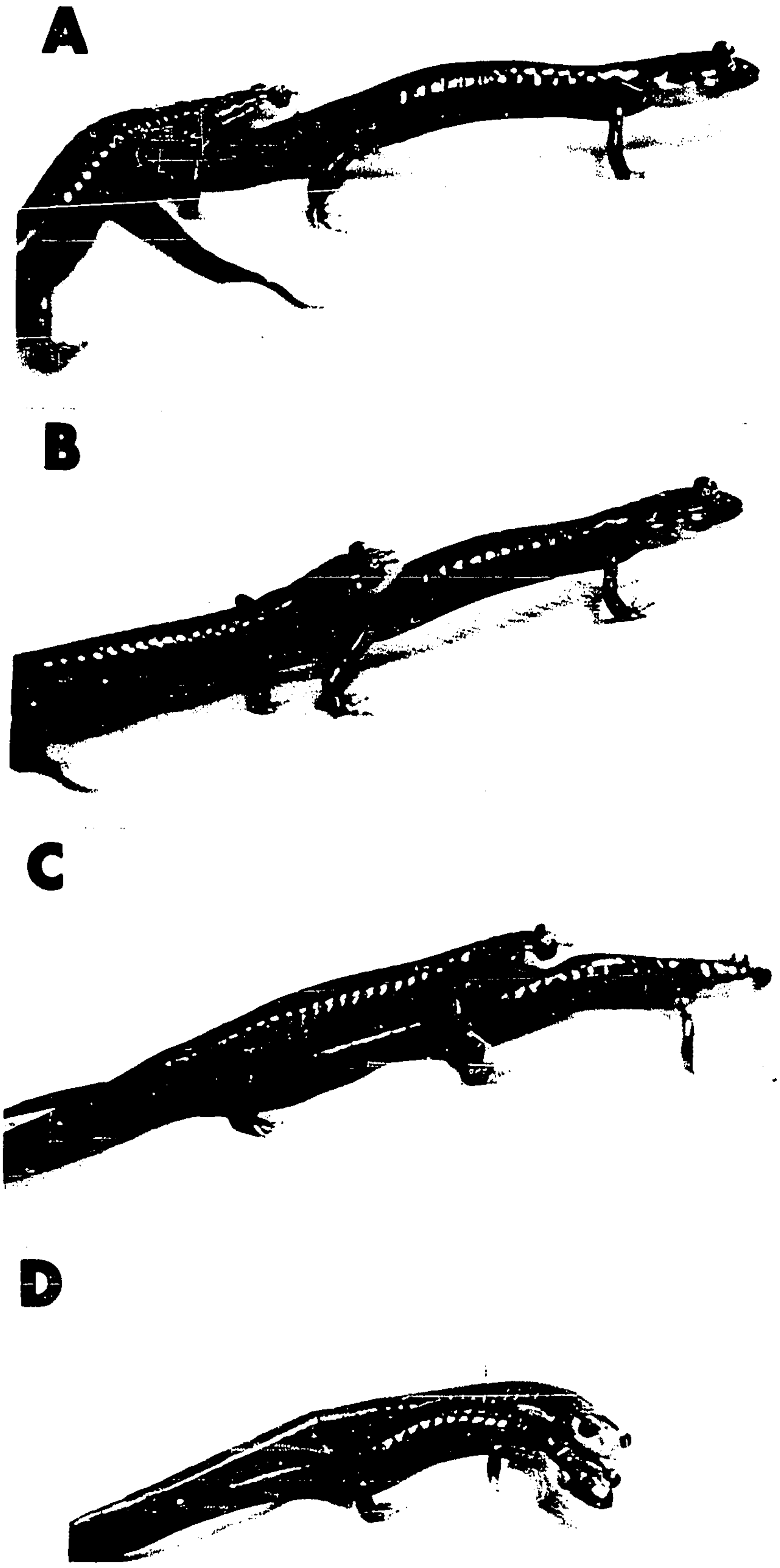

A
B
C
D

Figure 8. Courtship activities in Plethodon jordani.

Fig. A. The male (left) has moved along beside the female and is not contacting his lateral snout to the female's lateral snout. The female has turned her head slightly away from the male as he contacted her.

Fig. B. The male has turned his head under the female's chin, and now lifts his head in contact with her chin as he moves forward.

Fig. C. The male moves forward under the female's chin. The female has turned her head posterior over the dorsum of the male's body.

Fig. D. The female's chin has contacted the male's dorsal proximal tail as he moves forward, and he is arching his tail as he continues forward.

Fig. E. The male is stationary with his tail arched and undulating in contact with the female's chin and ventral neck.

(These figures are based on a series of photographs of two animals from Standing Indian Recreation Area, Macon Co., North Carolina; Plethodon jordani shermani. The total elapsed time is about two minutes).

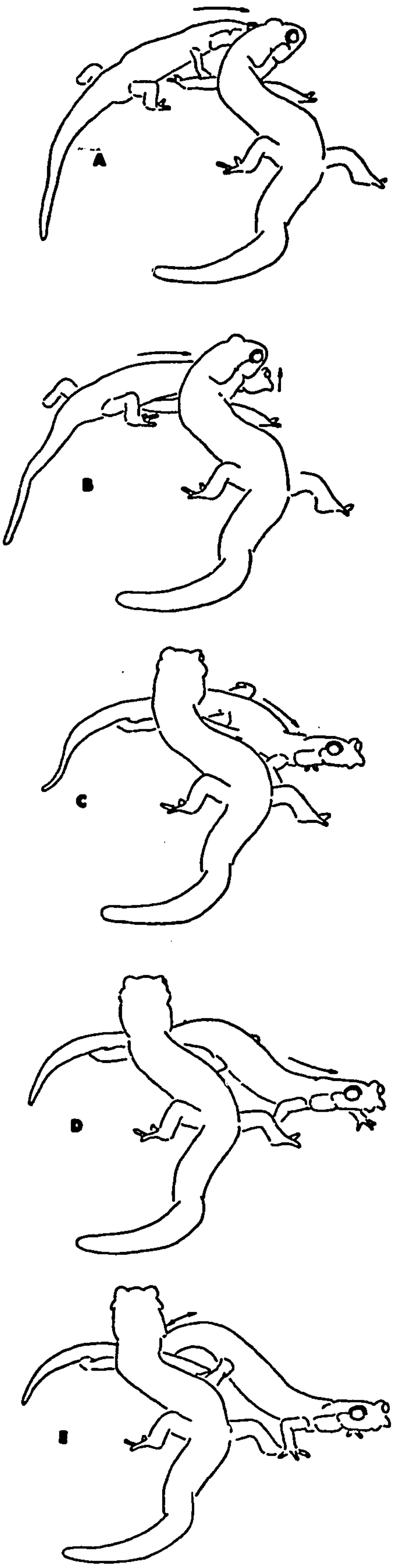

A
B
C
D
E

Figure 9. Courtship activities in Plethodon jordani, initiation of the tail-straddling walk.

Fig. A. The male is stationary while arching and undulating his tail under the female's chin. The female has turned her head from perpendicular to axial to the male's tail.

Fig. B. The female is now stepping astride the male's tail and sliding anterior along his tail. The male is just beginning to move forward while arching and undulating his tail.

Fig. C. The male (right) and the female (left) in a tail-straddling walk. The male is arching and undulating his tail under the female's chin, and the female has moved completely astride his tail. The male's mental gland can be seen as a low projection from his chin just below his eye. Notice too the male's and the female's nasolabial cirri, just below the nare.

(These animals are from Standing Indian Recreation Area, Macon Co., North Carolina; Plethodon jordani shermani. Total elapsed time is about five minutes.)

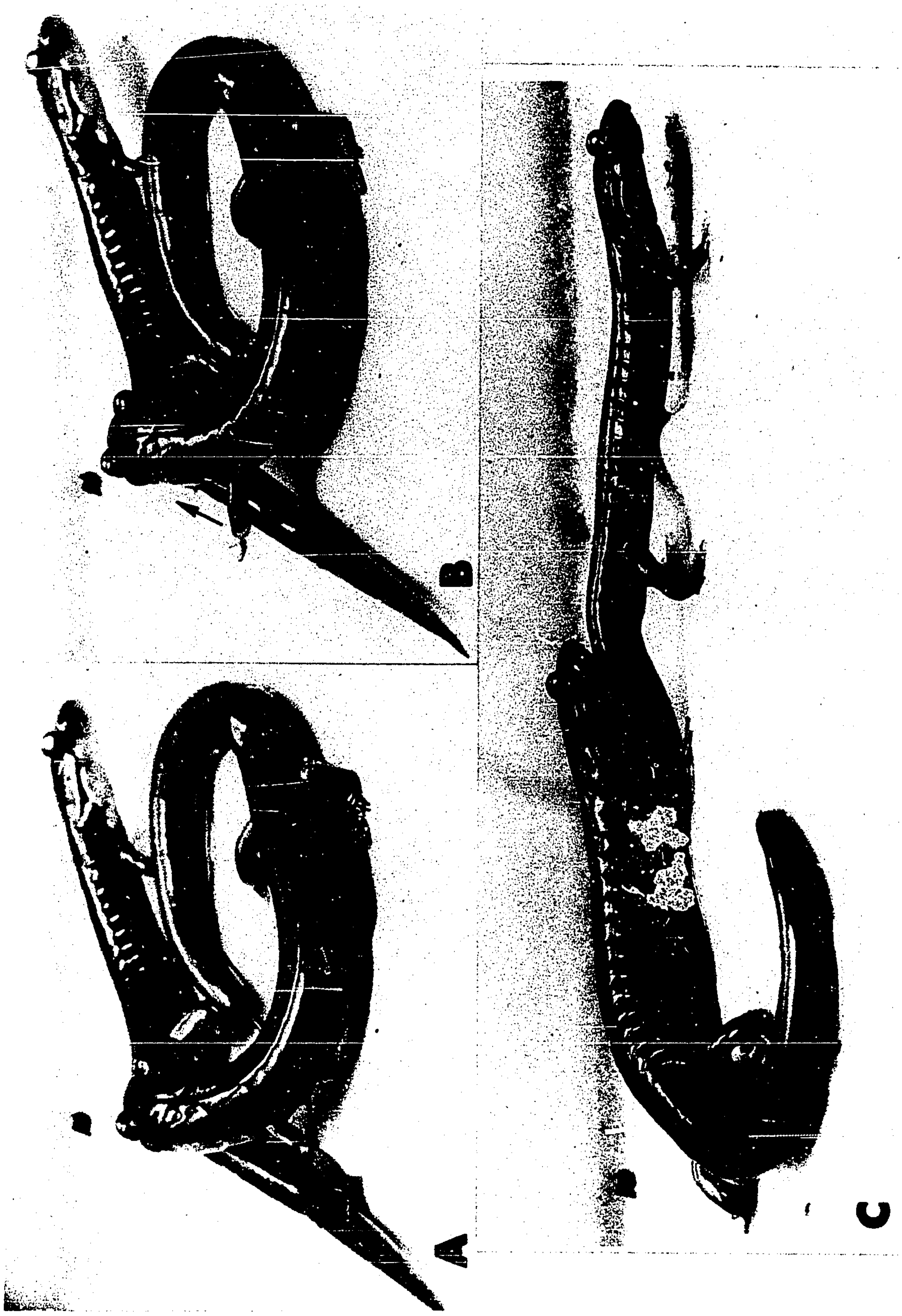

A
B
C

Figure 10. Courtship activities in Plethodon jordani; spermatophore deposition and sperm transfer. (Based on a 16mm. movie of animals from Standing Indian Recreation Area, Macon Co., North Carolina; Plethodon jordani shermani. Total elapsed time about five minutes).

Fig. A. The male is in the process of depositing a spermatophore as the female straddles his undulating tail. (Male is on left).

Fig. B. The male has completed spermatophore deposition and begins to move forward as he flexes his proximal tail to one side and out from under the female.

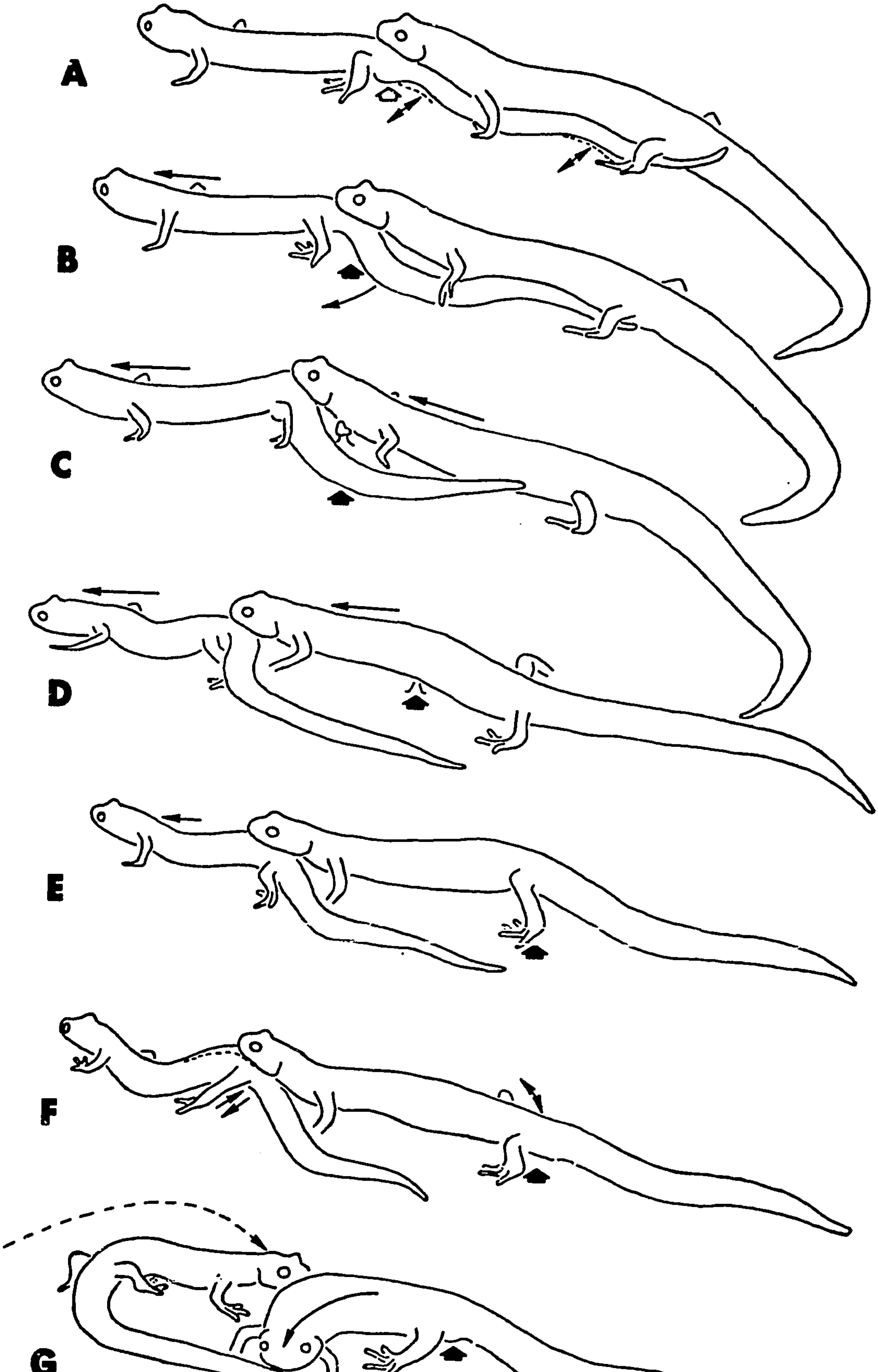
Fig. C. The male continues forward with his tail flexed to one side, and the female is now moving forward with her chin resting on the male's dorsal tail base. The spermatophore is visible in contact with the female's lateral neck.

Fig. D. The male continues forward with his tail flexed laterally and with his body in a sigmoid lateral flexure. As the female moves forward, the spermatophore is in continuous contact with her venter.

Fig. E. The spermatophore has contacted the female's vent, and she has stopped with her vent in contact with it. The male continues forward.

Fig. F. The female has lowered her vent upon the spermatophore and inserted it into her cloaca. The male has stopped in front of the female, has leaned backward on his hindlimbs, and is now extending and flexing on his hindlimbs.

Fig. G. The male has just swung back towards the female, and she is now departing from the male and the spermatophore.


A
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F
G

B. Variables affecting male reproductive success during a courtship season

In the next several sections I will present observations on specific aspects and variables of courtship behavior in each of the three species. The reader should refer to Fig. 24 in order to visualize the relationships between the various aspects and variables of courtship. Note that each variable could have a pronounced effect on the reproductive success of a male during a courtship encounter. The major hypothesis to be tested is that the social context of courtship has a major impact on the evolution of courtship behavior. The goals are then to discover whether there are significant differences between species in aspects of courtship behavior which effect the reproductive success of males and to then decide whether these differences are due to differences in the context, particularly the social context, in which courtship behavior occurs.

1. Number of spermatophores deposited per courtship.

Estimates of the number of spermatophores deposited per courtship in Ambystoma maculatum from Goss Pond and A. tigrinum were made by pooling data from two sources. Animals were placed in cylinders of fiber glass window screening (20 inches in diameter by 12 inches high), and the cylinder was half submerged in water in Burt Pond on the E.S.G.R. at night. The next morning the animals were removed, and the spermatophores were collected from the cylinder and counted under a binocular scope. Alternatively spermatophores were collected from large aquaria after courtship behavior had terminated, and the spermatophores were counted. In both cases single pairs of animals which had not yet courted were placed together. Spermatophore counts refer to the number of spermatophore depositions (eg. a triple spermatophore structure counts as three spermatophore depositions). Estimates for *A. maculatum* from the E.S.G.R. were obtained by the first method above. When calculating means, courtships in which no spermatophores were deposited were excluded.

In *Plethodon jordani* counts of spermatophores were made in each container housing a pair each morning, and the spermatophores were then removed.

Ambystoma maculatum males from Goss Pond deposited a mean of 20.8 spermatophores per courtship (n=11, S.D.=14.4 range = 4 to 55). *Ambystoma maculatum* males from the E.S.G.R. deposited a mean of 43.6 spermatophores per courtship (n=21, S.D.=20.9, range = 10 to 81).

Ambystoma tigrinum males from the E.S.G.R. deposited a mean of 15.6 spermatophores per courtship (n=8, S.D.=5.9, range = 8 to 24).

Plethodon jordani males from Whitetop Mtn., Virginia deposited a mean of 1.04 spermatophores per courtship (n=51, S.D.=0.20, range = 1 to 2, 49 observations with 1 spermatophore and 2 observations with 2 spermatophores).

Ambystoma maculatum males from the E.S.G.R. deposited significantly more spermatophores per courtship than *A. maculatum* males from Goss Pond (T test yields p=0.002).

Ambystoma maculatum males from the E.S.G.R. deposited significantly more spermatophores per courtship than E.S.G.R. *A. tigrinum* (T test yields p=0.00001). Goss Pond *A. maculatum*, however, did not deposit significantly more spermatophores than E.S.G.R. *A. tigrinum* (T test yields p=0.15).

Both *Ambystoma* species deposited many more spermatophores per courtship than *Plethodon jordani*, and the differences are of course significant.

2. Probability of successful sperm transfer per courtship.

In order to become inseminated during courtship, the female must first locate a spermatophore and then remove the sperm mass from it. I have considered insemination as a two-part process, since only the first part of the process, the location of a spermatophore by the female, could be observed in all three species.

a. Probability of spermatophore location per spermatophore deposition.

The conditional probability that the female successfully locates a spermatophore with her vent, given that a spermatophore has been deposited, p(L/SD), was estimated for each species as the total number of times females lowered their vents upon spermatophores divided by the total number of spermatophores deposited by the males during all courtship records for each species.

The total number of spermatophores deposited, the total number of successful spermatophore locations by females, and the probability of spermatophore location per spermatophore deposition, p(L/SD), are shown for each species in Table 1. The observations on _A. maculatum_ are based only on animals from Goss Pond.

Calculations of Chi Square based on 2x2 contingency tables of numbers of spermatophores deposited and numbers of spermatophores located are shown in Table 2. These calculations are designed to test the null hypothesis that there are no differences between species in the probability of locating spermatophores per spermatophore deposition.

The probability of spermatophore location per spermatophore deposition, p(L/SD), is significantly smaller in _A. maculatum_ (p(L/SD)=0.39) than in _Plethodon jordani_ (p(L/SD)=0.92) (Chi Square=12.34, d.f.=1, $p<0.001$). This

Table 1. The probability of spermatophore location per spermatophore deposition in *Ambystoma maculatum*, *A. tigrinum* and *Plethodon jordani*.

	Ambystoma maculatum (Goss Pond)	*Ambystoma tigrinum*	*Plethodon jordani*
Total number of spermatophores deposited.	131	28	25
Total number of spermatophores located by the females.	51	17	23
Probability of spermatophore location per spermatophore deposition.	0.389	0.607	0.920
Total number of successful sperm transfers.	unknown	unknown	14
Probability of sperm transfer per spermatophore location.	($\geqslant$ 0.608)	($\geqslant$ 0.608)	0.608
Probability of sperm transfer per spermatophore deposition.	($\geqslant$ 0.236)	($\geqslant$ 0.369)	0.560
Probability of sperm transfer per courtship	($\geqslant$ 0.996)	($\geqslant$ 0.992)	0.574

Table 2. Chi Square tests for species differences in the probability of spermatophore location per spermatophore deposition.

	Ambystoma maculatum	*Plethodon jordani*	Total
Total number of spermatophores deposited	131	25	156
Observed number of spermatophores located	51	23	74
Expected number of spermatophores located	62.1	11.9	

Expected probability of spermatophore location = 74/156 = 0.47

Chi Square = 12.34

	Ambystoma maculatum	*Ambystoma tigrinum*	Total
Total number of spermatophores deposited	131	28	159
Observed number of spermatophores located	51	17	68
Expected number of spermatophores located	56.0	12.0	

Expected probability of spermatophore location = 68/159 = 0.43

Chi Square = 2.53

	Ambystoma tigrinum	*Plethodon jordani*	Total
Total number of spermatophores deposited	28	25	53
Observed number of spermatophores located	17	23	40
Expected number of spermatophores located	21.1	18.9	

Expected probability of spermatophore location = 40/53 = 0.75

Chi Square = 1.69

probability in *A. trigrinum* (p(L/SD)=0.62) is not significantly different from *A. maculatum* (chi Square=2.53, d.f.=1, p>0.1) or from *Plethodon jordani* (Chi Square=1.69, d.f.=1, p>0.1).

Thus given that a spermatophore has been deposited, the probability that the female will locate it is higher in *Plethodon jordani* than in *Ambystoma maculatum*, and *Ambystoma tigrinum* is probably intermediate between these two species.

b. Probability of sperm transfer per spermatophore location.

The success of the female in actually retrieving sperm from the spermatophore, once the spermatophore has been located, could be accurately determined only for *Plethodon jordani*. The calculation was based only on successful sperm transfers. A sperm transfer was termed successful only if the female departed from the spermatophore with the sperm cap held in her cloacal lips. Sperm transfer was considered unsuccessful if the female failed to locate the spermatophore, if she did locate it but then failed to remove the sperm cap, or if she removed the sperm cap but then lost the sperm cap as she moved away from the spermatophore.

The probability of sperm *transfer* per spermatophore location, p(T/L), was estimated as the total number of successful sperm transfers divided by the total number of spermatophores located by females with the vent (see Table 1). This conditional probability was 0.61 in *Plethodon jordani*. Given that the female has located a spermatophore with her vent, the probability that she will successfully retrieve sperm from the spermatophore is 0.61.

The sperm mass of *Plethodon jordani* is a coherent, nearly spherical mass which rests cap-like on a spiked spermatophore base. Organ and

Lowenthal (1963) have found that the sperm cap is surrounded with a thick covering. Therefore either the entire mass of sperm is removed by the female or none of it. In contrast, the sperm mass in *Ambystoma maculatum* and in *A. tigrinum* is "simply" a mixture of spermatozoa and matrix perched on the apex of the spermatophore base. Consequently when a female of *Ambystoma maculatum* or *A. tigrinum* moves off of a spermatophore, she may remove the entire sperm mass, only a portion of it may be removed, or the sperm mass may appear unchanged. For this reason one cannot determine whether the female has removed sperm when she departs from the spermatophore (that is without examining her cloaca and thereby disturbing her subsequent behavior). However, since the sperm masses of *A. maculatum* and *A. tigrinum* are smaller in relation to the size of the female than in *Plethodon jordani*, it seems likely the *Ambystoma* females have less difficulty in successfully removing sperm from the spermatophore than do *Plethodon jordani* females. For this reason I have tentatively estimated the probability of sperm transfer per spermatophore location in the two *Ambystoma* species as at least as high as in *Plethodon jordani* (ie.$\geq$ 0.608 in Table 1).

c. Probability of sperm transfer per spermatophore deposition.

The probability of successful sperm transfer given that a spermatophore has been deposited, p(T/SD), was estimated in *Plethodon jordani* as the total number of successful sperm transfers divided by the total number of spermatophores deposited (see Table 1). This is mathematically equivalent to p(T/L) p(L/SD), or 0.56.

p(T/L) was assumed to be 0.608 for *Ambystoma maculatum* and *A. tigrinum*. The probability of successful sperm transfer per spermatophore deposition was then estimated as ($\geq$ 0.608) p(L/SD), or 0.24 for *A. tigrinum*.

d. Probability of sperm transfer per courtship.

The probability of successful sperm transfer per courtship, p(T/C), was estimated as the probability of at least one successful sperm transfer per courtship.

1-p(T/SD) is the probability of failing to transfer sperm per spermatophore deposition. If n is the number of spermatophores deposited per courtship, then $(1-p(T/SD))^n$ is the probability of n successive failures to transfer sperm with n spermatophore depositions. This last expression assumes that the probability of sperm transfer per spermatophore deposition remains unchanged during a sequence of spermatophore depositions or spermatophore locations. $1-(1-p(T/SD))^n$ is then the probability of at least one sperm transfer in n spermatophore depositions.

This last expression was used to estimate the probability of sperm transfer per courtship for each species, using p(T/SD) as previously estimated and the mean number of spermatophores per courtship as n (see Table 1).

3. Time per spermatophore deposition.

The time per spermatophore deposition was estimated for each species by dividing the total elapsed time during which animals were observed courting by the total number of spermatophores deposited. Time per spermatophore deposition therefore refers to the courtship time required per spermatophore deposition rather than to the duration of the act of spermatophore deposition.

In a total of 178.7 minutes Goss Pond *Ambystoma maculatum* males deposited 131 spermatophores or 1.36 minutes per spermatophore.

In a total of 126.4 minutes *Ambystoma tigrinum* males deposited 28 spermatophores or 4.52 minutes per spermatophore.

In a total of 1398.0 minutes (23.29 hours) *Plethodon jordani* males deposited 25 spermatophores or 55.9 minutes per spermatophore.

4. Variability in the site of spermatophore deposition.

From motion pictures of Ambystoma males depositing spermatophores, two aspects of the site of spermatophore deposition were noted; the direction the male was facing at the onset of spermatophore deposition in relation to the female and the distance of the spermatophore from the female's body at the onset of spermatophore deposition. The latter distance was measured as the distance from the spermatophore to the closest point of the female's outline (head, trunk or tail). This distance was measured in terms of female snout-vent lengths in order to standardize for different sized females.

The results of these tabulations are shown in Figure 11. The direction the male was facing and the site of spermatophore deposition was noted in 25 observations of Plethodon jordani pairs at the onset of spermatophore deposition. Both variables were so remarkably constant from observation to observation that no actual measurements were tabulated. In each case the male faced straight away from the female (ie at a 0° angle) with the spermatophore located within a few millimeters of the female's snout at the onset of spermatophore deposition.

In contrast, the site of spermatophore deposition and the angle the male faces at the onset of spermatophore deposition are remarkably variable in Ambystoma maculatum (Fig. 11). In Ambystoma tigrinum spermatophores are usually deposited in the vicinity of the female's head with the male facing straight away from the female (Fig. 11).

Statistical analyses

a. Angle of male orientation during spermatophore deposition.

The angle of male orientation at the onset of spermatophore deposition was measured as the number of degrees deviation from parallel to the female and facing in the same direction. Means, standard deviations, variances and ranges are shown in Table 3 for *Ambystoma maculatum* and *A. tigrinum*.

The variance in angle of male orientation is significantly larger in *A. maculatum* than in *A. tigrinum* (F=3.59, d.f.=(77,18), p=0.001 (one sided test)). The mean deviation from 0° is also significantly larger in *A. maculatum* (82.1°) than in *A. tigrinum* (21.5°) (T corrected for unequal variance yields p less than 10^{-6}).

Within *Ambystoma maculatum*, *de novo* and secondary spermatophore depositions do not differ significantly in mean angle of male orientation or in variance about the mean (F=1.04, d.f.=(28,48), p=0.4; T=1.07, p=0.29).

b. Distance of the spermatophore from the female's body.

Means, standard deviations, variances and ranges are shown in Table 3 for *A. maculatum* and *A. tigrinum*.

Variance in the distance of the spermatophore from the female's body is significantly larger in *A. maculatum* than in *A. tigrinum* (F=2.9, d.f.=(77,18), p=0.0003 (one sided test)). The mean distance from the spermatophore to the female's body is also significantly larger in A. maculatum (T corrected for unequal variance = 4.01, p=0.0001 (one sided test)).

Within *Ambystoma maculatum* the mean distance of the spermatophore from the female and the variance about this mean are both significantly larger for secondary spermatophore depositions than for spermatophores deposited *de novo* (F=2.71, d.f.=(28,48), p=0.002 (one sided test); and T corrected for unequal variance yields p=0.015 (one sided test)).

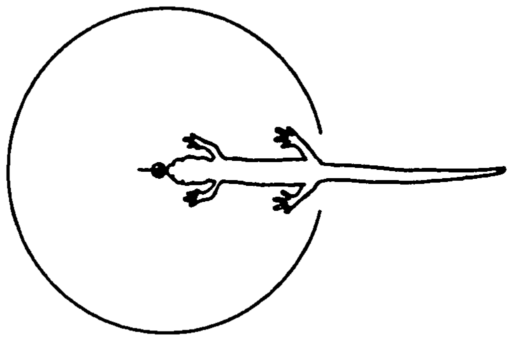
Figure 11. Sites of spermatophore deposition in relation to the female's body in *Ambystoma maculatum*, *Ambystoma tigrinum* and *Plethodon jordani*.

Solid circles indicate the sites of spermatophores deposited *de novo* (ie. upon the substrate).

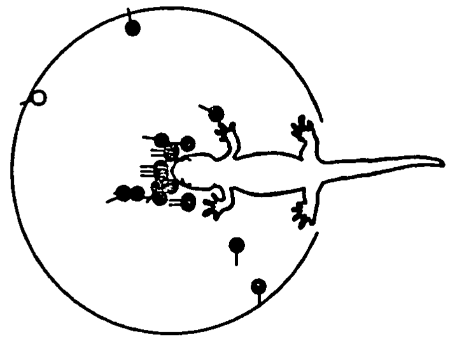
Open circles indicate the sites of spermatophores deposited on top of pre-existing spermatophores.

Short lines from circles indicate the direction the male was facing during spermatophore deposition.

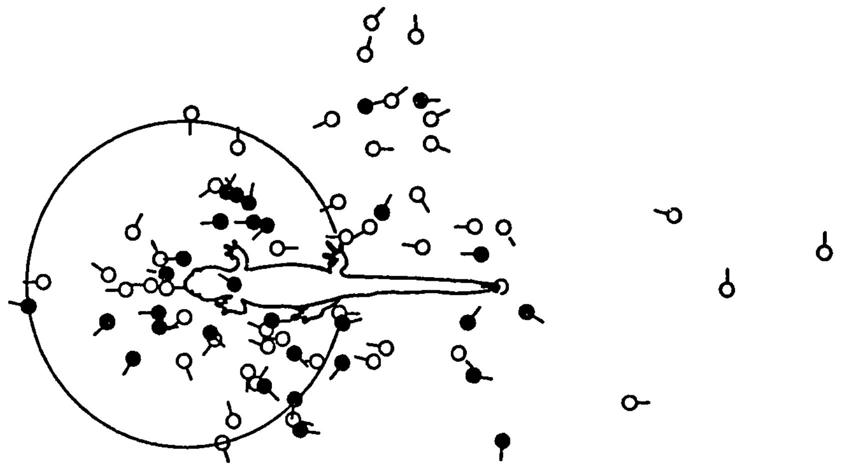
Large circle indicates a radius one snout-vent length from the female's snout.



PLETHODON JORDANI
N = 25



AMBYSTOMA TIGRINUM
N = 19



AMBYSTOMA MACULATUM
N = 78

Table 3. Variability in site of spermatophore deposition in *Ambystoma maculatum* and *Ambystoma tigrinum*.

	A. maculatum			*A. tigrinum*
	de novo spermatophores	secondary spermatophores	all spermatophores	all spermatophores
Number of observations	29	49	78	19
ANGLE THE MALE WAS FACING DURING SPERMATOPHORE DEPOSITION				
mean (degrees)	91.8	76.3	82.1	21.5
standard deviation	62.8	61.7	62.2	32.8
variance	3947	3803	3863	1077
range	(0 - 180)	(0 - 180)	(0 - 180)	(0 - 90)
DISTANCE OF THE SPERMATOPHORE FROM THE FEMALE'S BODY				
mean	0.41	0.61	0.54	0.21
standard deviation	0.31	0.51	0.46	0.27
variance	0.10	0.27	0.21	0.07
range	(0.0 - 1.15)	(0.5 - 2.17)	(0.0 - 2.17)	(0.03 - 0.97)

(Variables underlined show statistically significant differences between the two species)

5. Analysis of communication between sexual partners during courtship.

When I compared my impressions of courtship behavior in plethodontid and ambystomatid salamanders, I was plagued with two questions; "Why do male plethodontids court at such a 'painstakingly' slow pace, and why do they take so long to deposit a spermatophore?". It seemed likely that both of these characteristics increased the probability that the female would locate and retrieve sperm from the spermatophore.

The analysis in this section was then designed to test the following hypothesis; the more sexual partners affect each other's behavior between spermatophore depositions, the more likely it is that the female will locate the spermatophore. Since female *Plethodon jordani* are more likely to locate a specific spermatophore than *Ambystoma maculatum* females, the hypothesis may be stated in more specific terms; in *Plethodon jordani* sexual partners affect each other's behavior more per spermatophore deposition than in *Ambystoma maculatum*. The analysis is based on the courtships of *single* pairs of animals in each species which were observed in the laboratory.

An analogy will help make the spirit and the complexity of the analysis more understandable. Suppose that a public speaker has the goal of communicating as much information as possible to an audience during a lecture. He can accomplish this goal in three ways. He can speak for a longer period of time, he can speak faster (increase the number of words per minute), or he can increase the information content of each word (or sentence). The analysis of this section is similar to comparing the total information content of lectures delivered by two speakers. To make the comparison we must determine each of the three aspects of the lectures mentioned above, for the total information content of a lecture can be viewed as the product of these three aspects. In salamander terms we are asking, "Do *Plethodon jordani* males communicate more information to the female "per lecture" (ie. per spermatophore deposition)?". We have already found that male *Plethodon jordani* "lecture for a longer period of time" than do *A. maculatum* males (ie. more courtship time is expended per spermatophore). We must now determine the "speaking rates" (ie. the number of courtship acts per minute) and the "information content of each word" (ie. the extent to which secual partners affect each other's behavior per courtship act) in order to calculate "how much information is communicated per lecture" (ie. the extent to which sexual partners affect each other's behavior per spermatophore deposition) in each of the two species.

Information theory was used to estimate the extent to which sexual partners affect each other's behavior in each of the two species. In most lectures information is passed only from the lecturer to the audience. During courtship encounters, however, both the male and the female affect each other's behavior. In other words, information is passed both from the male to the female and from the female to the male. The analysis in this section partitions the flow of information between sexual partners into these two aspects.

To accomplish this task, I have analyzed the flow of information from specific components of behavior of one sexual partner to specific components of behavior in the other sexual partner (the specific components of behavior which were considered in the two salamander species will be discussed shortly). A further, and somewhat strained, extention of the lecture analogy will help clarify this additional complexity in analysis. Suppose we recognize two components of behavior both in the lecturer and in his audience; facial expressions and audible sounds, such as speech or laughter. We might then ask "How much do the facial expressions of the speaker affect both the facial expressions and the audible sounds of the audience?", and conversely "How much do the facial expressions of the audience affect both the facial expressions and the audible sounds of the speaker?". In terms of courting salamanders, I have asked "How much does a specific component of male behavior (eg. male tail undulation) affect all components of female behavior?" and conversely "How much does a specific component of female behavior (eg. female tail undulation) affect all components of male behavior?" in each of the two species. Each component of behavior provides a sample of how much one sexual partner affects the other partner's behavior. The samples for each species were then compared to determine whether the two species differ in the extent to which sexual partners influence each other's behavior.

The analysis which follows will strike some readers as needlessly complex. Nevertheless this numerical approach has two main virtues. First, the complexity of the analysis should not obscure the simplicity of the results. Information theory allows us to reduce the complicated process of communication to a single metric. This metric tells us how effective each species is in affecting behavior during courtship. Second, the analysis can be applied to many other communication processes. The standardization techniques I have employed allow one to correct for differences between species in the number of behavioral elements which are used during communication. The behavioral coding scheme I have employed has the virtue of broad applicability in behavioral investigations. This scheme does remove some of the subjectivity in recognizing behavioral acts, but much labor is required to apply such a scheme. An investigator must decide whether the results of such an analysis will warrant the labor of coding behavior in this way.

I will first discuss the behavioral coding scheme which both describes the behavioral components which were considered in each species and allows one to compare the "speaking rates" of the two species. I will then turn to the actual analysis of communication during courtship which is based on this coding scheme. Finally, I will compare the extent to which sexual partners influence each other's behavior in the two species, in order to test the hypothesis above.

Hazlett and Bossert (1965) and Altmann (1965) provide examples of the use of information theory to analyse communication between conspecific animals. For a more formal derivation of some of the information theoretic measures I have used, see Garner (1962).

a. A behavioral coding scheme.

A coding scheme was devised for each species which describes the behavior of each sexual partner in terms of a set of behavioral components. Each behavioral component describes either the movements of a particular body region, the spatial orientation of a particular body region, the body region(s) contacting the other sexual partner, or the body region(s) being contacted by the other sexual partner.

In so far as possible the same behavioral components were used to describe the behavior in each of the two species. And within each species the same behavioral components were used to describe the male's and the female's behavior. Thus in Ambystoma maculatum 10 behavioral components were used to describe the male's behavior, and 10 components were used to describe the female's behavior. In Plethodon jordani 11 components were used for each sexual partner.

Each of the behavioral components consists of a set of component states which describe the particular, mutually exclusive activities happening at that behavioral component. For example, the behavioral component called tail undulation has two states; tail not undulating (the state called 0), or tail undulating (the state called 1). The components, and the component states of each component, which were used to code the courtship behavior of each species are shown in Table 4 (_Ambystoma maculatum_) and Table 5 (_Plethodon jordani_).

During a recording session for _Plethodon jordani_ the ongoing states of each component of male behavior and of female behavior were spoken into a tape recorder. As soon as the state of at least one component changed, in either the male or the female, a new series of component states were spoken into the tape recorder. The tape recorded records of courtship behavior which were later transcribed and then recoded, using numbers, rather than verbal phrases, for the names of component states.

Courtship behavior happens so rapidly in _Ambystoma maculatum_, that it was impossible to describe the behavior verbally as it happened. Instead, courtship encounters were filmed, and the behavior was later recoded directly from the movies while watching them frame by frame.

An example of _Plethodon jordani_ behavior, when coded in final form, is:-

	Male components											Female components										
component name	1	2	3	4	5	6	7	8	9	10	11	1	2	3	4	5	6	7	8	9	10	11
act 1	1	1	0	0	0	10	0	0	0	0	0	0	0	0	0	3	0	0	0	0	0	0
act 2	1	1	0	0	0	9	0	0	0	0	0	0	0	0	1	3	0	0	0	0	0	0
act 3	1	0	0	1	0	8	0	0	0	0	0	0	0	0	1	3	0	0	0	0	0	0

Table 5 can be consulted for the verbal names of the components and their component states. The first row says that the male is simultaneously arching his tail (component 1), undulating his tail (2), not performing a foot dance (3), his whole body is stationary (4), he is not contacting the female with his anterior body (5), but the female is contacting his tail at a point 1 vent length posterior to his vent (6), he is not moving his head up or down (7), not turning his head sideways (8), his longitudinal body axis is straight (9), his tail is straight (10), and his vent is raised from the substrate (11). The first row also indicates that, simultaneously with all of the preceding male activities, the female is holding her tail level (1), her tail is not undulating (2), she is not performing a foot dance (3), her whole body is stationary (4), her chin is in contact with the male (5), there is no posterior contact to her body (6), she is not moving her head up or down (7), she is not turning her head (8), her longitudinal body axis is straight (9), and her tail is straight (10), and her vent is not in contact with a spermatophore (11).

The second row says that the male's behavior has remained unchanged, except that the female is now contacting the male's tail 1/2 vent length posterior to his vent (male component 6), and simultaneously the female is moving forward now (female component 4). The third line says that all components are unchanged from the second line, except that now the male is moving forward (male component 4), he has stopped undulating his tail (2), and the female is now contacting the male's tail just at the rear margin of his vent (6).

Sequences totaling 800 such rows were coded for Ambystoma maculatum, and sequences totaling 1113 such rows were codes for Plethodon jordani.

Each row, such as in the example above, will be termed an act. Each act describes the activities ocurring simultaneously in both the male and the female. Each act differs, by definition, from the act preceding it by one or more change in component state.

Table 4. Coding scheme for courtship behavior in *Ambystoma maculatum*

MALE P	NAME OF COMPONENT	NAME OF COMPONENT STATES	FEMALE P
.891	1 Tail angle	0 Tail level	.992
.109		1 Tail raised	.008
.795	2 Tail undulation	0 Tail not undulating	1.000
.205		1 Tail undulating	
.859	3 Limbs adpressed	0 Hindlimbs not adpressed	.844
.141		1 Hindlimbs adpressed	.156
.290	4 Progress	0 Stationary	.691
.704		1 Move slowly forward	.292
		2 Swim rapidly along substrate	.001
.006		3 Swim to or from surface of water	.015
.485	5 Contact to anterior body	0 No contact	.606
.293		1 Lateral snout or snout	.105
.016		2 Cheek	.022
.064		3 Chin	.055
.092		4 Dorsal head or neck	.048
.001		5 Forelimbs	.029
.031		6 Forebody	.109
.010		7 Hindbody	.019
.001		8 Hindlimb	.001
.001		9 Sacrum	
.002		10 Cloaca	.001
.002		11 Tail	.005

Table 4. Coding scheme for courtship behavior in Ambystoma maculatum (continued)

MALE P	NAME OF COMPONENT	NAME OF COMPONENT STATES	FEMALE P
.743	6 Contact to posterior body	0 No contact	.622
.002		1 Forebody	.005
.029		2 Hindbody	.069
.005		3 Hindlimb	.031
.019		4 Sacrum	.029
.090		5 Foretail	.092
.091		6 Hindtail	.116
.001		7 Lateral snout or snout	.001
.902	7 Head action	0 Head level	.998
.058		1 Raising head	.002
.040		2 Pressing head down	
.961	8 Head orientation	0 Stationary	.978
.022		1 Turning head towards sexual partner	.014
.016		2 Turning head away from sexual partner	.008
.989	9 Head swinging	0 Not swinging head laterally	1.000
.011		1 Swinging head laterally	
.799	10 Vent position	0 Raised above substrate	.751
.022		1 Adpressed to substrate	
.025		2 Extruding a spermatophore	
.030		3 Midbody in contact with spermatophore	.048
.032		4 Vent in contact with a spermatophore	.048
.091		5 Vent lowered on a spermatophore	.154

Table 5. Coding scheme for courtship behavior in *Plethodon jordani*.

MALE P	NAME OF COMPONENT	NAME OF COMPONENT STATES	FEMALE P
.694	1 Tail angle	0 Tail level	.874
.306		1 Tail arched	.126
.001		2 Tail arch accentuated	
.713	2 Tail undulation	0 Tail not undulating	.875
.287		1 Tail undulating	.125
.648	3 Foot action	0 Foot dance absent	.988
.347		1 Foot dance present	.012
.005		2 Extending and flexing on hindlimbs	
.489	4 Progress	0 Stationary	.745
.504		1 Moving forward	.251
.007		2 Moving backward	.004
.547	5 Contact to anterior body	0 No contact	.616
.210		1 Snout or lateral snout	.051
.005		2 Cheek	.035
.215		3 Chin	.164
.017		4 Dorsal head or neck	.027
.001		5 Forelimb	.051
.004		6 Forebody	.039
		7 Hindbody	.003
		8 Hindlimb	.004
		9 Sacrum	.002
		10 Dorsal tail at mid-vent	.001
		11 Foretail	.005
		12 Hindtail	.001

Table 5. Coding scheme for courtship behavior in Plethodon jordani (continued)

MALE P	NAME OF COMPONENT	NAME OF COMPONENT STATES	FEMALE P
.685	6 Contact to posterior body	0 No contact	.585
.002		1 Chin	.042
.004		2 Dorsal head or neck	
.003		3 Forebody	.001
.017		4 Hindbody	.032
.002		5 Hindlimb	.039
.007		6 Sacrum	.008
.034		7 Dorsal tail at mid-vent	
.048		8 Dorsal tail just posterior to vent	
.026		9 Dorsal tail 1/2 vent length post. to vent	
.033		10 Dorsal tail 1 vent length post. to vent	
.003		11 Dorsal tail 1 & 1/2 vent length post. to vent	
.029		12 Foretail	.144
.101		13 Hindtail	.091
.003		14 Contact is other than sexual partner	.003
.003		15 Contact to body region other than above	.005
.924	7 Head action	0 Vertical head angle stationary	.967
.003		1 Raising head	.028
.003		2 Lowering head	.003
.066		3 Tapping substrate	.003
.003		4 Tapping spermatophore	
.001		5 Eating spermatophore	
.934	8 Head orientation	0 Lateral head angle stationary	.812
.044		1 Turning head towards sexual partner	.120
.022		2 Turning head away from sexual partner	.068

Table 5. Coding scheme for courtship behavior in <u>Plethodon Jordani</u> (continued)

MALE P	NAME OF COMPONENT		NAME OF COMPONENT STATES		FEMALE P
.987	9	Longitudinal body axis	0	Straight	.906
.004			1	U-shaped	.039
.009			2	Circular	.056
.967	10	Tail position	0	Tail straight	.998
.033			1	Tail flexed laterally	.002
.966	11	Vent action	0	Raised or in contact with substrate (male)	
.031			1	In contact with substrate during tail-straddling walk (male)	
.004			2	Extruding spermatophore	
			3	No contact with spermatophore (female)	.974
			4	Midbody in contact with spermatophore (Fem.)	.008
			5	Vent in contact with spermatophore (Fem.)	.007
			6	Vent lowered on spermatophore (female)	.011
			7	Lift off spermatophore and remove spermcap (female)	.002

b. Courtship rate (acts per minute)

In two pairs of Ambystoma maculatum 800 acts occurred in 10.58 minutes, and in six pairs of Plethodon jordani 1113 acts occurred in 311.28 minutes. In Ambystoma maculatum courtship occurs at a much faster rate (75.65 acts per minute) than in Plethodon jordani (3.58 acts per minute).

c. Information transmitted between sexual partners per act.

Information theory was used to measure the extent to which the state of a particular component of one sexual partner (eg. male tail undulation) could be predicted from a knowledge of the states of each of the components of the other sexual partner in the immediate preceding act.

Let $p(m)_i$ represent the probability of occurrence of the ith state of the mth component of the male. For each component there were 1113 observations of state for Plethodon jordani and 800 observations of state for Ambystoma maculatum (ie. one observation in each act). $p(m)_i$ was estimated as the number of occurrences of the ith component state divided by the total number of observations of that component (or 1113 for P. jordani and 800 for A. maculatum). Similarly let $p(f)j$ represent the probability of occurrence of the jth component state at the fth component of the female. These probabilities are shown in Table 4 for A. maculatum and in Table 5 for P. jordani.

If each of the component states of a particular component were equally probable, it would be maximally difficult to guess which component state was occurring in any given act. That is to say, the uncertainty about the state of a component is highest when the states are equi-probable. If, for example, a component has 2 equi-probable states, then the uncertainty of that component is:-

$$\log_2 2 = -(1/2 \log_2 1/2 + 1/2 \log_2 1/2) = 1 \text{ bit}$$

If component m has r states, the maximum uncertainty of that component is:-

$$H(m)_{max} = \log_2 r \tag{1}$$

The maximum uncertainty which can be expressed by a component is then simply a function of the number of states in that component.

Since some of the component states were never observed (for example, notice in Table 4 that female A. maculatum were never observed to undulate their tails, component 2), $H(m)_{max}$, the maximum uncertainty of the male's mth component, and $H(f)_{max}$, the maximum uncertainty of the female's fth component, were calculated from the number states observed in each component and not from the potential number of states.

The realized uncertainty of the male component m was calculated as:-

$$H(m) = -\sum_i p(m)_i \log_2 p(m)_i \tag{2}$$

Similarly the realized uncertainty of the female component f was calculated as:-

$$H(f) = -\sum_j p(f)_j \log_2 p(f)_j \tag{3}$$

The maximum and realized uncertainties of each of the components in the female and in the male are shown in Tables 6 and 7.

Since the number of states differs from component to component, the ratios $H(m)/H(m)_{max}$ or $H(f)/H(f)_{max}$ were calculated for each component and are also shown in Tables 6 and 7. These ratios vary from 0.0, when only one component state occurs, to 1.0, when all component states are equiprobable. $H(m)/H(m)_{max}$ will be referred to as the standardized uncertainty of male component m, and $H(f)/H(f)_{max}$ will be called the standardized uncertainty of female component f.

Let $p(m_i/f_j)$ be the probability that component state i of male component m occurred in the n+1th act, given that component state j of the female component f occurred in the nth act. This transition probability (or conditional probability) was estimated as the number of times state i of male component m occurred in the next act following the occurrence of state j of the female component f divided by the number of times acts containing state j in female component f were followed by another act.

Then

$$-p(f)_j \sum_i p(m_i/f_j) \log_2 p(m_i/f_j) \qquad (4)$$

represents the average uncertainty in male component m, when the state j of the female component f occured in the preceding act. These conditional uncertainties for each component state of a particular female component, f, are summed to yield

$$HC(m,f) = - \sum_j p(f)_j \sum_i p(m_i/f_j) \log_2 p(m_i/f_j) \qquad (5)$$

HC(m,f) represents the average uncertainty of the male component m in the n+1th act, when the component state of the female's component f is known for the nth act.

H(m) represents the total uncertainty of the male component m, and

$$HT(m,f) = H(m) - HC(m,f) \qquad (6)$$

represents the uncertainty in the male component m which can be predicted from a knowledge of the component state of female component f in the preceding act. HT(m,f) will be referred to as the average amount of information transmitted from the female's fth component to the male's mth component in two act sequences.

If we sum the information transmitted from each female component to a particular male component, m, we have a measure of the total information transmitted from the female's behavior in an act to a particular male component in the next act,

$$\sum_{f} HT(m,f)$$

The ratio

$$\sum_{f} HT(m,f) \ / \ H(m)$$

measures the proportion of the uncertainty in the male component m which can be predicted from the female's behavior in the preceding act. When this ratio is 0.0 the female has no effect on the male's mth component in the next act. The mathematical significance of various values of this ratio are shown diagramatically, with Venn diagrams, in Figure 12. The central circular area in each cluster represents the total uncertainty in male component m, H(m). Each circular area bordering the central circle represents the total uncertainty in a particular female component (eg. $H(f_2)$ represents the uncertainty in female component (2). The area of intersection between each H(f) and H(m) represents HT(m,f), or the amount of information transmitted from that female component to the male component. The sum of these intersections, in each cluster, represents

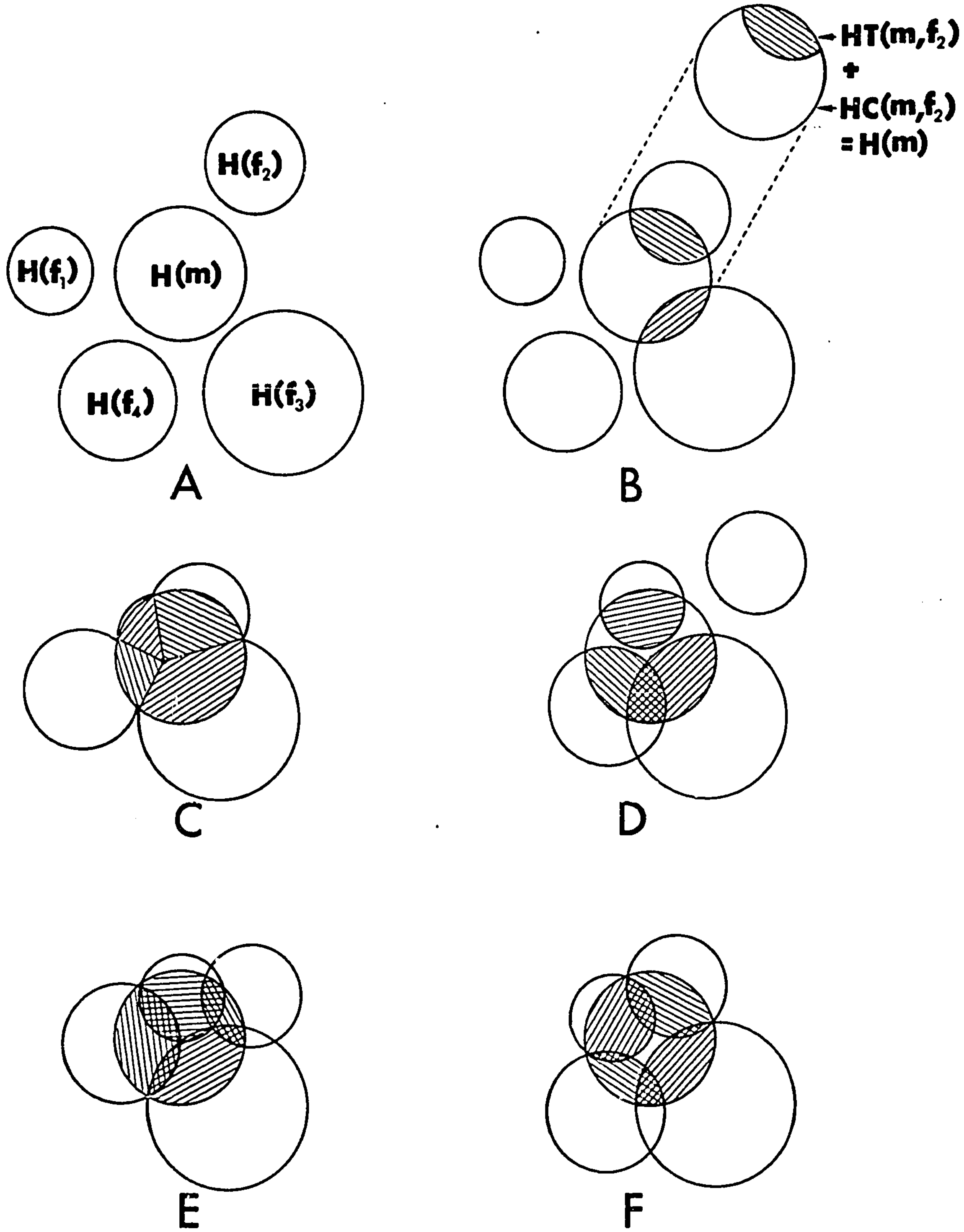
$$\sum_{f} HT(m,f)$$

The ratio

$$\sum_{f} HT(m,f)/H(m)$$

is equal to 0.0 only when there is no information transmitted from any female component (Fig. 12A). The ratio is greater than zero when at least one female component to the male's subsequent behavior at component m (eg. Fig. 12B). When the ratio is equal to one, the sum of the areas of intersection is equal to H(m). This may be because taken together the

Figure 12. Venn diagrams indicating two types of redundancy in the information transmitted between sexual partners during courtship.


H(f₂)
H(f₁)
H(m)
H(f₄)
H(f₃)
A
HT(m,f₂)
+
HC(m,f₂)
= H(m)
B
C
D
E
F

female components reduce the entire uncertainty of subsequent male behavior at component m (Fig. 12C), or because the information transmitted from a particular female component is redundant with information transmitted from another female component, and redundant and non-redundant information transmitted sum to H(m) (Fig. 12D). When the ratio is greater than one it is certain that some of the information transmitted female components is redundant, but the male's total uncertainty may (Fig. 12E) or may not be (Fig. 12F) completely reduced by information transmitted from the female.

Thus the ratio $\sum_f HT(m,f)/H(m)$ measures the sum of both non-redundant and redundant information which is transmitted from female components. This ratio will be termed the total information transmitted from female components to the male component m. Similarly,

$$\sum_m HT(f,m)/H(f)$$

is the total information transmitted from male components to the female component F in two act sequences.

$$\sum_m HT(m_x,m)/H(m_x)$$

is the total information transmitted from male components to the particular male component m_x in two act sequences.

$$\sum_f HT(f_y,f)/H(f_y)$$

is the total information transmitted from female components to the particular female component f_y in two act sequences. With appropriate substitutions, these last three ratios were calculated in the same way as $\sum_f HT(m,f)/H(m)$, and the same considerations hold for interpretation. The results of these calculations are shown in Tables 6 and 7.

Table 6. Information transmitted from the female to behavioral components of the male in <u>Plethodon jordani</u> and in <u>Ambystoma maculatum</u>.

		NAME OF COMPONENT	No. OF STATES	UNCERTAINTY OF COMPONENT			INFORMATION TRANSMITTED FROM	
				ACTUAL $H(m)$	POTENTIAL $H(m)_{max}$	STANDARD $H(m)/H(m)_{max}$	FEMALE TO MALE $\sum_f HT(m,f)/H(m)$	MALE TO MALE $\sum_m HT(m_x,m)/H(m_x)$
Plethodon jordani	1	Tail angle	3	.898	1.585	.566	.322	1.373
	2	Tail undulation	2	.864	1.000	.864	.412	1.572
	3	Foot action	3	.976	1.585	.616	.210	.804
	4	Progress	3	1.054	1.585	.665	.097	.332
	5	Contact (anterior)	7	1.611	2.807	.574	.404	.735
	6	Contact (posterior)	16	1.844	4.000	.461	.643	1.349
	7	Head action	6	.443	2.585	.171	.282	.451
	8	Head orientation	3	.410	1.585	.259	.336	.558
	9	Body axis	3	.108	1.585	.068	1.753	1.870
	10	Tail axis	2	.210	1.000	.210	1.047	1.790
	11	Vent action	3	.231	1.585	.146	.747	1.796
MALE		Mean				.418	.568	1.148
		Standard				.260	.476	.584
Ambystoma maculatum	1	Tail angle	2	.496	1.000	.496	.210	1.558
	2	Tail undulation	2	.732	1.000	.732	.209	1.859
	3	Limb action	2	.588	1.000	.588	.262	2.211
	4	Progress	3	.920	1.585	.580	.158	1.298
	5	Contact (anterior)	12	2.000	3.585	.558	.216	.946
	6	Contact (posterior)	9	1.381	3.170	.436	.329	.792
	7	Head action	3	.556	1.585	.351	.248	.797
	8	Head orientation	3	.274	1.585	.173	.215	.274
	9	Head swinging	2	.089	1.000	.089	.315	1.438
	10	Vent action	6	1.143	2.585	.442	.268	1.464
MALE		Mean				.444	.243	1.264
		Standard deviation				.196	.052	.571

Table 7. Information transmitted from the male to behavioral components of the female in Plethodon jordani and in Ambystoma maculatum.

		NAME OF COMPONENT	No. OF STATES	UNCERTAINTY OF COMPONENT			INFORMATION TRANSMITTED FROM	
				ACTUAL $H(f)$	POTENTIAL $H(f)_{max}$	STANDARD $H(f)/H(f)_{max}$	MALE TO FEMALE $\sum_{m} HT(f,m)/H(f)$	FEMALE TO FEMALE $\sum_{f} HT(f_y,F)/H(f_y)$
FEMALE Plethodon jordani	1	Tail angle	2	.546	1.000	.546	.348	2.408
	2	Tail undulation	2	.543	1.000	.543	.423	2.365
	3	Foot action	2	.092	1.000	.092	2.457	3.022
	4	Progress	3	.852	1.585	.538	.096	.221
	5	Contact (anterior)	13	1.922	3.700	.519	.398	.592
	6	Contact (posterior)	10	2.024	3.322	.609	.543	1.030
	7	Head action	4	.237	2.000	.118	.297	.422
	8	Head orientation	3	.874	1.585	.551	.148	.737
	9	Body axis	3	.543	1.585	.342	.300	.545
	10	Tail axis	2	.019	1.000	.019	.342	.526
	11	Vent action	4	.249	2.000	.124	1.331	1.161
		Mean				.364	.608	1.184
		Standard deviation				.229	.695	.959
FEMALE Ambystoma maculatum	1	Tail angle	2	.064	1.000	.092	1.443	1.250
	2	Tail undulation	1	.000	.000			
	3	Limb action	2	.625	1.000	.625	.223	1.472
	4	Progress	4	.990	2.000	.495	.198	.620
	5	Contact (anterior)	11	2.006	3.459	.580	.350	.497
	6	Contact (posterior)	9	1.889	3.170	.596	.322	.536
	7	Head action	2	.025	1.000	.025	.722	.800
	8	Head orientation	3	.177	1.585	.112	.221	.237
	9	Head swinging	1	.000	.000			
	10	Vent action	4	1.143	2.000	.572	.091	1.110
		Mean				.384	.446	.815
		Standard deviation				.266	.444	.424

Statistical analyses

There are eight estimates, one from each component, for each of the standardized variables $H(f)/H(f)_{max}$, $\sum_m HT(f,m)/H(f)$, and $\sum_f HT(f_y,f)/H(f)$ for female Ambystoma maculatum, and there are 11 estimates for each of these variables in female Plethodon jordani. For the analagous variables in male Ambystoma maculatum there are 10 estimates, and there are 11 estimates for male Plethodon jordani. There is one estimate from each component, and these will be treated as samples from a statistical population of many possible components. We can now ask if there are statistically significant differences within and between the two species in these variables. Means and standard deviations for each variable are shown in Tables 6 and 7.

Mann-Whitney U tests show that within each species there is no significant difference between the standardized uncertainty of female and male components (ie. between $H(f)/H(f)_{max}$ and $H(m)/H(m)_{max}$ within each species. Likewise, between species there is no significant difference between the standardized uncertainty of male components and no difference between the standardized uncertainty of female components.

Within each species there is no significant difference between the extent to which females affect male behavior and the extent to which males affect female behavior (Mann-Whitney U tests show no significant difference between $\sum_f HT(m,f)/H(m)$ and $\sum_m HT(f,m)/H(f)$ in both species).

Plethodon jordani females affect the male's subsequent behavior more than Ambystoma maculatum females affect the male's subsequent behavior (U=20.5, .001 p .01; comparing $\sum_f HT(m,f)/H(m)$ between species). But there is no significant difference between the two species in the extent to which the male affects the female's subsequent behavior (ie. in $\sum_m HT(f,m)/H(f)$ between species).

Within each species, each sexual partner affects its own subsequent behavior more than does the sexual partner (note that in Table 6 $\sum_{m} HT(m_x,m)/H(m_x)$ is almost invariably larger than $\sum_{f} HT(m,f)/H(m)$ for each male component, and that in Table 7 $\sum_{f} HT(fy,f)/H(f_y)$ is almost invariably larger than $\sum_{m} HT(f,m)/H(f)$ for each female component). Between species, however, there is no significant difference in the extent to which sexual partners affect their own subsequent behavior.

Since there is no significant difference between species in the amount of information transmitted from the male to the female, I will estimate this amount of transmitted information as the mean of observations combined from both species (.539). This amount of information transmitted plus the information transmitted from the female to the male (which is significantly different in the two species), I will term the total amount of information transmitted between sexual partners per act. This sum is (.539 + .568) or 1.107 for Plethodon jordani and (.539 + .243) or .782 for Ambystoma maculatum.

d. Information transmitted between sexual partners per unit time.

I will estimate the average rate of information transmission between sexual partners as simply the product of courtship rate (acts/minute) and information transmitted between sexual partners per act, for each species.

The average rate of information transmission between sexual partners is (3.58 acts/min X 1.107 units/act) or 3.963 for Plethodon jordani and (75.65 acts/min X .782 units/act) or 59.158 for Ambystoma maculatum.

Ambystoma maculatum pairs court at a faster rate and affect each other's behavior at a faster rate than pairs of Plethodon jordani.

e. Information transmitted between sexual partners per spermatophore deposition.

I will estimate the average amount of information transmitted between sexual partners per spermatophore deposition as the product of the rate of information transmission between sexual partners and the average time per spermatophore deposition in each species.

The average amount of information transmitted between sexual partners per spermatophore deposition is (3.963 units/min X 55.90 min/spermatophore) or 221.53 in *Plethodon jordani* and (59.158 units/min X 1.36 min/spermatophore) or 80.46 in *Ambystoma maculatum*.

Therefore, for each spermatophore deposited, *Plethodon jordani* pairs affect each other's behavior nearly three times as much as *Ambystoma maculatum* pairs. This difference is largely due to the fact that *Plethodon jordani* males court for a much longer time before depositing a spermatophore.

6. A closer look at the dynamics of communication during courtship.

In the preceding section I used information theory to reduce the complexities of communication during courtship to a single metric in Plethodon jordani and in Ambystoma maculatum. This approach allowed us to compare the impact of communication processes in each species, but it obscured the differences between species in the behavioral mechanisms employed during courtship. In this section I will take a closer look at the dynamics of communication during courtship.

Ambystoma maculatum males court rapidly and deposit many spermatophores in a wide variety of sites. Plethodon jordani males court slowly and deposit a single spermatophore in a very specific site. Do male Plethodon jordani employ special behavioral mechanisms to accomplish this specifity in the site of spermatophore deposition? The peculiar tail-straddling walk of Plethodon jordani accomplishes just this function and thereby increases the female's chances of locating the spermatophore. The tail-straddling walk is characteristic of the entire family Plethodontidae and is an excellent example of a behavioral mechanism which has evolved to increase the reproductive success of each spermatophore deposited by the male. In section (a) I will examine this special mechanism in detail.

In the next section, (b), I will compare the overall complexity of courtship mechanisms in the three species. Is the female more likely to locate the male's spermatophore if his courtship is complex? In order to test this hypothesis I have applied the technique, borrowed from computer sciences, of modeling behavior in terms of stepwise procedures or algorithms. This technique forces one to make specific hypotheses about the mechanisms which control behavior. In addition the models which I propose give an overview of the complexity of behavior during courtship in each species and give a tentative answer to the question above.

a. Behavioral homeostasis during the tail-straddling walk of *Plethodon jordani*.

In *Plethodon jordani*, spermatophore deposition is always preceded by a tail-straddling walk in which the female straddles the male's tail with her forelimbs, and her hindlimbs, and rests her chin on the dorsum of the male's anterior tail. Both animals walk forward, intermittently, with the female in this position, but the female's snout remains over a very small area on the male's tail. Fig. 13 shows six successive photographs, taken during a period of approximately 10 minutes, of a pair of *Plethodon jordani* in a tail-straddling walk. Notice that the position of the female's snout is remarkably constant in relation to the male's hindlimbs. What are the behavioral mechanisms responsible for this constancy in female position? Is one or the other sexual partner responsible for this constancy, while the other sexual partner is simply a passive participant? Or are both the male's and the female's behavior responsible for the constancy of female position?

A series of close observations on 18 pairs of courting *Plethodon jordani* was made to answer these questions (24 sets of observations). In particular these observations allow us to determine whether the position of the female's snout on the male's tail influences forward progress by the male and by the female.

Eight regions were recognized on the male's tail (see Fig. 15C). Each region is one male-vent-length long, so that the sizes of the regions are standardized to correct for the differing sizes of courting males. Region 4 is centred about the posterior limit of the male's vent, and the regional position of the female's snout was reckoned from this point. The animal's were observed from the side, so that this scheme for noting female snout position could be applied very easily. Regions 2 through 7 are of equal

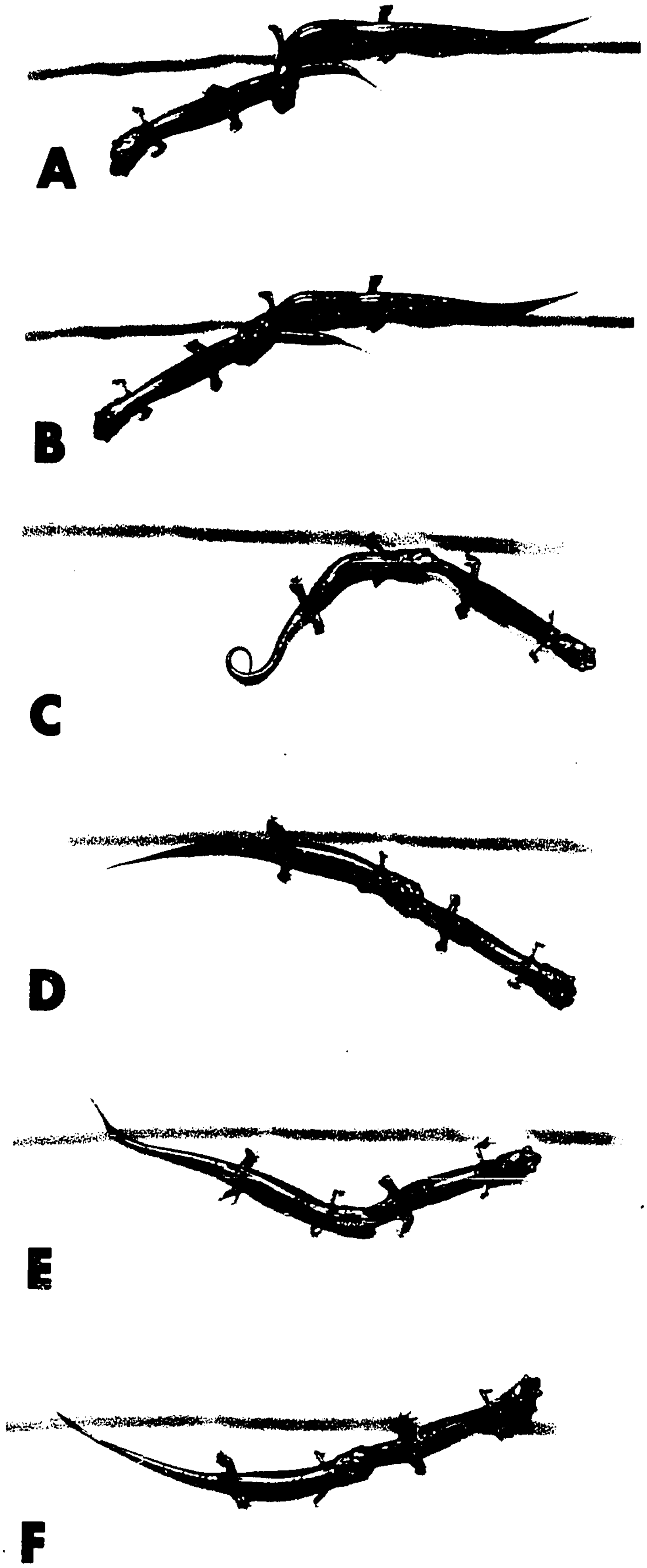
Figure 13. The tail-straddling walk of Plethodon jordani (dorsal views).

Fig. A. The male is stationary while arching and undulating his tail under the female's chin.

Fig. B. The female has turned her head axial and anterior along the male's tail as he continues to arch and undulate his tail.

Figs. B,C,D,E,F. The female has stepped astride the male's arched and undulating tail. Notice the remarkable constancy in the position of the female's snout in relation to the male's hindlimbs, and that the female's chin remains axial on the male's tail.

(These photographs are of a pair of animals from Highlands, Macon Co., North Carolina; Plethodon jordani melaventris).


A
B
C
D
E
F

length (one half of the male's vent length), while region 1 is any dorsal position anterior to the insertion of the male's hindlimbs, and the region 8 is any point posterior to 1 and 1/2 vent lengths posterior to the rear margin of the male's vent.

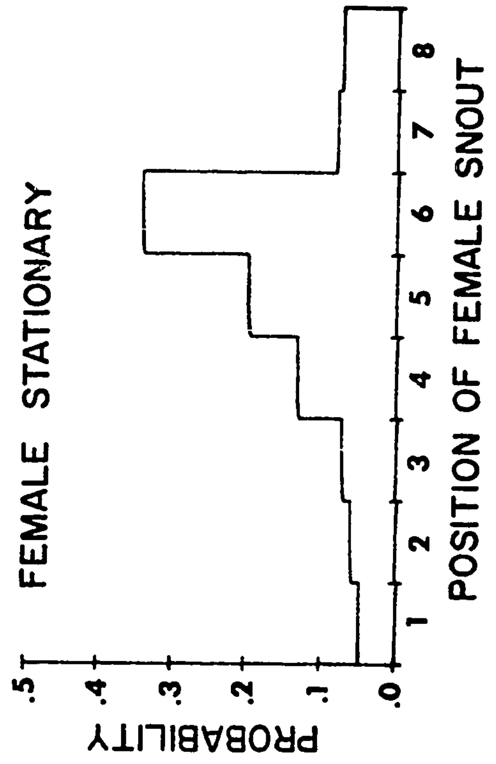
During recording sessions I make continuous observations on the position of the female's snout and whether the male and the female were moving forward at that position, whenever the female's chin was in contact with the male's dorsal body or tail and his vent was raised above the substrate.

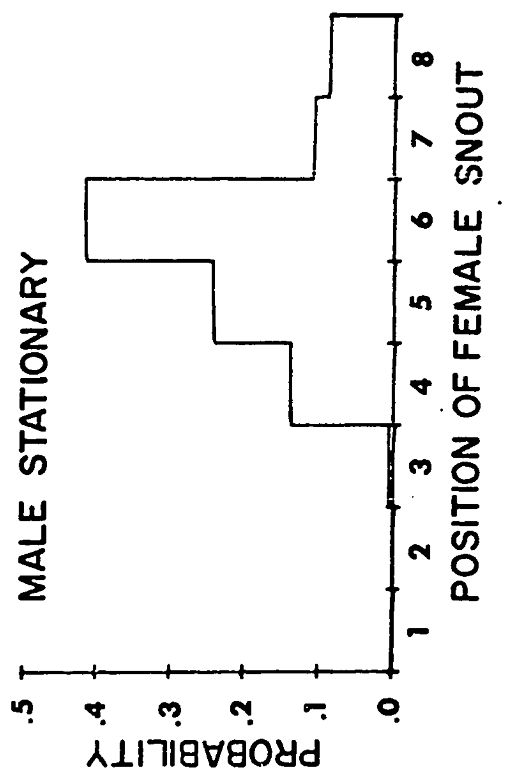
The probability of the female's snout being in each of the eight tail regions, given that the male is stationary, is shown in Fig. 14 (based on 151 observations of female snout position with the male stationary). The probability of the female's snout being in each of the eight tail regions, given that the male is moving forward, is shown in Fig. 14 (based on 108 observations of female snout position with the male moving forward). The analagous probability distributions for the female are also shown in Fig. 14 (based on 167 observations for females stationary and on 167 observations for females moving forward).

When the male is moving forward, the female's snout is in a more anterior position along his tail (mean = 3.8, variance = 1.67) than when the male is stationary (mean = 5.7, variance = 1.25) ($T=12.6$, d.f.=257,$p<10^{-6}$) (see Fig. 14). In contrast, there is no significant difference in mean female snout position when the female is moving forward (mean = 5.2, variance = 1.37) and when she is stationary (mean - 5.1, variance = 3.04) (T corrected for unequal variance = -0.74, d.f. 292, p=0.46) (see Fig. 14).

From the same data we can also calculate the probability that the male is moving forward, given that the female's snout is at a particular position, (the proportion of observations in which the male was moving forward, given

Figure 14. Probabilities that the female's snout is in each of eight position along the male's tail during the tail-straddling walk of <u>Plethodon jordani</u> given that the male or the female is stationary.


FEMALE STATIONARY
PROBABILITY
.0
.1
.2
.3
.4
.5
1
2
3
4
5
6
7
8
POSITION OF FEMALE SNOUT


MALE STATIONARY
PROBABILITY
.0
.1
.2
.3
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.5
1
2
3
4
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6
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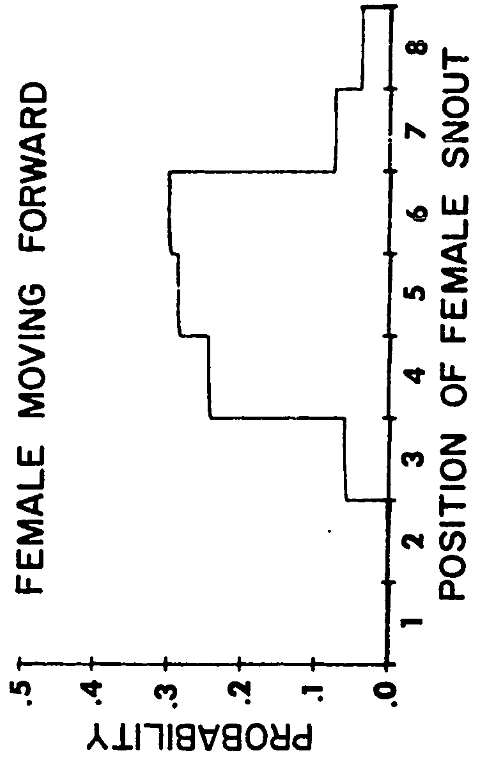
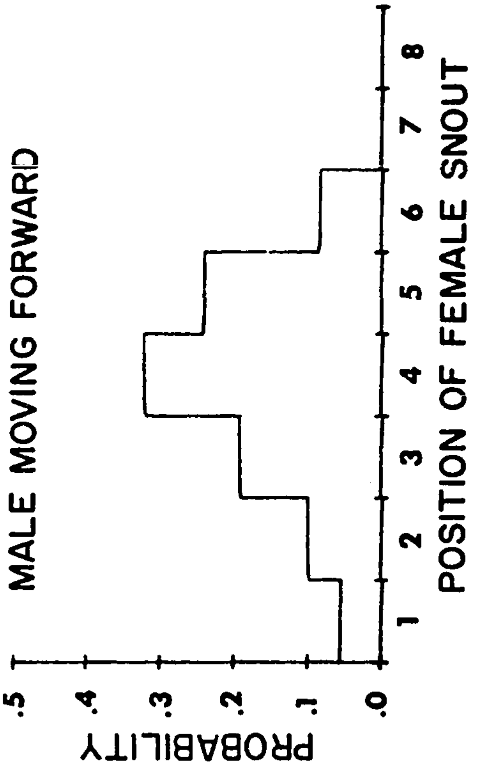
8
POSITION OF FEMALE SNOUT


FEMALE MOVING FORWARD
PROBABILITY
.0
.1
.2
.3
.4
.5
1
2
3
4
5
6
7
8
POSITION OF FEMALE SNOUT


MALE MOVING FORWARD
PROBABILITY
.0
.1
.2
.3
.4
.5
1
2
3
4
5
6
7
8
POSITION OF FEMALE SNOUT

female snout position), and the probability that the female is moving forward, given female snout position, (the proportion of observations in which the female was moving forward, given female snout position). These probabilities are shown in Fig. 15. Notice (Fig. 15B) that as the female's snout position drops posteriorly from region 1 to region 8, the probability of forward progress by the male drops suddenly from 1.0 to 0.0. A Chi Square test shows this trend to be highly significant (see Table 8). Notice also (Fig. 15A) that the female is most likely to be moving forward when her snout is in region 4. When her snout is anterior or posterior to this region, she is less likely to move forward. A Chi Square test shows that this trend is statistically significant, but barely so (see Table 8).

These last two analyses allow us to answer the questions posed above. The constancy in female snout position is certainly produced by the male's behavior and probably also by the female's behavior. Regulation of female snout position is produced in the following way. When the female's snout slips posteriorly along the male's tail, the male tends to stop. He remains stationary until the female slides forward. As the female slides forward along his tail, the probability that the male will move forward gradually increases, and finally he moves forward. When the male does move forward, the female's snout will slip posteriorly, and the cycle of regulation begins again.

The female is most likely to move forward when her snout is in region 4. At the same time the male tends to move forward when her snout is anterior to this same point, and this has the effect of moving her snout back towards region 4. When she slides posterior to region 4, she tends to stop. The male then remains stationary until she slides forward again to region 4, and the regulatory cycle continues.

These regulatory interactions between the male and the female can be

Figure 15. Forward progress as a function of female snout position during the tail-straddling walk of <u>Plethodon jordani</u>.

Fig. A. The probability that the female is moving forward as a function of her snout position on the male's tail.

Fig. B. The probability that the male is moving forward as a function of the position of the female's snout on his tail.

Fig. C. A lateral view of a male (right) and a female (left) in a tail-straddling walk, showing the 8 regions used to describe the female's snout position in Fig. A. and B.

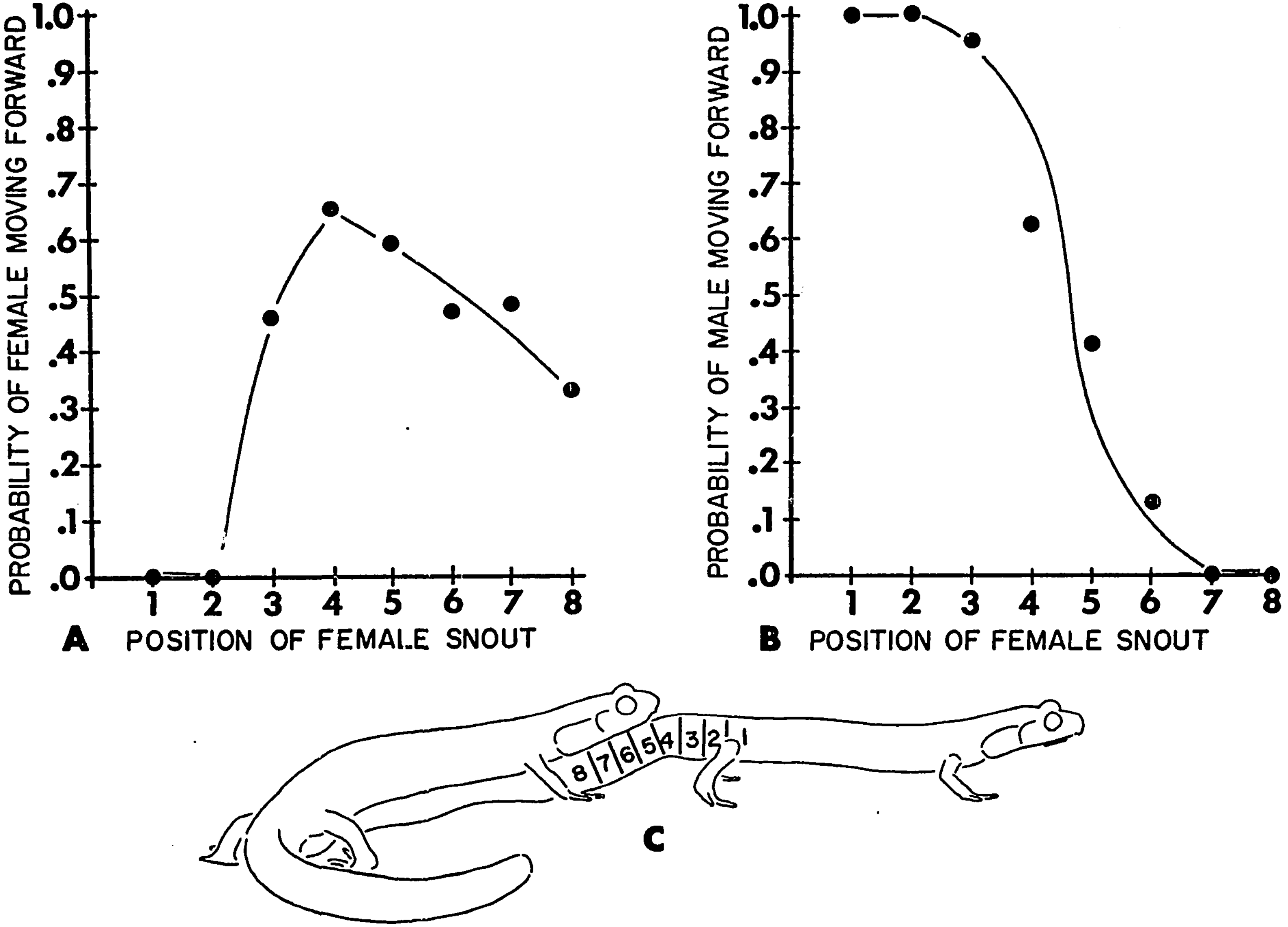

PROBABILITY OF FEMALE MOVING FORWARD
1.0
.9
.8
.7
.6
.5
.4
.3
.2
.1
.0
1
2
3
4
5
6
7
8
A
POSITION OF FEMALE SNOUT
PROBABILITY OF MALE MOVING FORWARD
1.0
.9
.8
.7
.6
.5
.4
.3
.2
.1
.0
1
2
3
4
5
6
7
8
B
POSITION OF FEMALE SNOUT
8
7
6
5
4
3
2
1
C

Table 8. Chi Square tests of some communication processes during the tail-straddling walk of *Plethodon jordani*.

A. *Hypothesis*: The male's tendency to move forward is independent of the female's snout position.

Female snout position	1	2	3	4	5	6	7	8	TOTAL
Total No. of observations of male progress	6	11	22	56	63	72	16	13	259
No. of observed cases in which male was moving forward	6	11	21	35	26	9	0	0	108
							9		
Expected No. of cases	2.5	4.6	9.2	23.3	26.2		42.0		

Expected probability of forward progress = 108/259 = 0.416

Chi Square = 61.0, d.f. = 5, $p < 0.001$

B. *Hypothesis*: The female's tendency to move forward is independent of the female's snout position.

Female snout position	1	2	3	4	5	6	7	8	TOTAL
Total No. of observations of female progress	8	10	22	63	81	107	25	18	334
No. of observed cases in which female was moving forward	0	0	10	41	48	50	12	6	167
		10							
Expected No. of cases		20.0		31.5	40.5	53.5	12.5	9.0	

Expected probability of forward progress = 167/334 = 0.500

Chi Square = 11.12, d.f. = 5, p = 0.05

best appreciated when they are expressed diagramatically. Two such diagramatic representations are shown in Fig. 16, a discrete state model, and in Fig. 17, a continuous state model. Every such model will clarify some aspects of a phenomenon while sacrificing some aspects of reality. The models in Fig. 16 and Fig. 17 are not exceptions. Both models seek to clarify the regulatory roles of the male's and the female's behavior in adjusting the position of the female's snout, but each model sacrifices a different aspect of reality. In both models the behavioral output from each sexual partner, forward progress, is a function of female snout position.

In the first model, Fig. 16, the behavioral output, forward progress, consists of two discrete states (stationary or moving forward), and forward progress is a probabilistic function of female snout position. Each animal continuously receives female snout position as a stimulus input, and then makes a probabilistic decision, based on this stimulus input, to either move forward or remain stationary. The male's behavior either moves the female's snout position posterior or leaves it unchanged. While, on the other hand, the female's behavior either moves her snout anterior or leaves its position unchanged. Jointly their decision making processes and behavioral outputs maintain the female's snout on the male's anterior tail.

In the second model, Fig. 17, behavioral output is a continuous variable, velocity, but velocity is a deterministic function of female snout position. As in the first model, each animal continuously receives female snout position as a stimulus input. The further anterior the female's snout, the faster the male moves forward. He is stationary with the female's snout in region 8, and his velocity increases monotonically as the female moves anterior to this region. The female moves forward fastest when her snout is in region 4, and she slows down when her snout

Figure 16. A discrete state model of the regulatory processes during the tail-straddling walk of Plethodon jordani.

The decision making processes of the male are shown in the upper, large, dotted box. The male receives the current position of the female's snout on his tail as a stimulus input. If the female's snout is anterior to region 4 on his tail, the male is most likely to move forward. If the female's snout is not anterior to region 4, the male is most likely to remain stationary.

The decision making processes of the female are shown in the lower, large, dotted box. The female receives the current position of her snout on the male's tail as a stimulus input. If her snout is in region 4, she is most likely to move forward along the male's tail. If her snout is not in region 4, the female is most likely to remain stationary.

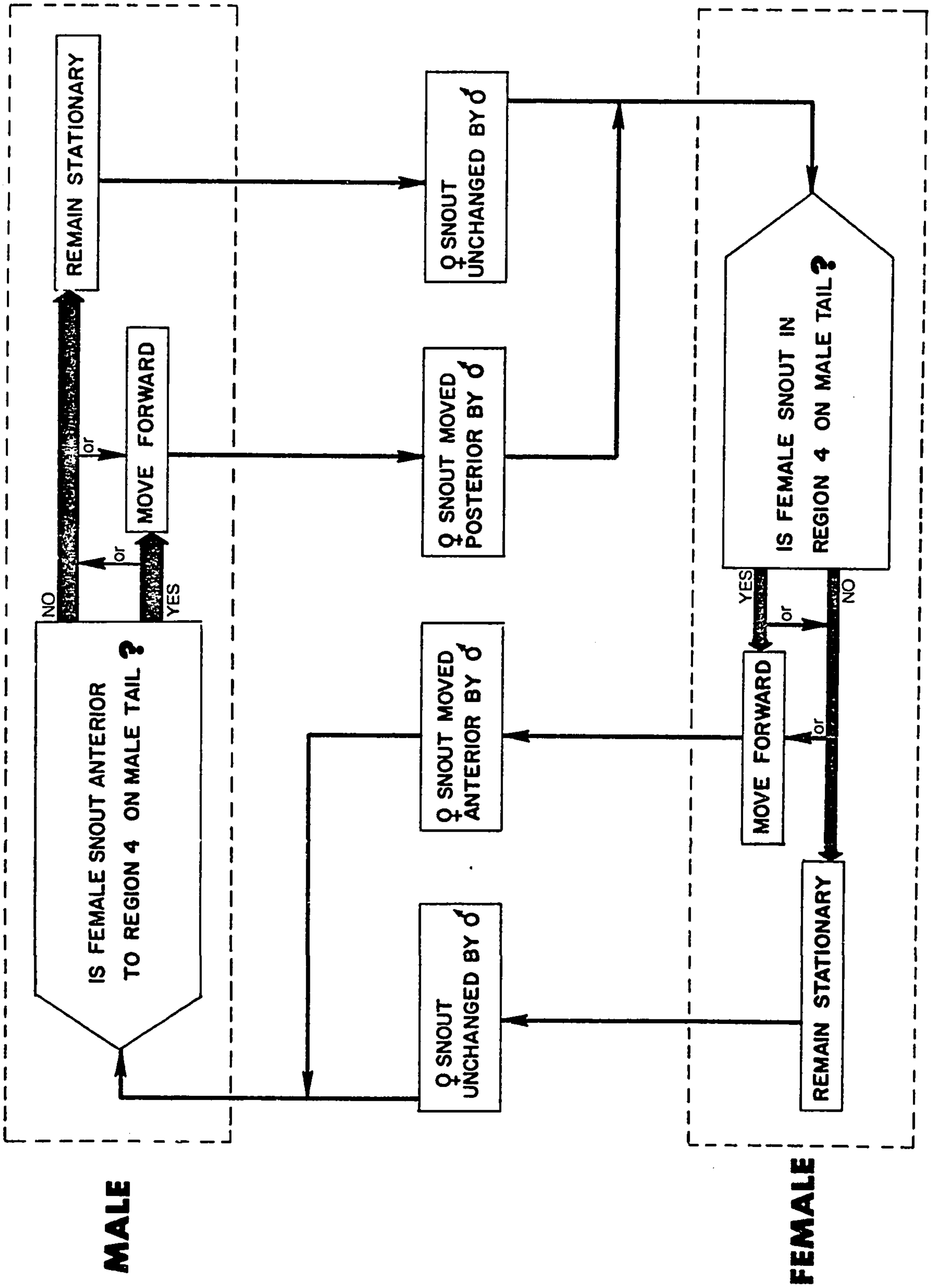
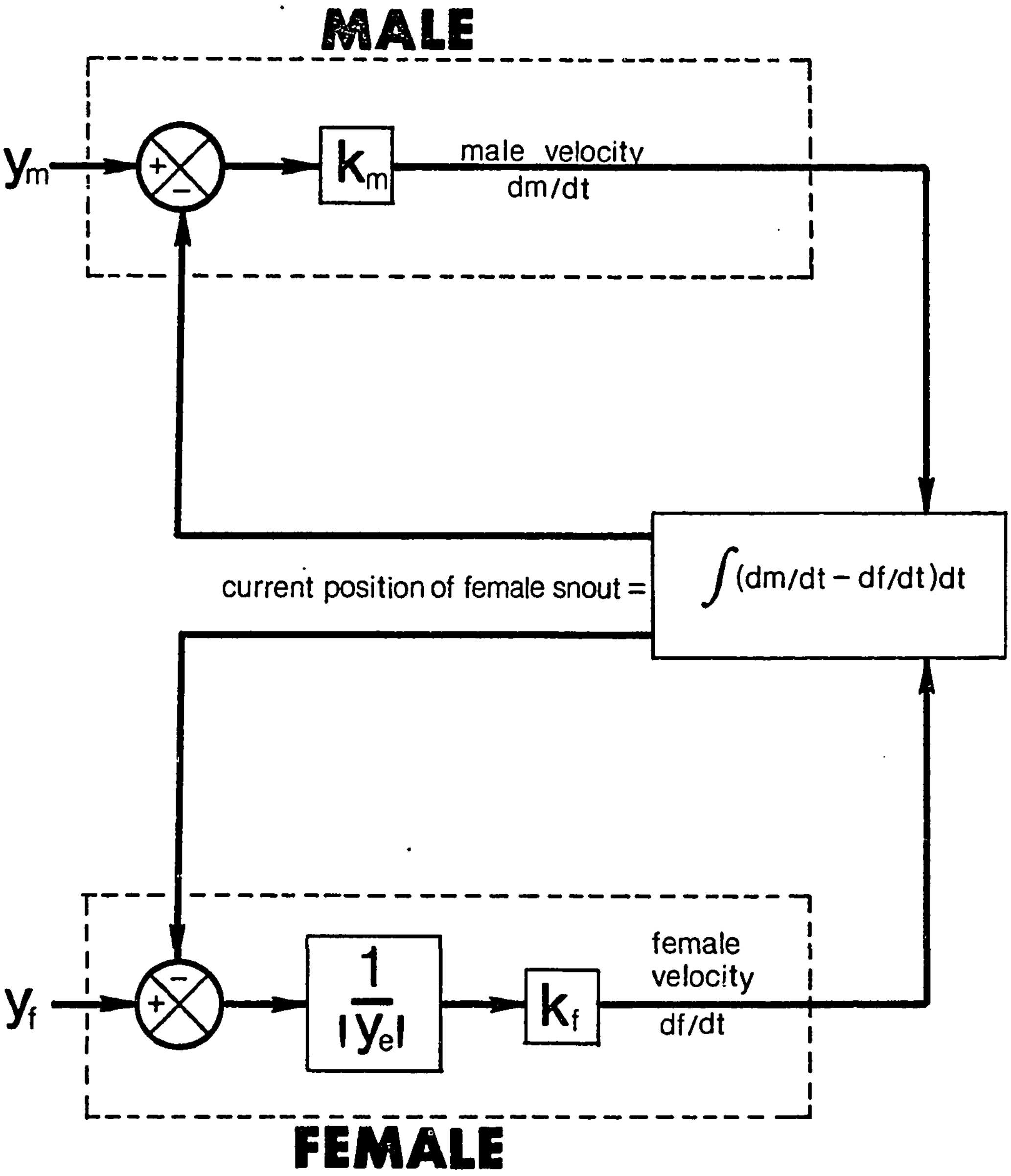

MALE
IS FEMALE SNOUT ANTERIOR TO REGION 4 ON MALE TAIL?
NO
YES
or
MOVE FORWARD
or
REMAIN STATIONARY
♀ SNOUT UNCHANGED BY ♂
♀ SNOUT MOVED POSTERIOR BY ♂
♀ SNOUT MOVED ANTERIOR BY ♂
♀ SNOUT UNCHANGED BY ♂
FEMALE
IS FEMALE SNOUT IN REGION 4 ON MALE TAIL?
YES
NO
or
MOVE FORWARD
or
REMAIN STATIONARY

Figure 17. A continuous state model of the regulatory processes during the tail-straddling walk of *Plethodon jordani*.

The decision making processes of the male are shown in a large dotted box. The male receives the current position of the female's snout as a stimulus input. This position is compared (circle with cross bars) with a reference point (Ym, the region 8 on the male's tail) to yield a deviation of the female's current position from this reference point. This deviation is multiplied by a constant (k_m) to determine the male's velocity (dm/dt). Thus the male moves forward faster, the more anterior the female's snout.

The decision making processes of the female are shown in the lower, large dotted box. The female receives the current position of her snout on the male's tail as a stimulus input. This position is compared with a reference point on the male's tail (yf, region 4 on the male's tail) to yield a deviation of the female's snout from this reference point. The inverse of the absolute value of this deviation (or $1/|y_e|$) is multiplied by a constant (kf) to determine the female's current velocity. Thus the female moves forward fastest, when her snout is in region 4, and her velocity decreases when her snout is anterior or posterior to this region.


MALE
y_m
+
−
k_m
male velocity
dm/dt
current position of female snout =
$\int$(dm/dt − df/dt)dt
y_f
+
−
$\frac{1}{|y_e|}$
k_f
female
velocity
df/dt
FEMALE

lies anterior or posterior to this point.

In both models the male and the female behave as regulators of female snout position. The first model emphasizes the probabilistic influence of female snout position on forward progress, but forward progress is unrealistically treated as a two state behavioral output. The second model treats the behavioral output more realistically as a continuous variable, velocity, but when the female's snout is at a particular position, this invariably produces a particular velocity.

On one occasion I was able to experimentally manipulate a male during the tail-straddling walk. The results of this one experimental session reaffirm the foregoing conclusions about the role of the female's snout position in determining forward progress by the male. As a male was approaching a female, and contacting her with his snout while performing a foot dance, I reached into the container and placed the stainless steel handle of a scalpel in contact with the male's anterior tail in an attempt to simulate the contact of a female's chin to his tail. The handle was held perpendicular in contact with his tail, so that the length of contact was only 1 cm. The male immediately arched and undulated his tail, while holding his vent above the substrate. I touched my fingers to the ground on either side of the male's tail, so that the handle contacted his tail very lightly. For the next twenty minutes I found that I could regulate the male's forward progress by changing the position of the handle on his tail. Movement of the forward edge of the handle anterior to approximately region 5 caused the male to move forward. Whenever the handle was moved anterior to region 2, the male moved forward very rapidly. Each time I held the handle stationary as the male moved forward, he would continue forward and then stop when the contact slipped posteriorly along his tail. After approximately twenty minutes of "tail-straddling walk" with the handle simulating a female, the male stopped and deposited a spermatophore.

The remarkable success of this one experimental session in producing male tail-straddling walk responses in the absence of a female, suggests that the male is responding solely to tactile contact to his dorsal tail during the tail-straddling walk. Furthermore, although a female would contact the male's tail along the entire length of his tail, tail-straddling walk behavior by the male can be produced with only an anterior contact. This suggests that during a tail-straddling walk with a female, only the most anterior contact of the female's chin on the male's tail is responsible for regulating male progress.

Additional experiments of this kind should do much to unravel the sensory cues which govern behavior during the tail-straddling walk. In particular, it would be illuminating to know the sensory modalities (eg. tactile or chemoreceptive) used by the female to regulate her progress during the tail-straddling walk.

b. Behavioral algorithms for courtship behavior and the complexity of programming for courtship behavior in *Ambystoma maculatum*, *Ambystoma tigrinum* and *Plethodon jordani*.

In this section models are presented which attempt to represent the underlying dynamics of courtship behavior in *A. maculatum*, *A. tigrinum* and *Plethodon jordani*. The purpose of these models is to elucidate the behavioral mechanisms which cause animals to switch from one activity to another during courtship. For each species two models are presented; one to represent the mechanisms controlling male behavior and one to represent the mechanisms controlling female behavior.

Although the models at first appear complex, they are actually composed of only three elements. The first type of element is the behavioral action. These correspond to the actions presented earlier in the catalogs of actions for each species. The other two elements, conditional statements and stochastic branch points, are used to represent the behavioral mechanisms which govern transitions from one type of behavioral action to another. Conditional statements take the form of questions which ask whether or not a particular stimulus is being received from the sexual partner. They are used to represent how and when stimulus input from the sexual partner changes the behavior of the other sexual partner. Stochastic branch points are used to represent situations in which the "decision" to change courtship behavior to one of two or more alternative actions appears to be simply probabilistic and independent of the current stimulus input from the sexual partner.

The models were constructed in the following way. When one action (A) was observed to always lead to another action (B), then an arrow is drawn leading from A to B. When observations showed that action B follows A only when a particular stimulus is given by the sexual partner, and C follows A when this stimulus is not given, then a conditional statement, composed of the relevant stimulus, is drawn between A and the actions B and C. Sometimes several conditional statements are inserted between actions. In such cases the conditional statement in such a hierarchy. The first conditional statement in such a hierarchy determines a change in the sequence of performed actions, regardless of the input stimuli which are present in conditional statements lower in the hierarchy. The same consideration holds for the second, third, ... conditional statements in the hierarchy. Stochastic branch points were inserted whenever changes in behavior could not be related to particular stimuli from the sexual partner.

No model serves all purposes equally well. The models of this section attempt to represent courtship behavior as the result of interactions between a stepwise procedure, or algorithm, for the male and a separate stepwise procedure for the female. They are meant to portray courtship behavior in each species as realistically as possible in order to make meaningful comparisons between species, and, more importantly, to suggest specific hypotheses for future behavioral analyses. I will briefly discuss the virtues and the limitations of this type of behavioral modeling, and then turn to discussion of the models themselves.

The utility of this type of modeling can be best appreciated when it is compared with other modes of describing or explaining the interactions between animals. Investigations of courtship behavior have invariably shown that the behavioral sequences are not completely stereotyped. The central problems are then to describe this variability in behavioral sequence, to elucidate the behavioral basis for this variability, and to determine whether the variability has nay adaptive significance.

Several investigators have described variability in behavioral sequence by presenting the frequencies with which particular behavioral actions follow other behavioral actions (either in the form of diagrams or in tabular form as matrices of transition frequencies or probabilities) (eg. Baerends, Brouwer and Waterbolk, 1955; Bastock and Manning, 1955). Behavioral data compressed in this way have also been treated as predictive models by some workers (eg. Nelson, 1964; Altmann, 1965). Models of this kind can be used to test whether the behavioral actions in a sequence are probabilistically independent of the preceding actions in a sequence. For example, Nelson (1964) found that courtship actions of male glandulocaudine fish were probabilistically dependent only upon the immediate preceding action and independent of earlier actions in a sequence (the mathematical analog of such a situation is a first order Markov process). Descriptions or models of this kind do portray some of the variability in courtship sequence, but they tell us relatively little about the decision making processes in the animal, and in particular they do not indicate whether the sexual partner influences decisions to change behavior.

"Chain response diagrams" (Hinde, 1966) (commonly called "stickleback diagrams") do provide this type of information, but they presume that the behavioral sequences are invariant. Such diagrams indicate the stimuli which are required from one sexual partner to elicit a new behavior from the other sexual partner. Courtship behavior is viewed as an alternating exchange of stimuli between the male and the female, with each male action providing the eliciting stimulus for the next female action, and with each female action providing the eliciting stimulus for the next male action. (Tinbergen, 1951; Prechtl, 1951; Eibl-Eibesfeldt, 1954). Such diagrams suggest fruitful hypotheses about how courtship behavior is controlled, but they presume that changes in behavior are obligatory once the sexual partner provides a particular stimulus. Consequently, if viewed as realistic models of courtship behavior, these diagrams portray courtship behavior as more stereotyped than it actually is (Morris, 1958; Barlow,1962).

The models which follow incorporate the virtues of both of the preceding classes of descriptions or models. They realistically portray the variability present in behavioral sequence, and they focus attention on how this variability is produced during courtship encounters. At the same time they possess limitations, for in many instances the causal basis for variability in sequence remains unresolved. The variability in sequence indicated by stochastic branch points could be due to consistent differences between individuals, to differences between courtships within an individual, or to differences within individuals within a courtship (eg. a gradual change in the tendency to respond to a particular stimulus situation). Alternatively, stimuli from the sexual partner might actually be responsible for switching behavior in the other animal. If the role of such stimuli goes undetected, then a stochastic branch point, rather than a conditional statement, is incorporated into the courtship algorithm. In other words, many alternative explanations for variability in behavioral sequence remain to be tested. Courtship models of this kind will always represent a set of working hypotheses about the underlying dynamics of courtship behavior. Ideally tables of the frequencies of transition between courtship actions should be the basic data from which the courtship algorithms are constructed, since the algorithms should account for all observed transitions between actions in each sex. These are provisional models, and they have yet to be compared with actual tabulations of transition frequencies. At this point the models are simply reasonable first approximations to the dynamics of courtship behavior in each species, but they suggest many specific causal hypotheses for further testing. (See Eberhard (1969) and Robinson (1969) for similar algorithmic models of behavioral processes in one animal which do not include stochastic branch points.)

Provisional courtship algorithms for Ambystoma maculatum, Ambystoma tigrinum and Plethodon jordani are shown in Figs. 18, 19, 20. In each diagram rectangles represent courtship actions, triangles represent conditional statements, and stochastic branch points are represented by solid circles. The algorithms should be read in the following way. Begin, for example, at the top of the algorithm for male Ambystoma maculatum (Fig. 18), and consider only the first three conditional statements. If the female is far from the male (the state of conditional statement 1), the male should move forward rapidly (A). If the female is close to the male (conditional statement 1), but the male's snout does not contact the female (conditional statement 2), the male should move towards the female (B). If, however, his snout does contact the female (conditional statement 2), and he does not contact a spermatophore with his vent (3), the male should perform nudging and head swinging while moving along the length of the female (C). If his vent does contact a spermatophore (3), the male should stop and adpress his hindlimbs (F). He may then (see stochastic branch point after F) either deposit a spermatophore (G) (in this case on the pre-existing spermatophore he has located), or perform actions A, B or F, depending upon the stimulus situation which occurs next.

Diagrammatic algorithms of this kind allow considerable compression of information, compared with verbal descriptions of the same logical structure. These algorithms are, in fact, simply formal diagrammatic representations of the discussions of temporal relations which were given earlier for each species.

Figure 18. Algorithms for courtship behavior in male *Ambystoma maculatum* and male *Ambystoma tigrinum*.

Ambystoma maculatum (on left)

MALE ACTIONS (rectangles)

A. Move forward rapidly
B. Approach female.
C. Perform nudging and head swinging while moving along the length of the female.
D. Lift head and turn head towards side of body contacted.
E. Shuffle vent in contact with substrate, move away from female.
F. Remain stationary and adpress hindlimbs against tail base.
G. Deposit a spermatophore.

CONDITIONAL STATEMENTS (triangles) ("yes" exits on left).

1. Is the female near?
2. Does the male's snout contact the female?
3. Does the male's midbody or vent contact a spermatophore?
4. Is there contact to the male's dorsal head?
5. Is there contact to the male's dorsal head, midbody or tail?
6. Is there contact to the male's dorsal midbody or tail?

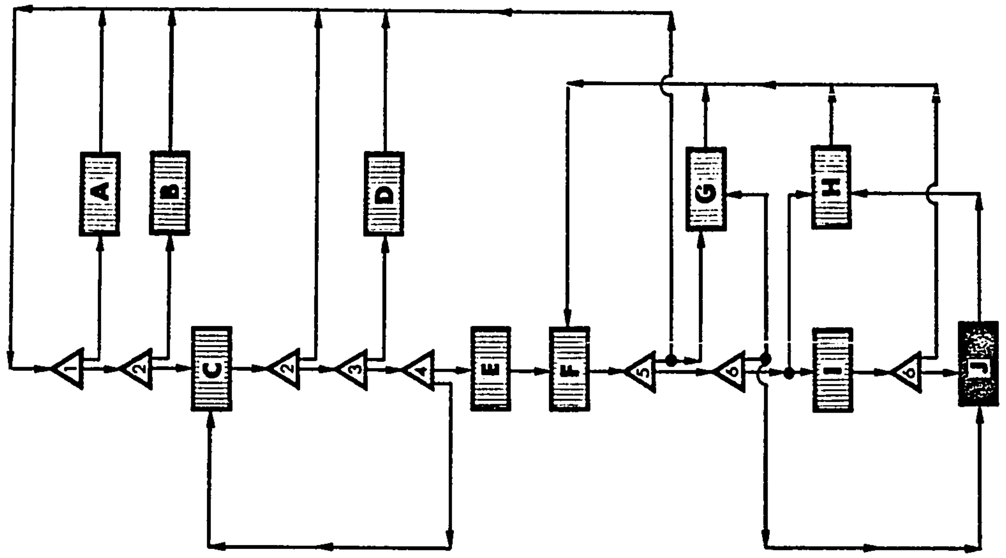
Ambystoma tigrinum (on right)

MALE ACTIONS (rectangles)

A. Move forward rapidly.
B. Approach the female.
C. Perform nudging, head swinging and lifting while moving along the length of the female.
D. Shove the female through the water.
E. Move short distance (less than one tail length) away from female and pause.
F. Remain stationary and perform tail tapping.
G. Back up short distance.
H. Move forward with tail raised, undulate tail.
I. Remain stationary, undulate tail rapidly and adpress hindlimbs.
J. Deposit spermatophore.

CONDITIONAL STATEMENTS (triangles) ("yes exits on left).

1. Is the female near?
2. Does the male's snout contact the female?
3. Is there contact to the male's head or foremidbody?
4. Is the female stationary?
5. Is there contact to the male's tail?
6. Is there contact to the male's tail base or cloaca?


A
B
D
G
H
1
2
C
2
3
4
E
F
5
6
I
6
J

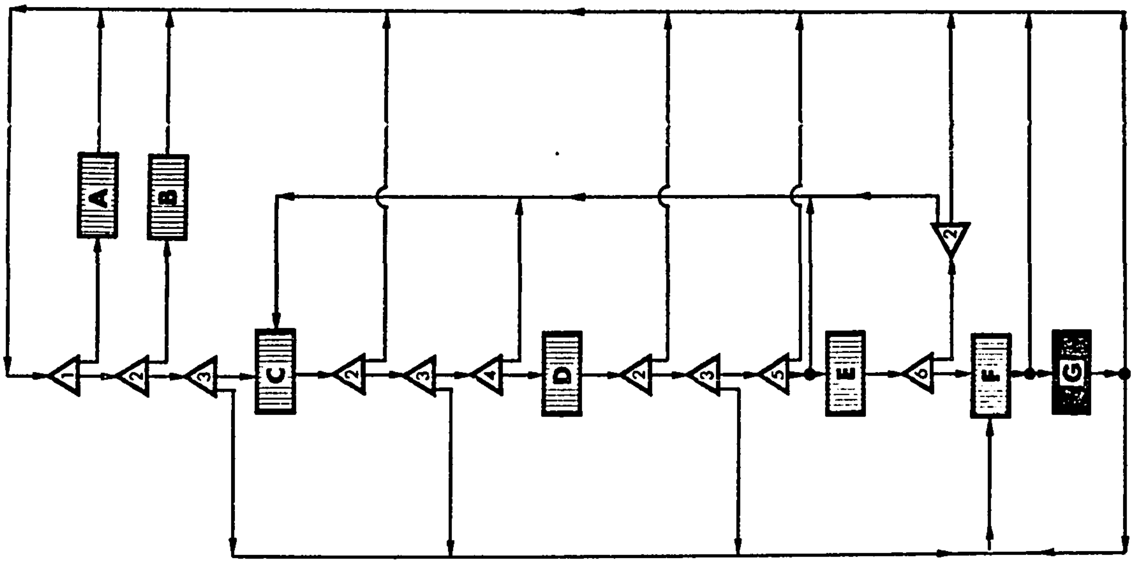

A
B
1
2
3
C
2
3
4
D
2
3
5
E
6
F
G
2

Figure 19. An algorithm for courtship behavior in male *Plethodon jordani*.

MALE ACTIONS (rectangles)

A. Move forward while tapping substrate.
B. Approach the female rapidly.
C. Approach the female slowly.
D. Perform tapping, nudging, head sliding and foot dance while moving along beside the female.
E. Turn head under female's chin, lift and crawl forward.
F. Move forward while arching tail.
G. Remain stationary with tail arched and undulating.
H. Turn back towards female.
I. Slap mental gland on the female's snout or dorsal head.
J. Slide vent in contact with substrate.
K. Remain stationary with vent in contact with substrate.
L. Deposit spermatophore.
M. Move forward with tail flexed to one side.
N. Remain stationary with tail flexed to one side and perform extention and flexion of hindlimbs.
O. Swing rapidly back towards female.
P. Move forward tapping substrate.
Q. Bite the female.
R. Eat the spermatophore.
S. Terminate courtship.

CONDITIONAL STATEMENTS (triangles)

1. Is the female present in visual field? ("yes" exits on left).
2. Is the female very near? ("yes" exits on left).
3. Does the male's snout contact the female? ("yes" exits on left).
4. Is there contact to the male's dorsal midbody or tail? ("yes" exits on left).
5. Is the male's head opposite the female's chin? ("yes" exits on left).
6. Is the contact anterior to region 4 on tail? ("yes" exits on left).
7. Does the male's snout contact the spermatophore? ("yes" exits below and "no" exits above).

STOCHASTIC BRANCH POINTS are indicated with solid circles.

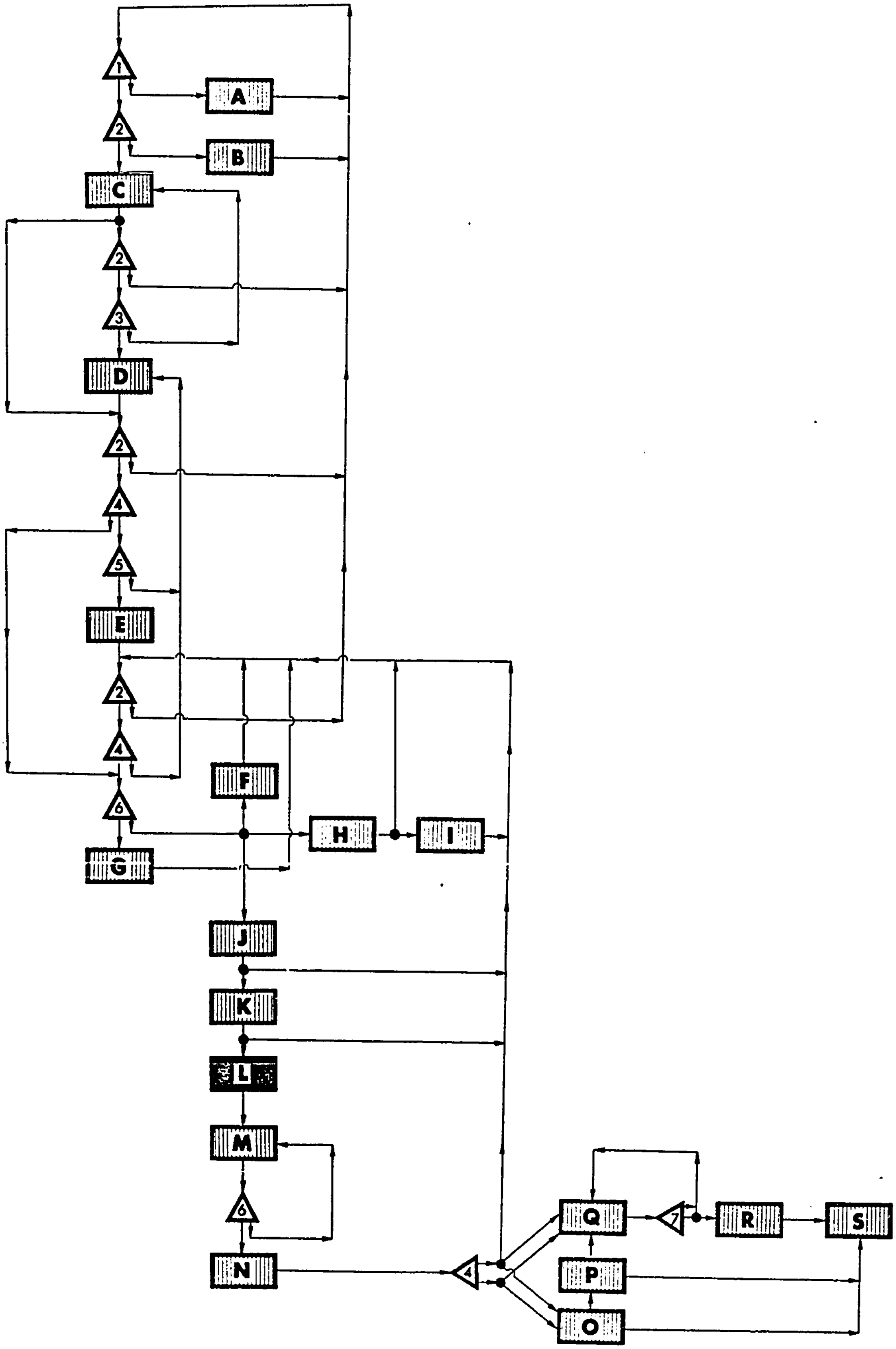

1
A
2
B
C
2
3
D
2
4
5
E
2
4
6
F
H
I
G
J
K
L
M
6
N
4
Q
7
R
S
P
O

Figure 20. Algorithms for courtship behavior in female *Ambystoma maculatum*, female *Ambystoma tigrinum*, and female *Plethodon jordani*.

Ambystoma maculatum (left, above)

FEMALE ACTIONS (rectangles)

A. Remain stationary.
B. Move forward, (away from male).
C. Turn towards and rub male with snout.
D. Move forward keeping spermatophore in contact with ventral midline.
E. Lower vent on spermatophore and pause.

CONDITIONAL STATEMENTS (triangles)

1. Is a spermatophore in contact with the ventral midbody? ("yes" exits on right).
2. Is there contact to the female's dorsal or lateral body (not a spermatophore)? ("yes" exits on left).
3. Does the spermatophore contact the vent? ("yes" exits below.

Ambystoma tigrinum (left, below)

FEMALE ACTIONS (rectangles)

A. Remain stationary.
B. Move forward (away from male).
C. Turn towards and rub the male with the snout.
F. Move towards the male's cloaca.
G. Nudge the male's cloaca with the snout.
D. Move forward keeping spermatophore in contact with ventral midline.
E. Lower vent on the spermatophore and pause.

CONDITIONAL STATEMENTS (triangles)

1. Is a spermatophore in contact with the ventral midbody? ("yes" exits on right).
2. Is there contact to the female's dorsal or lateral body (not a spermatophore)? ("yes" exits on left).
3. Does the male's tail contact the female's body? ("yes" exits on left).
4. Female's snout contacts the male's cloaca? ("yes" on right).
5. Does the spermatophore contact the vent? ("yes" exits below).

Cont/.

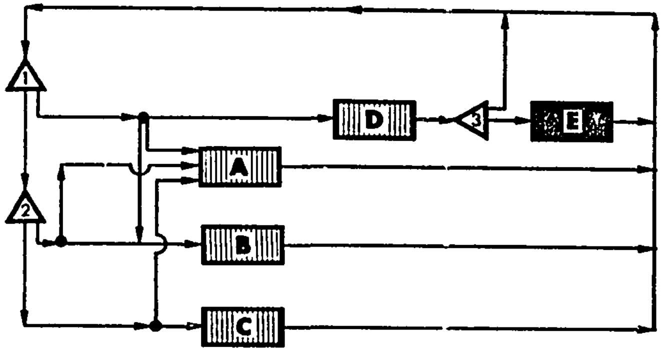
Plethodon jordani (right)

FEMALE ACTIONS (rectangles)

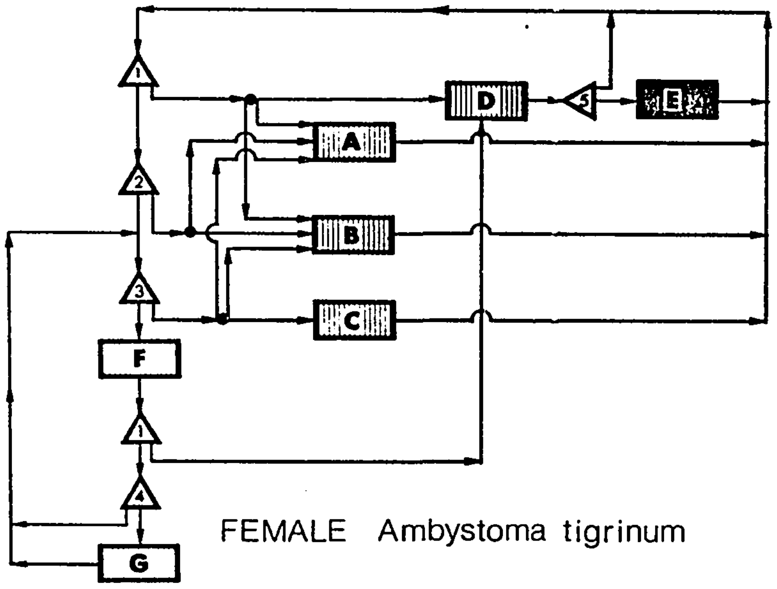
A. Remain stationary.
B. Move forward (away from male).
C. Raise head.
D. Move forward towards the male.
E. Move forward with chin in contact with male's tail while astride tail with forelimbs. Maintain head axial on male's tail.
F. Remain stationary with chin in contact with male's tail.
G. Lower vent on spermatophore.
H. Lift vent off of spermatophore.
I. Move away and terminate courtship activities.

CONDITIONAL STATEMENTS (triangles)

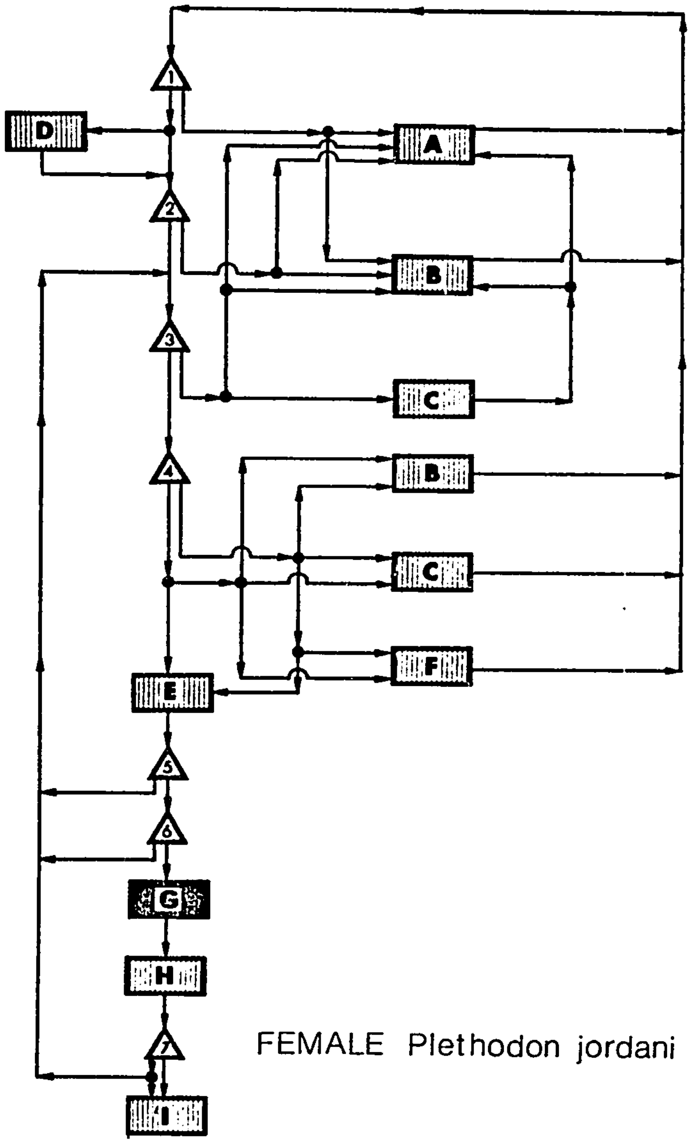
1. Is there contact to the female's body? ("yes" exits on left).
2. Is there contact to the female's cheek or chin? ("yes" exits on left).
3. Is the male's tail undulating in contact with the female's chin? ("yes" exits on left).
4. Is the female's snout in region 4 on the male's tail? ("yes" exits on left).
5. Is a spermatophore in contact with the ventral midbody? ("yes" exits on right).
6. Is a spermatophore in contact with the vent? ("yes" exits on right).
7. Is a sperm mass present in the female's cloaca? ("yes" exits on right).



FEMALE Ambystoma maculatum



FEMALE Ambystoma tigrinum



FEMALE Plethodon jordani

Behavioral programs, behavioral algorithms, and the adaptive significance of programming conventions.

Ethologists seem to have no name for the whole system of conventions which animals use to determine the behavioral responses they give in particular behavioral contexts and to particular stimuli. It is clear that not only observable behavioral actions, but also whole systems of internal rules or conventions can be typical for a species. By analogy with the sets of instructions (computer programs) which can be used to direct computing machines to perform specific tasks, I will refer to the system of internal conventions which animals use to direct their activities as behavioral programs. Behavioral algorithms are then attempts to reproduce the logical structure of the animal's behavioral program.

It is convenient to use the activity of spermatophore deposition as a reference point when discussing male courtship algorithms. With respect to this reference point, there are two classes of programming conventions; those that loop forward towards spermatophore deposition (ie. shorten the behavioral route to spermatophore deposition) and those that loop backward (ie. lengthen the behavioral route before spermatophore deposition).

For example, _Ambystoma maculatum_ males will cease any on-going activity when they are in close contact with the female, and deposit a spermatophore on top of a pre-existing spermatophore, if a spermatophore contacts the male's vent (see Fig. 18). (A similar programming convention probably exists in _A. tigrinum_, but my observations are not extensive enough to describe its logical structure in detail, and so it is omitted from Fig. 18). The adaptive significance of this loop forward programming convention will be discussed in detail later in relation to other aspects of courtship.

Plethodon jordani males usually initiates tail-straddling walks by slowly crawling under the female's chin and then pausing while arching and undulating the tail, until the female steps astride the tail. Sometimes, however, the female will actively approach the male and place her chin on his tail as he crawls beside her. In such cases, the male deletes lifting and crawling under the female's chin, and immediately moves forward in a tail-straddling walk (see forward loop from conditional statement 4 after action D in Fig. 19). It would appear that this programming convention allows the male to shorten the behavioral sequence preceding spermatophore deposition when the male encounters a female which is particularly sexually receptive.

Most programming conventions take the form of directing the male to perform some action, which has already been performed, if the female does not give a particular response (ie. loop backward programming conventions). Thus, in all three species if the female repeatedly moves away from the male, the male will continue to approach her and perform various modes of head contact, but he will not deposit a spermatophore. The prevalence of loop backward programming conventions causes the male to require many specific behavioral responses by the female before he deposits a spermatophore. Presumably the females which give these specific behavioral responses are also the females which are most likely to retrieve sperm from the spermatophore once it is deposited. Thus males tend to present spermatophores only to females which are likely to be inseminated by them.

The logical structure of female courtship algorithms is much more difficult to characterize. The most striking feature of these algorithms (Fig. 20) is that they are composed of many stochastic branch points. Observations showed that females in the same stimulus situation gave a wide variety of behavioral responses, and in most cases I was unable to formulate specific hypotheses about whether the immediate preceding behavior of the male was responsible for changing female behavior. I suspect that this variability in female response comes from two principal sources. Upon initiation of courtship by the male, some females consistently flee from the male, while others actively participate in courtship. It is clear, then, that females come to courtship situations with differing tendencies to engage in courtship (eg. some females are gravid and some are not). Secondly, some females which at first flee from the male or do not respond to his courtship activities do eventually engage in active courtship. It seems likely that during a courtship encounter, males are able to change the tendency of the female to court (and to be inseminated) by the repetition of certain courtship actions (such as rubbing, nudging and the application or presentation of glandular body regions).

Complexity of programming for courtship behavior.

The courtship algorithm for male *Plethodon jordani* (Fig. 19) is much more complex than the male courtship algorithms of the two *Ambystoma* species (Fig. 18). The early portions of the algorithms, which are responsible for keeping the male in close contact with the female, are quite comparable in all three species. But male *Plethodon jordani* possess elaborate programming for regulating activities during tail-straddling walk which precedes spermatophore deposition.

The male courtship algorithms of *Ambystoma maculatum* and *A. tigrinum* are rather similar in overall complexity, but like *Plethodon jordani*, male *A. tigrinum* have rather complex programming which is responsible for regulating the position of the male in relation to the female just before spermatophore deposition.

Females of *Plethodon jordani* probably have more complex courtship programming than the females of the two *Ambystoma* species, but the difference is not so striking as in the males (Fig. 20).

7. Behavioral interactions between males during the courtship season.

a. Ambystoma maculatum

In the field during the courtship season, usually several *A. maculatum* males are found courting a female simultaneously. Occasionally a single male can be found courting and depositing spermatophores with a single female. In the field, however, the density of males is so high that frequently additional males locate and join such a courting pair and initiate courtship with the female. When several males court a female simultaneously, they rub and nudge each other as well as the female, but agonistic behaviors such as biting were never observed between males in the field (or in the laboratory). Each of the courting males may deposit spermatophores, either *de novo* or on pre-existing spermatophores. These courtship interactions between several males and a female are exceedingly confusing to watch in the field, because the participating males and the female are in continuous rapid motion.

What are the effects of multiple courting males on the reproductive success of individual males during courtship encounters? And do the males change their behavior in any way when other males are present during courtship? To answer these questions detailed observations were made on the behavior of each of three pairs of animals (1 male with 1 female) and on each of three trios of animals (2 males with 1 female) during courtship in the laboratory.

Males were collected on land as they migrated to ponds on the E.S.G.R. on the night of April 12, 1971. Females were collected on the same night on land as they migrated to Goss pond. (I was unable to use both males and females from the same pond for these experiments because large numbers of animals were required for other experiments). The females and the males had therefore not yet courted that courtship season.

During observation sessions the animals were placed in a large circular washtub with a corrugated bottom 53.5 cm in diameter, and filled with well water to a depth of 20 cm. The observations were made in the evening, and the container was illuminated with dim light. Water temperature was 46°F. The washtub was emptied, scrubbed and refilled with water between each set of observations. Each pair or trio was observed for 90 minutes and then released. All observations were completed within five days of the date of capture.

During an observation session I verbally noted into a tape recorder whenever a male initiated spermatophore deposition, whenever the female located and squatted upon a spermatophore, and whenever interference occured between animals during spermatophore deposition or location. When two males were courting with a female I was able to recognize each male as an individual by differences in size or the pattern of dorsal spots. I could therefore tell which male was depositing a spermatophore, but due to the large numbers of spermatophores I could not tell which male's spermatophore the female was locating. At the end of 90 minutes, I separated the animals, examined the female's cloaca for sperm and counted the number of spermatophores.

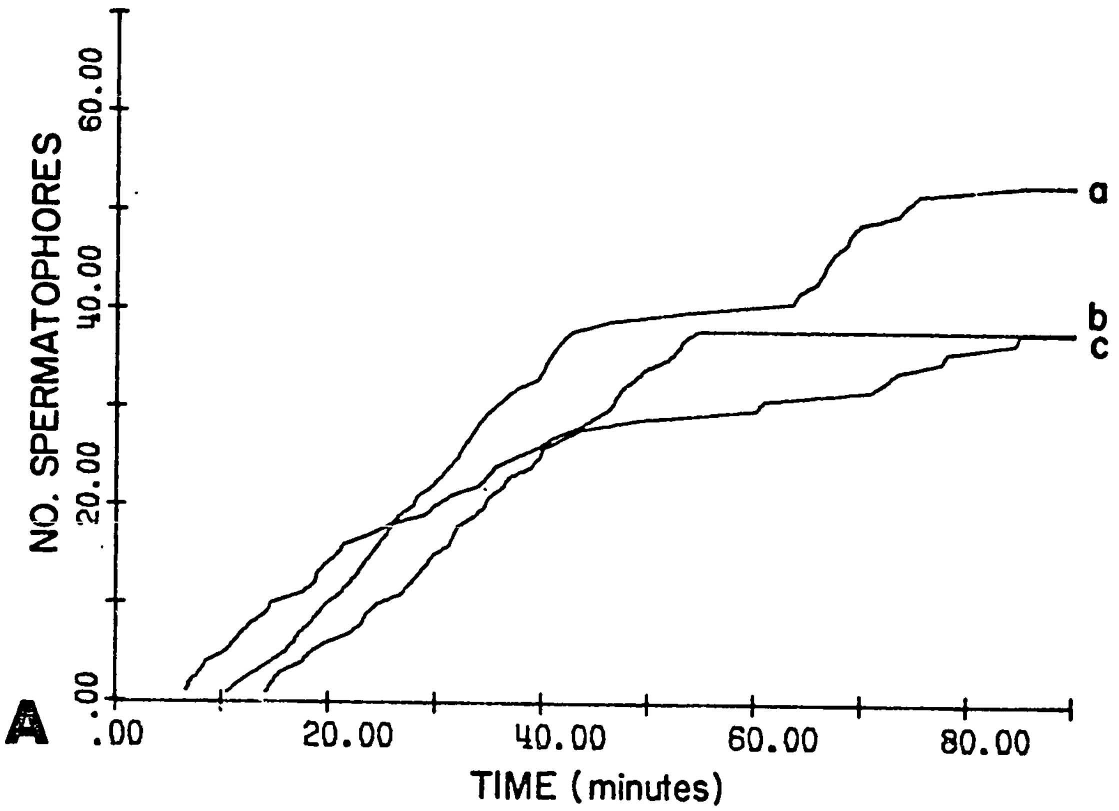
Paper records of the observations were made later by assigning different writing pens on an Esterline-Angus recorder to the events 'onset of spermatophore deposition' (one pen for each male, if two were present) and 'onset of spermatophore location by the female'. and then depressing the appropriate pens via a keyboard while listening to the magnetic tapes. The times between various behavioral events were then measured directly from these paper records.

I found that the activities of the animals followed a very predictable course. Upon introduction, the animals sank slowly or swam to the bottom

Figure 21. Spermatophore deposition as function of time in *Ambystoma maculatum* males courting alone with a female in the presence of another male.

Fig. A. Males courting alone with a female. The cumulative number of spermatophores deposited is shown as a function of time for each of three males (a,b,c). In each case the male and female were introduced into the same tank at 0 time.

Fig. B. Males courting a female in the presence of another male. The cumulative number of spermatophores deposited is shown as a function of time for each of six males. Males d and d' were courting the same female simultaneously, and similarly for males e and e', and males f and f'. Vertical lines connect the cumulative spermatophore depositions of each pair of males which courted the same female. In each case the males and the female were introduced into the same tank at 0 time.


A
NO. SPERMATOPHORES
.00
20.00
40.00
60.00
TIME (minutes)
.00
20.00
40.00
60.00
80.00
a
b
c

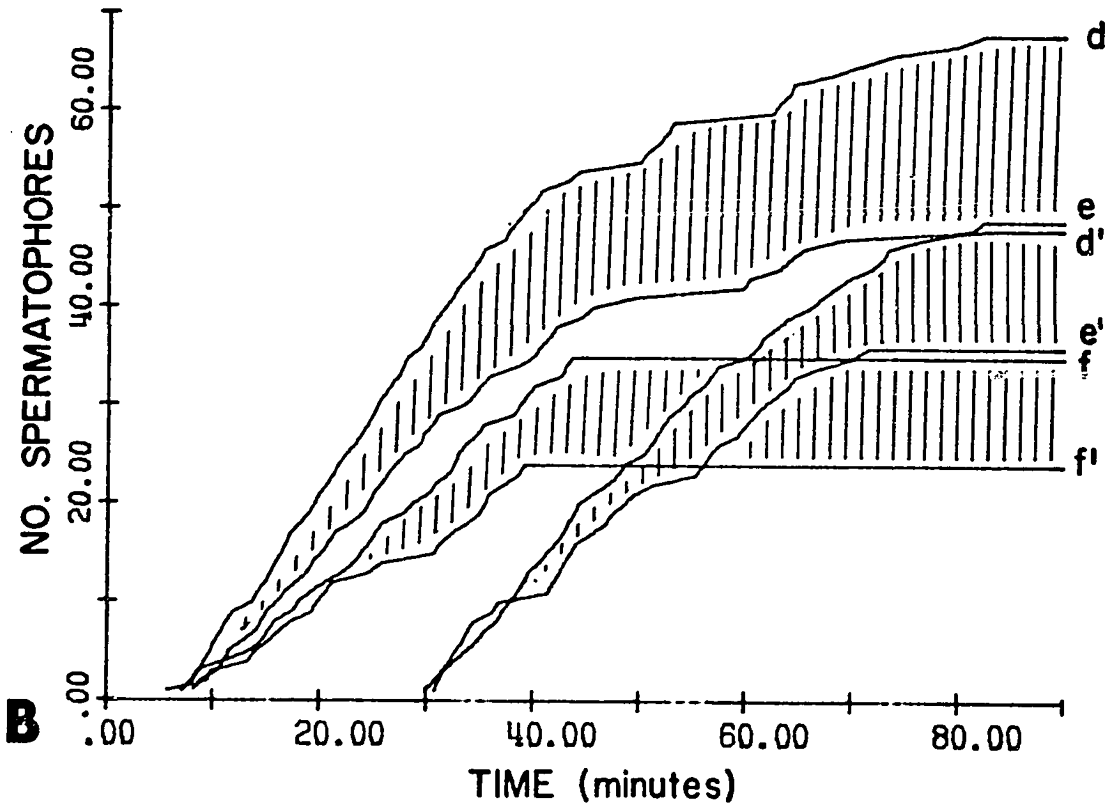
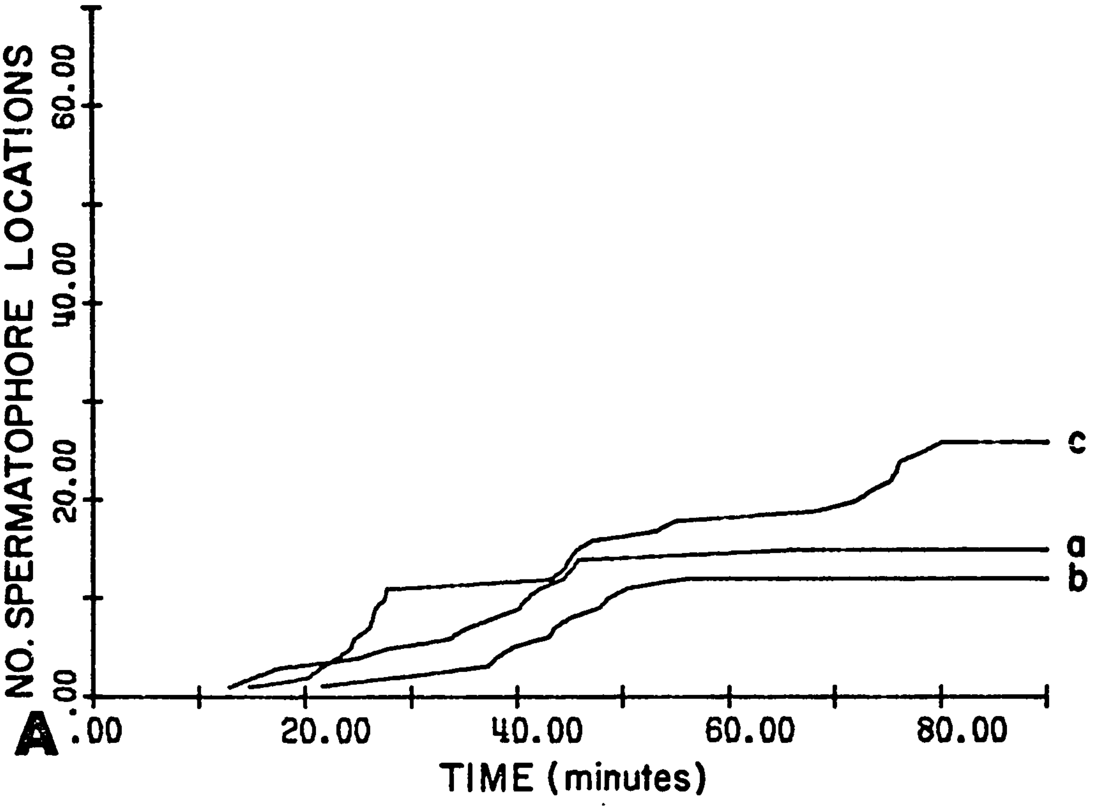

B
NO. SPERMATOPHORES
.00
20.00
40.00
60.00
TIME (minutes)
.00
20.00
40.00
60.00
80.00
d
e
d'
e'
f
f'

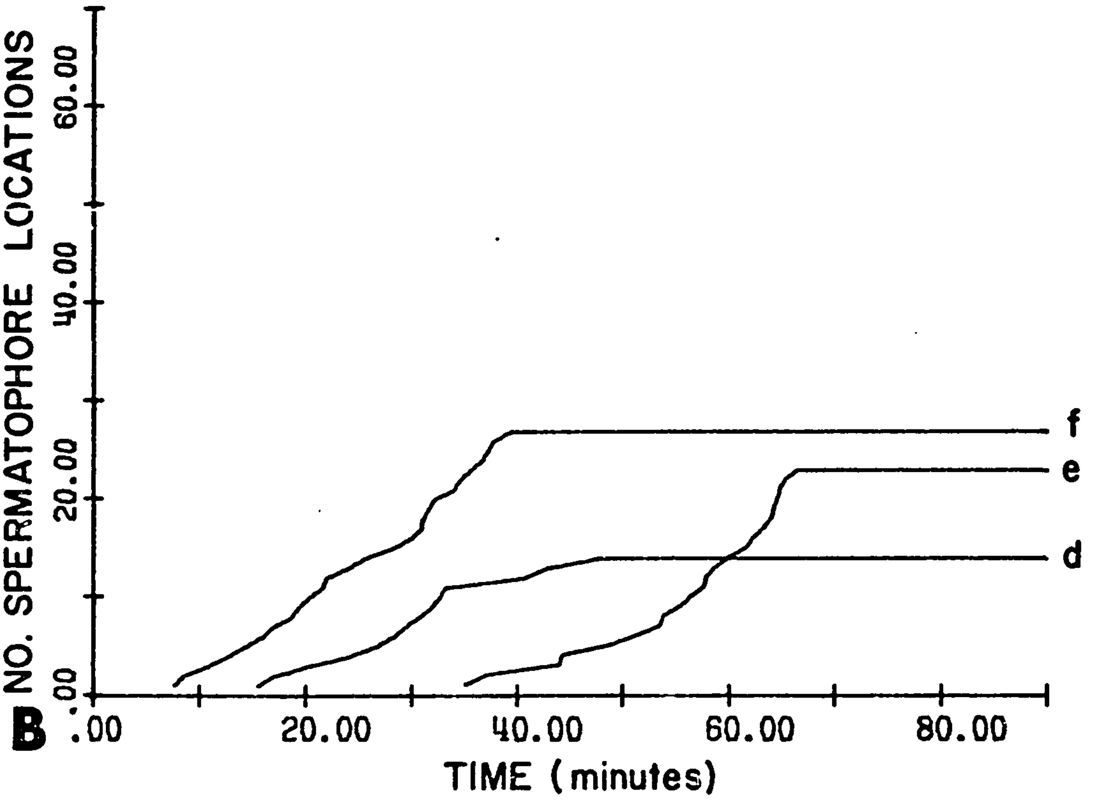
Figure 22. Spermatophore location by the female as a function of time in females courting with one male and with two males in *Ambystoma maculatum*.

Fig. A. Females courting with one male. The cumulative number of times the female located spermatophores with her vent (and then squatted upon them) is shown as a function of time for each of three females. Female a was courting with male a in Fig. 21 and similarly for female b and female c.

Fig. B. Females courting with two males. The cumulative number of times the female located spermatophores with her vent (and then squatted upon them) is shown as function of time for each of three females. Female f was courting with males f and f' in Fig. 21, and similarly for female e and female d.

In each case the female and male(s) were introduced into the same container at 0 time.


A
NO. SPERMATOPHORE LOCATIONS
.00
20.00
40.00
60.00
TIME (minutes)
.00
20.00
40.00
60.00
80.00
c
a
b


B
NO. SPERMATOPHORE LOCATIONS
.00
20.00
40.00
60.00
TIME (minutes)
.00
20.00
40.00
60.00
80.00
f
e
d

of the container and remained motionless for a few minutes. Invariably the female then began to move slowly about the bottom of the container, while slowly shifting her vent laterally against the bottom by stepping from side to side with her hindlimbs. The male(s) then also began to move slowly about the container, but without the vent shuffling shown by the female. After a few minutes the male(s) contacted the female one or a very few times, and then began courtship and increased their rate of movement markedly. Spermatophore depositions by the male and spermatophore locations by the female then occurred for 30 to 80 minutes. The female's behavior then changed abruptly. Instead of moving continuously about locating and squatting upon spermatophores, she began swimming at the surface of the container, around and around its periphery. When she landed, she moved forward rapidly and did not orient to or squat upon spermatophores.

When two males are present with a female, each male does not behave neutrally towards the other male. Both males periodically rub, nudge and lift the female, but the bulk of behavioral interactions are between the two males. The males nudge, rub and lift each other just as they behave towards the female.

These interactions between males have two dramatic consequences. First, one male can inhibit the other male from depositing a spermatophore by nudging him. A male which has begun spermatophore deposition on a pre-existing spermatophore, may be pushed off of that spermatophore by the other male. Or a male which has begun a de novo spermatophore deposition may suddenly stop and not deposit a spermatophore when nudged by the other male. Second, one male may immediately deposit a spermatophore on top of a spermatophore just constructed by the other male. On several occasions I watched one male approach the other male, nudge his cloaca as he deposited a spermatophore upon the first male's spermatophore as the first male departed. As previously mentioned, such secondary spermatophore usually render the sperm masses below inaccessible to the female. On two occasions the first male circled around, nudged the second male's cloaca and deposited a teriary spermatophore upon the second male's spermatophore.

None of the male behaviors above are unique to interactions between males. A male may inhibit a female from recovering sperm from a spermatophore by nudging and dislodging her. A male may follow behind a female and deposit a spermatophore on top of the spermatophore she departs from. However, when a male directs these behaviors towards another male, they have the effect of reducing the other male's reproductive success.

When two males court simultaneously with one female, they deposit no more spermatophores each (mean=43.3) than does a single male (mean=43.0) (U test=7.0, $p > .05$). Consequently when two males are present, twice as many spermatophores are deposited (mean=86.7) as when one male is present (mean=43.0).

At the same time, the female locates no more spermatophores per courtship when two males are present (mean=21.3) than when one male is present (mean=17.7) (U=3.0, $p > 0.05$). Therefore, when one male is present the probability of the female locating a spermatophore per spermatophore deposition is higher (p(L/SD)=0.41) than when two males are present (p(L/SD)=0.25) (see Table 10 for Chi Square Test). Consequently when multiple males are present each participating male will experience a lower probability of reproductive success than when courting the female alone.

Can males compensate for the interfering effects of other males upon their spermatophore depositions and deposit spermatophores at the same or a faster rate than when courting the female alone? The distributions of times between spermatophore depositions (measured from the onset of one spermatophore deposition to the onset of the next) are shown in Fig. 23.,

Table 9. The numbers of spermatophores deposited by males courting along with a female and in the presence of another male, and the numbers of spermatophores located by females. in _Ambystoma maculatum_.

	ONE MALE			TWO MALES		
	Name of male	Number of spermatophores deposited	Number of spermatophores located by female	Name of male	Number of spermatophores deposited	Number of spermatophores located by female
	a	53	15	d	68	14
				d'	48	
	b	38	12	e	49	23
				e'	36	
	c	38	26	f	35	27
				f'	24	
No. spermatophores deposited per male		mean = 43.00 (S.D.=8.66)			mean = 43.33 (S.D.=15.23)	
Total No. of spermatophores deposited per female		mean = 43.00			mean = 86.67	
No. of spermatophores located by female		mean = 17.67 (S.D.=7.37)			mean = 21.33 (S.D.=6.66)	

for one and for two males courting with a female. The mean time between spermatophore depositions is 1.53 minutes (S.D.=1.898, n=126) for single males and 1.24 minutes (S.D.=1.489, n=254) for males courting in the presence of another male. Since the distributions of times between spermatophore depositions are highly skewed to the left (see Fig. 23), this variable was transformed, by taking its logarithm to the base 10, to produce more nearly normal distributions for statistical testing. Normal probability plots showed the transformed distributions. A T test based on the two transformed distributions shows that males deposit spermatophores at a significantly faster rate when another male is present during courtship. The mean of $\log_{10}$ time between spermatophore depositions is 1.74 (variance=.087, n=254) for males courting with another male present and 1.81 (variance=.106, n=126) for solitary males (T=2.05, d.f.=378, p=0.02 (one tailed test)). There is no significant difference in variance (F=1.22, d.f.=(125,253), p=0.095).

The distributions of times between spermatophore locations by the female are similarly skewed to the left for females courting with one male (mean=3.05 minutes, S.D.=3.96, n=50) and with two males (mean=1.56 minutes, S.D.=1.43, n=61). These distributions too were transformed, by taking $\log_{10}$ of time between spermatophore locations, to yield more nearly normal distributions for statistical testing. A T test shows that females courting with two males locate spermatophores at a faster rate than females courting with a single male. The mean of $\log_{10}$ of time between spermatophore locations is 2.01 (variance=.221, n=50) for females courting with a single male and 1.83 (variance=.136, n=61) for females courting with two males (T corrected for unequal variance = 2.27, d.f.$\approx$ 93.5, p=0.013 (one tailed test)). Variance is significantly larger for females courting with one male (F=1.619, d.f.=(49,60), p=0.019 (one tailed test)).

TABLE 10. A Chi Square test of the hypothesis that the probability of the female locating a spermatophore per spermatophore deposition is independent of the number of courting males in *Ambystoma maculatum*.

	ONE MALE	TWO MALES	TOTAL
Total number of spermatophores deposited	129	260	389
Observed number of spermatophore locations by females	53	64	117
Expected number of spermatophore locations by females	38.8	78.2	

Hypothesis: The probability of the female locating a spermatophore per spermatophore deposition is the same with one as with two males.

Expected probability of female locating a spermatophore per spermatophore deposition = 117/389 = 0.3008

Chi Square = 7.78, d.f.=1, $0.005 > p < 0.01$

Figure 23. Times between spermatophore depositions for male *Ambystoma maculatum* courting along with a female and for males courting in the presence of another male.

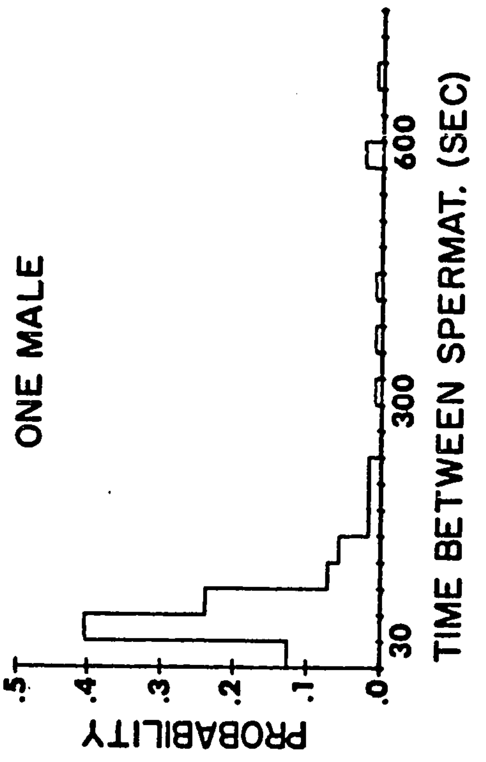
Upper left. The times between successive spermatophore depositions for males courting alone with a female (n=126). Observations on three males are combined.

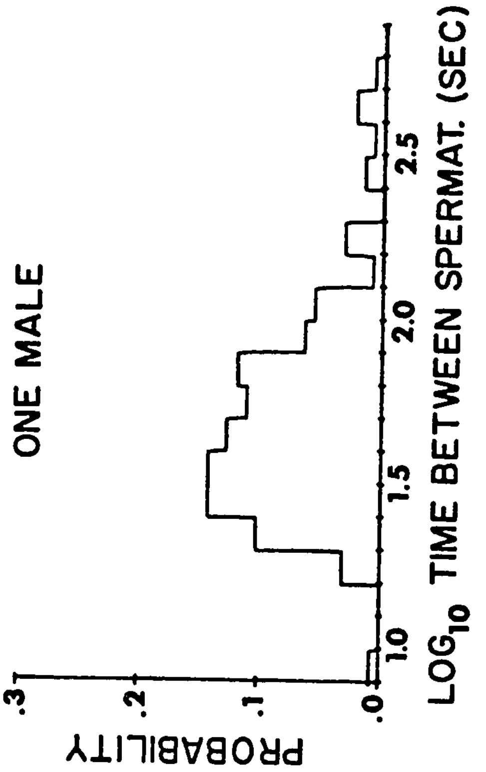
Upper right. The same distribution transformed by taking $\log_{10}$ of the time between successive spermatophore deposition.

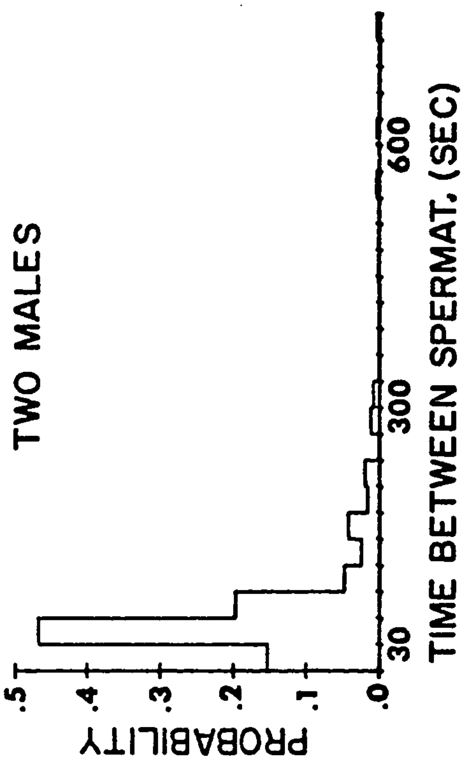
Lower left. The times between successive spermatophore depositions for males courting with a female in the presence of another male (n=254). Observations on six males are combined.

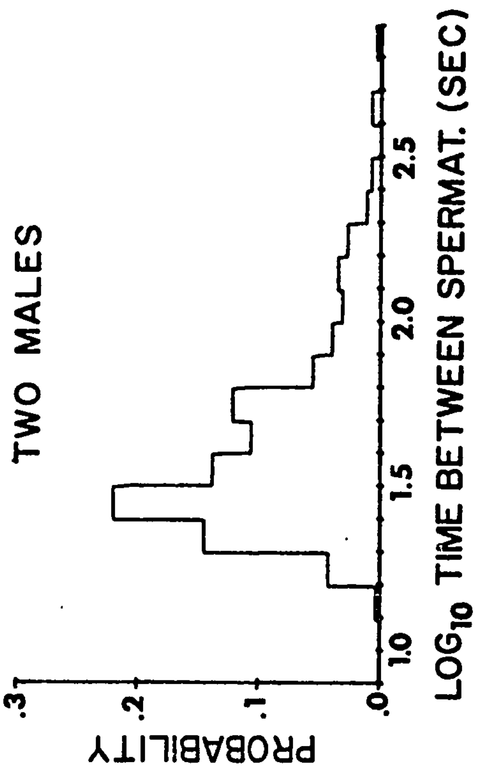
Lower right. The same distribution transfored by taking $\log_{10}$ of the time between successive spermatophore depositions.

(NOTE: When two males are courting with the same female, the time between successive spermatophore depositions is measured as the time from one male's spermatophore deposition to his next spermatophore deposition, and not from the time of one male's spermatophore deposition to the other male's spermatophore deposition).


ONE MALE
PROBABILITY
.0
.1
.2
.3
.4
.5
30
300
600
TIME BETWEEN SPERMAT. (SEC)


ONE MALE
PROBABILITY
.0
.1
.2
.3
1.0
1.5
2.0
2.5
LOG10 TIME BETWEEN SPERMAT. (SEC)


TWO MALES
PROBABILITY
.0
.1
.2
.3
.4
.5
30
300
600
TIME BETWEEN SPERMAT. (SEC)


TWO MALES
PROBABILITY
.0
.1
.2
.3
1.0
1.5
2.0
2.5
LOG10 TIME BETWEEN SPERMAT. (SEC)

In summary, when two males court with a female, they deposit no more spermatophores each than when courting alone, but they do deposit spermatophores at a faster rate. When females court with two males, they locate no more spermatophores than with a single male, but they locate spermatophores at a faster rate and with less variance in the time between spermatophore locations.

Unfortunately, time did not permit me to make observations on interactions between courting males of *Ambystoma tigrinum*.

b. *Plethodon jordani*

Organ (1958) observed two different types of interactions between males during the courtship season. First, one male repeatedly interrupted courtship with a female and bit other males in the container. Second, Organ observed two males engaged in a homosexual courtship. Two males courted a female simultaneously and then began courting each other. One male then deposited a spermatophore as the second male straddled his tail, just as a female would. Organ also found a pair of animals in the field engaged in a tail-straddling walk and found them both to be males. I found that both of these types of behavior were common when two or more males were housed with one or more females. When one courting male pursues and bites another male, the pursued male flees. Sometimes, as Organ (1958) observed, an attacking male may dash forwards and bite a female. Frequently, however, the male resumes courtship with a female after attacking another male. Interactions of this kind are not restricted to captive specimens. Hutchison (1959) observed two males pursuing and biting each other in the field.

Homosexual courtships between males were so frequent during my observations in 1968 that in subsequent years I housed only one male and one female together so that I could confine my observations to heterosexual interactions. Homosexual interactions between males take a rather predictable course. When several males were housed together with a female, frequently a second, "intruding", male would approach a courting, heterosexual pair. The intruding male nudges and slides his mental gland along the female's length while periodically performing a foot dance. If the intruding male contacts the other male's dorsal tail, he slides his mental gland along it. The first male then arches and undulates his tail, just as if a female had so contacted him. The two males then move forward in a tail-straddling walk away from the female. The intruding male then behaves very much like a female, for he pauses periodically as the other male leads him forward and his chin rests continually on the leading male's dorsal tail. When the leading male stops and begins spermatophore deposition, the intruding male again behaves very much like a female. During the 3-4 minutes required for spermatophore deposition, the intruding male remains essentially motionless astride the leading male's tail with his snout resting on the leading male's tail base. After spermatophore deposition the indtruding male moves forward behind the leading male, just as a female would, but he does not stop over the spermatophore. At this point the intruding male may either depart from the leading male, or the leading male may suddenly swing around and bite the intruding male. In the latter case the intruding male flees rapidly.

The following points suggest that homosexual courtship in Plethodon jordani is not simply a sexual pathology peculiar to captivity, but rather a behavioral device used by males to depress the reproductive success of other males. First, intruding males, which induced another male to deposit a spermatophore, were later observed to court and deposit spermatophores with females in the same evening. Intruding males are, therefore, not obligate homosexuals. Second, once a male has deposited a spermatophore, he usually does not court and deposit spermatophores for several days. When a single male is housed with a female the mean time between spermatophore depositions is seven days! Thus, a male which is induced to deposit a spermatophore by another male is unable to inseminate a female for several days. Third, females only locate spermatophores when they straddle a male's tail during and after spermatophore deposition. Thus spermatophores deposited during homosexual courtships are reproductive failures. They are never located by, and never inseminate, females. Fourth, homosexual courtships do not occur, and spermatophores are not deposited, unless females are present in a container. Homosexual courtships only occur when two courting males converge on and initiate courtship with the same female. Fifth, the behavior of the intruding male, once the other male begins a tail-straddling walk, is remarkably similar to a female. Sixth, homosexual courtships between males occur in the field (Organ, 1958), as well as in captivity.

James Organ and I have discussed the phenomenon of homosexual courtship in *Plethodon* (it also occurs in *P. glutinosus*, *P. ouachitae* and *P. yonahlossee*) at length. At first I regarded the phenonmenon as simply a hindrance to observations of heterosexual courtship, and Organ regarded it as an example of the imperfections of sex recognition in *Plethodon*. I think the six points above suggest quite another interpretation. There is every reason to believe that natural selection has selected for males with the capacity to distract other males from a female and then induce them to deposit spermatophores which serve no reproductive function. Such males depress the fitness of the other male and at the same time are able to return to and inseminate the female. All observations to date support this hypothesis, and it may profitably be used to design critical experiments.

Agonistic interactions between courting males probably serve the same function. If a courting male attacks an intruding male, the intruding male flees, the attacking male can then resume courtship with the female, the intruding male is then unlikely to again intrude, and the attacking male is unlikely to be "duped" into an unprofitable spermatophore deposition (as described above). In addition agonistic interactions between males probably serve to disperse males so that intrusions during courtship are unlikely in the first place.

8. Dispersion of animals in the field during the courtship season and the duration of the courtship season.

a. <u>Ambystoma maculatum</u>

During most of the year adults lead a terrestrial life, but in the early spring they migrate to small woodland ponds to breed. During the breeding season the arrivals of animals to ponds are clumped in time, so that most of the breeding adults will arrive at the pond on a very few successive nights or on each of a few nights separated by periods of non-migration. The critical environmental factors affecting the timing of breeding migration appear to be temperatures above freezing in conjunction with moisture provided by either snow melt or rain (Blanchard, 1930; Wright and Allen, 1909; Baldauf, 1952).

Within the ponds the courtship activities of a population are consumated on a very few nights, coinciding with the dates of arrival to the ponds and on a few nights following a major migration.

In southern Michigan small woodland ponds 100 meters or less in diameter are usually used for breeding, and frequently a few hundred animals are found courting simultaneously in such a pond. Over a five year period Husting (1965) found that a mean of 230.8 males and 123.6 females bred in a kidney-shaped pond 50 yards by 20 yards in southern Michigan. If the animals were evenly dispersed in the pond, this would result in a mean density of approximately .23 males/square yard and .12 females/square yard.

The effective density of courting animals in this pond is, however, much larger than this because animals tend to be clumped during courtship activities. At this particular pond in 1969, 1970 and 1971 I found that most of the courting animals were located in two or three small areas of a few square yards each. Frequently 10 to 50 animals were found courting in each of these areas simultaneously. Each aggregation of animals is composed mostly of males with only one or a very few participating females. This pattern of dispersion of courting animals was typical of the breeding ponds that I visited. Blanchard (1930) and Breder (1927) report similar observations.

Husing (1965) found that the sex ratio of breeding animals arriving at a pond was 1.87 males per female.

Within a population, egg laying begins a few days after the appearance of spermatophores in a pond (Wright, 1908). In the field females probably cease courtship activities and begin laying eggs after only one, or a very few, nights of courtship.

b. Ambystoma tigrinum

Like Ambystoma maculatum, adults of Ambystoma tigrinum lead terrestrial lives for most of the year and then migrate to ponds in the early spring for courtship and egg laying. Most of the adults breeding in a pond arrive during a few nights of migration.

I was unable to observe courtship in the field. Henry Wilbur (pers. comm.)reports that Ambystoma tigrinum were observed courting as single pairs separated by a few meters from other courting pairs in Burt Pond on the E.S.G.R. Agregations of courting animals, as in Ambystoma maculatum, were not observed.

The courtship season probably lasts only a few days to a very few weeks. In 1971 in Burt Pond all courtship activities seemed to have occurred in a single night (Henry Wilbur, pers. comm.).

In the field eggs are found early in the spring, and females probably lay their eggs a few to several days after insemination.

c. *Plethodon jordani*

The entire life cycle of *Plethodon jordani* is terrestrial. At Whitetop Mtn., Virginia adults collected in the months of July, August and September courted in the laboratory. The courtship season is approximately three months long.

During the courtship season reproductive adults are found widely separated from each other. There is one exception to this pattern. During this period a male and a female may be found next to each other under the same surface object, but such pairs are also widely separated. Madison (1969) performed mark and recapture experiments with *Plethodon jordani* during the courtship season in North Carolina. Individuals were remarkably sedentary. Eighty per cent of recaptures occurred within a 20 foot radius of the initial point of capture in males, and within a 10 foot radius of the initial point of capture in females. When animals are displaced, they return to the initial area of capture with surprising accuracy (Madison (1969), Madison and Shoop (1970)). Madison (1969) found and marked 23 adult males and 22 adult females in one study area of 900 square yards. Male *Plethodon jordani* are much less dense than male *Ambystoma maculatum* during the courtship season (uniform densities of 0.04 male *P. jordani*/yd^2 versus 0.23 male *A. maculatum*/yd^2; 0.04 female *P. jordani*/yd^2 versus 0.12 female *A. maculatum*/yd^2; data from Husting (1965) and Madison (1969)). Furthermore, male *Plethodon jordani* are widely spaced and sedentary, whereas male *Ambystoma maculatum* are clumped and mobile during the courtship season. Consequently intrusions by other males during a courtship encounter are probably much more frequent in *A. maculatum* than in *P. jordani*.

The time from insemination to egg laying is unknown in *Plethodon jordani*, since egg clutches have never been found in the field. Since newly hatched young do not appear until early spring, it is likely that a few to several months elapse from the time of insemination to egg laying.

Table 11. Summary of courtship variables in *Ambystoma maculatum*, *Ambystoma tigrinum* and *Plethodon jordani*

	Ambystoma maculatum	*Ambystoma tigrinum*	*Plethodon jordani*
Courtship rate (acts/min)	75.7		3.6
Information transmitted between sexual partners/act	0.78		1.11
Information transmitted between sexual partners/minute	59.16		3.96
Time/spermatophore deposition (min)	1.36	4.52	55.9
Information transmitted between sexual partners/spermatophore deposition	80.46		221.53
Variability in site of spermatophore deposition	+++	++	+
Complexity of male programming	+	++	+++
Probability of female locating spermatophore per spermatophore deposition	0.39	0.61	0.92
Mean number of spermatophores/courtship	20.9 (Goss) 43.6 (E.S.G.R.)	15.6	1.04
Probability of sperm transfer per spermatophore deposition	($\geq$ 0.236)	($\geq$ 0.369)	0.560
Probability of sperm transfer per courtship	($\geq$ 0.996) (Goss) ($\geq$ 0.999) (E.S.G.R.)	($\geq$ 0.999)	0.574

The order +, ++, +++ indicates increasing values of a particular variable).

DISCUSSION

The functional relationships between courtship variables will be discussed first, and then the adaptive significance of interspecific differences will be discussed.

a. Functional relationships among courtship variables.

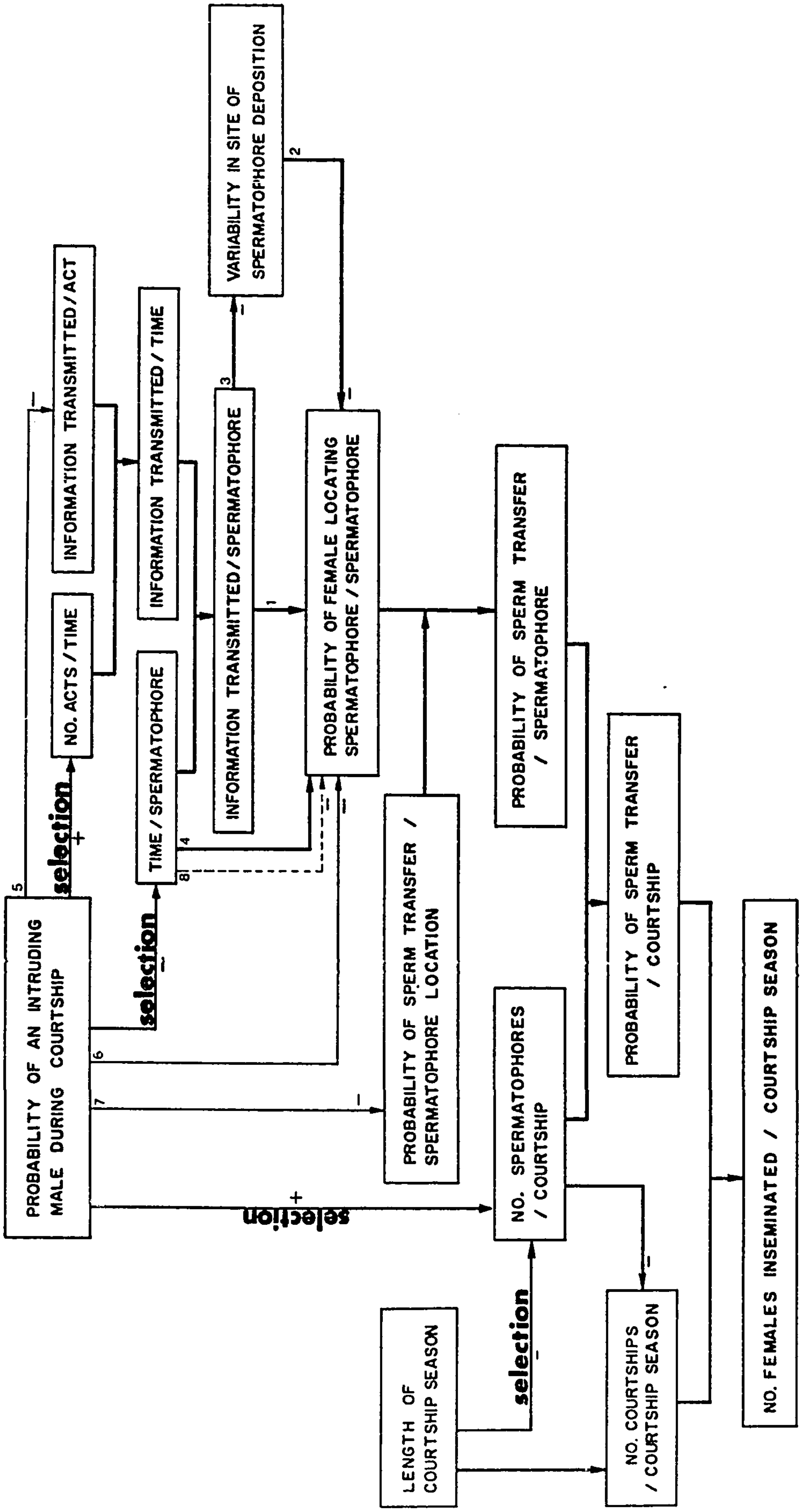
It appears that the more sexual partners affect each others behavior between spermatophore depositions, the more likely it is that the female will locate the spermatophore (arrow 1 in Fig. 24). This functional relationship is supported by the observation that in *Plethodon jordani* more information is transmitted between sexual partners per spermatophore deposition, and the female is more likely to locate a spermatophore than in *Ambystoma maculatum*.

The more variable the site of spermatophore deposition, the less likely is the female to locate the spermatophore (arrow 2 in Fig. 24). This relationship is supported by the observation that in the three species *A. maculatum*, *A. tigrinum* and *P. jordani* there is an inverse relationship between these two variables (see Table 11).

Note that the species, *Plethodon jordani*, which has the most complex male programming for courtship behavior and in which sexual partners affect each others behavior the most between spermatophore depositions, is also the species in which the site of spermatophore deposition is the lease variable (Table 11). It seems likely then that by affecting each others behavior more between spermatophore depositions, pairs of *Plethodon jordani* are able to reduce the variability in the site of spermatophore deposition (arrow 3 in Fig. 24). In large part this is accomplished by the male's elaborate programming conventions for regulating the position of the

Figure 24. Functional relationships among courtship variables and the effects of natural selection.

The reproductive success of a male during a courtship season (ie. the number of females he inseminates) will be determined by two variables; (1) his reproductive success with each female (ie. the probability of sperm transfer per courtship), and (2) the number of courtships he performs that courtship season. The effects of other courtship variables upon those two variables are shown in the figure. Two variables are extrinsic to a pair of courting animals (the probability that another male will intrude during courtship and the length of the courtship season). All arrows between variables represent positive influences unless otherwise noted. As the variable at the start of the arrow increases, so will the variable to which the arrow leads. Arrows with a negative sign indicate that as the variable at the start of the arrow increases, the variable at the end of the arrow will decrease. Four arrows indicate the effects of natural selection arising from the two variables extrinsic to the courting animals. The dotted arrow (8) indicates that when another male has intruded, a male can increase the probability that the female will locate his (rather than the other male's spermatophores) by depositing spermatophores at a faster rate.


PROBABILITY OF AN INTRUDING MALE DURING COURTSHIP
selection
+
selection
-
selection
+
NO. ACTS / TIME
INFORMATION TRANSMITTED / ACT
TIME / SPERMATOPHORE
INFORMATION TRANSMITTED / TIME
INFORMATION TRANSMITTED / SPERMATOPHORE
VARIABILITY IN SITE OF SPERMATOPHORE DEPOSITION
PROBABILITY OF FEMALE LOCATING SPERMATOPHORE / SPERMATOPHORE
PROBABILITY OF SPERM TRANSFER / SPERMATOPHORE LOCATION
PROBABILITY OF SPERM TRANSFER / SPERMATOPHORE
NO. SPERMATOPHORES / COURTSHIP
PROBABILITY OF SPERM TRANSFER / COURTSHIP
LENGTH OF COURTSHIP SEASON
selection
-
NO. COURTSHIPS / COURTSHIP SEASON
NO. FEMALES INSEMINATED / COURTSHIP SEASON
1
2
3
4
5
6
7
8

female just before spermatophore deposition (ie. during the tail-straddling walk).

The more time the male takes per spermatophore deposition, the more likely is the female to locate the spermatophore (Table 11). This relationship is probably due in part to pairs being able to affect each others behavior more between spermatophore depositions by taking more time between spermatophore depositions. But in addition, males which take more time before depositing spermatophores will give non-receptive females (which tend to ignore spermatophores) a greater chance to depart from the courtship before spermatophores are deposited. Consequently because spermatophores are deposited with a biased sample of females, the probability that the female will locate the spermatophore is higher. This direct functional relationship(s) between the time per spermatophore deposition and the probability of spermatophore location per spermatophore deposition is shown by arrow 4 in Fig. 24.

Thus the interspecific differences in rate of information transmission between sexual partners, the amount of information transmitted between sexual partners per spermatophore deposition, variability in the site of spermatophore deposition and the probability of successful spermatophore location per spermatophore deposition can all be explained in terms of interspecific differences in (1) rate of courtship and (2) time required per spermatophore deposition.

b. The adaptive significance of interspecific differences in courtship variables.

What, then, is the adaptive significance of interspecific differences in these last two variables and in the number of spermatophores deposited per courtship?

The entire reproductive biology of *Ambystoma maculatum* is tied to breeding in small, temporary woodland ponds. Because of the nearly synchronous arrival of many animals to these small ponds, courtship behavior occurs in much more crowded circumstances than in *Plethodon jordani*. Indeed, field observations show that frequently several males of *A. maculatum* court a single female simultaneously. The presence of these additional courting males probably has several effects upon the reproductive success of each individual male participant. All of these effects will tend to reduce the reproductive success of each male by lowering the probability that the female will locate and be inseminated by his spermatophores. First, additional males will interfere with the communication processes between a particular male and the female (arrow 5 in Fig. 24). This will have the effect of reducing the probability that the female will locate the spermatophores deposited by that male. Second, additional males will reduce directly the probability that the female will locate spermatophores in a number of ways (all shown with arrow 6 in Fig. 24). Laboratory experiments showed that females locate no more spermatophores when two males are present than with one solitary male, despite the fact that two males deposit twice as many spermatophores as one male. Consequently the probability of the female locating the spermatophore of a particular male is reduced when additional males are present. In addition, by nudging and pushing the female, males can interfere with the process of spermatophore location by the female, and this effect will be increased with additional males. Finally, males tend to deposit spermatophores on top of pre-existing spermatophores. Thus a particular male will have some of his spermatophores rendered inaccessible to the female (ie. the effective number of his spermatophores will be reduced) when other males are present.

When the female has located the spermatophore of a particular male, other males may dislodge her from that spermatophore by nudging and rubbing her and so reduce the probability of successful sperm transfer (arrow 7 in Fig. 24).

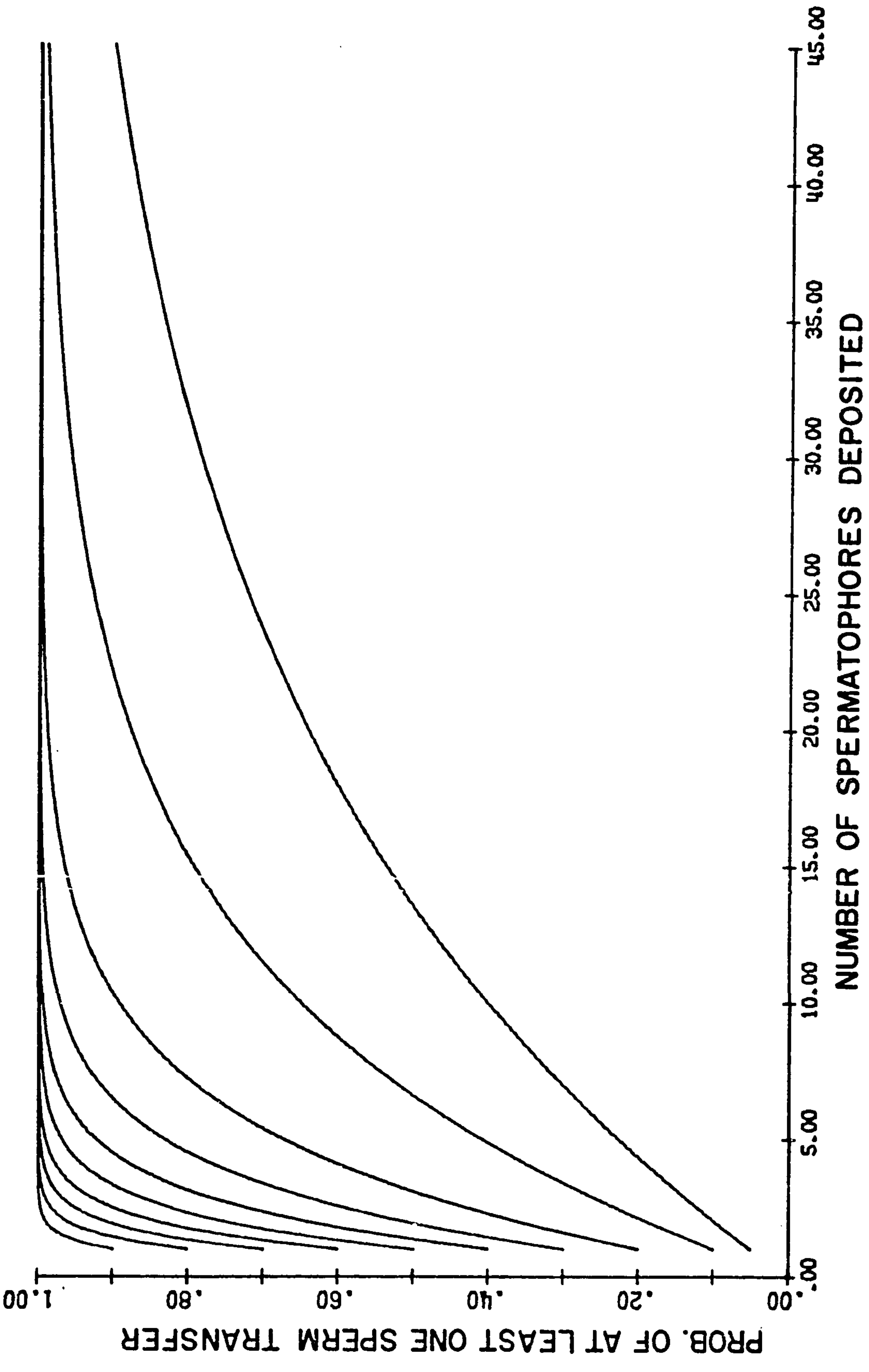
Thus courtship in crowded circumstances will tend to reduce the reproductive success of each participating male (compared with his expected success when courting without other males present) by reducing the probability that the female will locate his spermatophores.

The high likelihood of other males participating in courtship in Ambystoma maculatum is probably the selective pressure responsible for rapid courtship rate, rapid spermatophore deposition rate and the large numbers of spermatophores deposited by each male in this species. When other males are simultaneously courting a female, the male which deposits spermatophores at a slow rate will find that the female will be inseminated by the spermatophores of other males. Hence when courtship occurs in crowded circumstances, selection will favor males with rapid spermatophore deposition rates. This is probably the major adaptive significance of rapid courtship rate as well. But in addition, males which perform more courtship acts per unit time will be favored by natural selection, since they should transmit more information to the female per spermatophore deposition and thereby increase the probability that the female will locate their spermatophores. In crowded circumstances, natural selection should also favor males which deposit many spermatophores per courtship. Such a male will compensate for the reduction in probability of successful sperm transfer due to the presence of other males by simply giving the female more opportunities to find his spermatophores. When a single male courts a female the probability of successful sperm transfer was estimated as about 0.24, and the male deposits a mean of 20 or 40 (depending on population)

Figure 25. The probability of sperm transfer per courtship as a function of the number of spermatophores deposited and the probability of success with each spermatophore.

Each line represents the probability of sperm transfer per courtship as a function of the number of spermatophores deposited for a particular probability of success with each spermatophore. Locate one spermatophore deposited on the X axis and read upward. The first line represents the function above when the probability of sperm transfer per spermatophore is 0.05; the second line represents the function when this probability is 0.1; the third line shows the function when the probability is 0.2, etc.

The function is calculated with the assumption that the probability of sperm transfer per spermatophore is stationary and independent of the past history of spermatophore locations by the female during a courtship (see p. 62 for the function).


PROB. OF AT LEAST ONE SPERM TRANSFER
.00
.20
.40
.60
.80
1.00
NUMBER OF SPERMATOPHORES DEPOSITED
.00
5.00
10.00
15.00
20.00
25.00
30.00
35.00
40.00
45.00

spermatophores per courtship with a female. From Fig. 25 we can see that the probability of sperm transfer per courtship is essentially 1.0 when only 20 spermatophores have been deposited with a success of 0.24 per spermatophore. A male which deposits 40 spermatophores per courtship is very likely to inseminate the female even if the probability of success with each spermatophore is only 0.05. It is very likely that the probability of success per spermatophore is this low in the field when other males are simultaneously depositing spermatophores with a female. Hence male *Ambystoma maculatum* routinely deposit 40 or more spermatophores with a female in the "expectation" that other males will intrude and reduce the likelihood that each spermatophore will inseminate the female. One male deposited 81 spermatophores with a female in a single evening when no other males were present.

The converse of most of these arguments apply to the evolution of *Plethodon jordani* courtship behavior. In this species it is much less likely that additional males will intrude during a courtship encounter. During the courtship season pairs of *P. jordani* are widely spaced. The entire breeding population is not forced into a small area for courtship activities as in *Ambystoma maculatum*. Consequently, all of the selective pressures which result from crowded circumstances are relaxed in *Plethodon jordani*. Males court very slowly and take a long time for each spermatophore deposition. Consequently when a spermatophore is deposited it is in a very specific site close to the female, and the female is very likely to locate the spermatophore with her vent.

Males which deposit many spermatophores per courtship will have fewer spermatophores to expend on females encountered later in the courtship season. In *Ambystoma maculatum*, females are available for courtship for a very short period of time. They arrive for courtship on a very few nights and, due to the high density of males, they are inseminated very rapidly and then depart from the courting pool of females to lay their eggs. Under these circumstances, selection will not favor males which conserve spermatophores early in the season in order to inseminate females which might be encountered later. But in *Plethodon jordani*, females are available for courtship for a considerably longer period of time. Consequently selection will favor males which deposit few spermatophores per courtship, since such males will be able to inseminate females encountered later in the courtship season.

In summary, consideration of only two variables, (1) the probability of additional males intruding during courtship encounters and (2) the length of the courtship season, enables us to account for the many differences between *Ambystoma maculatum* and *Plethodon jordani* in courtship variables. Where animals are forced to court in crowded circumstances and the courtship season is short, selection will favor rapid deposition of many spermatophores per courtship. But when intrusions by other males are unlikely and there are many opportunities for courtship during a courtship season, selection will favor leisurely deposition of a very few spermatophores per courtship.

Ambystoma tigrinum males take a longer time per spermatophore deposition and deposit fewer spermatophores per courtship than *A. maculatum* males. But they do not take as long per spermatophore deposition as *Plethodon jordani*, and they deposit many more spermatophores per courtship. As in *A. maculatum*, the courtship season of *A. tigrinum* is short, and the population courts in relatively more crowded circumstances than *Plethodon jordani*. Thus the courtship differences between *Ambystoma tigrinum* and *Plethodon jordani* can be accounted for by the arguments above. What is the adaptive significance of the differences between *A. tigrinum* and

A. maculatum? Apparently the large courtship aggregations characteristic of A. maculatum are not characteristic of A. tigrinum. Courting pairs may even be regularly spaced, even though large numbers of animals are courting in the same pond. Thus intrusions and spermatophore depositions by additional males are probably less likely in A. tigrinum than in A. maculatum, but additional field work is required to conclusively establish this difference. But if it is so, the selective pressures due to intrusions by other males are relaxed somewhat in A. tigrinum, and selection may have favored males which expend more time per spermatophore deposition (thereby increasing the probability that the female will locate the spermatophore(s)), and which deposit fewer spermatophores per courtship (and are thereby able to court with more females per courtship season).

The tendency of Ambystoma males to deposit spermatophores on top of other spermatophores is probably an adaptive response to courtship in crowded circumstances with other males. In Ambystoma maculatum particularly, when a male encounters a pre-existing spermatophore it is likely to be the spermatophore of another male. (When more than two males are present this probability is greater than half, and in the field frequently a dozen or more males court a female simultaneously). When a male deposits his own spermatophore on top of this spermatophore, he renders the sperm of another male inaccessible to the female while increasing the likelihood that the female will find his own spermatophore. Even if the male deposits a spermatophore on top of his own spermatophore, the original sperm mass may have already been dislodged or removed by the female.

The specific differences in behavioral interactions between males during the courtship season also appear to be adaptive. By attacking other males during the courtship season, male Plethodon jordani probably chase other males from their immediate vicinity and so reduce the probability that another male will intrude during a courtship encounter. When a male encounters another male courting a female, by joining the courtship and behaving as a female he may cause the original male to expend a spermatophore which the female cannot retrieve. He thereby depresses the reproductive success of the original male and may himself be able to inseminate the female. Ambystoma maculatum males actively depress the fitness of other courting males by following behind them and covering the other male's sperm with their own spermatophore. In addition males are able to actively inhibit the spermatophore depositions of other males by dislodging them from a spermatophore deposition in the presence of other courting males and thereby increase the likelihood that the female will be inseminated by their own spermatophores before she departs from the courtship encounter.

It would probably not be adaptive for males of Ambystoma maculatum to actively bite and pursue other males as it is for Plethodon jordani. Since the density of male A. maculatum is so high, a male which interrupts his courtship activities to pursue other males would be continually engaged in male-male interactions, and other males would inseminate the female.

No attempt has yet been made to observe interactions between courting males of Ambystoma tigrinum. The spectacular male behavior of shoving the female long distances through the water (Fig. 4), may have the effect of removing the female from the vicinity of other males, and thus insuring the male's monopoly of the sexually active female. Experiments should be performed to see whether the frequency of this behavior increases in the presence of other males. This behavior may be responsible for the absence of massive courtship aggregations in Ambystoma tigrinum.

Several authors (Williams, 1966; Tinkle, 1969; Gadgil & Bossert, 1970) have suggested that species with short adult life expectancies should expend more energy in reproduction each breeding season than species with longer life expectancies. In annual species, for example, there is no selection to conserve energy for reproduction in subsequent years. In terms of number of spermatophores per courtship, male *Ambystoma maculatum* certainly expend more energy than *Plethodon jordani*, and despite the shorter courtship season they probably expend more energy per breeding season than male *Plethodon jordani*. Unfortunately age specific survivorship of males is known, rather imperfectly, for only one of these species. Husting (1965) estimated yearly survivorship of male *A. maculatum* in Michigan at 0.76 to 0.94, depending on the method of estimation. Male *Ambystoma maculatum* are then very likely to survive to the next breeding season following their first breeding season, and I was able to capture a few males eleven years after Husting marked them as sexually mature adults. *Desmognathus* are the most closely related salamanders to *Plethodon jordani* for which male survivorship is known. *Desmognathus ochrophaeus* is a salamander of comparable size (but one with aquatic larvae). Sexual maturity is attained after 4 years, and the probability of a male surviving to the third breeding season from the first breeding season is approximately 0.20 (Organ, 1961a), and in each of five species of *Desmognathus* male survivorship decreases with age. If any comparison can be made of male survivorship in these two species, it is that the probability of a male surviving to breed in successive courtship seasons is lower in *Plethodon jordani* than in *Ambystoma maculatum*. Thus the species with the largest expenditure of reproductive energy per courtship season has probably the greater likelihood of surviving to breed in subsequent years. Differences in male survivorship do not explain the differences in courtship variables in these two species.

Plethodon jordani is sympatric with more congeneric species than either *Ambystoma maculatum* or *A. tigrinum*. The long time required before spermatophore deposition and the complex programming of male behavior in *Plethodon jordani* might be the result of selection to avoid matings with other species. Although five congeneric species are sympatric with *P. jordani* on Whitetop Mtn., the courtship seasons are displaced in time so that during its courtship season *Plethodon jordani* is sympatric with no more species of courting congeners than either *Ambystoma* species. Furthermore, evidence from a variety of sources suggests that courtship behavior between sympatric, heterospecific salamanders is terminated abruptly upon or shortly after initial contact. The various studies of the role of behavior in reproductive isolation in salamanders will be reviewed in the next chapter, but it appears that male *Plethodon jordani* do not use their complex behavioral programming for species identification during courtship.

CHAPTER II

THE EVOLUTION OF COURTSHIP BEHAVIOR

INTRODUCTION

In this chapter I present my observations on the courtship behavior of salamanders, together with summaries of information available in the literature.

For the species for which the most complete behavioral information is available, I have selected 25 behavioral characters. I have attempted to reconstruct the phylogeny of salamanders from these behavioral characters. Using this phylogeny I then discuss the evolutionary history of courtship behavior, the evolutionary relations between courtship behavior and sexual dimorphisms, and the selective pressures responsible for evolutionary modification of courtship behavior.

There are many ways to construct hypotheses about evolution from behavioral data. Some ethologists have arranged the behaviors of different species in graded series and then discussed the evolutionary modification of behavior (eg. Lorenz, 1935/translation in Lorenz, 1970 (see p. 191)); Salthe, 1967). Other ethologists have suggested that behavioral characters should be reflected upon an accepted phylogeny based on morphology in order to infer how behavior has changed during evolution (eg. Hinde and Tinbergen, 1958). Unfortunately morphologists are seldom in agreement about the phylogeny of any group of organisms. This is the case with salamanders. I have taken the tact of inferring the phylogeny of salamanders from their courtship behavior, without including the morphological characters which are usually used by salamander systematists (eg. aspects of osteology and musculature). I then discuss evolutionary modification of behavior and compare behavioral with osteological interpretations of phylogeny. Of course osteology and behavior share the same phylogenetic history, but by separating behavioral from osteological inference I hope to focus attention on unresolved systematic problems in salamanders.

There are approximately 300 species of living salamanders, and about 200 of these are in one family, the Plethodontidae (Brame, 1967). Something is known about the courtship behavior of 71 species of salamanders, or about 20 per cent of the living species.

Collecting data for the animals I have observed are given in Appendix II as well as the dates on which courtship was observed. The reader should refer to Appendix I for general information about the various genera of salamanders. I have indicated the mode of fertilization, the site of fertilization, the time of courtship, type of larvae and the geographical distribution of each genus for which courtship information is available.

MATERIALS AND METHODS

Observations of courtship behavior were made in the following species m indicates that movies, and p indicates that still photos, were made of courtship behavior); *Cryptobranchus bishopi* (m), *Rhyacotriton olympicus* (p), *Ambystoma maculatum* (m,p), *A. texanum* (m,p), *A. opacum* (p), *A. tigrinum* (m), *A. mexicanum* (m,p), *A. laterale* (m,p), *Taricha granulosa* (m,p), *T. torosa* (p), *Notophthalmus viridescens* (m,p), *Triturus cristatus* (m,p), *T. helveticus* (p), *T. alpestris* (p), *T. vulgaris*, *Cynops pyrrhogaster* (Hiroshima) (m,p), *Paramesotriton hongkongensis*, *Pleurodeles waltl* (m,p), *Salamandra salamandra* (m,p), *Pseudotriton ruber* (p), *Eurycea bislineata* (m), *Desmognathus fuscus*, *D. ochrophaeus*, *D. monticola*, *Plethodon cinereus*, *P. richmondi*, *P. welleri*, *P. yonahlossee*, *P. caddoensis*, *P. jordani* (m,p), *P. glutinosus*, *Aneides lugubris*, *Ensatina eschscholtzia*, *Bolitoglossa subpalmata*, *B. flavimembris* and *Euproctus asper*. The localities from which these animals came are shown in Appendix I. Unless otherwise indicated, line drawings were made from the still photographs and movies above.

Courtship accounts for each species were compiled from tape recorded observations, handwritten notes and sketches, still photographs and movies.

RESULTS

A. Accounts of courtship behavior. Family CRYPTOBRANCHIDAE

Cryptobranchus alleganiensis

Smith (1909) found that the eggs of Cryptobranchus could be successfully inseminated outside of the female's by artificial means, and that eggs removed from the female's body were invariably infertile unless artificially exposed to sperm. He also observed ovoposition and spermiation in an outdoor enclosure and so established that fertilization is external in Cryptobranchus. Smith observed a female, with a short string of eggs protruding from her cloaca, crawling about and dragging the eggs on the substrate. A male followed the female. The female stopped occasionally and made lateral and vertical swaying movements of her posterior body. The female then crawled under a rock, and more of the egg string was extruded. With the female motionless, the male moved over or beside the eggs, either alongside or over the female. In this position the male executed swaying lateral and vertical movements of his posterior body while raising and lowering his posterior body with his hindlimbs. Simultaneously the male extruded a white, ropy or cloudy mass consisting of seminal fluid and secretions of the cloacal glands. The seminal materials fell either upon the eggs or beside them and were diffused among the eggs by the male's own movements or by the movements of other animals in the vicinity.

I was able to observe ovoposition in captive Cryptobranchus bishopi, but I can add little to Smith's (1909) observations. Several males and several females were housed in a large aquarium and separated from each other by a sliding glass partition. After two weeks in captivity, two females were found to be laying eggs one evening, and the glass partition was then removed. During ovoposition two egg strings (one from each oviduct) are extruded simultaneously from the female's cloaca. During ovoposition the female crawls about actively, and as the egg strings are caught on objects on the substrate they are pulled from the female's cloaca. Some of the males crawled among the egg strings and ate some of the eggs, but I never observed sperm discharge such as Smith (1909) described. The males never actively followed the females as they discharged their egg strings. A portion of the eggs was later isolated, and they failed to develop. I removed one of the males from the observation tank as he lay among the egg strings. He extruded a small quantity of whitish fluid from his cloaca as I held him. I prepared a smear of this fluid, and found that it contained many active spermatozoa. For some reason the males failed to show reproductive behavior in the presence of ovopositing females.

Andrias japonicus

Kerbert (1904) observed ovoposition and spermiation in a captive pair of animals. A few weeks before breeding occurred the male became very active and formed a depression in the sand substrate of the aquarium. On September 19 the female released a short string of four eggs and then began releasing two very long egg strings simultaneously. During ovoposition the female swam about the container. The male was more active than the female and swam continually through the egg mass which lay in the sandy depression. A few minutes later he rested quietly near the egg mass. Kerbert then noticed that the male's tail and skin on his rump showed an undulatory, quivering movement, and that the male was releasing sperm. The male released a grey-white substance which contained the sperm and made the water turbid. After ovoposition the female moved to the back of the container and remained motionless. The male, however, crept among the egg strings and enveloped himself in them or rested beside them. He periodically moved his entire body in a pendulum-like movement, which Kerbert suggests may have ventilated the eggs and developing embryos. The male dashed at the female and chased her away whenever she approached the eggs. She was finally removed from the container. Kerbert (1904) rejected the notion that the male was actually fertilizing the eggs externally when he released sperm near them (the eggs were fertile), no doubt because the generalization that fertilization was internal in salamanders had just been established. In light of Smith's (1909) later work on Cryptobranchus it is certain that Kerbert did in fact observe external fertilization in Andrias.

While he does not provide a description of breeding behavior, Kudo (1938) apparently observed the phenomenon and notes that fertilization is external in Andrias japonicus. He also found that the female departed from the brood, while the male remained with it.

Family HYNOBIIDAE

Hynobius lichenatus

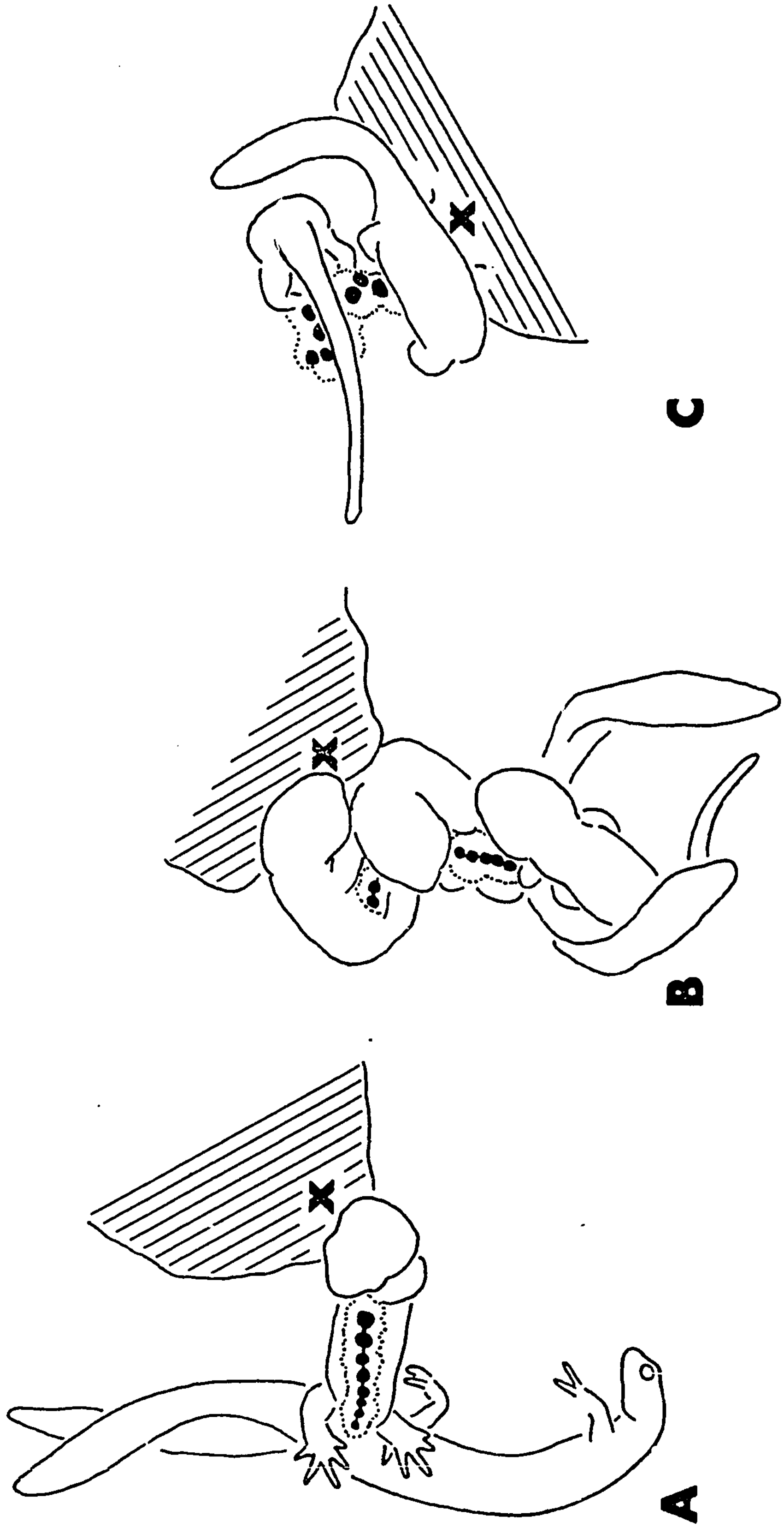
Sasaki (1924) observed the processes of ovoposition and spermiation in captive specimens. Several males and several females were housed in the same observation tank. Spawning was nocturnal and usually occurred in the early hours of the morning. The female crawls about slowly and seeks a hard object for the attachment of her egg sacs. The egg sacs consist of two elongate, corrugated sacs which are joined at one end. The female adpresses her cloaca to the ovoposition site and attaches the egg sacs at their juncture to the selected object while arching her body and stretching her limbs out to the side. Finally with a backward movement the female attempts to draw the egg sacs out of her oviducts. Males in the vicinity rapidly approach such a spawning female and immediately clasp the emerging egg sacs, rather than the female. Sasaki observed two types of male behavior on the egg sacs. A male may orient his body lengthwise along the egg sac while clasping the egg sac near its point of attachment with his forelimbs. In this position the male pushes the female backward with his hindlimbs by extending and flexing his body. By this action the male forces the egg sacs from the female's oviducts and simultaneously rubs his cloaca upon them (see Fig. 26A). Alternatively, the male may coil his body in spirals around the egg sacs while clasping the egg sacs with both his forelimbs and hindlimbs and in this position rub his cloaca on the egg sac (see Fig. 26B). Presumably this vigorous application of the male's cloaca to the egg sac as the male clasps the sac is synchronous with the release of sperm, since Sasaki found that egg sacs discharged in the absence of males never developed. Once the female has discharged her egg sacs, she departs from the ovoposition site. The males continue to cling to the egg sacs for several minutes and remain near the egg sacs for two or three hours.

Figure 26. Reproductive behavior in Hynobius lichenatus (after Sasaki, 1924).

Fig. A. A female (left) has attached the end of her egg sacs to a rock at the site marked with an X. A male (right) has approached the female and her egg sacs and is not clasping the egg sacs, near their point of attachment, with his forelimbs while applying his cloaca to the egg sacs and pushing the female away with his hindlimbs.

Fig. B. The female has now discharged the egg sacs from her oviducts and retreated from the site of ovoposition. Two additional males have approached the egg sacs, so that now three males are clasping the egg sacs with their forelimbs and hindlimbs and applying their cloaca to the egg sacs as they fertilize the ova.

Fig. C. Two males are clasping and fertilizing egg sacs which are attached to a rock at the site marked with an X. Note the clasping posture of the upper male's hindlimbs as he applies his cloaca to the egg sacs.


C
X
B
X
A
X

Hynobius nebulosus

The observations of Thorn (1962, 1963, 1966) and Rehberg (1962) provide the most complete account to date of breeding behavior in a hynobiidspecies. Thorn (1963,1966) found that with the onset of the breeding season and in the absence of females, a captive male will tend to reside near a particular site in an aquarium where there are vertical stems or leaves of aquatic plants. This will later be the site of ovoposition. In the vicinity of this site the male frequently assumed a characteristic posture with the head raised slightly while extended on his forelimbs. Periodically the male undulated his tail laterally. When a gravid female was introduced into the aquarium, she moved actively about without approaching the male. When in the vicinity of the female, the male nudged her and then performed a rhythmic jerking, lateral movement of his body which was most pronounced in the male's pelvic region. In the vicinity of the female, the male also projected his gular region outward while raising his head slightly. This had the effect of exposing a white gular spot which is found only in males. When the female paused, the male turned his head towards her head. Whenever the female moved forward again, the male raised his body upward, and then repeated the pelvic jerking movement and the gular swelling action. This last series of actions was repeated several times. The male then moved away from the female and towards the future ovoposition site. Upon reaching this site the male leaned vertically upon the vertical leaves of a plant. The female then rapidly approached the site. She climbed upward along the vertical leaves while clasping them with all four limbs until her anterior body emerged from the water. She applied her cloaca to the leaves and attached the base of the two egg sacs to them. The female then fell backward in the water, pivoting about the point of attachment of the egg sacs. The male then rapidly approached the female and entwined with her. The male pressed the female's venter against him by grasping her with his hindlimbs. The two egg sacs, one from each oviduct, were then expelled from the female, and she fell to the substrate. The male meanwhile clasped the egg sacs and remained motionless. The female then moved away. As she departed, the male approached her and again performed the jerking pelvic movement. The female then moved out of the water, and the male returned to the egg sacs. He entwined among them while clasping them with his forelimbs. He then arched his back upward and clasped the egg sacs with his hindlimbs. In this position he executed rhythmic movements of his hindlimbs and possibly rubbed them against the egg sacs. The male then released the egg sacs with his limbs and penetrated among them. The male then tended to remain on the substrate beneath the egg sacs and occasionally executed tail undulations with his tail straight. The eggs were fertile.

Thorn (1962) also found that the male continues to remain near the eggs once he has fertilized them, and that he will rapidly approach other males which come near the eggs. Males which are so approached then flee from the resident male. In this context too, the resident male performs lateral tail undulations. The male will also bite inanimate objects which are thrust in or near the egg sacs.

Rehberg (1962) also observed a male fertilizing egg sacs. The male clasped one end of the egg sac with his forelimbs while bending his head down. The male then arched his back upward, clasped the other end of the egg sac with his hindlimbs and shoved the egg sac through his hindlimbs and against his cloaca. This series of actions was very rapid (one and a half to two seconds in duration) and was repeated several times.

Hynobius keyserlingi

Dybowski (1870) notes that the females lay their eggs in organized string-like clumps and attach them to plant stalks and other objects near the water surface. The males discharge milt upon the eggs while moving actively back and forth.

Ranodon sibericus

Bannikov (1958) reports that fertilization is external in *Ranodon sibericus*. The male attaches a spermatophore to the underside of a stone lying under water or, less frequently, to twigs and branches projecting in the water. The spermatophore consists of two mucilaginous clumps which are filled with spermatozoa. These clumps are 5-6 mm in diameter, but can be elongated to a length of 40 mm! The female attaches one end of her egg sac(s) to the underside of the spermatophore. Usually two egg sacs are attached to each spermatophore, but sometimes one or three egg sacs are attached. Bannikov suggests that the sperm reach the ova through the mucus junction between the spermatophore and the egg sac. The behavior accompanying spermiation and ovoposition has apparently not been observed.

Family AMBYSTOMATIDAE

Rhyacotriton olympicus

Catalog of male actions.

A.) NUDGING The male contacts his snout or lateral snout to the female's lateral body (Fig. 27B).

B.) HEAD-SWINGING The male swings his head from side to side, arhythmically, with his chin in contact with the female's dorsum.

C.) HEAD-SLIDING The male moves forward sliding his chin along the female's dorsum.

D.) LIFTING The male turns his head under the female's chin and lifts his head contacting the dorsum of his head to the female's chin.

E.) TAIL CURLED UPWARD This action begins with the male's tail level, in contact with the substrate, and directed straight backward. The male slowly raises the distal tail (Fig. 27C), gradually curling the tail upward until the tail tip is directly above the male's midbody (Fig. 27D). With the tail curled in this position, the last entimeter of the tail is slowly swung rhythmically back and forth (Figs. 27D, 28A, 28B). This posture, with the tail curled upward and with the tail tip swinging laterally, is frequently maintained for several minutes. The ventral surfaces of the male's tail and his vent lobes are bright yellow in contrast to his dull brown dorsal coloration. When he performs this tail curling action, he presents a striking visual effect. He appears from the rear, even in dim light, as a vertical light line (his tail) with two light ovals (his vent lobes) near the base of the line on either side.

F.) TAIL ARCHED AND TAIL UNDULATING The male's proximal tail is arched upward and undulated laterally (Fig. 28C).

Temporal relations (Rhyacotriton olympicus)

The processes of spermatophore deposition and sperm transfer have not yet been observed. Preliminary courtship encounters were nocturnal and invariably took place on "land" even when pairs were maintained in sloping aquaria with half of the substrate submerged and half exposed. Spermatophores were discovered on several occasions and were always attached to the substrate on land. Usually one (but on one occasion three) spermatophore was deposited by a male housed with a female.

Preliminary courtship encounters take the following, rather variable, course. A sexually active male will approach a female as she moves about. In close proximity to the female, the male may stop abruptly, if the female remains stationary, and perform tail curled upward (E) (Fig. 28A,28B) without contacting her. Alternatively he may approach the female (Fig.27A) and begin contacting her with his head (via nudging, head-swinging or head-sliding) as he moves along her length (Fig. 27B). If she remains stationary as the male contacts her with his head, the male may move away from her (Fig. 27C), stop and perform tail curled upward (Fig. 27D), while facing away from her.

On several occasions males performed lifting when they reached the female's head, after first moving along the length of the female. The male then crawls forward under the female's chin, pauses when his dorsal proximal tail contacts her chin (or some other region of her body as in Fig. 28C), and then arches and undulates his tail. In all cases the female remained stationary. The male may then cease tail arch and tail undulation, and resume head contact with the female, or he may move forward and initiate tail curled upward.

On many occasions I observed males initiating and performing tail curled upward when not approaching females or other animals. Frequently a male moved about the container, stopped and performed the characteristic tail curled action, and then terminated the action after a few minutes, moved forward again and resumed tail curled upward.

When several males were housed together with females, I frequently observed males pursuing and biting other males. I never saw interactions of this kind between males and females or between females.

Figure 27. Courtship activities in *Rhyacotriton olympicus*.

Fig. A. A male (left) has approached a female (right) and pauses momentarily. Note the male's enlarged vent lobes.

Fig. B. The male moves posterior along the length of the female nudging her with his snout.

Fig. C. As the male moves away from the female, he begins to curl his tail upward.

Fig. D. The male pauses while facing away from the female with his tail curled upward and with his tail tip undulating from side to side.

(From photographs taken at night of courting animals).

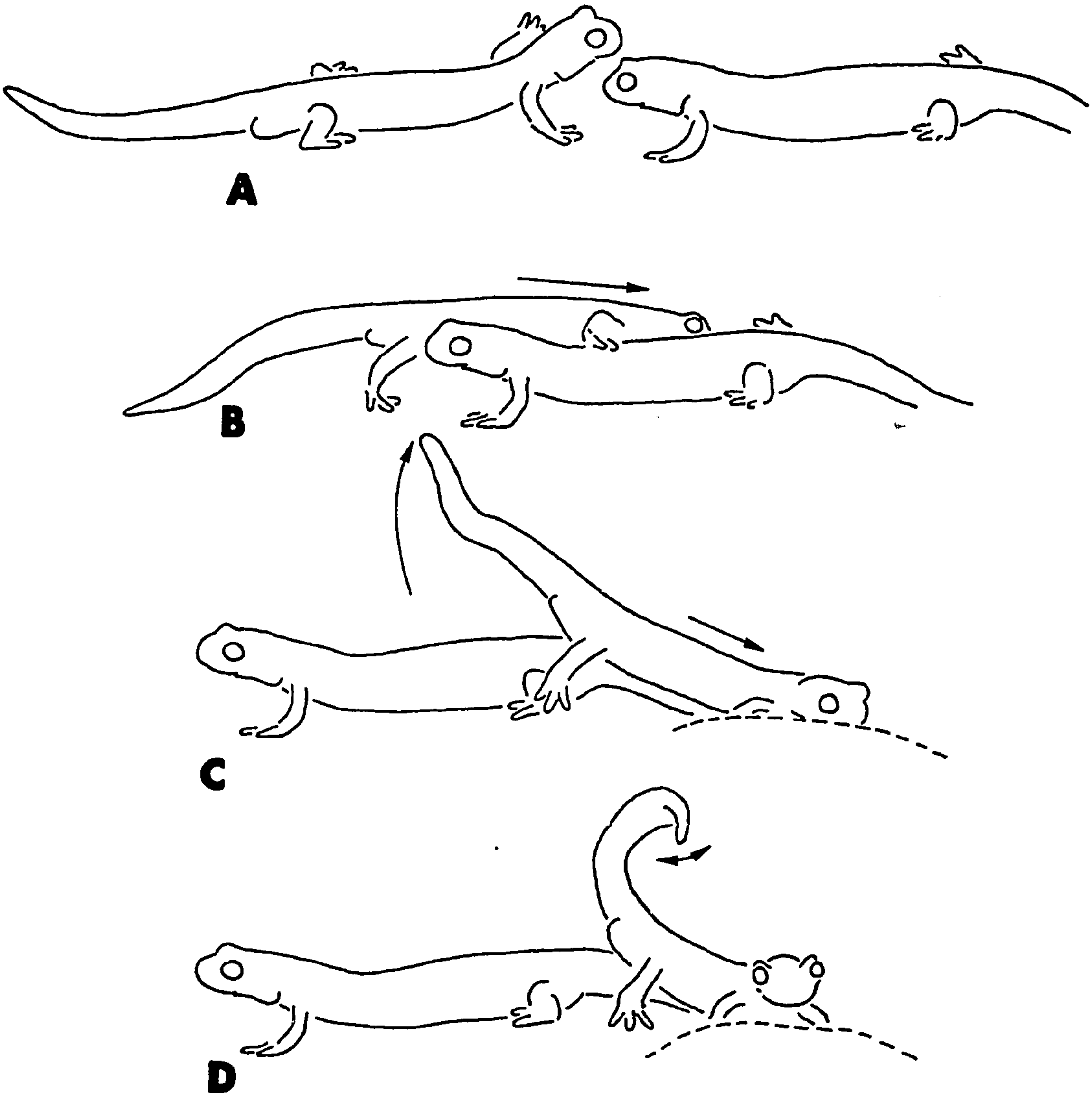

A
B
C
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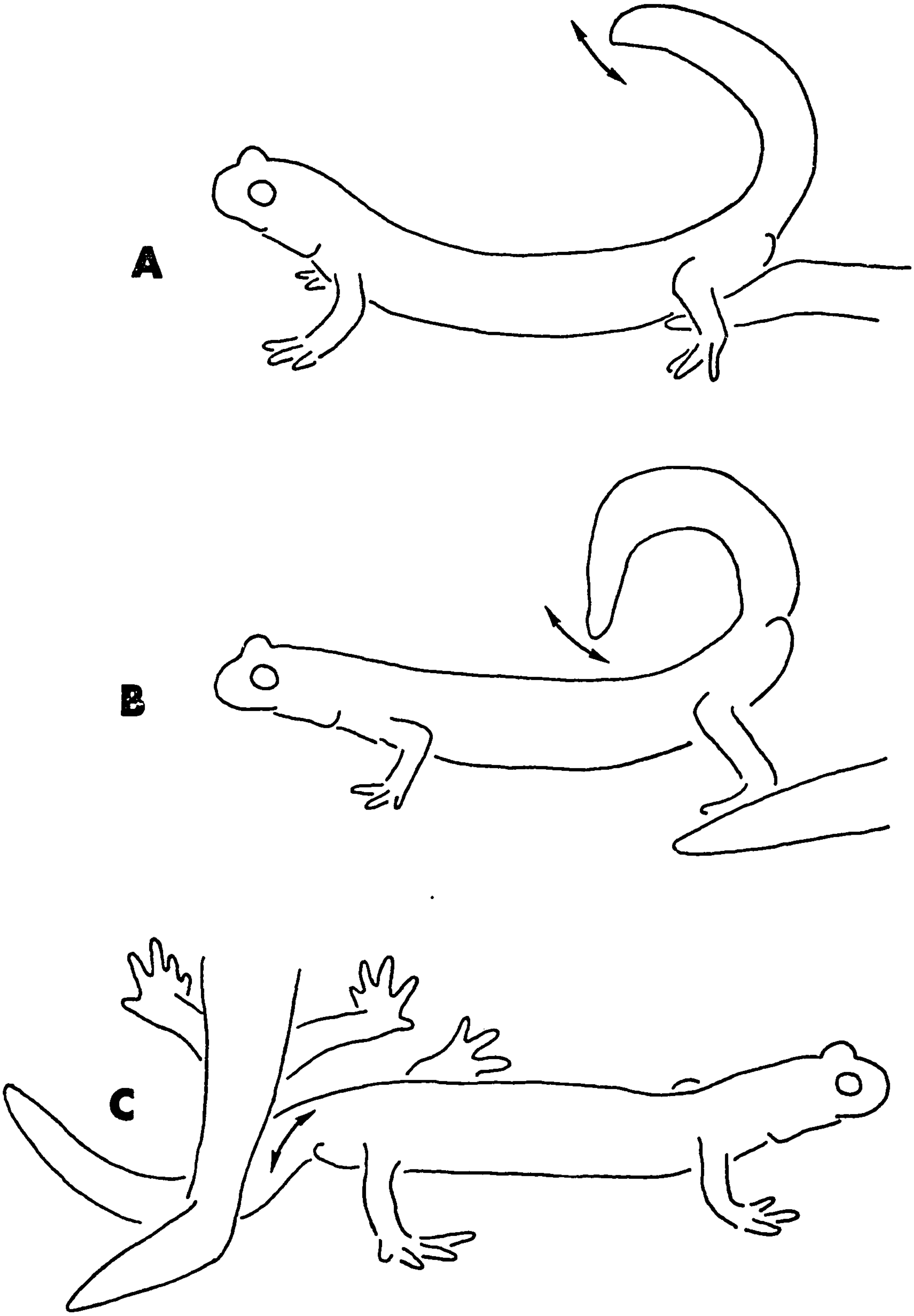
Figure 28. Courtship activities in Rhyacotriton olympicus.

Fig. A. A male facing away from a female with his tail curled upward and his tail tip undulating from side to side. Just the distal tail of the female is visible.

Fig. B. Another male in the same position, but with the tail curled further over his back as he undulates his tail tip.

Fig. C. A male (right) has crawled under the tail of a female as she rests vertically on the back pane of the container. The male is stationary as he arches his proximal tail upward and undulates his tail laterally, in contact with the female's tail.

(From photographs of courting animals, taken at night).


A
B
C

Ambystoma texanum

Catalog of male actions

A.) NUDGING The male contacts his snout or lateral snout to the female's lateral body (Fig. 29C, H).

B.) HEAD-SWINGING The male swings his head from side to side with his chin or mentum in contact with the female's dorsal body. The male may simultaneously press his head downward (Fig. 29A).

C.) LIFTING The male lifts his head with his snout, dorsal head or dorsal midbody in contact with the female's ventral body. He may simultaneously turn his head sharply to one side towards the female (Fig. 29B, D).

D.) VENT-SHUFFLING The male shuffles his vent laterally in contact with the substrate by swinging the entire posterior body and tail from side to side. This action may be performed with the male stationary or while moving forward.

E.) STATIONARY WITH HINDLIMBS ADPRESSED While stationary the male adpresses his hindlimbs against his lateral tail base and raises them slightly above the substrate. The forelimbs are outstretched perpendicular to the body. The body is arched upward slightly so that only the pectoral region, sacrum and vent contact the substrate. The entire tail is arched upward so that the distal tail may be raised as much as 90° to the substrate. The tail may be undulated slowly.

F.) SPERMATOPHORE DEPOSITION When spermatophore deposition occurs it follows the action just described (E) with the male continuing in the same posture (Fig. 29E, F). Spermatophore deposition terminates with the male lowering his tail and then raising the proximal tail upward slightly as he moves forward off of the spermatophore.

Temporal relations (Ambystoma texanum)

Upon contacting or recontacting the female, a sexually active male moves repidly along her length while performing nudging, head-swinging and lifting (Fig. 29A, B, C, D). The male may move along beside the female either anteriad or posteriad while performing these actions and may cross diagonally over the top of the female. When the male reaches the female's head or tail, he tends to turn sharply towards the female and lift his head under her head (Fig. 29B) or tail (Fig. 29D) and then continue along the opposite side of the female in the direction he has turned.

When the male looses contact with the female, he moves forward rapidly, turning repeatedly until he recontacts her. He then resumes nudging, head-swinging and lifting as he moves along beside her. The male tends to turn towards objects contacting his lateral body on one side. The female shows this same tendency. In addition, the female may nudge and perform head-swinging and lifting towards the male. Thus courting pairs tend to mill around in a small area, with both animals repeatedly turning towards each other and nudging and rubbing each other's bodies. Or the female, particularly at the initiation of courtship, may remain essentially stationary as the male circles around and over her while nudging, rubbing and lifting.

Periodically the male ceases nudging and rubbing of the female and moves forward shuffling his vent against the substrate. He may then reapproach the female and resume nudging and rubbing or he may pause and adpress his hindlimbs. He may then reapproach the female without depositing a spermatophore, or continue in the same posture and deposit a spermatophore (Fig. 29E, F).

Spermatophores may either be deposited de novo upon the substrate, or they may be deposited upon pre-existing spermatophore (secondary spermatophore deposition). When the male contacts a pre-existing spermatophore with his ventral body, he shifts his body laterally as he moves forward so the spermatophore slides posterior in contact with his ventral midline. If the spermatophore contacts his vent, he stops, shuffles his vent upon it and lowers his vent upon it. If the spermatophore then enters his cloaca, he either moves away from it without depositing a spermatophore, or he deposits a new spermatophore base with sperm mass upon the pre-existing structure. Such secondary spermatophores cover the sperm mass of the original spermatophore, if sperm is still present, and render it inaccessible to the female.

Following spermatophore deposition the male either moves forward shuffling his vent against the substrate and then deposits another spermatophore (particularly if he should encounter a pre-existing spermatophore), or he moves forward, turning repeatedly, until he contacts the female. He then resumes nudging, head-swinging and lifting.

Females were observed to locate and squat upon several spermatophores during a courtship. The female orients to spermatophores which contact her ventral body just as the male does. She lifts and shifts her body over and towards the spermatophore as she moves forward. The spermatophore then slides posteriorly in contact with her ventral midline. If the spermatophore contacts her vent, she stops and lowers her vent, squatting upon the spermatophore. Nearly the entire spermatophore is inserted into her cloaca. The female remains stationary and assumes the same posture employed by the male when depositing spermatophores. She adpresses her hindlimbs against her tail base, arches her midbody upward so that only the pectoral region, sacrum and vent contact the substrate. The forelimbs are outstretched, and she lifts her tail upward to as much as 90° with the substrate. She then lowers her tail and moves forward off of the spermatophore. She may remove the entire sperm mass, only a portion of it, or the sperm mass may appear unchanged after her departure.

Sometimes, however, the female does not orient to and squat upon spermatophores which contact her ventral body. Even when orienting to or squatting upon a spermatophore, she may be dislodged from it by the male's nudgings or other activities.

The male activity of spermatophore deposition and the female activity of spermatophore location are not coordinated in any way. Either activity may occur with the pair separated by several body lengths, and either activity can occur while the other animal performs any activity. Garton (1972) observed courtship in Ambystoma texanum from Illinois. My observations agree very well with those of Garton. We both find that A. texanum males do not clasp the female and that females usually locate spermatophores independent of the male's activities.

Garton (1972) supplies the following additions to my observations. Single males courting with a female deposited a minimum of 23 spermatophores in one case and 33 spermatophores in another. When three males were housed together in the absence of a female no courtship activities occurred. When a female was introduced, courtship began within 10 minutes. The males nudged each other as well as the female and deposited 123 spermatophores. Garton found three concentrations of A. texanum spermatophores in the field. These concentrations contained 72, 78 and over 100 spermatophores each. Each concentration certainly represents the efforts of more than one male. Garton concludes that Ambystoma texanum form courtship aggregations just as Ambystoma maculatum does. I agree that both the elements and temporal patterning of courtship are very similar in these two species. Someone should attempt to see Ambystoma texanum courting in the field.

Wyman (1971) has recently provided an account of courtship behavior in *Ambystoma texanum*. I find two major discrepancies between my observations and Wyman's description. (1) Wyman notes that the male clasps the female with his forelimbs just anterior to the female's forelimbs while astride her dorsum. I never observed behavior of this kind. I have re-examined my movies of courtship behavior in *A. texanum* and still fail to see any suggestion of dorsal clasping of the female. (2) Wyman found that the female located spermatophores while following behind the mole immediately after spermatophore deposition. I found that female's usually locate spermatophores by continually turning and moving about in the vicinity of the male, and only infrequently does the female locate a spermatophore by following behind the male. Wyman injected animals with chorionic gonadotropin or *Rana* pituitaries in order to induce courtship behavior. Perhaps this hormonal supplement is responsible for the differences in our observations. I did not inject animals with hormones and neither did Garton. Wyman's animals were from McLean Co., Illinois. Since Garton's observations on animals from Jackson Co., Illinois and my observations on animals from Washtenaw Co., Michigan depart from Wyman's descriptions on the same points, I doubt that the discrepancies are due to geographic variation in courtship behavior.

Figure 29. Courtship activities in *Ambystoma texanum*.

Fig. A. A male (right) presses his snout downward on the dorsum of the female's back as he moves anterior along the female.

Fig. B. A male (left) turns his head towards the female and lifts under her chin.

Fig. C. The male moves posterior along the length of the female while nudging her with his snout.

Fig. D. The male turns towards the female as he crawls under her tail.

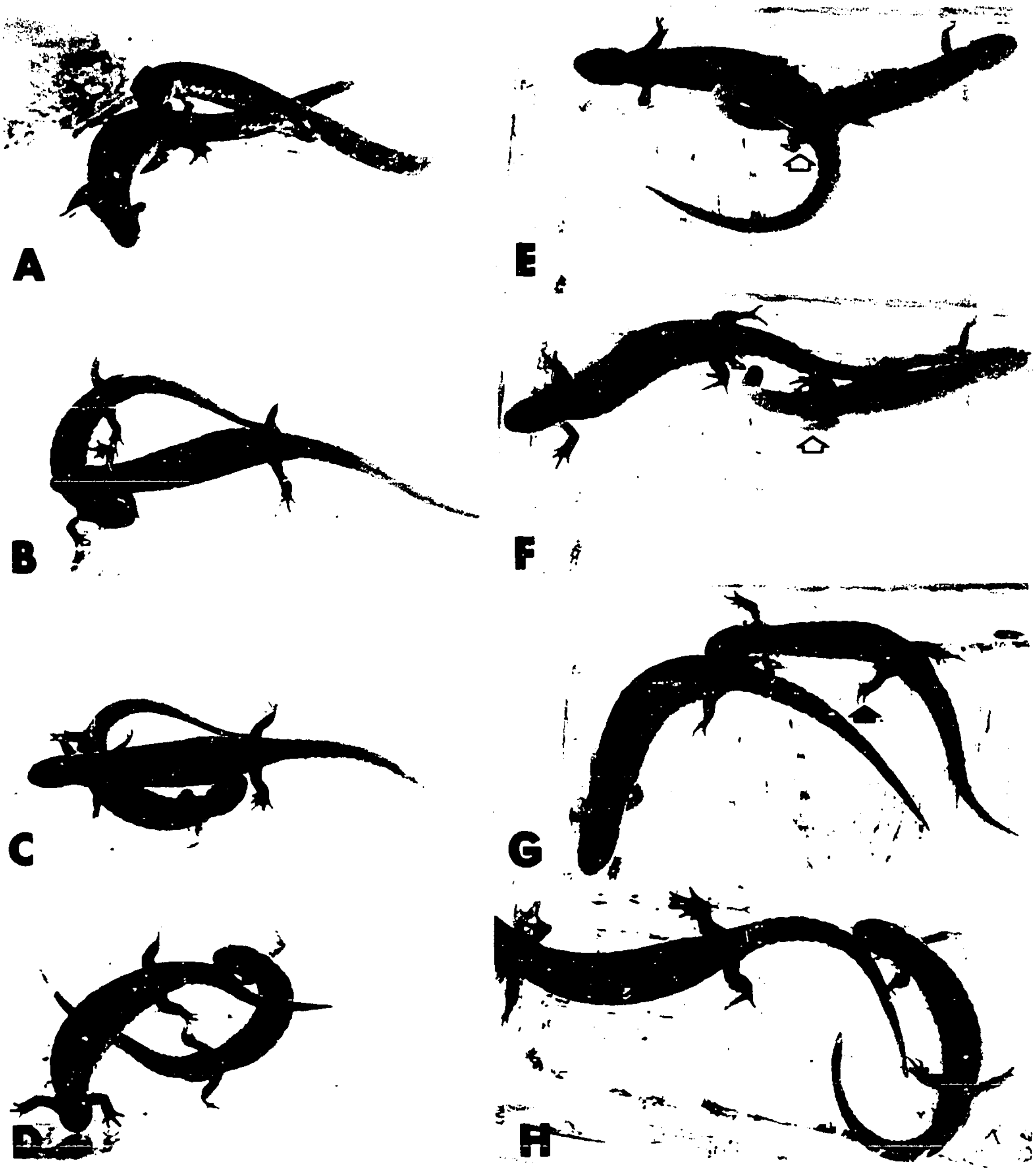
Fig. E. A male in the process of spermatophore deposition as the female crawls over the dorsum of his sacrum.

Fig. F. The male continues to deposit a spermatophore as the female moves away from him. Note that the male's hindlimbs are adpressed against his tail base and that his tail is arched upward with the distal tail perpendicular to the substrate.

Fig. G. The male has turned and reapproached the female and now moves forward while nudging her with his snout. The spermatophore deposited in Fig. F lies just above the solid arrow head.

Fig. H. A male nudges the female's tail as he moves anterior along her length.

(These animals are from Washtenaw Co., Michigan).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Ambystoma annulatum

Spotila and Beumer (1970) found adults migrating into small artificial ponds (100 meters or less in diameter) in Arkansas during or just after rains in September and October. Courtship activities began immediately, and eggs were laid within two days. They placed 34 males and nine females in a tank 104 cm by 38 cm with 2 to 10 cm of water on October 15. The animals were collected earlier the same evening.

Initially only a few animals were engaged in courtship activity, but later 25-30 males were actively courting simultaneously. According to Spotila and Beumer, the male approaches and nudges the female's body and cloaca with his snout. He then turns and swims off a short distance, pauses and deposits a spermatophore. During spermatophore deposition the male grasps the substrate with his hindfeet, pressing his cloaca to the substrate. The tail is bent to one side and raised slightly with slight tail undulation. After 7-10 seconds in this posture the male lifts his tail, raising his cloaca off the spermatophore, and swims away. The male may either return immediately to the female, or he may deposit as many as four spermatophore in succession. One male deposited nine spermatophores in two minutes. Males may deposit spermatophores on top of or beside pre-existing spermatophores. Spermatophores may even by deposited on the bodies and tail of other salamanders.

As more and more male's initiated courtship activities, they seemed to nudge both males and females indiscriminately. Initially males apparently restricted their activities to nudging females. The females were not observed to pick up sperm masses from spermatophores and appeared to not actively participate in courtship.

In a breeding pond spermatophores were found concentrated in several small areas, 100 cm^2 or less in each area. There were 54 to 120 sperm caps on four to 30 structures in each of these areas of spermatophore concentration. Presumably aggregations of courting animals also occur in the field.

Ambystoma opacum

Catalog of male actions.

A.) NUDGING The male contacts his snout or lateral snout to the female's lateral body (Fig. 30A, B, E).

B.) HEAD-SWINGING The male swings his head from side to side with his chin or mentum in contact with the female's dorsum. The male may press his head down while performing this action. This action is also performed with the male raising his head with his dorsal head in contact with the female's venter.

C.) LIFTING The male lifts his head with the dorsum of his head, snout or midbody in contact with the female's ventral body. He may simultaneously turn his head sharply to one side towards the female (Fig. 30C, F).

D.) BODY-FLEXING The male rapidly flexes both his head and sacrum laterally in the same direction while simultaneously extending on the forelimb and hindlimb on the opposite side of his body. The head is also lifted upward as the flexing action is performed (Fig. 30G).

E.) VENT-SHUFFLING The male shuffles his vent laterally in contact with the substrate by shifting from side to side on his hindlimbs.

F.) STATIONARY WITH HINDLIMBS OUTSTRETCHED The male pauses with his vent in contact with the substrate and with the hindlimbs stretched out to the side perpendicular to his body. The tail is level and is undulated laterally. The entire ventral surface of the body is in contact with the substrate.

G.) SPERMATOPHORE DEPOSITION When spermatophore deposition occurs it follows the action just described (F). The male continues in the same posture with lateral undulation of his level tail. The tail undulations then cease, and the male lifts his sacrum upward and with a slight upward arch of the tail moves forward off of the spermatophore.

Temporal relations (Ambystoma opacum)

Upon contacting or, recontacting a female, the male moves anteriad or posteriad along the length of the female. While moving along beside her, the male continuously nudges the female and performs head-swinging upon her dorsum. When the male reaches the head, or the tail, of the female, he usually turns his head towards the female and under her head, or tail, and performs lifting. After first lifting, the male may perform body-flexing one to several times in rapid succession with the female's chin or tail resting on the dorsum of his midbody. If the female remains stationary, the male then moves posteriad along the female (if lifting, with or without body-flexing, occurred under the female's chin) or anteriad (if lifting, with or without body-flexing, occurred under the female's tail) while resuming nudging or head swinging. Thus when the female remains stationary, the male tends to circle around and around the female in the same direction (Fig. 30 A, B, C, D, E, F).

When the female moves away from the male, he tends to follow along beside or behind her while nudging and head-swinging. When the female has broken contact with the male, and if she moves forward in front of him, he may approach her directly and rapidly from a distance of approximately 20 cm or less. He then resumes nudging, head-swinging, lifting and body-flexing. When the male is not in contact with the female, or not actively approaching her, he moves forward repeatedly, turning occasionally, until either the female moves across his path or he stumbles into her.

Both the male and the female have a marked tendency to arch the tail upward when the proximal dorsal tail is contacted by the other animal.

After repeatedly performing the actions of nudging, head-swinging, lifting and body-flexing, and if the female remains stationary, the male may suddenly move a few centimeters away from her, shuffle his vent against the substrate and begin tail undulations. He may then either cease tail undulations and reapproach the female without depositing a spermatophore, or he may deposit a spermatophore and then reapproach the female.

Spermatophore depositions are of two types. The male may either deposit a spermatophore de novo, directly on the substrate, or he may deposit a spermatophore on top of a pre-existing one (secondary spermatophore deposition). In the latter case the new spermatophore base completely sheaths the sperm mass of the original spermatophore as well as the apical portion of the spermatophore base. Secondary spermatophore depositions occur when the male contacts a pre-existing spermatophore with his ventral midbody. The male crawls forward over the spermatophore with his ventral midbody in contact with it. If his vent contacts the spermatophore, he shuffles his vent momentarily on top of it and then squats on the spermatophore, inserting it into his cloaca. He then assumes the same posture and performs the same actions as in a de novo spermatophore deposition. Finally he arches his tail slightly as he moves forward off of the spermatophore, leaving a new spermatophore base and sperm mass, and rendering the sperm mass of the original spermatophore, if still present, inaccessible to the female. My observations are insufficient to tell whether these two types of spermatophore depositions differ in behavioral context.

The female locates spermatophores just as the male does before he deposits a secondary spermatophore. When a spermatophore contacts the female's ventral midbody, she shifts her body laterally as she moves forward so that the spermatophore slides posteriorly in contact with her ventral midline. If the spermatophore then contacts her vent, she stops and lowers her vent upon it, inserting very nearly the entire spermatophore into her cloaca. She then pauses motionless on the spermatophore with her tail level and not undulating and with her hindlimbs held out to the side of her body but not stretched out to the side. When, after several seconds, she moves forward off of the spermatophore, she may, or may not, arch her proximal tail upward. The male does not orient to every spermatophore which contacts his venter, and similarly the female may move over spermatophores without squatting upon them.

During a courtship a female will squat upon several spermatophores. For example, in one courtship the male deposited three spermatophores, one of which was a secondary spermatophore, or a total of two functional spermatophores before the female succeeded in locating a spermatophore. The female then located and squatted on the same double spermatophore 10 times as the male continued to interact with her without depositing additional spermatophores. This is perhaps an exceptional record for successful location of single spermatophore structure. The double spermatophore lay along the front pane of the tank, and so it lay directly in the female's path whenever she moved along parallel to the front pane.

The male activity of spermatophore deposition and the female activity of spermatophore location are in many ways independent. While the male tends to deposit spermatophores in close proximity to the female, he may depsoit a spermatophore as the female departs from him. The female may locate and squat upon a spermatophore when she is several centimeters away from the male. And she may locate spermatophores as the male nudges her and performs head swinging, lifting or body flexing.

Ambystoma opacum is unusual among species of the genus Ambystoma in that courtship occurs in the basins of temporary ponds before they have filled with water, rather than under-water. The female lays her eggs in a small depression on the margin of the pond and remains with them until they are inundated with water as the pond is filled by fall rains.

Noble and Brady (1933) observed courtship in A. opacum from several localities both in the field and in the laboratory. They observed the male actions which I have termed nudging, head swinging, lifting and body flexing as well as the processes of spermatophore deposition and sperm recovery by the female. While my observations are essentially in agreement with theirs, I disagree with two points of emphasis. Noble and Brady describe a courtship "waltz" in which the male and female simulteneously nudge each other's cloacae while moving in a circular path. They suggest that such encounters are frequent and commonly last for several minutes. In my observations this type of interaction was quite infrequent and of very short duration (several seconds) when it did occur. I think it can be best viewed as a consequence of a tendency in both the male and the female to turn in the direction of a lateral contact. If the animals happen to face in opposite directions while contacting each other's bodies laterally, this will result in both animals moving in a circular path. Secondly, Noble and Brady note that on six of the eight occasions in which females located spermatophores, the female followed directly behind the male after spermatophore deposition and located the spermatophore just deposited. In my observations females more commonly encountered spermatophores by moving continually about the region in which they were deposited, rather than by following behind the male. Both of these differences in emphasis may be the result of differences between females in tendency to follow the male and to respond to lateral body contact. In other species of Ambystoma (eg. A. tigrinum) some females consistently follow the male and others do not. Perhaps my sample of females did not include females with a tendency to follow the male during and after spermatophore deposition.

Figure 30. Courtship activities in *Ambystoma opacum*

(Figures A,B,C,D,E, and F are a sequence of photographs of one courting pair (elapsed time about 30 seconds), and Fig. G and H show another courting pair).

Fig. A. A male approaching a female and contacting her tail with his snout.

Fig. B. The male moves along the length of the female while nudging her with his snout. A previously deposited spermatophore can be seen on the far left.

Fig. C. The male turns his head towards the female and lifts his head under her chin as he crawls forward.

Fig. D. The male now moves posteriorly along the length of the female and continues to nudge her with his snout.

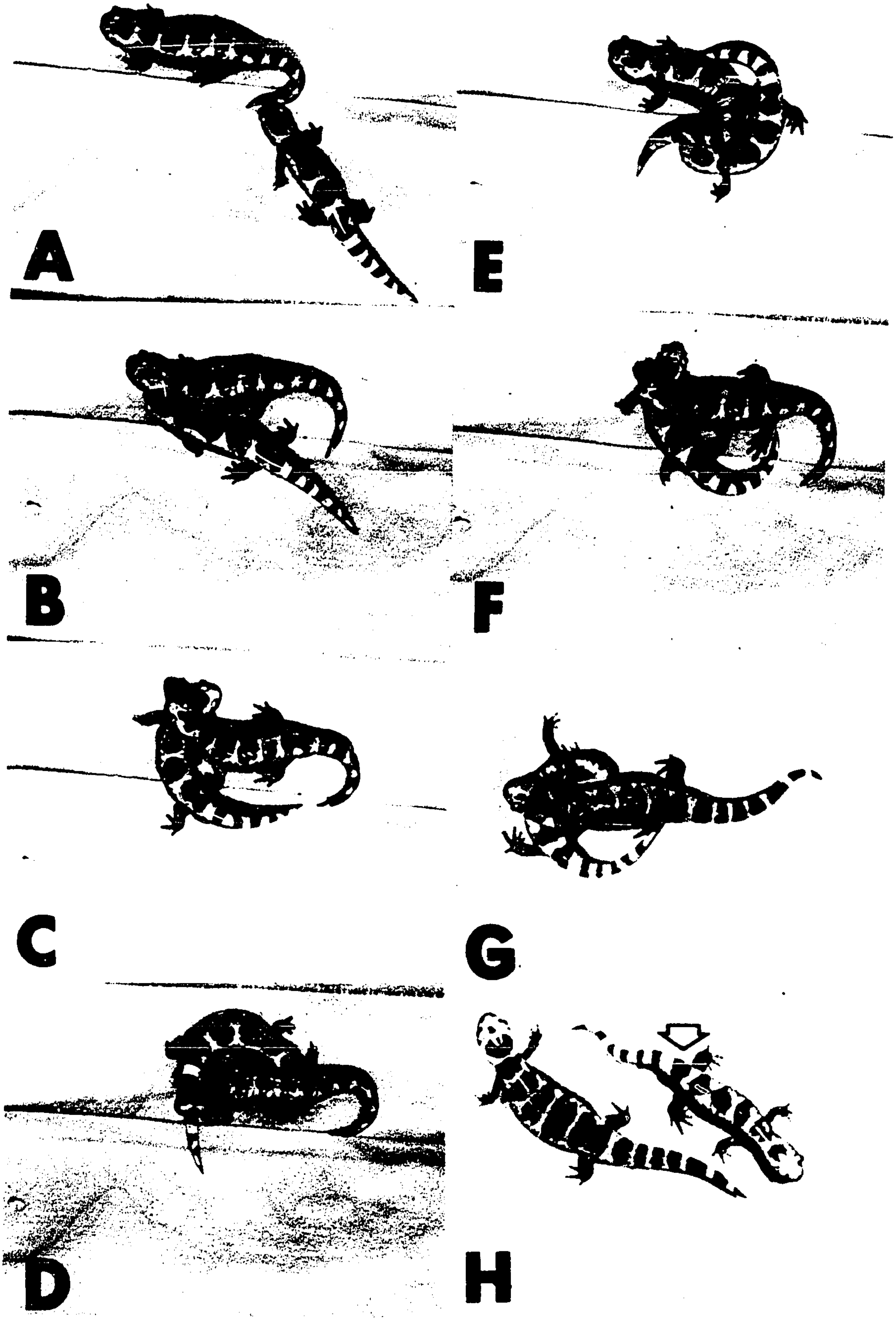
Fig. E. The male turns and moves anterior along the opposite side of the female after reaching her tail.

Fig. F. The male has again reached the female's head and now begins to turn and lift under her chin.

Fig. G. A male performing body-flexing under a female's chin.

Fig. H. The male (right) has moved a short distance away from the female and is now in the process of depositing a spermatophore. His tail is undulating laterally. The open arrow indicates the site of the future spermatophore.

(These animals are from Alabama).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Ambystoma mexicanum

Catalog of male actions.

A.) NUDGING The male contacts his snout or lateral snout to the female's lateral body.

B.) HEAD-SWINGING The male swings his head laterally from side to side with his chin in contact with the female's dorsal body.

C.) HEAD-SLIDING While moving forward the male slides his chin in contact with the female's dorsum.

D.) LIFTING The male lifts his head with his snout or dorsal head in contact with the female's venter. The male may simultaneously turn his head to the side towards the female.

E.) SHOVING The male swims vigorously while shoving his snout against the female's lateral or ventral midbody. The female is thus pushed rapidly through the water (Fig. 31A, B).

The following actions are performed with the male facing away from the female.

F.) STATIONARY WITH TAIL TAPPING While stationary and with the tail directed straight backward, the male repeatedly raises and lowers his tail, tapping the ventral surface lightly on the female's dorsum or the substrate (Fig. 31C, 32B,C and D, 33H, 34D). On each upward stroke the tail is raised 45° to 90°. The tail is also slowly undulated laterally while being raised and lowered.

G.) BACKING UP The male backs up a few centimeters with the tail level, or nearly so, and directed straight backward.

H.) MOVING FORWARD The male moves forward with the tail directed backwards while repeatedly raising and lowering the tail with slight lateral tail undulations (Fig. 32A, 33E, G).

I.) STATIONARY WITH HINDLIMBS ADPRESSED While stationary, the male adpresses his hindlimbs against his lateral tail base, arches the midbody upward slightly, raises the tail 60° to 90° and undulates the tail rapidly in this position (Fig. 33F).

J.) SPERMATOPHORE DEPOSITION When spermatophore deposition occurs it follows the preceding action (I) with the male continuing in the same posture and with the same actions. The forelimbs are outstretched and the forefeet are raised slightly from the substrate. Spermatophore deposition terminates with the male ceasing tail undulations and raising the tail upward as he moves forward off of the spermatophore (Fig. 33G).

Temporal relations (Ambystoma mexicanum)

When a sexually active male contacts a female, he moves rapidly along her length contacting her with his head in a variety of ways. As he moves forward the male performs nudging, head-swinging, head-sliding, lifting and periodically shoving.

The male moves either anteriad or posteriad along the length of the female and turns upon reaching either end of the female and continues along her opposite side. Upon reaching the female's head, the male may lift his head under the female's chin. In form of execution lifting grades into the action of shoving. The male may turn his head under the female's chin and lift his head upward (lifting) as he crawls beneath her chin; the male may lift his head forcefully under the female's body, lifting her whole body off the substrate while the male remains stationary or moves forward slowly (Fig. 34B); or the male may swim rapidly forward while lifting the female's whole body off the substrate thus shoving her rapidly through the water (shoving) (Fig. 31A). The actions of lifting and shoving simply represent two ends of a continuum, with shoving representing the end of the continuum with the most forceful upward lifting of the female and the fastest forward progress by the male. The male may swing his head from side to side with the dorsum of his head in contact with the female's venter as he performs lifting or shoving.

The female may actively and persistently turn towards and contact the male with her head as he contacts her. Such active females may perform nudging, head-sliding, head-swinging and lifting just as the male does. Alternatively, the female may simply remain motionless as the male contacts her, or the female may repeatedly move away from the male when he contacts her.

If the female does move away from the male as he contacts her with his head, the male rapidly reapproaches her and reinitiates nudging, head-swinging, head-sliding, lifting and shoving.

Such bouts of head contact are terminated abruptly by the male moving away from the female and pausing with his vent less than one tail length from the female (Fig. 34D). The male then immediately initiates tail tapping. If on each downward stroke, the male's tail tails to contact the female's body, the male may back up and resume tail-tapping. If the male's tail still fails to contact the female, or if she does not nudge his tail base or cloaca, the male turns and reapproaches the female and reinitiates head contact.

If, however, the female actively nudges the male's tail base or cloaca as he pauses facing away from her performing tail-tapping, the male moves forward (Fig. 32A, 33E). He continues forward so long as the female nudges his tail base or cloaca. Whenever such nudging contact ceases, the male stops and performs tail-tapping. He may also stop and back up thus contacting his cloaca to the female's snout, or by shifting laterally on his hindlimbs, he may lightly rub his cloacal papillae across the female's snout or the dorsum of her head (Fig. 32D).

Thus the male moves forward in fits and starts, subject to the contingencies above, and with the female moving forward intermittently behind him while nudging his tail base and cloaca. Should the female depart from the male, he pauses and performs tail-tapping and may back up slightly. He then reapproaches the female and frequently reinitiates head contact by shoving the female.

If the female continues to nudge the male's cloaca or tail as he moves away from her, both animals move forward 10 cm to half a meter and the male stops and deposits a spermatophore (Fig. 33F). He first stops and undulates his tail rapidly while holding his tail at a 60° to 90° angle.

After spermatophore deposition, the male moves forward slightly on a straight course (Fig 33G) and pauses and resumes tail-tapping if the female fails to move forward and nudge his tail base or cloaca (Fig.33H). Continued forward progress by the male then follows the same contingencies as before spermatophore deposition. If the female continues to move forward behind him nudging his tail base or cloaca, the male continues forward and may deposit additional spermatophores in front of the female while continuously facing away from her.

As the female follows behind a male, the spermatophores he deposits lie directly in her forward path. If a spermatophore contacts her venter as she moves forward behind the male, (see Fig. 32A and Fig. 34F), she shifts her body to and fro laterally (Fig. 34G) as she moves forward so that the spermatophore slides posteriorly in contact with her ventral midline (Fig. 32B). If the spermatophore contacts her vent, she shuffles her vent laterally over the top of it and then squats upon it, lowering her vent to the substrate and inserting the whole spermatophore into her cloaca (Fig. 32C). She then adpresses her hindlimbs backward against her tail base (Fig. 34H) just as the male does while depositing a spermatophore, but she keeps her tail level and may undulate her tail base slightly while squatting on the spermatophore. After pausing for several seconds on the spermatophore, she moves forward off of it, lifting her tail slightly. She may remove the entire sperm mass from the apex of the spermatophore (see spermatophore in Fig. 33G and H), but usually only a portion is removed and sometimes the sperm mass appears just as massive as before located by the female. The female may locate and squat upon several spermatophores during a courtship.

The female may fail to locate the spermatophore just deposited by the male, and she may locate spermatophores deposited much earlier by the male.

If the male contacts a spermatophore with his venter as he moves forward facing away from the female, he may orient to it and squat upon it, just as the female does, and deposit a secondary spermatophore. The bases of such secondary spermatophores completely sheath the original spermatophore and render the original sperm mass, if still present, inaccessible to the female.

Gasco (1881) provides a lively description of courtship behavior in captive animals. Gasco observed the male behaviors which I have called shoving, nudging and head sliding. He observed males depositing spermatophores on top of pre-existing spermatophores as well as on the substrate. He notes that a female which had located a multiple spermatophore structure with her vent grasped the spermatophore structure laterally with her hindlimbs. Several authors have concluded from Gasco's description that the female actively stuffs the spermatophore into her cloaca with her hindlimbs. I found that the female simply adpresses her hindlimbs against her tail base or the base of the spermatophore. She does not actively push the spermatophore into her cloaca with her hindlimbs. The female inserts the spermatophore into her cloaca by lowering her sacrum while shuffling her vent laterally over the spermatophore.

Figure 31. Courtship activities in *Ambystoma mexicanum*

Fig. A. The male (below) is shoving a female rapidly through the water while lifting her upward (0 sec).

Fig. B. The male has now stopped shoving the female. He now moves his head rapidly towards the female's head, and over her head and then moves away from the female along the path indicated with the dotted line (1.8 sec to 3.9 sec).

Fig. C. The male then pauses in front of the female and performs tail-tapping with his tail raised high. The male's cloaca papillae lie just in front of the female's snout, and she is beginning to move forward towards the male (8.0 sec). Two spermatophores, previously deposited by the male, lie in contact with the female's lateral body as she moves forward.

(These figures are taken from a 16mm. movie of one continuous sequence of courtship activities. Total elapsed time from Fig. A to C is 8.0 seconds).

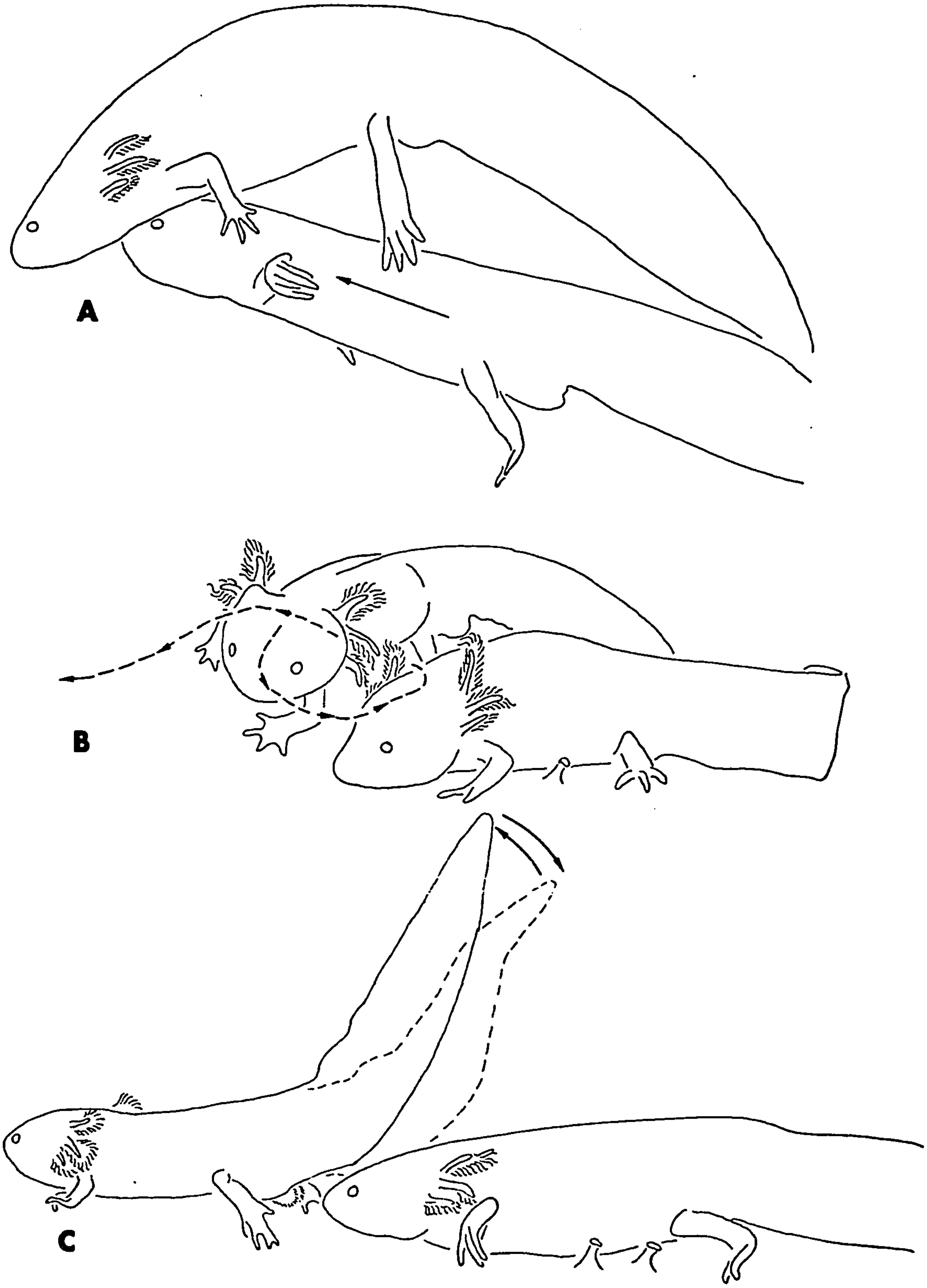
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Figure 32. Courtship activities in Ambystoma mexicanum; location of a spermatophore by a female.

Fig. A. A spermatophore lies in contact with the female's forelimb as she follows behind the male and nudges his tail base (o sec).

Fig. B. The female shifts her body towards and over the spermatophore as it contacts her lateral body and continues forward (4.3 sec).

Fig. C. The spermatophore has contacted the female's vent and she has stopped and lowered her vent upon it, inserting the spermatophore into her cloaca. The male has paused in front of her and performs tail-tapping (9.7 sec).

Fig. D. The female continues to remain stationary with the spermatophore inserted into her cloaca. The male has backed up slightly and is now rubbing his cloacal papillae from side to side over the female's snout. The female has turned her snout towards the male's cloaca (13.4 sec).

(Sequence continued in Figure 33).

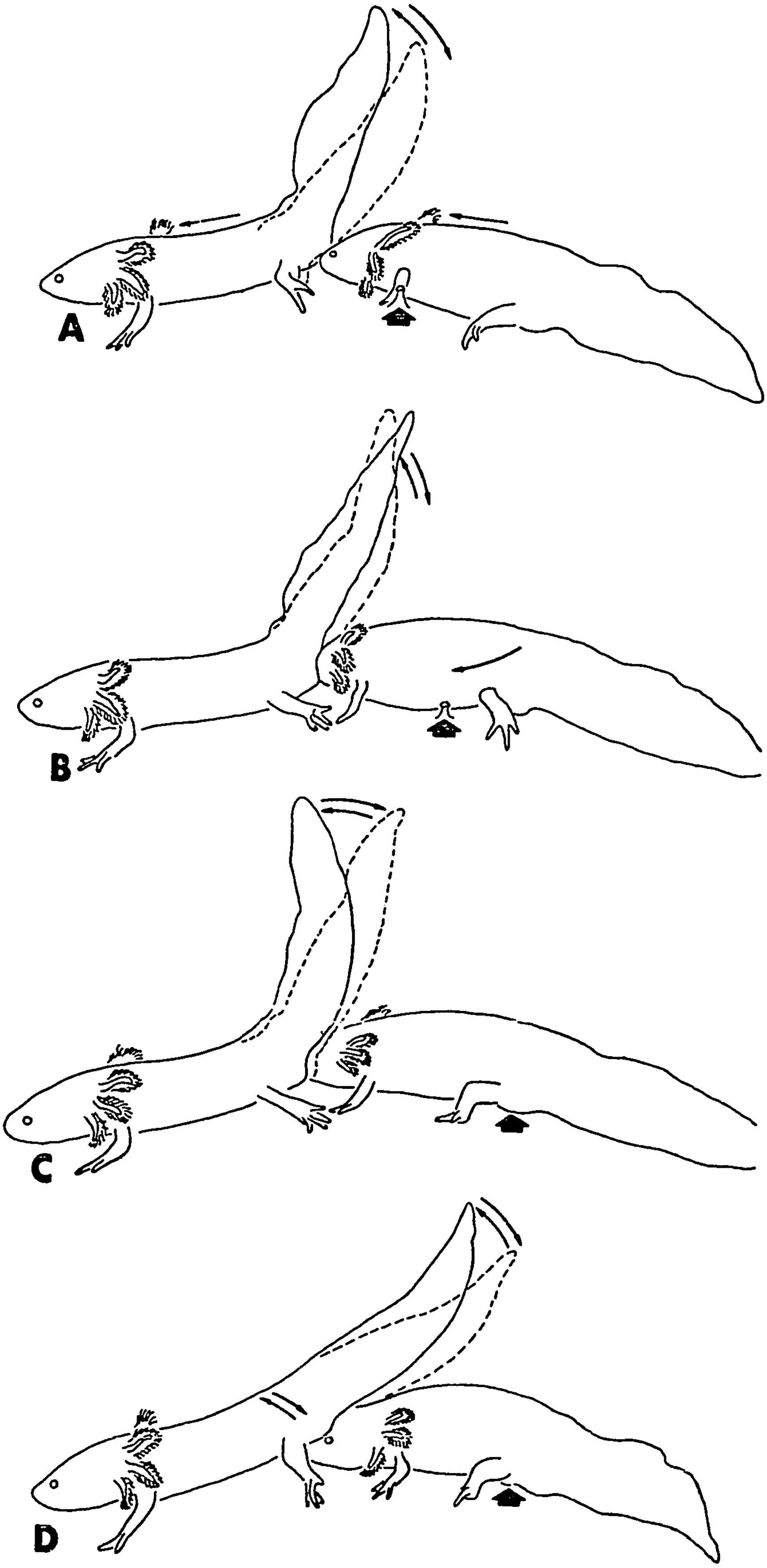
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Figure 33. Courtship activities in *Ambystoma mexicanum*; spermatophore deposition (continued from Figure 32).

Fig. E. The female has now moved forward off of the spermatophore and the male and female move forward as the female nudges the male's cloaca with her snout (31.6 sec).

Fig. F. The male has now stopped and is in the process of depositing a spermatophore. His hindlimbs are adpressed against his tail base, and his tail is undulating rapidly. The female is stationary with her snout in contact with his lateral tail (40.0 sec).

Fig. G. The male is now moving forward off of the spermatophore which is visible just behind his cloaca (above the solid arrow). He performs tail-tapping as he moves forward. The female has departed from the male (45.5 sec).

Fig. H. The female fails to contact the male's anterior tail or cloaca. The male stops just in front of the spermatophore and performs tail-tapping (46.5 sec).

(This, and the preceding figure, are taken from a 16mm. movie of one continuous sequence. Total elapsed time is 46.5 seconds).

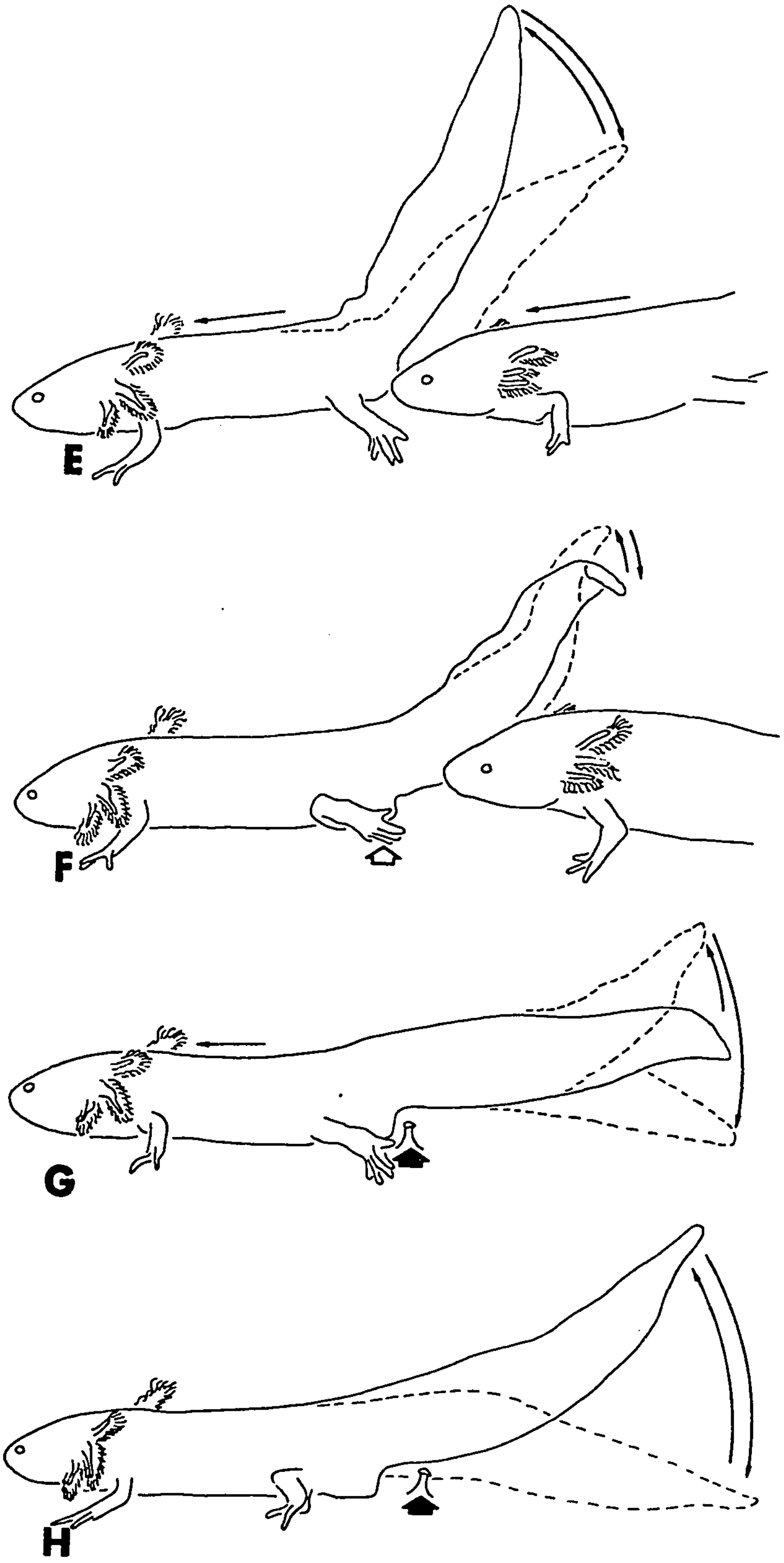
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Figure 34. Courtship activities in *Ambystoma mexicanum* (dorsal views).

Fig. A. A male (above) is approaching a female and nudging her snout as he moves forward.

Fig. B. A male (below) performing shoving and thereby lifts the female up into the water.

Fig. C. A male turns to move a short distance away from the female (right) after contacting her with his snout.

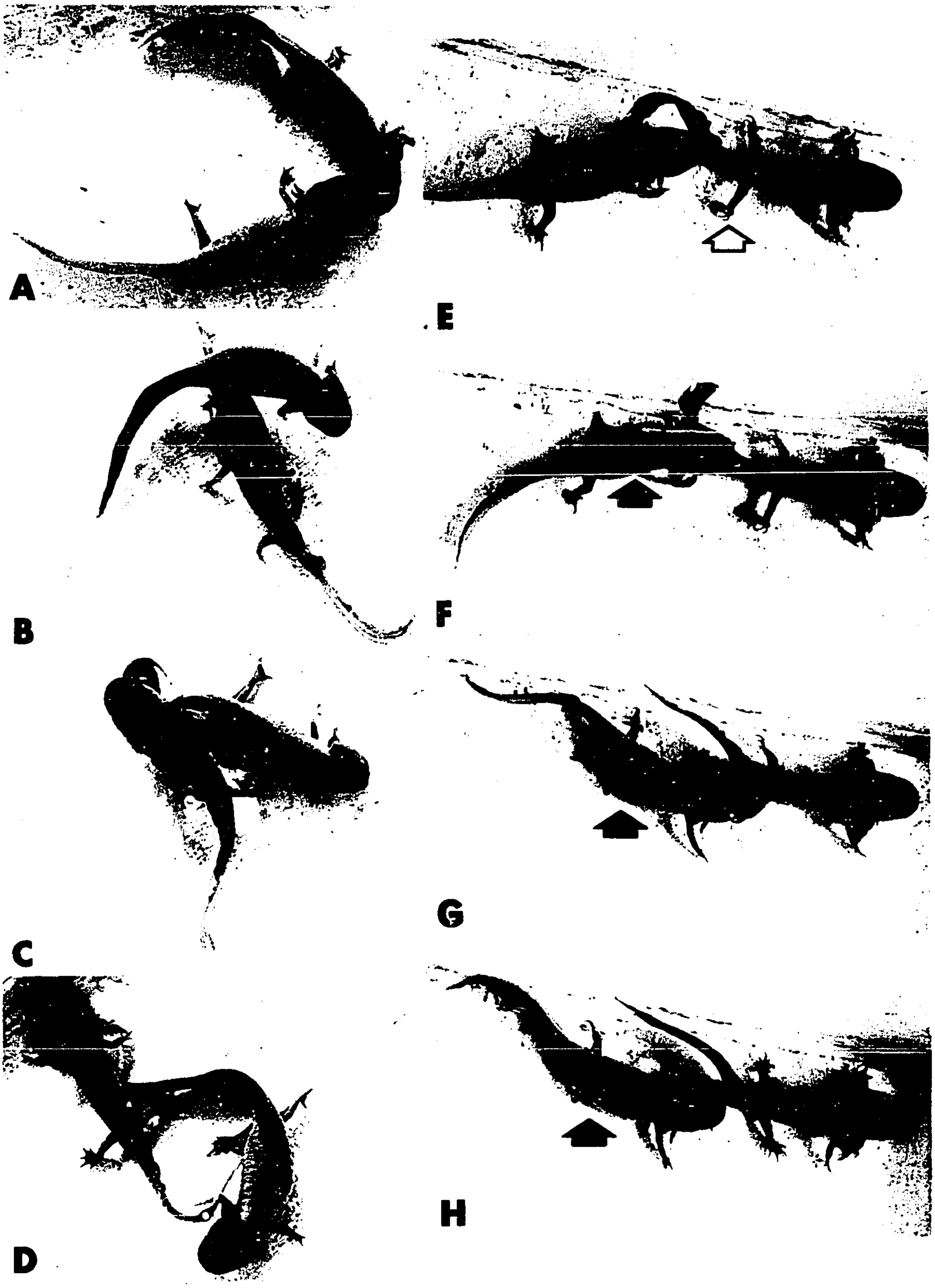
Fig. D. A male pauses after moving away from a female and performs tail-tapping. The female is beginning to turn and move towards the male.

Fig. E. A male (right) in the process of depositing a spermatophore as the female nudges his ventral tail base with her snout. The open arrow indicates the site of the spermatophore he is depositing.

Fig. F. The female is moving forward behind the male, and the spermatophore now lies in contact with her ventral body.

Fig. G. The female has shifted her posterior body to one side and stops with the spermatophore in contact with her vent.

Fig. H. The female adpresses her hindlimbs with the spermatophore inserted into her cloaca.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Ambystoma dumerilii

Brandon (1970) was able to observe courtship behavior in two pairs of captive animals. At 11.50 am on September 14, Brandon first noticed that a pair was courting, 50 minutes after the pair was placed together. The male was moving forward with his tail raised 30° to 40° and directed posterior and undulating from side to side. His cloaca was swollen and the posterior margins appeared to be everted. The female was moving closely behind him with her snout rubbing from side to side on the underside of his tail four centimeters posterior to his cloaca. The male stopped occasionally as the pair moved forward. Sometimes he backed up slightly, and occasionally the female's snout contacted his posterior cloaca. Periodically the male stopped with the female directly behind him and deposited a spermatophore. During spermatophore deposition the male's body was rigid and straight and the hindlimbs were extended with the plantar surfaces facing posteriad. The male moved off of the spermatophore, and the female moved forward behind him. The female moved forward over the spermatophore and appeared to locate it tactilly. When the spermatophore contacted her vent, she swayed on her hindlimbs and settled upon it. The pair then continued forward as before.

Whenever the female departed from the male, rather than moving forward behind him in contact with his tail, the male turned and approached her. He then shoved her sideways through the water by swimming with his snout against her side. The male then stopped swimming, nudged the female's body briefly with his snout, and stopped with his cloaca directly in front of her snout. Both animals then moved forward as described above.

In this fashion, periods of spermatophore deposition and sperm transfer alternated with the shorter periods with the male actively shoving the female through the water. During the four periods when the male moved forward with the female behind him, the male deposited four (or possibly five) spermatophores, then two, then one and finally one spermatophore. The last eight spermatophores were deposited in 24 minutes with intervals as short as one minute between spermatophore depositions. In all, nine spermatophores were deposited, and the female settled on spermatophores at least five times. Finally 38 minutes after the observations began, the male and female remained separated from each other and no longer approached each other.

Initial courtship interactions were observed in another pair on October 27. The male repeatedly moved anteriad along the length of the female, nudging her with his snout, paused with his cloaca directly in front of the female's snout, and then resumed nudging of the female. For 20 minutes the female "either pushed him away or simply moved off to one side". After 45 minutes the female did follow the male briefly, and in this context two spermatophores were deposited. The container was small, and the female did not locate either spermatophore.

In larger tanks five courtships were obtained in five pairs (including the first courtship described above). A mean of 13.0 spermatophores were deposited per courtship (16, 14, 13, 9). Fertile eggs were laid beginning 23-24 hours after courtship.

Ambystoma talpoideum

Shoop (1960) observed courtship in outdoor, aquatic enclosures in Louisiana on the evening of February 7. He found that upon initial contact the male nudges the female and moves along her length. Both animals may nudge each other's cloacae simultaneously and move in a circular path. The male then moves away from the female swinging his pelvis and proximal tail from side to side while undulating his distal tail as the female moves behind him contacting her head to his tail. If the female nudges the male's cloaca after the pair makes forward progress for 1-11 minutes, the male stops and deposits a spermatophore. During spermatophore deposition the male is apparently motionless with the hindlimbs stretched outward and directed posterior. Following spermatophore deposition the male moves forward resuming the lateral swinging of his pelvis and lateral tail. If the female locates the spermatophore with her vent as she moves forward over it, she pauses and assumes the same posture assumed by the male during spermatophore deposition. Rarely the female may follow behind the male as she moves forward towards and over the spermatophore. Shoop suggests that the female terminates her courtship activities once she picks up a single sperm mass.

A female may be courted by many males, and many spermatophores may be deposited before she successfully locates a spermatophore. One female did not locate the first six spermatophores deposited, but did locate the seventh.

Ambystoma laterale

Catalog of male actions

The following actions are performed by the male while facing towards the female but not clasping her.

A.) NUDGING The male contacts his snout or lateral snout to the female's lateral body (Fig. 35A, 38B).

B.) LIFTING The male turns his head towards the female and under her chin and lifts his head under her chin.

The following actions are performed by the male while clasping the female.

C.) CLASPING The male clasps the female, usually while astride her dorsum, by gripping her firmly with his forelimbs just anterior or posterior to the insertion of her forelimbs (Fig. 35C, 36B, C, 38E, I).

D.) HEAD-SWINGING The male presses his chin downward on the surface of the female's head and swings his head back and forth laterally through an arc of 90° to 100° and consequently rubs his chin on the female's head. The male does not open his mouth during head-swinging. Head-swinging may take two forms, single swings and sustained swinging. Single head-swings are associated with clasping just behind the insertion of the female's forelimbs. While maintaining this clasping position, the male drives himself forward with rapid, alternate treadings of the hindlimbs, swings his head once across the female's dorsal head or snout and pauses. Sustained head-swinging is associated with clasping of the female's neck (Fig. 36B, C). The chin is swung back and forth several times across the female's snout, but treading with the hindlimbs does not accompany the rubbing. During sustained rubbing of the female's head, the male's hind-body may be over the dorsum of the female's back or resting off to one side of the female on the substrate (Fig. 35C).

E.) TRAVELING WHILE CLASPING The male releases the female with his forelimbs and turns his head 180° and then reclasps the female's dorsum while facing posterior. As he releases the female, the male's hindlimbs move off of her dorsum. The male then moves posteriad along the dorsum of the female by shuffling forward with his forelimbs, as in climbing a telephone pole (Fig. 38C). The hindlimbs, however, simply drape over the dorsum of the female. They do not clasp, but are moved as in crawling. When the male's snout reaches the middle of the female, he releases with his forelimbs, turns 180°, reclasps the female's dorsum and moves anterior along the female (Fig. 38D). The male pauses when his head again reaches the dorsum of the female's head (Fig. 38E). While moving anterior or posterior along the female, the male's snout is pressed downward slightly, and the male swings his head from side to side.

F.) SWIMMING WHILE CLASPING The male undulates his tail vigorously while making rapid treading movements with his hindlimbs and thereby pushes the pair forward through the water.

G.) DISMOUNT FROM CLASPING The male releases the female with his forelimbs and crawls directly forward over the dorsum of the female's head.

The following actions are performed by the male while facing away from the female.

H.) MOVING FORWARD WITH TAIL RAISED The male moves forward with the tail raised at a 45° angle and directed straight backward. The tail is not undulated.

I.) VENT-SHUFFLING While stationary the male undulates his tail laterally with the tail level. Rapid lateral movements of the sacrum cause the vent to shuffle back and forth against the substrate (Fig. 37A).

J.) SPERMATOPHORE DEPOSITION The hindlimbs are adpressed backward against the male's tail base and are raised slightly upward. The forelimbs are extended upward and forward. Simultaneously the tail is undulated slowly with the tail level and with the vent adpressed to the substrate, (Fig.38B). Spermatophore deposition terminates with the male ceasing tail undulations and raising the tail 20° to 80° as the male moves forward off of the spermatophore.

Temporal relations (Ambystoma laterale)

When a male encounters a female, he briefly moves along beside her while nudging her. If he reaches her head he may perform lifting. Usually these interactions are very brief, and the male moves onto the female's dorsum and clasps her with his forelimbs (Fig. 35B, C). He may move anteriorly, in which case he pauses while clasping the female just anterior or posterior to the insertion of her forelimbs (Fig. 35B, C), or he may move posteriorly (Fig. 38B, C). In this case, as in traveling while clasping, the male releases the female in the vicinity of her tail, turns and moves anterior along her dorsum (Fig. 38D). While clasping,bouts of head-swinging alternate with periods in which the male rests motionless. Periodically the male performs traveling while clasping, and I was unable to discover whether any stimuli from the female elicits this behavior.

Some females swim vigorously when clasped by the male and may dislodge him.

After clasping the female for a few to several minutes, the male suddenly dismounts from the female, moving directly over her head. Dismounting was usually immediately preceded by a sustained bout of head-swinging on the female's snout. The male then moves forward away from the female with his tail raised, and he continues forward so long as the female moves forward and contacts his proximal tail or lateral vent (eg. with her snout). The male pauses and shuffles his vent against the substrate when the female fails to contact his lateral tail (Fig. 37A). After a few to several seconds of intermittent forward progress, subject to these conventions, the male pauses and initiates spermatophore deposition (Fig. 37B). After spermatophore deposition, the male again moves forward with tail raised (Fig. 37C). He continues forward in this posture if the female continues to contact his proximal tail, and pauses and performs vent-shuffling when contact is broken (Fig. 37D). He may then deposit additional spermatophores if the female continues to contact him.

If the male contacts a pre-existing spermatophore with his venter, he may move on top of it and deposit a second spermatophore on top of the first structure. Such secondary spermatophore depositions only occur if the female follows behind the male.

Thus the courtship behavior of the male consists of a series of alternations between clasping the female and dismountings during which spermatophores may or may not be deposited depending on whether the female follows behind him. For example, in Fig. 38F, the female fails to follow the male after he has dismounted from her. The male turns and reapproaches the female (Fig. 38G) and reclasps her (Fig. 38H, I).

The female may locate spermatophores while moving forward behind the male immediately after he deposits them, while the male is clasping her, or while the male nudges her prior to reclasping her, or while the male nudges her prior to reclasping her. If a spermatophore contacts the female's venter in any of these contexts, she moves forward, shifting her body laterally, so that the spermatophore moves towards her midline and passes posteriad towards her vent as she moves forward (Fig. 37C to D). If the spermatophore contacts her vent, she pauses, lowers her vent upon it and inserts the entire spermatophore into her cloaca. While resting on the spermatophore she adpresses her hindlimbs against the base of her tail. Her tail is held level and is not undulated (Fig. 37D). After several seconds she then moves forward off of the spermatophore and may, or may not, remove part or all of the sperm mass.

When moving forward slowly, while the male is or is not clasping her, the female may shift her sacrum back and forth by stepping slowly first to one side and then to the other with her hindlimbs. This behavior probably increases the female's chances of tactilly locating a spermatophore.

My observations are in good agreement with descriptions of Ambystoma laterale courtship provided by Kumpf and Yeaton (1932), Storez (1969) and Uzzell (1969).

Uzzell (1964) concluded that Kumpf and Yeaton (1932) observed courtship behavior in Ambystoma laterale and not A. jeffersonianum. Just as Storez (1969), Uzzell (1964, 1969) and I found, bouts of spermatophore deposition were always preceded by dorsal clasping of the female (Kumpf and Yeaton, 1932). Storez (1969) also observed the actions I have called head swinging, traveling while clasping and swimming while clasping. Storez(1969) suggests that the male dismounts from the female, and then initiates spermatophore deposition, when the female lifts her head during clasping. On many occasions I have seen males dismount from the female when the female made no perceptible head movement.

I agree with Uzzell (1969) that spermatophores are usually deposited by the male as the female follows behind him nudging his cloaca or tail base (see Fig. 37). Uzzell notes that this female response is not a necessary requirement for spermatophore deposition. Again I agree, but the exceptions that I observed further clarify the rule that the female does provide the cue for spermatophore deposition by contacting the male in specific ways. I did observe males depositing spermatophores when the female had not nudged the male's anterior tail or cloaca with her snout, but in these instances contact to the male's tail base or cloaca was nevertheless present just before the male initiated spermatophore deposition. In one instance, for example, the male dismounted over the female's head when her snout abutted against the side of the tank. The male then turned and moved posterior along beside the female. He then initiated spermatophore deposition when the female's hindlimb and then her tail contacted his anterior tail and cloaca. In addition when the male dismounts from the female and she does not contact his anterior tail or cloaca, the male turns and reapproaches her without depositing a spermatophore (as in Fig. 38).

Uzzell (1969) notes that males will clasp available objects with their hindlimbs during spermatophore deposition, and females will clasp available objects with their hindlimbs during sperm retrieval. When objects are not available, as in my observation tanks, these clasping behaviors are not shown.

Storez (1969) found that males would approach a clasping pair and attempt to clasp them. In these instances the clasping male swam away from the intruder with the female. Storez (1969) suggests that this behavior is used by males to transport the female away from intruders and thereby insure that she will be inseminated. I see the selective advantage falling specifically on the male which transports the female away and then inseminates her successfully, rather than upon the female. Experiments should be performed to test Storez's hypothesis. I may note that this transporting behavior is not peculiar to instances in which other males are present, as Storez (1969) suggests. Males courting along with a female also perform this behavior.

Uzzell (1969) found that male A. laterale deposited means of 34.9 spermatophores (range 29-46, n=9) in Cook Co., Illinois and 19.3 spermatophores (range 1-32, n=4) in Livingston Co., Michigan with one to two females; presumably in a single evening. When more than one male is present with a female, the total number of spermatophores deposited by the males is always less than the mean spermatophore deposition total for one male multiplied by the number of males present (Uzzell, 1969). Before we can understand the basis for this depression in spermatophore production, observations must be made of interactions between males, and their individual spermatophore productions, during courtship with a single female.

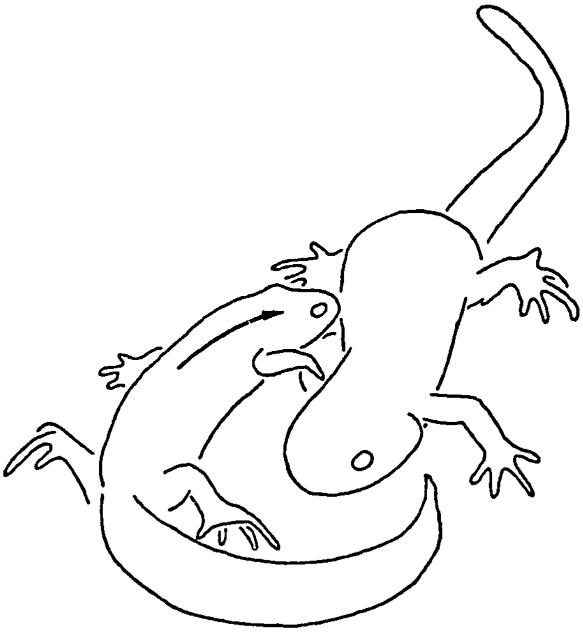
Figure 35. Courtship activities in *Ambystoma laterale*; initiation of dorsal clasping.

Fig. A. The male (left) has approached a female and is nudging her lateral body with his snout.

Fig. B. The male moves his snout onto the dorsum of the female's back and turns his head anterior along her body as he moves forward.

Fig. C. The male has moved anterior along the female's dorsum and is now clasping the female around her neck, just anterior to her forelimbs, with his forelimbs.

The above are based on a 16mm. movie of one continuous sequence. These animals are from the vicinity of Whitmore Lake, Livingston Co., Michigan).



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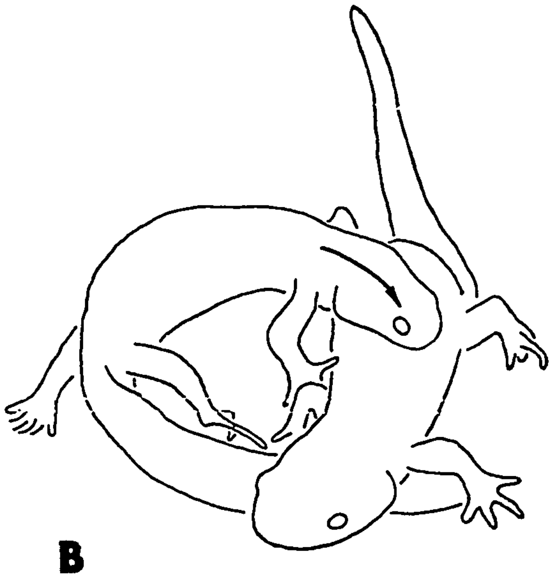

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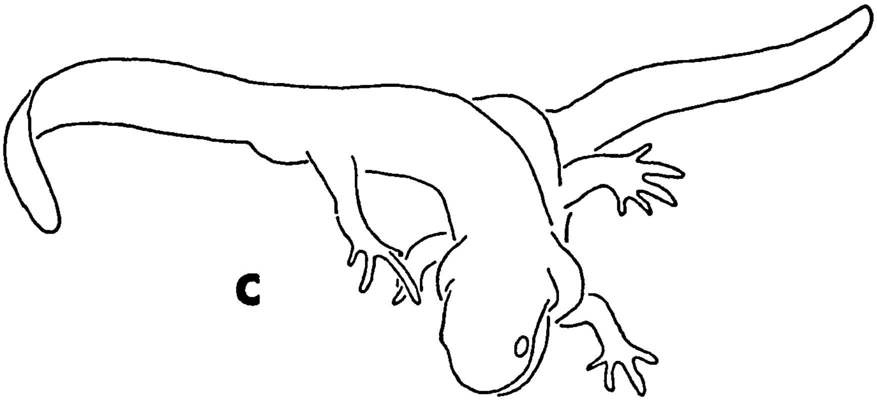

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Figure 36. Courtship activities in Ambystoma laterale; head swinging during dorsal clasping of the female.

Fig. A. The male pauses astride the female's dorsum.

Fig. B. The male clasps the female's neck firmly with his forelimbs and begins head-swinging by swinging his head to the right with his chin in contact with the female's snout.

Fig. C. The male continues head-swinging by swinging his head to the left.

(The above are based on a 16mm. movie of one continuous sequence. These animals are from the vicinity of Whitmore Lake, Livingston Co., Michigan).

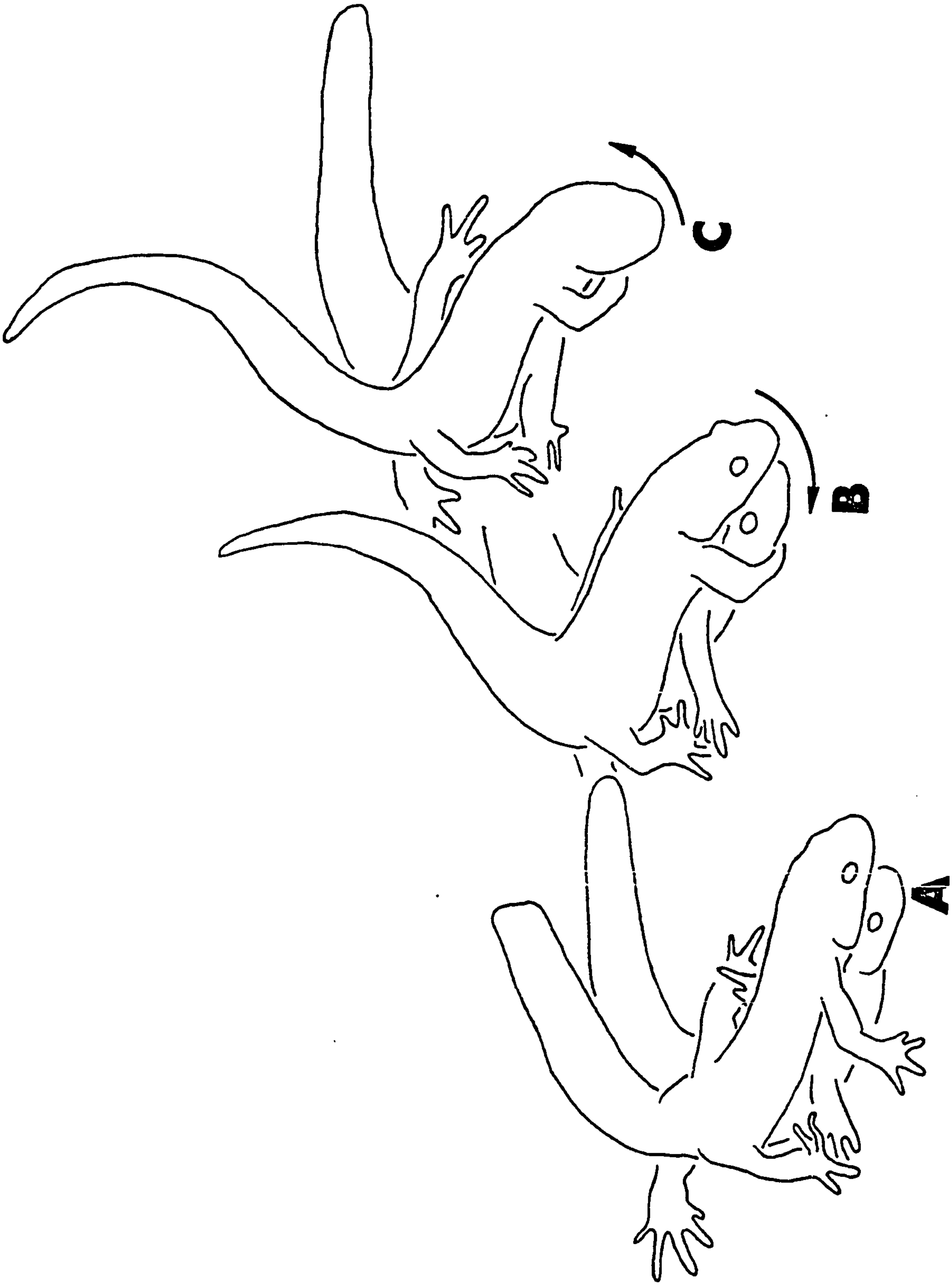
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Figure 37. Courtship activities in Ambystoma laterale; spermatophore deposition by the male and spermatophore location by the female.

Fig. A. The male has dismounted from the female and now pauses in front of her and performs vent-shuffling.

Fig. B. The female has turned towards the male and nudges his lateral cloaca with her snout. The male is in the process of depositing a spermatophore. His tail undulates laterally.

Fig. C. The male is now moving forward away from the spermatophore (visible above the arrow head) as the female moves behind him nudging his hindlimb with her snout.

Fig. D. The female contacted the spermatophore with her ventral body as she moved forward and then lowered her vent on it when the spermatophore contacted her vent. She now pauses with the spermatophore inserted into her cloaca. The male pauses in front of the female and reinitiates vent-shuffling (only his tail is visible).

(Taken from a 16mm. movie of one continuous sequence.
These animals are from the vicinity of Whitmore Lake, Livingston Co., Michigan).

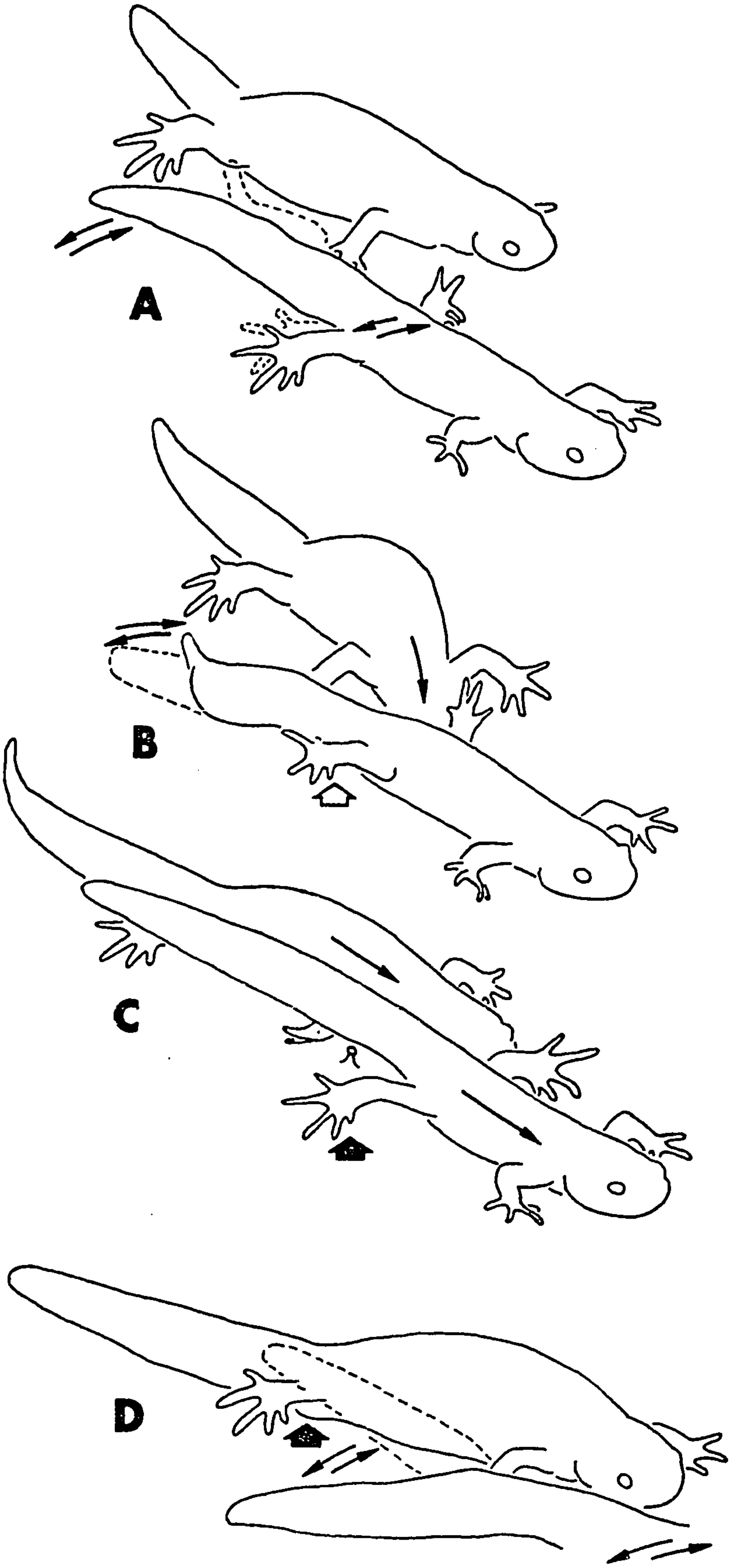
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Figure 38. Courtship activities in <u>Ambystoma laterale</u> (dorsal views). (Figures A through E represent one sequence, and Figures F through I show another sequence).

Fig. A. The male (left) pauses in front of the female and performs vent-shuffling. The female is stationary with a spermatophore inserted into her cloaca, and she fails to contact the male's anterior tail or cloaca.

Fig. B. The male has turned and moved back towards the female, and now nudges her with his snout.

Fig. C. The male has moved onto the dorsum of the female and is moving posterior while astride her (traveling while clasping).

Fig. D. The male is turning and moving anterior along the female's dorsum while gripping her with his forelimbs.

Fig. E. The male has reached the female's head, and now clasps her near her neck and performs hindlimb-treading. The female has now moved forward off of the spermatophore.

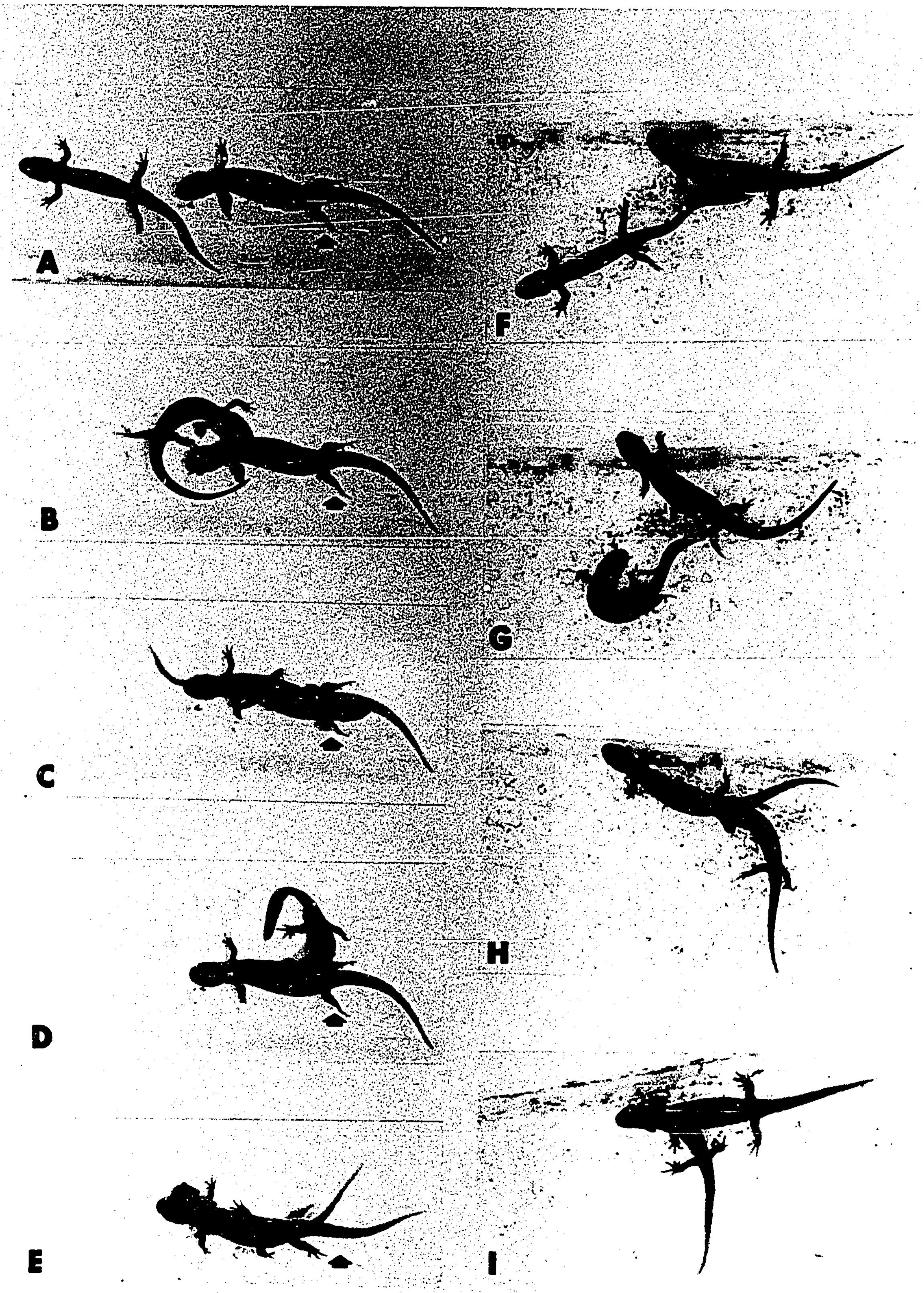
Fig. F. A male performs vent-shuffling as the female (right) fails to contact his anterior tail.

Fig. G. The male is now turning and beginning to move back towards the female.

Fig. H. The male contacts the female's posterior body and now begins to move onto her dorsum.

Fig. I. The male has reached the female's head and now clasps her firmly about the neck with his forelimbs.

(These animals are from the vicinity of Whitmore Lake, Livingston Co., Michigan).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Ambystoma jeffersonianum

Mohr (1930, 1931) observed several aspects of courtship, in the field. He observed males clasping the female with his forelimbs, just behind the female's forelimbs. In this position the male rubs the dorsum and sides of the female's head with his snout. On one occasion a male was observed undulating his tail and posterior body and periodically clutching the substrate with his hindlimbs. A female approached him and nudged his cloaca. The male then deposited a spermatophore. The male moved away from the spermatophore with the female following behind him. She then paused with her cloaca over the spermatophore. The female then again followed directly behind the male, and they moved out of view.

Uzzell (1964) observed courtship in both A. jeffersonianum and A. laterale and detected no differences in courtship behavior between these two species.

Ambystoma macrodactylum

Anderson (1961) provides us with a very fine account of courtship behavior in Ambystoma macrodactylum croceum. After encountering a female, the male moves onto and along the female's dorsum. The male may move onto the female in the vicinity of her pelvis and then move anteriorly towards her head with his chin pressed against her dorsum and with his forelimbs held lightly against her sides. Alternatively, he may move onto the female's dorsum after encountering her head on. He then moves posteriorly along her dorsum, until his chin reaches her tail. He then turns and moves anteriorly towards her head. Once the male's snout reaches the female's snout as he moves anteriorly along her dorsum, the male clasps the female firmly with his forelimbs just behind her forelimbs. While clasping the female in this position, the male's hindlimbs are sprawled out to the sides with the planter surfaces facing posteriorly. In one instance the male repeatedly contacted the female's vent region with his hindlimbs, but usually the hindlimbs are held in the position just described. Almost invariably the female swims rapidly when the male first clasps her with his forelimbs. Once the female rests on the substrate, the male begins swinging his head from side to side, rubbing his chin on the dorsum of the female's head and snout. Initially the male's head stops at the midline of the female's head during lateral head swings. Later the male's head movement changes to a smooth lateral swing without halting at the female's midline. The male's snout and lateral snout, as well as his chin, now tend to contact the female's dorsal head, and the male contacts the female's nares and snout more frequently as he swings his head. The male may relax his forelimb grip as he performs these head movements, if the female is quiescent. The male does not open his mouth while swinging his head laterally. If the female struggles, the male tightens his forelimb grip and resumes the halting lateral swings of his head. Anderson suggests that the gradual change in the form of execution of the head swing of the male is associated with a change towards a more quiescent attitude on the part of the female.

The male then releases the female and slides straight forward over the top of her head. The male then pauses immediately in front of the female and raises his distal tail to 90°. He then begins lateral undulations of his tail tip and moves forward slowly away from the female. The female may then move forward towards the male. If she does, she contacts her snout to the male's tail base, cloaca or the base of his hindlimbs. When the female so contacts the male, he raises his tail even higher. As he moves forward the male undulates his pelvis laterally, rubbing his vent on the substrate while continuing to undulate his tail. The pelvic undulation becomes more vigorous as the male moves forward with the female behind him.

If the female fails to follow the male, the male remounts and clasps the female again as described above. He may then dismount from the female over her head and again move forward in front of her snout.

Finally the male stops and deposits a spermatophore. Presumably the male continues to undulate his raised tail during spermatophore deposition, but Anderson does not explicitly describe the male's behavior during this act. As the male deposits a spermatophore the female may rub her vent on the substrate and undulate her distal tail slowly with her tail raised slightly. After spermatophore deposition, the male moves forward on a straight course, and the female moves forward behind him once again. As she moves forward the female passes over the top of the spermatophore and pauses with her vent over the spermatophore. The female then raises and holds her tail at a 60° angle and pauses over the spermatophore. The male may then deposit another spermatophore in front of the female as she rests in this position. Usually, however, the female departs after one spermatophore deposition, and the male must reclasp her and dismount before depositing additional spermatophores.

The female does not invariably retrieve sperm from a spermatophore. Anderson observed at least eight spermatophore depositions and saw only four retrievals of sperm by females.

One male deposited 15 spermatophores in a five hour period. Three spermatophores were deposited in 15 minutes and two others within 80 seconds.

Ambystoma gracile

Two observers, Knudsen (1960) and Licht (1969), have provided accounts of courtship behavior. Additional observations are much needed for this species both to clarify inconsistencies between these two accounts (eg. in the position assumed by the male during clasping) and to provide detailed descriptions of spermatophore deposition and sperm transfer.

In early February in Washington, Knudsen (1960) observed courtship between a metamorphosed male and a neotenic female in the field and also in a metamophosed pair in the laboratory. He notes that the male may approach the female either laterally or from behind and then slowly straddle her body. The male then suddenly clasps the female behind the forelimbs with his hindlimbs. Some females swim forward and escape from the male, and others remain passive. In the latter case the male swims actively with the female while clasping her and occasionally remains stationary. While clasping the female, the male moves his tail as in swimming. He may also hold the distal tail straight and lash the tail from side to side by bending the tail at its base and consequently rub his cloaca against the female's back. The male may then dismount from the female and press his vent to the substrate. The male may repeatedly and rapidly alternate between clasping and dismounting. The male may also move posteriad along the female's dorsum and then stop and clasp the female's tail with his hindlimbs. In this position the male executes a series of contractions of the hindlimbs, forcing the narrow dorsal edge of the female's tail between his cloacal folds. Knudsen notes that this activity is generally followed by spermatophore deposition on the substrate or other objects. Sperm transfer was not observed.

Licht (1969) observed courtship on March 7 in a pair of animals which had recently been captured in Vancouver, British Columbia. Like Knudsen, Licht found that the male approached the female laterally and then straddled her. But in contrast to Knudsen, Licht found that the male seized the female's body with his forelimbs, rather than hindlimbs, and moved forward to clasp the female just behind her forelimbs with his forelimbs so that his snout was directly over her snout. In this position the male's hindlimbs were either wrapped around the female's hindlimbs, or held firmly against her abdomen, just anterior to her hindlimbs. The male continually moved his hindlimbs in a forward jerking motion which forced the hindlimbs of the female forward. The male also, (perhaps simultaneously), vigorously rubbed his chin from side to side over the female's snout. The male's tail was lashed from side to side, and often his cloaca was rubbed over the dorsum of the female's tail. Both Knudsen and Licht noted that the male's cloaca was distended while clasping the female.

Whenever Licht observed the pair courting during the first two days in captivity, the male was clasping the female as described above. On the third day the male frequently dismounted from the female, and then remounted her a few minutes later after first nudging her flanks or tail with his snout. No spermatophore deposition was observed, but a sperm mass was found in the female's cloaca on the third day.

THE EVOLUTION OF COURTSHIP BEHAVIOR
IN SALAMANDERS

by

Stevan James Arnold

Volume II

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1972

Doctoral Committee:

Associate Professor Arnold G. Kluge, Co-Chairman
Professor Richard D. Alexander, Co-Chairman
Associate Professor Brian A. Hazlett
Professor John A. Jacquez

Family SALAMANDRIDAE

Taricha granulosa

Catalog of male actions.

The following actions are performed by the male while facing towards the female.

A.) NUDGING The male contacts his snout lightly to the female's dorsal or lateral body.

B.) CAPTURE (See section on temporal relations).

The following actions are performed by the male while clasping the female.

C.) FORELIMB-CLASPING During clasping the forelimbs of the male firmly grasp the pectoral region of the female just posterior to the insertion of her forelimbs (Fig. 39). The toes of the male's forefeet overlap on the female's chest.

D.) HINDLIMB-JERKING While clasping the female with the forelimbs, both hindlimbs are simultaneously jerked upward (Fig. 40A). As the upward jerk begins, the toes are flexed inward. During leg-jerking the toes may stroke the female's lateral hindbody, her hindlimbs, cloaca or tail - depending on the male's relative position while clasping. On the upward jerk, the male's legs may force the female's hindlimbs upward, and the male's toes may interlock with those of the female.

E.) HINDLIMB-TREADING The hindlimbs are alternatively moved forward and then backward much as in walking. (In Taricha granulosa this action was executed my males with the female slowly moving forward, and the male's hindfeet struck the substrate on each backward stroke as the male walked forward while clasping the female with the forelimbs. Taricha torosa males showed this same action in the same context, but in addition they sometimes treaded with alternate hindlimbs while stationary with the female).

F.) CHIN-PRESSING From a position with the snout resting on the dorsum of the female's head posterior to her eyes (Fig. 40A), the male shifts suddenly forward by driving with his tail. As his body moves forward, the male bends his head down and opens his mouth, pressing his chin against the female's snout (Fig. 40B). As his body shifts backward his chin may force the female's snout upward due to its hooked position over her snout. See also Fig. 39B.

G.) CHIN-RUBBING Chin-rubbing is initiated just as chin pressing, but with his mouth open and with chin hooked over the female's snout, the male swings his head from side to side several times, thereby rubbing his chin on the female's snout.

H.) TAIL UNDULATION Slow tail undulations of large amplitude may occur with the tail directed backwards, and not flexed, and with the male stationary.

I.) SWIMMING WHILE CLASPING With strong sustained tail undulations the male drives the pair rapidly forward through the water just above the substrate.

J.) SURFACING FOR AIR Both animals give strong tail undulations as the pair moves upward to the surface, and both gulp air simultaneously before descending. During descent the pair may simply drift down, or the male may drive them down with rapid tail undulations.

Temporal relations (*Taricha granulosa*)

Upon encountering a female, the male nudges her very briefly. He may then either move slowly onto her dorsum and clasp her firmly with both forelimbs and hindlimbs, or he may move forward in a short and rapid burst

Figure 39. Dorsal clasping of the female in *Taricha granulosa* and *Notophthalmus viridescens*.

Fig. A. A *Taricha granulosa* male clasps the female with his forelimbs and hindlimbs. Height of the tail is sexually dimorphic during the breeding season. The male possess horny excrescences on the undersides of both his forelimbs and hindlimbs.

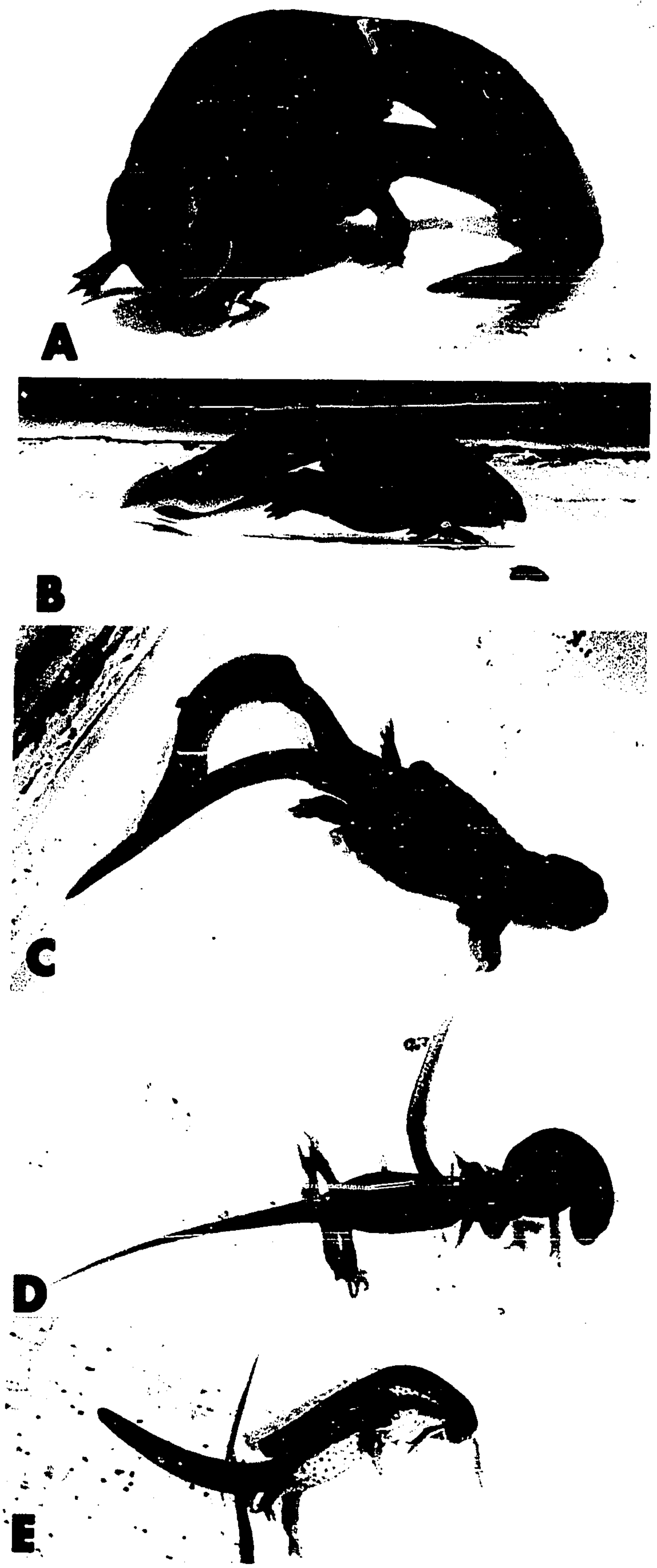
Fig. B. A *Taricha granulosa* shifts forward while clasping and presses his chin on the female's snout by opening his mouth. The male possesses glands on his chin. The female is moving forward.

Fig. C. A dorsal view of a male *Taricha granulosa* as he clasps the female. The female's hindlimbs are adpressed by the pressure of the male's gripping hindlimbs.

Fig. D. A dorsal view of a male *Notophthalmus viridescens* as he clasps the female with his hindlimbs. The male is pressing glandular pits on his cheek against the female's snout. The male possesses horny excrescences only on his hindlimbs.

Fig. E. A pair of *Notophthalmus viridescens* which have toppled onto their sides as the male clasps the female with his hindlimbs and presses his glandular cheek pits against the female's snout.

(The *Taricha granulosa* are from Corvallis, Oregon, and the *Notophthalmus viridescens* are from Cass Pond, Washtenaw Co., Michigan).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E

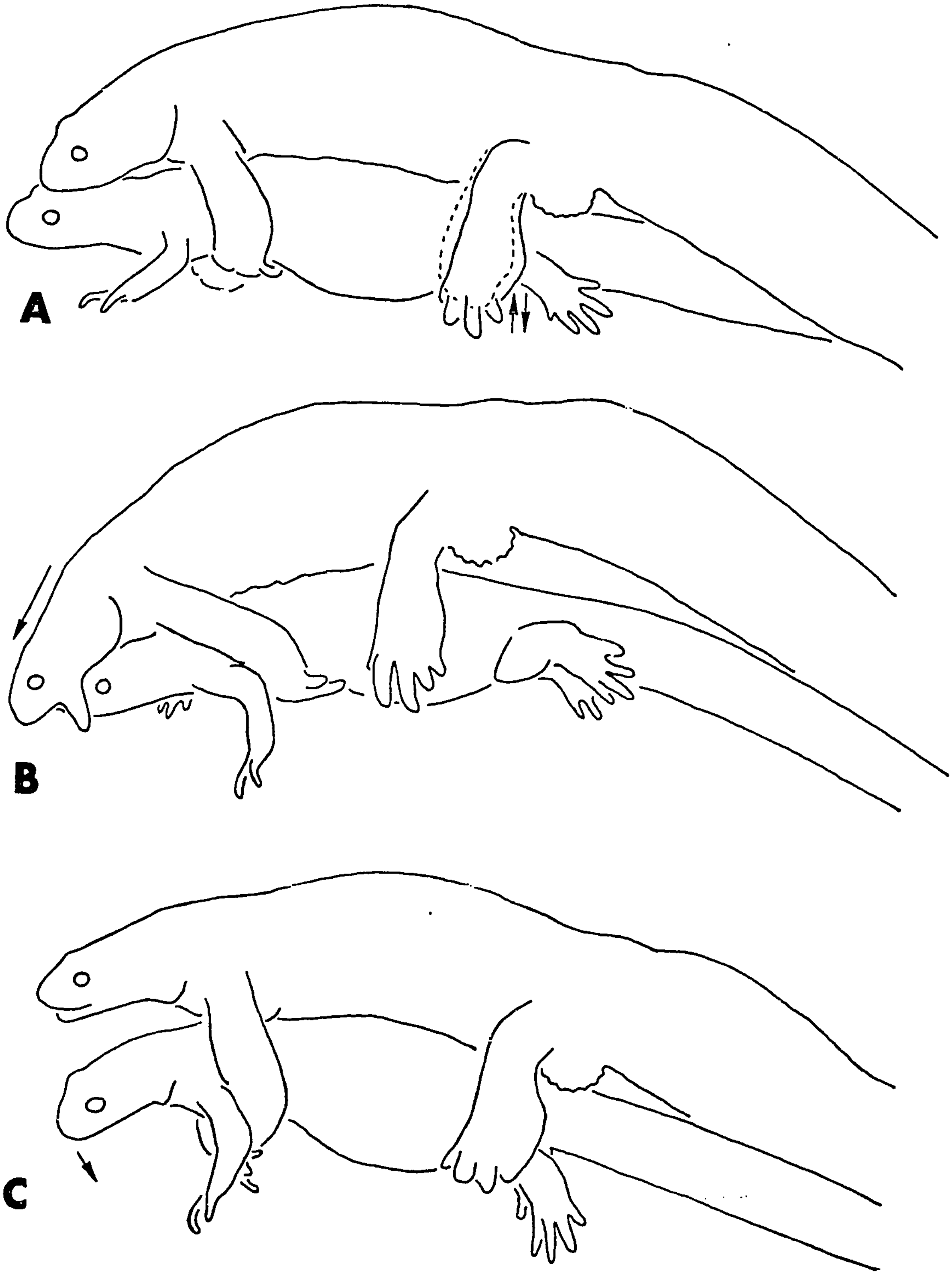
Figure 40. Courtship activities in Taricha granulosa; actions during clasping.

Fig. A. The male clasps the female firmly with his forelimbs and performs an upward, jerking motion with his hindlimbs. The hindlimbs jerk upward simultaneously and the toes are flexed on the upward stroke (0 sec).

Fig. B. The male has shifted forward rapidly and now presses glands on his chin against the female's snout by opening his mouth (1.1 sec).

Fig. C. The male has now shifted back to his former position, and the female is bending her head down (2.1 sec).

(Taken from a 16 mm. movie of one continuous sequence. Total elapsed time is 2.1 seconds. These animals are from Corvallis, Oregon).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by undulating his tail and clasp the female with both his forelimbs and his hindlimbs. Once the male has captured the female, he moves anterior towards her head by shuffling forelimbs and hindlimbs forward and then clasps her with his forelimbs just behind her forelimbs. If the male faces posterior along the female after capturing her, he shuffles forward with all four limbs and so moves posterior along her dorsum. When his head reaches the female's tail, the male releases the female with his forelimbs and turns his head and forebody anterior, all the while grasping the female firmly with his hindlimbs. He then regrasps the female with his forelimbs, releases with his hindlimbs and then shuffles anterior with all four limbs towards her head. Thus during capture of the female, the male employs both the forelimbs and hindlimbs to grasp the female's dorsum. Once the male reaches the female's head, his grip on the female is maintained principally by the forelimbs, which encircle the female firmly just behind her forelimbs (Fig. 39A), while the hindlimbs are pressed lightly against the female's abdomen or hindlimbs.

With both animals stationary during clasping, the male may give single hindlimb jerks separated by intervals of a few seconds with the male motionless. After several hindlimb jerks and pauses, the male suddenly shifts forward and gives chin-press (Fig. 40A, B) or chin-rub. This cycle of chin-press or rub separated by bouts of hindlimb jerking may go on for several hours with the male clasping the female continuously. When the female is moving forward slowly, the male may walk forward with his hindlimbs (hindlimb-treading) between chin presses or rubs. Chin-pressing or chin-rubbing may also be performed by the male while swimming during clasping. Whether stationary or moving forward, the female usually bends her head down or to the side in response to each chin-press (Fig. 40C) or rub. When she is moving forward, she stops momentarily while turning her head down, and so chin-press or rub may have the effect of arresting her forward progress. While clasping the male continually maintains his chin on the midline of the female's dorsal head. With each lateral turn of the female's head (Fig. 40A), the male turns his head laterally towards her dorsal midline. Tail undulations seem to occur sporadically during clasping and appear to show no regular temporal association with other male actions.

I was unable to observe spermatophore deposition and sperm transfer in Taricha, although on several occasions captive males deposited spermatophores with females when I was not present.

In Germany in 1896 Zeller obtained spermatophores from captive Taricha and provided a detailed description and figure of these remarkable spermatophores several years later (Zeller, 1905).

Ritter (1897) observed clasping animals in the field and in the laboratory. He found sperm masses in female cloacae and concluded that fertilization was internal. Since the male's swollen cloacal lips straddled the female's tail base, and he only observed clasping animals, Ritter speculated that sperm transfer occurred while the male still clasped the female.

Schreitmüller (1909) observed clasping in a captive pair of animals. He noted that the male clasps the female with his forelimbs behind her forelimbs while pressing his hindlimbs against her abdomen and provided a figure of the pair in this position. He found that the male periodically moves his hindlimbs forward in a jerking movement. The male also undulated his tail periodically. His cloacal lips were noticeably swollen and were rubbed against the female's dorsum. The male also pressed his head down against the female's head while simultaneously opening his mouth.

Hübener (1934) also observed clasping in a captive pair of Taricha.

On two occasions the female bit the male (on the tail and flank) as the male clasped her. Hübener observed the male moving his hindlimbs and pressing his chin against the female's head while opening his mouth.

Finally Smith (1941) described the process of sperm transfer in captive Taricha torosa. Sperm transfer was preceded by a lengthy period (usually two to three hours, but sometimes eight to ten hours!) during which the male clasps the female's dorsum as described by Schreitmüller. While clasping the female, the male performs repeated contractions of the hindlimbs (with a frequency as much as 70-80 contractions per minute) during which the hindfeet are drawn upward over the female's abdomen or hindlimbs. Smith notes too that the male periodically bends his head down, hooking his chin over the female's snout while simultaneously opening his mouth. The male may also swing his head laterally with the mouth open and rub his chin back and forth over the female's snout. Prior to spermatophore deposition the male terminates clasping by moving forward off of the female, either directly over her head or obliquely off of one shoulder. The male then moves his body in an arc laterally. The female may then remain stationary or move away from the male. In such cases the male usually turns and reclasps the female without depositing a spermatophore. If, on the other hand, the female nudges the male's cloaca, the male initiates spermatophore deposition. During spermatophore deposition the male "vibrates tail and hindlegs with a general shuddering of pelvic and thoracolumbar regions". The male moves forward from the spermatophore, and the female moves forward nudging his cloaca and passes over the spermatophore. The female contacts the sperm mass lightly with her cloacal lips, and the sperm mass adheres between them and is removed from the spermatophore. Apparently, the male meanwhile continues the vibratory movements of the tail and body. He may then turn and reclasp the female, even though she has successfully removed the sperm mass.

Smith (1941) suggested that two glandular areas present in the male function during courtship. First, he found a group of glandular cells on the male's chin. These glands are located in the region which the male rubs on the female's snout during clasping, and Smith suggests that the repeated application of this glandular area to the female later influences the female to follow the male during spermatophore deposition. Secondly, the male's abdominal glands, located on the lateral posterior margins of the cloaca, are extruded during courtship, and Smith suggests that the female orients to these glands while locating the spermatophore..

Davis and Twitty (1964) have provided the most complete account to date on the courtship behavior of Taricha. In Taricha rivularis they found that after seizing the female and while clasping her, the male performs stroking movements with his hindlimbs and also hooks his chin over the female's snout and swings his head laterally. At night these clasping activities persist for approximately one hour, but for a longer period of time during the day. Finally the female raises her head slightly. The male then rubs his chin vigorously on the female's raised snout, releases a bubble of air and dismounts from her. The male dismounts by moving forward to the right or left side of the female's head. He then pauses with his right or left flank about two centimeters from the female's snout and with his body forming a slight angle to the long axis of the female's body. In this position the male deposits a spermatophore with his vent pressed to the substrate and with the hindlimbs widely outstretched, perpendicular to his body. Davis and Twitty (1964) do not mention the trembling body movements of the male during spermatophore deposition described by Smith (1941). The male moves off of the spermatophore by moving his pelvis laterally through a 90° arc. From photographs provided by Davis and Twitty (1964) it appears that the male holds one forelimb stationary while rotating the posterior body away from this forelimb. As his body rotates, the male's body forms a deep lateral curvature at the pelvis on the side facing the female. The male then pauses, with his body at approximately a 90° angle to the long axis of the female's body, and performs a lateral undulatory movement of the posterior body while "spasmodically striking the substratum with his outstretched feet". The female may then move forward towards the male and contact her snout to his shoulder. She then steps laterally while moving her snout posteriorly towards the male's pelvic concavity. If her vent then contacts the spermatophore, she lowers her vent upon it. Sometimes, however, the female approaches the male as he deposits the spermatophore and moves along his body. In such cases the female apparently has a lower probability of locating the spermatophore. The male usually reclasps the female depositing only one spermatophore.

Davis and Twitty (1964) also report that the courtships of *Taricha torosa* (*T. t. torosa* and *T. t. sierrae*) and *Taricha granulosa* are very similar to *Taricha rivularis*. They note the following differences. Some males of *Taricha torosa* reflex the distal tail forward and undulate their tails parallel to the body when they are placed in water which has contained females. Tail undulation with *reflexed* tail may also occur during clasping. The pelvic curvature during pivoting by the male is shallower in *T. torosa* and *T. granulosa* than in *T. rivularis*.

All descriptions on this genus are in general agreement on the basic actions performed by the male during clasping. I have provided some additional details on these actions and outlined their temporal patterning in the preceding section. Apparently only one spermatophore is deposited after dismounting from the female. Presumably the male may then deposit additional spermatophores after first reclasping the female, for I have found two fresh spermatophores in a tank with one pair of *Taricha granulosa* during a 24 hour period.

Notophthalmus viridescens

Catalog of male actions

The following actions are performed by the male while facing towards the female.

A.) SLOW APPROACH The male moves slowly forward on all four limbs while tracking the movements of another individual.

B.) SPRINGING FORWARD With rapid tail undulation, the male springs forward, lands on the toe tips with limbs extended and may then spring forward again.

C.) NUDGING The male lightly nudges the body of another individual with his snout.

D.) BODY UNDULATION WITH TAIL STRAIGHT With the forefeet resting on the substrate, slow lateral undulations of large amplitude proceed from the male's forebody along the entire length of his tail. The hindlimbs may be above the substrate, as the continuous undulations swing the sacrum from side to side, or the toes of the hindlimbs may lightly brush the substrate. The action suggests an acrobatic Hawaiian dancer with a tail (Fig. 42B, C). This action may be performed with the male stationary or while moving forward slowly. The cloacal papillae are everted.

E.) HINDLIMB CAPTURE Clasping is initiated by a very elaborate capture process. The male swims rapidly towards and in a parallel plane slightly above another individual (Fig. 41A). As his body comes over the individual below him, the male rapidly throws his head and forebody upward and backward (Fig. 41B). The forearms are thrown back (Fig. 41C). As the hindbody continues forward, the hindlimbs are rapidly opened and then quickly closed (Fig. 41C). The whole process is executed in less than a half a second. A fortunate male will capture the pursued individual with his massive hindlimbs. When the male captures another animal posterior to the neck, he shuffles forward with his hindlimbs, while maintaining a firm grasp, until he clasps the neck.

The following actions are performed by the male while clasping the female.

F.) HINDLIMB-CLASPING While clasping, the hindlimbs firmly grasp the female's neck with the toes overlapping on the ventral neck (Fig. 39).

G.) TAIL UNDULATION Two classes of tail undulations occur while clasping. The tail may be slowly undulated while straight or slightly reflexed to the side. Continuous gradations occur from this action to exceedingly rapid tail undulations with the tail reflexed forward along the side of the body (eg. Fig. 44F). Such rapid tail undulations with the tail bent forward always occur in bouts of short duration. Slow undulations with the tail directed backward are of more variable duration. Tail undulations of either type alternate with long periods with the tail motionless.

H.) TAIL-JERKING With the tail bent in an S-shape, the tail base is repeatedly jerked laterally (Fig. 45D). This action can be very distinct and yet often grades temporally into tail undulation.

I.) CHEEK-PRESSING The cheek is pressed against the female's snout, but the head is held stationary (Fig. 44E).

J.) CHEEK-RUBBING The male presses his cheek firmly against the female's snout, and moves his head forward in jerks around the side of the female's head. As a consequence the male rubs his cheek against the female's snout (Fig. 45D). The region of the male's cheek which is applied to the female's snout during this and the preceding action, cheek pressing, contains the male's genial pits.

K.) CHANGING OF CHEEKS The male switches from head bent to one side and pressed against the female's snout (Fig. 46A) to the same position with the other cheek (Fig. 46C) by straightening and turning his head (Fig. 46B).

L.) THRASHING The male violently thrashes his body and tail laterally, frequently lifting the pair off the substrate and driving them through the water (Fig. 45E). This action grades into changing of cheeks (G).

M.) FOREARM-RUBBING The male lifts the forearm closest to the female's snout, turning his cheek away from the female's snout (Fig. 44A). The forelimb is rotated towards the female's snout (Fig. 44B), the forearm is brought down and rubs in contact with the female's snout (Fig.44D). The forearm is pushed down around the tip of the female's snout and moved posteriorly along the female's chin (Fig. 44E), as the male again presses his cheek against the female's snout (Fig. 44E). The whole process is executed in a little more than one second (see Fig. 44). In some instances the forearm is lifted and rubbed posterior along the female's chin without a downward stroke across her snout.

The following actions are performed by the male while facing away from the female.

N.) DISMOUNTING With straightened body and tail, the male releases the captured individual with his hindlimbs and slides either anteriorly (over the head) or posteriorly (over the tail), depending upon the clasping position (Fig. 45F).

O.) BODY UNDULATION WITH TAIL FLEXED The male is stationary with the tail flexed to one side at a 45° - 90° angle. Undulations of large amplitude proceed posteriorly from the male's anterior body to the end of his tail. The tail is level, the vent is held slightly above the substrate and the cloacal papillae are everted (Fig. 46G, 42E).

P.) MOVING FORWARD WITH FLEXED TAIL The male moves forward with the tail flexed to one side at the base at a 45° - 90° angle. Slow undulations of large amplitude are restricted to the length of the tail. The vent is held just above the substrate, and the cloacal papillae are everted (Fig. 47A, 48G).

Q). SPERMATOPHORE DEPOSITION The male is stationary with the vent adpressed to the substrate. Slow undulations proceed from the base along the length of the tail. The tail is level and flexed to one side at a 45° angle, The forelimbs are held motionless with the palms on the substrate, but the hindlimbs alternatively move forward with a flexure of the toes preceding each forward motion (Fig. 47A, 48H, 49H).

R.) PIVOTING With the tail level and flexed to one side at a 45° - 90° and undulating slowly, the male turns his head to the other side and moves forward. The sacrum is moved laterally through a 90° arc, while the male pivots about the inner forelimb as he moves forward (see Fig. 47A to D, Fig. 48H to J, Fig. 49A to E). The flexed tail gradually straightens during the turn and is straight and undulating at the completion of the turn. Pivoting thus begins with body undulation with tail flexed and terminates in body undulation with tail straight with the body now perpendicular to the initial position.

Temporal relations (Notophthalmus viridescens)

In Taricha, spermatophores are deposited only after a lengthy period of clasping. In contrast, Notophthalmus males sometimes deposit spermatophores, and transfer sperm to the female, without first clasping the female. The "decision" to clasp the female is not a random decision. The male changes his behavior dramatically depending on how the female responds to his first approaches. If the female swims or moves away from the male as he approaches her, the male springs rapidly towards her and may attempt to clasp her (as in Fig. 41). But if the female remains stationary, or actively approaches the male, the male usually does not try to clasp her. Instead the male begins undulating his body and tail with his tail essentially straight (Fig. 42B). In two instances the female repeatedly nudged the male as he performed this action (Fig. 42C). The male turned away from the female (Fig. 42D), and undulated his body with his tail flexed to one side (Fig. 42E). In both instances the female persistently nudged the male's tail base. The male then moved forward with his tail flexed and deposited a spermatophore without clasping the female.

Humphries (1955) also found that male Notophthalmus viridescens can delete clasping prior to spermatophore deposition. He observed this short circuiting of courtship by males only in the presence of females implanted with anterior pituitary lobes. By manipulating the positions of males and implanted females, Humphries found that capture and clasping frequently occurred when the male contacted the female posterior to the pelvis, whereas if the female is placed in contact with the male's head, the male may begin body undulation and then deposit a spermatophore without first clasping the female. Humphries suggested that the switch in male behavior is due to the relative positions of sexual partners upon contact. These observations together with my observations on unrestrained animals suggest that pursuit and captive attempts are given to females which move away from the male, while the response of body undulation with straight tail is given to females which remain in place or actively nudge the male. The critical stimuli are probably a combination of relative position of the female and direction of motion.

Clasping is always accomplished by the elaborate capture procedure previously described. Capture attempts are frequently abortive however

Figure 41. Courtship activities in Notophthalmus viridescens; a male attempting to capture a female with his hindlimbs.

Fig. A. A male (below) swims rapidly upward just above a female, as she swims upward slowly (o sec).

Fig. B. The male throws his anterior body backward as he lashes with his tail (0.23 sec).

Fig. C. The male has opened his hindlimbs widely and is now forcing them together (0.32 sec).

Fig. D. The male's hindlimbs fail to grasp the female's body. The female is now swimming forward rapidly (0.36 sec).

Fig. E. The female continues to swim forward rapidly. The male falls backward in the water with his hindfeet interlocked (0.41 sec).

(Taken from a 16mm. movie (22 fps). Total elapsed time is 0.41 seconds. These animals are from Goss Pond, Washtenaw Co., Michigan).

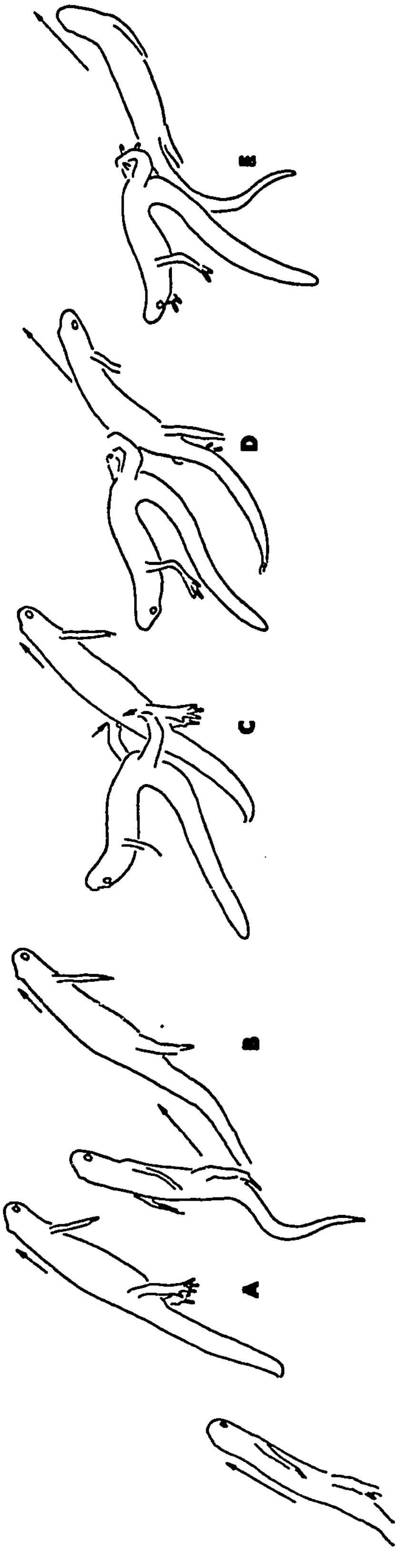
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Figure 42. Courtship activities in *Notophthalmus viridescens*; a male encounters a sexually receptive female.

Fig. A. The female (right) has gulped air at the surface and is drifting down to the substrate near a male (left).

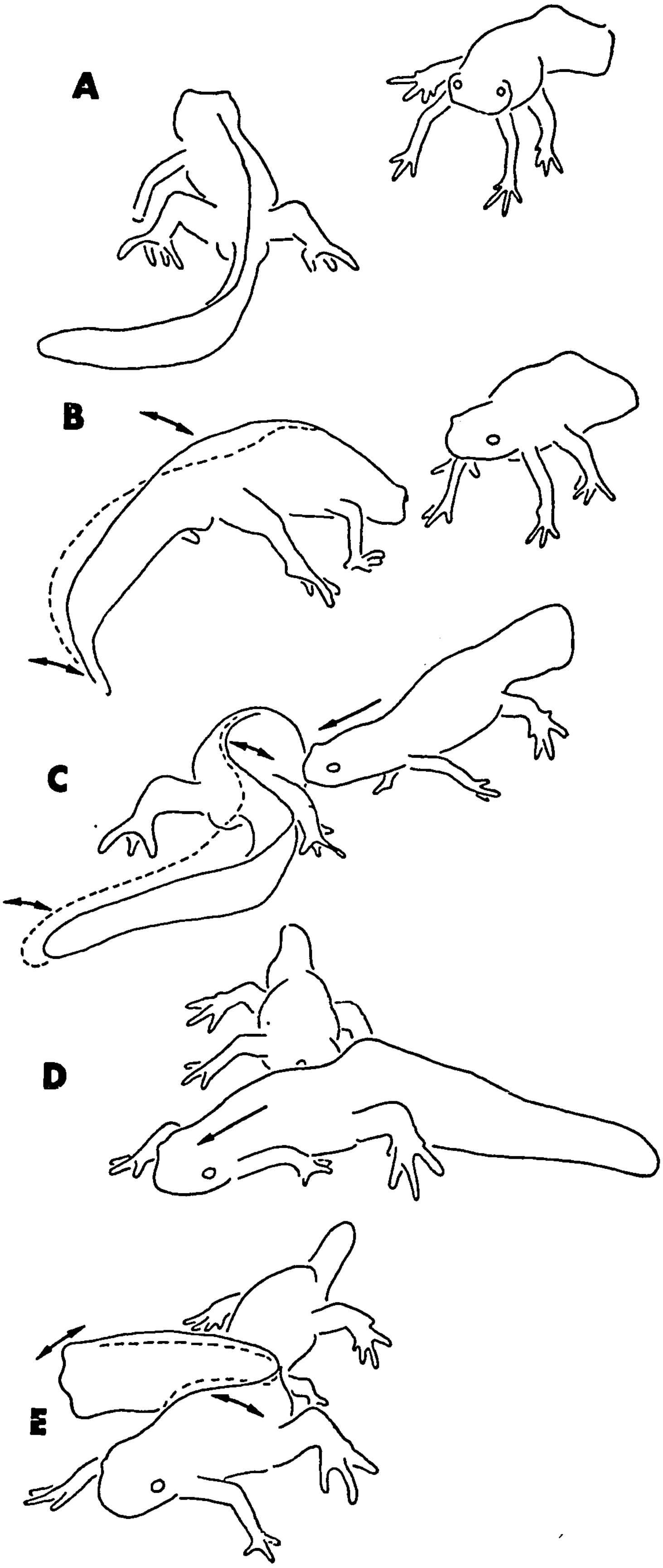
Fig. B. The female has remained stationary and turned towards the male. The male has turned towards the female and now undulates his body and tail with his forefeet resting on the substrate. He has not contacted the female.

Fig. C. The female is now approaching the male and contacting her snout to his lateral body. The male continues to undulate his body and tail with his tail straight.

Fig. D. The female continues to nudge the male's posterior body. The male has turned away from the female and now begins to move forward.

Fig. E. The female nudges the male's cloacal papillae and the male undulates his body and tail with his tail flexed to one side.

(Taken from a 16mm. movie of one continuous sequence. These animals are from Mountain Lake, Giles Co., Virginia).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(see Fig. 41). One male made nine unsuccessful capture attempts in 75 minutes, but was found clasping the female 45 minutes later. Individuals captured on the tail readily escape by swimming rapidly. Individuals (male or female) captured with the capturing male facing posterior are released. Notophthalmus viridescens males apparently have no provisions for dealing with such cases (eg. turning around while clasping).

Some females persistently bend their heads down sharply when they are captured: the male releases the female when she gives this response. When males are captured by another male, they invariably give this same head-down response and are released by the capturing male (Fig. 43). In some instances the male dismounts and departs from the female even though she does not give the head-down response.

During clasping the actions of the male follow a very complex but nevertheless predictable course. The beginnings of clasping bouts are characterized by rather long (few minutes) pauses with the male motionless with his head bent to one side. Such motionless periods terminate with the male rubbing his forearm on the female's snout (Fig. 42B to D), then pressing his cheek against her snout (Fig. 42E) and finally undulating his tail with the tail reflexed along the side of his body (Fig. 42F). Another motionless pause follows and the sequence is repeated over and over. Tail undulations with the tail reflexed or straight may also alternate with motionless pauses without any intervening actions by the male. Several such series of forearm, head and tail actions and long pauses are followed by a changing of cheeks.

Some 20 minutes prior to dismounting from the female, a rather rapid but smooth transition leads into a second phase of clasping. The sequences outlined above are executed much faster. The duration of intervals with the male motionless are rapidly reduced, so that the male moves into

Figure 43. A male Notophthalmus viridescens captures another male.

Fig. A. A female departed rapidly from a male as he nudged her with his snout. Another male nearby then began to swim forward slowly. The first male is shown as he swims rapidly towards and above this departing male.

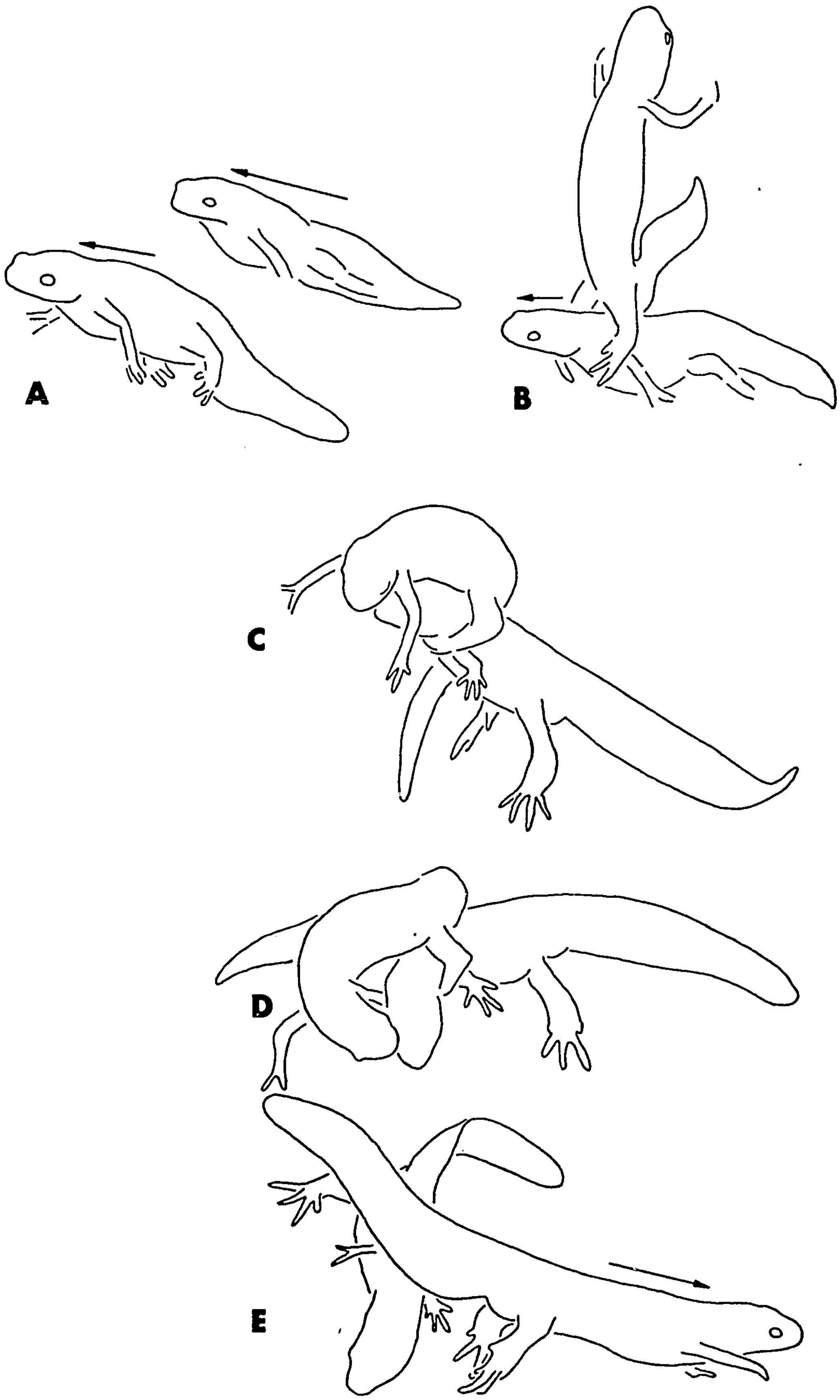
Fig. B. The male has thrown his anterior body upward, and backward, and is now rapidly forcing his hindlimbs together as the male below him continues to swim forward slowly.

Fig. C. The male has captured the other male about the neck with his hindlimbs.

Fig. D. The male contacts his snout to the other male's dorsal head, and the captured male bends his head down sharply.

Fig. E. The male has released the captured male and is now departing from him. The other male remains immobile with his head still bent down sharply.

(Taken from a 16mm. movie of one continuous sequence. These animals are from Mountain Lake, Giles Co., Virginia).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continuous activity. Arm-lifting or rubbing, cheek-pressing and then tail undulation with tail reflexed are executed rapidly in that sequence. Changing of cheeks increase in frequency of occurrence and follow tail undulation with tail recurved when they occur. During the rapid transition to the second phase of clasping, changing of cheeks grades, in form of execution, into thrashing. Instead of moving slowly from head bent to one side, to straight, to bent laterally in the other direction; the male straightens his body and performs one or a few lateral swings of tail and body before turning the other cheek to the female's snout. As the transition into the second phase of clasping proceeds, more and more lateral swings are inserted between the stationary adpressions of the cheeks to the female's snout. The speed as well as the amplitude of these lateral swings increases, so that during the second phase of clasping the male thrashes violently during changing of cheeks and frequently lifts the pair off the substrate, driving them forward or backward through the water. With the onset of thrashing the male's abdominal glands become pronounced white spots. In addition cheek-rubbing synchronous with tail jerking now follows bent tail undulation in the sequence of male actions. In this way the sequence of actions during the second phase of clasping becomes arm-lift or rub (Fig. 45A), cheek-press (Fig. 45B), tail undulation with tail reflexed (Fig. 45C), cheek-rubbing with tail-jerking (Fig. 45D), thrashing (Fig. 45E), arm-lift or rub, ...

The second phase of clasping lasts for several minutes and then thrashing is rapidly deleted from the sequence of actions. Tail-jerking, cheek-rubbing and arm-lifting or rubbing are also deleted. The third phase of clasping is composed of the repeated sequence, cheek-pressing with undulation of reflexed tail (Fig. 46A), changing of cheeks (Fig. 46B), cheek-pressing with undulation of reflexed tail (Fig. 46C), ... This

Figure 44. Male actions during clasping in *Notophthalmus viridescens*; forearm rubbing.

Fig. A. A male presses his cheek against the female's snout as he clasps her with his hindlimbs (0 sec).

Fig. B. The male initiates forearm-rubbing by turning his head slightly away from the female and is now lifting his forearm (0.28 sec).

Fig. C. The male moves his forearm towards the female's snout (0.44 sec).

Fig. D. With a downward motion, the male rubs his forearm across the female's nare (0.72 sec).

Fig. E. The male slides his forearm under the female's chin and again presses his cheek against her snout (1.17 sec).

Fig. F. The male continues to press his cheek against the female's snout and now undulates his tail with his tail reflexed (5.89 sec).

(Taken from a 16mm. movie of one contunuous sequence. Total elapsed time is 5.89 seconds. These animals are from Mountain Lake, Giles Co., Virginia).

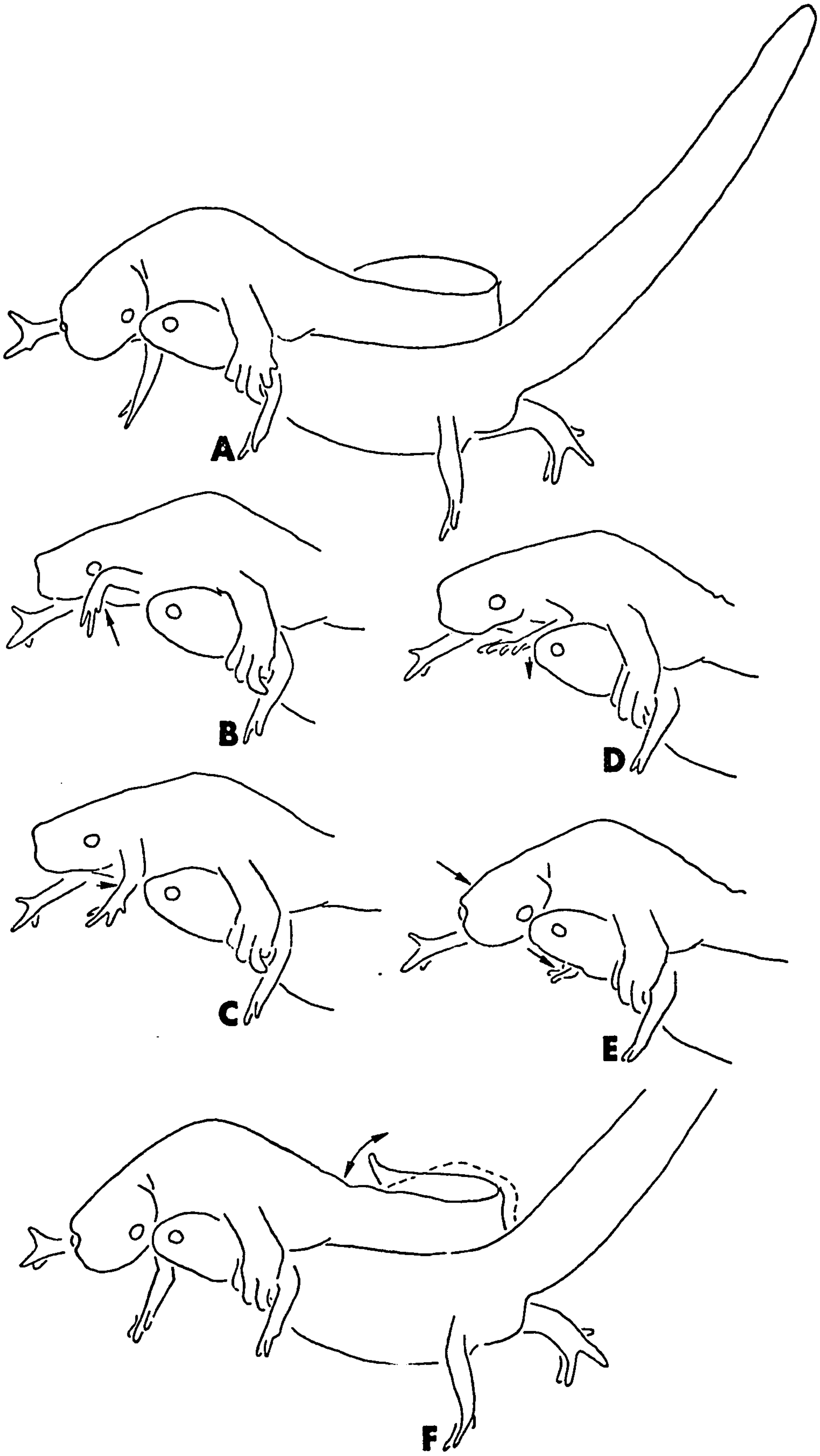
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Figure 45. Male actions during clasping in *Notophthalmus viridescens*.

Fig. A. A male in the process of rubbing his forearm on the female's snout (o sec).

Fig. B. The male presses his cheek against the female's snout as he moves his forearm under the female's chin (4.18 sec).

Fig. C. The male undulates his tail rapidly with his tail reflexed as he continues to press his cheek against the female's snout (5.73 sec).

Fig. D. The male rapidly and repeatedly jerks his tail base laterally as he rubs his glandular cheek pits on the female's snout (8.45 sec to 10.41 sec).

Fig. E. The male rapidly thrashes his body, and consequently the female, from side to side (11.27 sec to 11.36 sec).

Fig. F. The male has now pressed his other cheek to the female's snout He is undulating his tail rapidly with his tail reflexed (13.64 sec).

(Taken from a 16mm movie of one continuous sequence. Total elapsed time is 13.64 seconds. These animals are from Goss Pond, Washtenaw Co., Michigan).

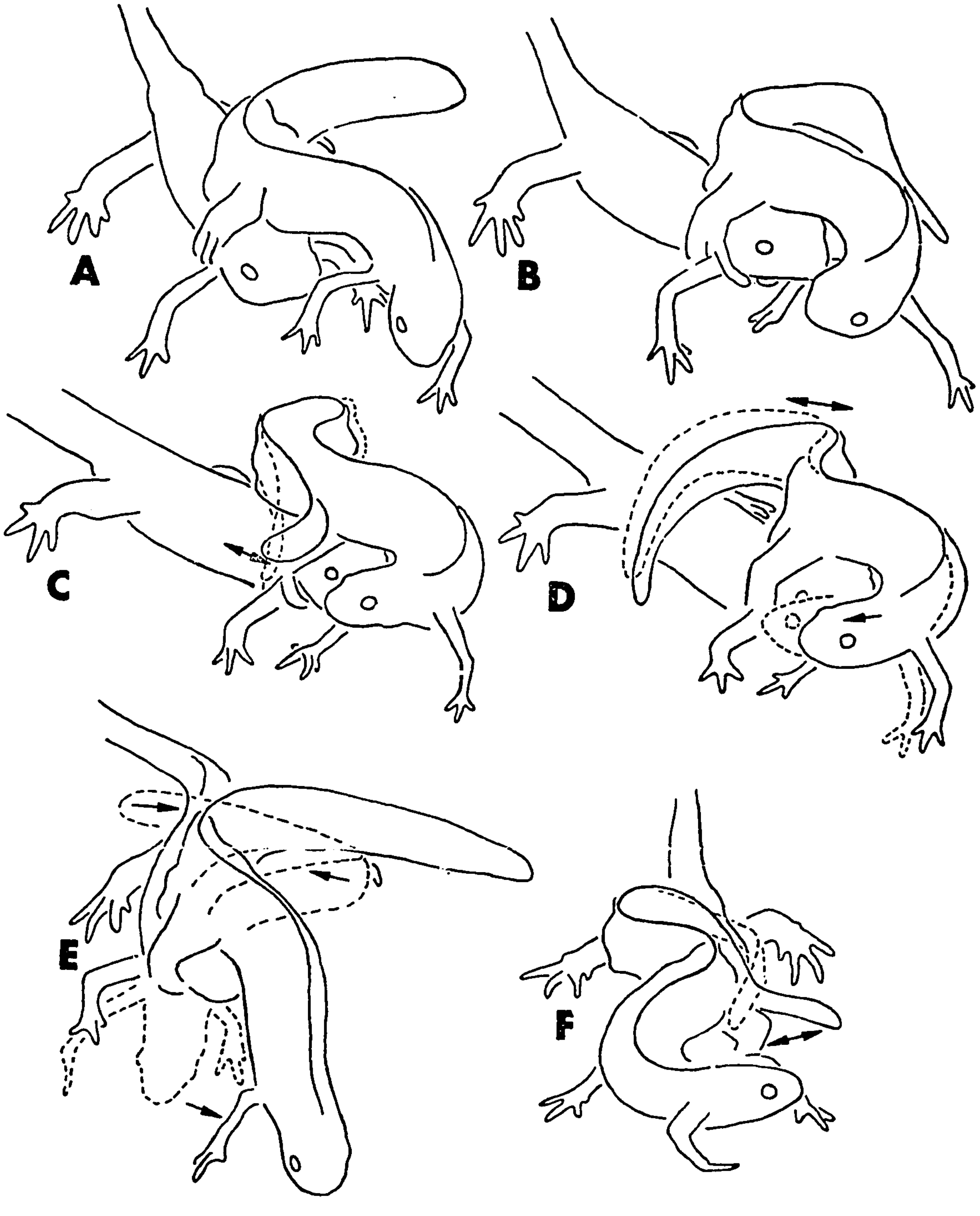
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Figure 46. Male actions during clasping in *Notophthalmus viridescens.*

Fig. A. The male presses his cheek against the female's snout while undulating his tail rapidly with the tail reflexed (0 sec).

Fig. B. The male is in the process of turning his other cheek towards the female's snout (1.00 sec).

Fig. C. The male presses his cheek against the female's snout. His tail is now reflexed on the opposite side, on the same side as his head. The male undulates his tail rapidly (1.61 sec).

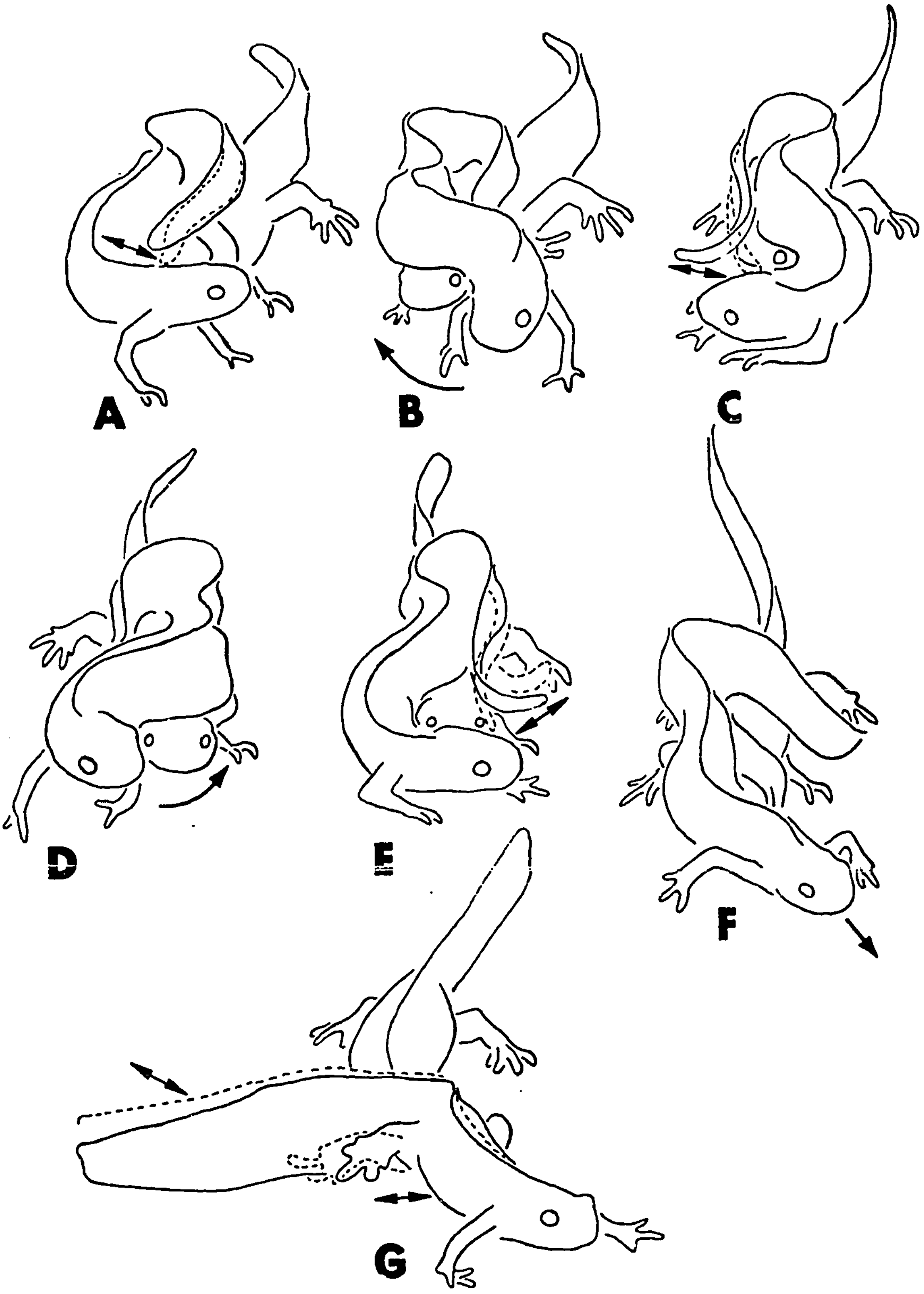
Fig. D. The male is in the process of turning his other cheek to the female's snout (3.00 sec).

Fig. E. The male presses this cheek against the female's snout. His tail is now reflexed on the same side and he is undulating his tail rapidly (3.67 sec).

Fig. F. The male has turned his cheek away from the female's snout and is now dismounting over the top of her head (5.22 sec).

Fig. G. The male pauses with his cloacal papillae in front of the female's snout and undulates his body with his tail flexed to one side (16.50 sec).

(Taken from a 16mm. movie of one continuous sequence. Total elapsed time is 16.5 seconds. The animals are from Mountain Lake, Giles Co., Va.)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sequence continues for several seconds and then finally the sequence is broken following undulation of reflexed tail (Fig. 46E) as the male straightens his body and dismounts over the female's head (Fig. 46F).

Upon dismounting from clasping, the male pauses with his vent half to one centimeter in front of the female's snout and performs body undulation with flexed tail (Fig. 46G). Frequently females depart from the male at this point and surface to gulp air. In these instances the male continues to perform body undulation with flexed tail for several minutes and does not move forward. He does not deposit a spermatophore. If, on the other hand, the female nudges the male's tail base, he moves forward with flexed tail. The male will continue forward only if the female continues to contact his tail base (as in Fig. 47A). With each contact the male moves forward half to one centimeter and pauses. Thus intermittent contact with his tail base causes the male to alternate between body undulation with flexed tail and moving forward with flexed tail. Continuous contact with his tail base causes the male to move forward continuously with flexed tail. If, during this forward progress, the female departs from the male, the male pauses, performs body undulation with flexed tail and does not deposit a spermatophore. After several seconds of continuous or discontinuous progress on a straight course, the male pauses and initiates spermatophore deposition. In all instances spermatophore depositions were initiated with the female's snout contacting the male's tail base or cloacal papillae (see Fig. 47B). Spermatophore deposition terminates with the male lifting his vent off the spermatophore and again performing body undulation with flexed tail. In a few instances the female departed during spermatophore deposition. The male then remained stationary after spermatophore deposition and performed body undulation with flexed tail. If, on the other hand, the female nudges the male's tail, after he lifts off of the spermatophore, the male makes a right angle turn by pivoting about the forelimb on the side opposite the side to which the tail is flexed (Fig. 47C). During all such instances the female moved forward continuously nudging the male's tail base and hindbody. While thus moving forward on a straight course while nudging the male, the female shifts from side to side slowly on her hindlimbs (and likewise she may shift laterally to and fro on her hindlimbs as she follows behind the male immediately after dismounting). If the spermatophore contacts the female's ventral or lateral body, she shifts actively in that direction, and the spermatophore may slide posteriorly in continuous contact with her ventral body as she moves forward (see Fig. 47C, to D, to Fig. 48E). If the spermatophore contacts her vent, the female rocks over the top of it and squats upon it (Fig. 48E). The sperm mass may then be dislodged from the spermatophore base and adhere to the female's cloacal cone (note sperm mass adhering to the female's lateral cloacal wall in Fig. 48G).

As the male completes the right angle turn by pivoting and performs body undulation with tail straight (see dorsal views of this process in Fig. 49A through E), the spermatophore lies approximately one snout-vent length away on a line perpendicular to his body. The male then remains stationary for a minute or more even though the female may persistently nudge his tail base or lateral hindbody, while she shifts laterally on her hindlimbs with her vent in the vicinity of the spermatophore (Fig.49D, E). Then after pausing, the male turns quickly and sharply from perpendicular to the female and stationary to parallel to the female and moving forward with tail flexed (see Fig. 49E to G for a dorsal view and Fig.48E to G for a lateral view). And so the sequence continues on, subject to the same contingencies outlined above. Following dismounting, one to three

Figure 47. Spermatophore depositions and sperm transfer in *Notophthalmus viridescens*.

Fig. A. The male has dismounted from the female after clasping her. He is now moving forward with his tail flexed and undulating. The female follows behind him nudging his tail base and cloacal papillae with her snout (0 sec).

Fig. B. The male has paused and is in the process of depositing a spermatophore. The female is stationary behind him with her snout in contact with his cloacal papillae and tail base (20.5 sec).

Fig. C. The male is moving forward away from the spermatophore by pivoting about his right forelimb. The female is moving forward with her snout in contact with the male's lateral tail base. The spermatophore is visible just below her neck (29.8 sec).

Fig. D. The male continues to pivot away from the spermatophore about his right forelimb. The female continues to nudge his lateral tail base as she moves forward, and the spermatophore is sliding posterior in contact with her venter as she moves forward (34.7 sec).

(The sequence is continued in Fig. 48).

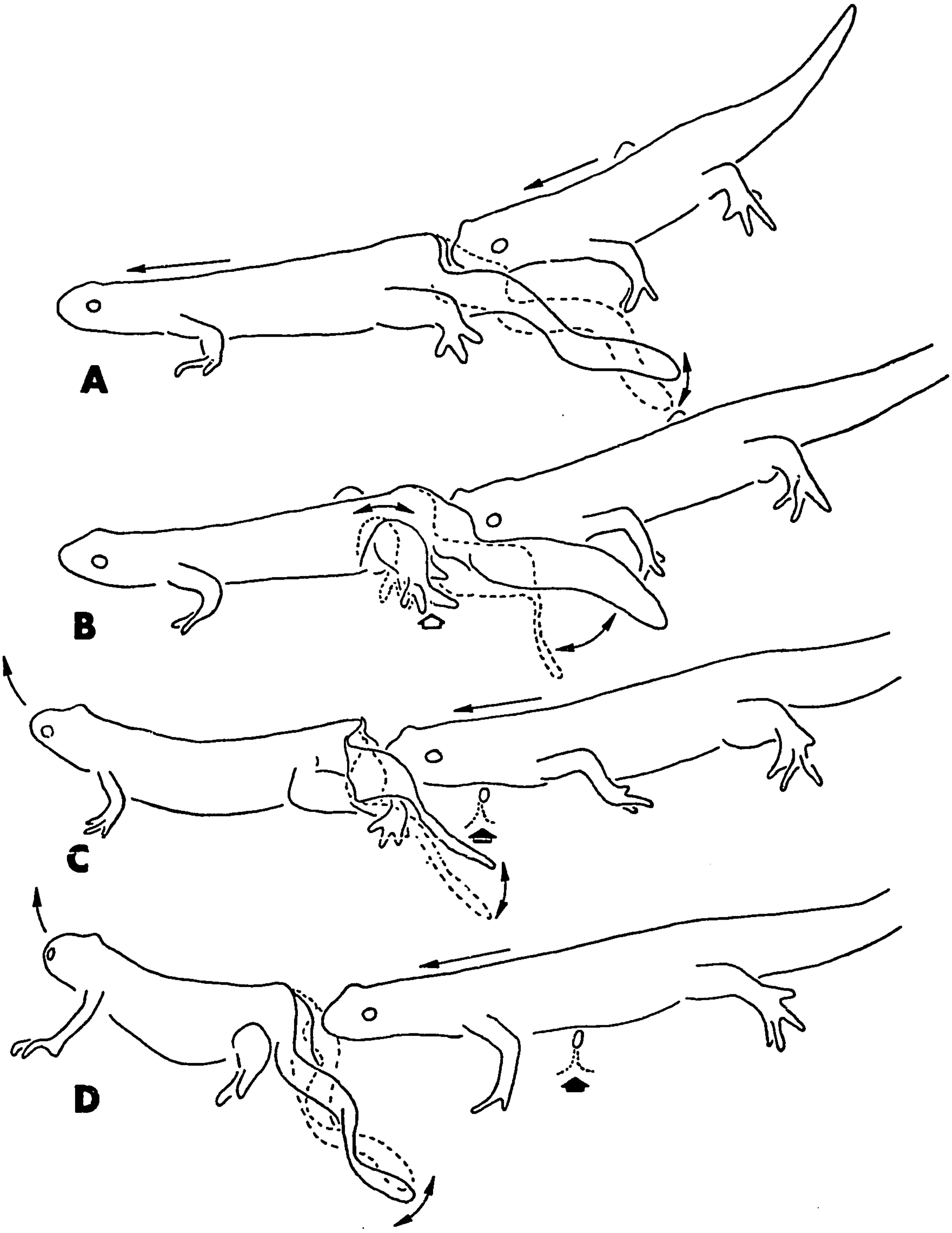
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Figure 48. Spermatophore deposition and sperm transfer in *Notophthalmus viridescens* (continued from Fig. 47).

Fig. E. The male has now paused and he is undulating his body and tail with his tail straight. As a consequence of pivoting after spermatophore deposition, his body axis now lies nearly perpendicular to the female's body axis. The female has stopped with her vent in contact with the spermatophore. Her snout contacts the male's lateral tail base (69.9 sec).

Fig. F. The female has moved forward off of the spermatophore and nudged the male's tail base. The male is making a 90° turn to the left as he continues to undulate his tail (139.0 sec or 2.31 min).

Fig. G. The male is now moving forward on a straight course after completing a 90° turn back to his former path (Fig. 47A). The female follows behind the male and nudges his lateral tail base. She successfully removes the sperm mass from the first spermatophore, and it can be seen adhering to her cloacal lip. The male's cloacal papillae are also visible now as well as his left abdominal gland (a small circle on the lateral, anterior margin of the cloaca) (149.7 sec or 2.49 min).

Fig. H. The male has now stopped and is in the process of depositing a second spermatophore. The female has stopped behind him with her snout in contact with his lateral tail base (158.4 sec or 2.64 min).

(Taken from a 16mm. movie of one continuous sequence. Total elapsed time is 2.64 minutes. Animals from Goss Pond, Washtenaw Co., Michigan).

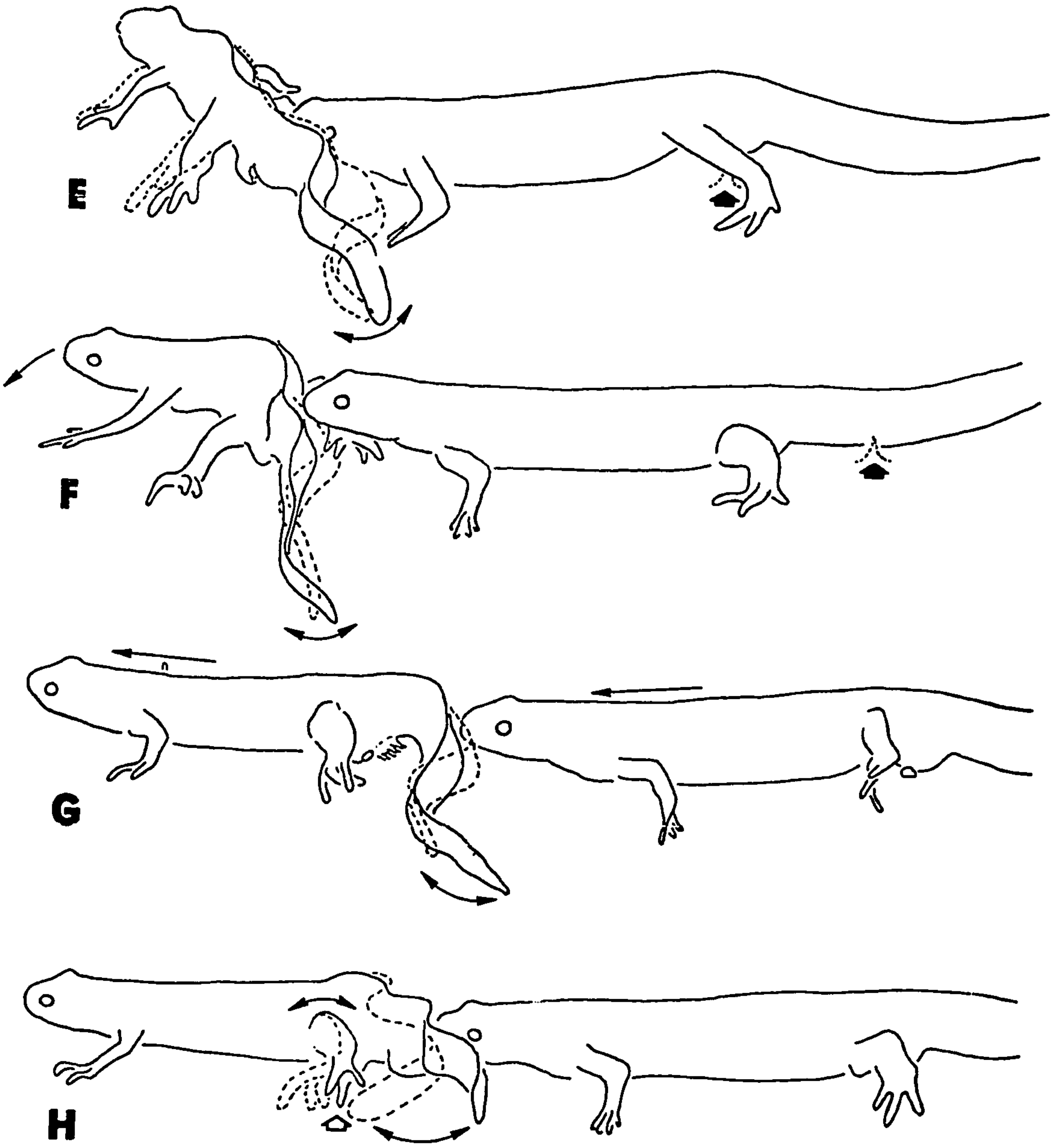
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Figure 49. Successive spermatophore depositions in Notophthalmus viridescens (dorsal views).

Fig. A. The male (right) has just completed spermatophore deposition and is just beginning to pivot to the left.

Fig. B. The male continues to pivot to the left. The female nudges his tail base and the spermatophore lies under her ventral

Fig. C. The male is now stationary with his body axis perpendicular to its former position (Fig. A). The spermatophore has now contacted the female's vent.

Fig. D. The male is stationary and continues to undulate his tail laterally. The female is stationary with her vent in contact with the spermatophore.

Fig. E. The female now begins to nudge the male's lateral tail base with her snout.

Fig. F. The female has moved forward off of the spermatophore and continues to nudge the male's lateral tail base. The male is now in the process of turning to the right.

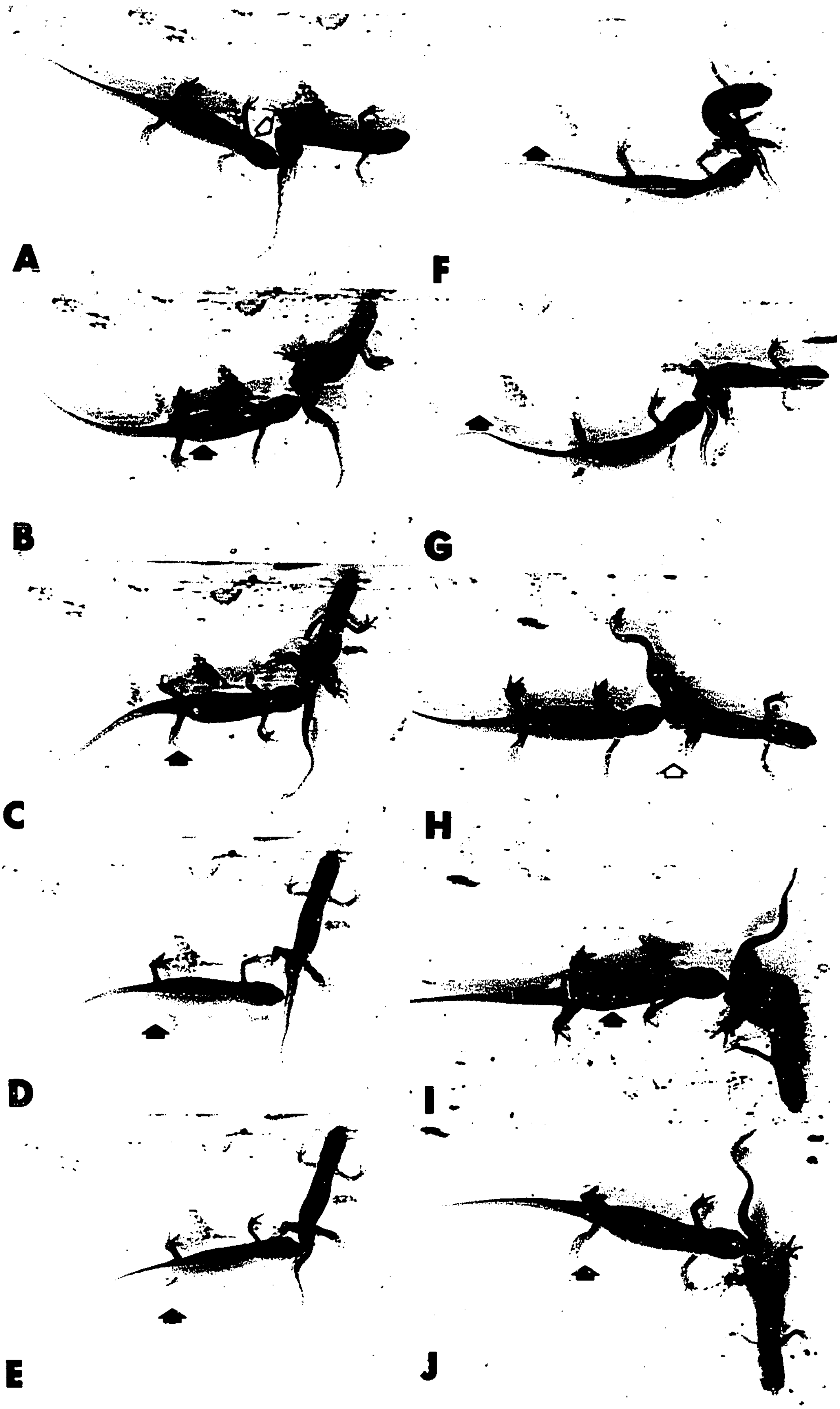
Fig. G. The male has just completed a 90° turn and begins to move forward on a straight course as the female nudges his tail base.

Fig. H. The male has again moved forward on a straight course. He has now stopped and is in the process of depositing a second spermatophore as the female nudges his tail base. Notice that the male has flexed his tail to the left.

Fig. I. The male moves off of the spermatophore by pivoting to the right (opposite to the direction in which his tail is flexed). The female has moved forward over the spermatophore and it lies in contact with her ventral hindbody as the male continues to pivot.

Fig. J. The male has now completed a 90° turn to the right and no longer pivots. He is stationary and is undulating his tail laterally. The female is stationary with her vent in contact with the second spermatophore, as she nudges the male's tail base with her snout.

(These animals are from Coss Pond, Washtenaw Co., Michigan).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spermatophores were deposited during this alternating sequence of forward progress, spermatophore deposition, right angle turn, forward progress, spermatophore deposition, right angle turn, ... In a few instances females, which had departed from the male and surfaced for air, reapproached him and nudged his tail base as he performed body undulation with tail flexed. The male then reinitiated forward progress.

Zeller (1890) observed that male Notophthalmus viridescens seize the female by springing upon the nape of her neck and clasping her firmly there with his hindlimbs. While clasping, the male undulates his tail with the tail reflexed and periodically swings and shakes the female vigorously back and forth. During clasping neither the female or the male surface for air. (I can, incidentally, confirm this observation of Zeller's. Notophthalmus viridescens apparently possess no provisions for obtaining air at the surface during clasping, unlike clasping Taricha or Ambystoma). Zeller noted that the male finally releases the female and moves directly in front of her and deposits a spermatophore. The female creeps slowly behind the male and takes up the sperm mass with her cloacal lips. The male may deposit a second and even a third spermatophore in succession.

Jordan (1891) reaffirmed Zeller's observations and makes several additional clarifications. Jordan observed that when a male first approaches a female, and if she remains quiescent, the male may perform body undulations similar to those observed at the time of spermatophore deposition. Jordan is undoubtedly referring to the male action I have called body undulation with tail straight. Jordan did not, however, observe spermatophore deposition immediately after this action, and hence without an intervening period of clasping. Instead he found that the male immediately springs onto the female and clasps her. Jordan recognized three distinct phases during clasping. At first the male and female remain relatively motionless, except for tail fanning on the part of the male. Then the male's behavior changes gradually into a second phase (of about ten minutes duration) during which the male vigorously jerks and drags the female about. Simultaneously the male's cloaca swells, and whitish papillae (the abdominal glands) project from the cloaca. Finally the male performs a few rapid bendings of his body (I have termed these changing of cheeks, see Fig. 46) and dismounts from the female. The male then performs rapid body undulations in front of the female and then deposits a spermatophore if the female nudges his cloaca with her head. The male then moves forward with the female following closely behind him, and the sperm mass of the spermatophore may adhere to the female's cloacal lips as they brush over it. As many as three spermatophores can be deposited in succession.

Humphries (1955) also observed the first two phases of clasping described by Jordan. He noted additionally that during the first phase of clasping the male alternatively applies his left and right cheeks to the female's snout while simultaneously undulating his tail.

Zeller (1890), Jordan (1891) and Humphries (1955) do not describe the characteristic 90° rotation of the male's body (pivoting) following each spermatophore deposition. This remarkable behavior can be appreciated only when the animals are observed from above, and for this reason it probably escaped the notice of these workers.

Male Notophthalmus viridescens possess an amazing array of secondary sexual characters, and all of them have clear functions during courtship behavior. The characters peculiar to the male include horny excrescences on the tips of the hind toes and inner surfaces of the hindlimbs, enlarged hindlimbs, broad tail, glandular pits on the cheeks, and eversible cloacal papillae. The horny growths on the hindlimbs are best developed during the courtship season, and undoubtedly increase the ability of the male to grip the female during capture and during clasping. Tail undulations with the tail reflexed along the side of the body create a water current towards the female's snout which probably serves to waft secretions from the male's everted cloacal papillae towards her nares. The male's cheek pits are firmly applied to or rubbed across the female's nares during the male actions of cheek-pressing and cheek-rubbing which occur during clasping. The cheek pits consist of three to four small depressions arranged in a longitudinal series which lies just below the black stripe proceding posteriorly from the male's eye. Cope (1889) first described these pits. Hilton (1902) found the cheek pits to be epidermal invaginations into which empty several glandular tubulues. During the breeding season the lumen of each tubule is packed with secretion. Rogoff (1927) tested Hilton's hypothesis that the application of these glandular cheek pits to the female's snout during clasping affects her subsequent behavior. Rogoff found that when the male's cheek pits were plugged with gum damar, the female did not remain quiescent and escaped from the male. When the female's nares were plugged, the female did not follow the male, and did not pick up sperm masses from the spermatophores he deposited. Rogoff concluded that secretions from the cheek pits were transferred to the female's nares during clasping and later induced her to follow the male before and after spermatophore deposition. Rogoff's interesting experiments are reported in an exceedingly brief note and could profitably be repeated.

When the male dismounts from the female after clasping, he pauses with his extruded cloacal papillae directly in front of her snout and performs slow, rhythmic tail undulations. The male's tail is simultaneously flexed to one side at the base. Consequently the cloacal papillae lie directly before her, unobstructed by the male's tail. Secretions from these papillae may very well enable the female to orient to the male's cloaca before, during and after spermatophore deposition. The female's snout is closely applied to these papillae when she follows the male at these times, except when the male makes right angle turns (see Fig. 48).

The male's forelimbs should be examined histologically during the breeding season, since during clasping the forelimbs, as well as the cheek, are applied to the female's nares (ie. during forearm-rubbing) (see Fig. 44).

I find that the cheek pits of male *Notophthalmus meridionalis* are remarkably larger than those of *N. viridescens*. In addition, Mecham (1968) finds that *N. meridionalis* males lack the horny growths on the hindlimbs characteristic of *N. viridescens*. The courtship behavior of *Notophthalmus meridionalis* has not been described, but in light of these differences in male characters we can very well expect interesting differences from *N. viridescens* in courtship behavior.

Triturus cristatus

Catalog of male actions.

The following actions are performed by the male while facing towards the female.

A.) SLOW APPROACH The male moves slowly towards the female by walking on all four limbs.

B.) NUDGING The male contacts his snout lightly to the female's lateral body.

C.) SPRINGING FORWARD The male springs forward rapidly with a quick undulation of his tail, lands on the tips of his toes with the limbs extended and may then spring forward again.

D.) LATERAL DISPLAY During the lateral display the long axis of the male's body is essentially perpendicular (within 30° on either side of perpendicular) to the long axis of the female's body. The male's head is turned to one side towards the female's head. The female's head is always within two centimeters of the male, and her snout lies directly opposite his cheek, forearm or anterior body. The male's body is continually arched upward (Fig. 50A, 51A, 52A). While in this posture the male performs the following actions.

E.) MOTIONLESS WITH TAIL CURVED With the palms of the forefeet resting on the substrate, the body is arched upwards with usually only the tips of toes of the hindfeet touching the substrate. The tail is level and slightly curved towards the female laterally (Fig. 50D).

F.) ROCK HINDBODY TOWARDS FEMALE With the forelimbs resting on the substrate and the body arched upward, the hindbody and tail are brought towards the female, and simultaneously the hindbody rotates laterally 45° so that the hindlimb opposite the female is raised far above the substrate (Fig. 50E). The hindlimb nearest the female may touch the substrate with just the toes or may be raised above the substrate. At the start of the action the tail may be undulated slowly with the tail straight, but it is then slightly flexed away from the female and undulated slowly as the hindbody and tail move towards the female.

G.) TAIL-SLAPPING This action is usually initiated after the male has brought his hindbody parallel to the female's body by rocking his hindbody towards her (F). With the forefeet resting on the substrate and the hindlimbs raised above the substrate, the male first turns his head rapidly away from the female (dashed arrow in Fig. 50F) so that instantaneously his body and tail are straight. Then very rapidly the head is swung again towards the female, while the extended tail is thrown away from the female in the opposite direction (see Fig. 50F for the instantaneous position of the male at this point in the action). Then very rapidly the extended tail is swung towards the female (Fig. 50G). During this forceful tail stroke the male's lateral tail frequently strikes the female's lateral body or head or it may pass over the top of her head (as in Fig. 50G). This tail stroke is delivered with such force that it may drive the female's body several centimeters laterally through the water and at the same time drive the male's body upward and laterally in the opposite direction! The entire action is executed in approximately 0.2 second.

H.) TAIL-SNAPPING With the male's body perpendicular to the female's long axis, or nearly so, and with the male's body arched upward, the tail is first coiled on the side towards the female. The tail is then rapidly unfurled (Fig. 50A), and the tail tip proceeds downward forcefully and then rapidly coils on the side away from the female (Fig. 50B). The action is similar to the downward snapping of a wet towel. The tail is then immediately recoiled on the side facing the female, and the action may then be repeated. During the downward stroke and snapping of the tail tip, the hindlimb on the side away from the female is raised upward (see Fig. 50A). As the tail is recoiled on the side facing the female, the male rocks towards the female on his hindlimbs so that his cheek or the insertion of his forelimb may nearly touch the female's snout. As the tail snaps downward the male rocks away from the female's snout about one centimeter. The action may be performed with the male in a handstand or with the hindlimb towards the female resting on the substrate (as in Fig. 50A, B).

I.) TAIL UNDULATION WITH TAIL REFLEXED The distal half of the tail is undulated with the tail recurved on the side facing the female (Fig. 50C).

The following actions are performed by the male while facing away from the female.

J.) MOVING FORWARD WITH S-SHAPED TAIL The male moves forward away from the female with the base of the tail straight but with the distal half of the tail S-shaped. The tail is level and is not undulated. The S-shaped distal tail flexure does not change from a forward to a backward directed S. (Fig. 51C).

K.) STATIONARY WITH S-SHAPED TAIL The male is stationary with the same tail position as in the action just described (J). The vent is adpressed to the substrate. The tail is level. The tail is jerked laterally and rapidly but with small amplitude of movement, so that the tail appears to vibrate. This tail action is intermittent. See Figs. 52B and 53A for dorsal views of this action and Figs 54C and 51D for lateral views.

L.) SPERMATOPHORE DEPOSITION The tail is held at a 45° angle with the tail curved laterally in an S-shape. During spermatophore deposition the tail is motionless. There are no movements of forelimbs or hindlimbs and the planter surfaces of all four limbs rest flat on the substrate. The hindlimbs are drawn up against the sides of the body with the feet directed perpendicular to the long axis of the body (see Fig. 53B for a dorsal view of spermatophore deposition and Fig. 54D for a lateral view).

M.) PIVOTING When pivoting to the right, for example, the male pivots about the right forelimb by stepping laterally with the hindlimbs and turning the head to the right. While pivoting to the right, the tail is reflexed along the right side of the male's body, and slow undulations pass along the reflexed portion of the tail. The body is arched upward, and the hindbody is concave on the side facing the female. The male pivots through approximately 100°. See Figs. 53D through H for a dorsal view of this process, and Figs. 54, 55E through G for a lateral view. Pivoting may, of course, occur to the right or to the left.

Temporal relations (Triturus cristatus)

The male approaches the female slowly and nudges her briefly with his snout. In all subsequent encounters with the female, however, the male approaches by springing forward and swimming rapidly behind and then parallel to her as she moves forward, and the male does not contact her with his snout. As the male moves parallel to the female as she moves forward, he turns his head towards her as he moves forward, and then rapidly springs perpendicular to her and in front of her snout and performs lateral display. On some occasions during such rapid approaches, the male springs perpendicular into lateral display while still parallel to the female. The female then simply continues forward with her path unobstructed. If, however, the male springs into lateral display in front of her, the female will stop or turn and continue forward on a new course.

When the female moves off repeatedly from the male, he may continue to reapproach her, or after several approaches he may simply move away from the female. Most frequently the lateral display is terminated by the female moving away from the male, and with the male then rapidly reapproaching her. If, however, the female remains stationary, the lateral display continues for a considerable period of time (approximately 10-30 minutes).

During the lateral display the male executes a remarkably complex series of actions, but they follow one another in a very predictable way. In Table 12 I show the frequencies of transition between these actions. Consideration of the frequencies of transition between acts taken three at a time, (see Table 13), however, shows that temporal structure is more complex than Table 12 indicates. The sequence motionless with tail curved (E), rock hindbody towards female (F), tail-slap (G) rock hindbody towards female (F), tail-snapping (H), tail undulation with tail reflexed (I), motionless with tail curved (E) ... is repeated over and over again during the lateral display. Sometimes, however, tail-slap (G) followed by rock hindbody towards female (F) is deleted from this sequence so that the sequence becomes E, F, H, I, E ... rather than E, F, G, F, H, I, E ...

A portion of this sequence is shown in Fig. 50; (H, I, E, F, G) or tail-snapping (H) (Fig. 50A and B), tail undulation with tail reflexed (E) (Fig. 50C), motionless with tail curved (E) (Fig. 50D), rock hindbody towards female (F) (Fig. 50E), tail-slap (G) (Fig. 50F through H).

We may note, incidentally, that the sequence of male actions during the male's lateral display is a second-order Markov process. The sequence is stochastic and not deterministic (note that in Table 13 the sequence E, F

Figure 50. Male actions during the lateral display in _Triturus cristatus_. (The male and female are seen in lateral view).

Fig. A. The male (left) begins tail-snapping by rapidly unfurling his tail as he raises the hindfoot on the side away from the female (o sec to 0.41 sec).

Fig. B. The male's tail continues downward and then furls quickly on the side away from the female. (0.50 sec).

Fig. C. The male has refurled his tail on the side facing the female, and is now undulating his tail with his tail reflexed (1.91 sec).

Fig. D. The male now pauses with his tail curved slightly towards the female (7.27 sec).

Fig. E. The male rocks his hindbody towards the female while undulating his distal tail (11.09 sec).

Fig. F. The male is in the process of performing tail-slapping. He has rapidly turned his head away from the female (dotted arrow) and is now swinging his head and tail towards the female very rapidly (solid arrows) (11.18 sec).

Fig. G. The action of tail-slapping continues as the male's tail passes rapidly over the dorsum of the female, and the male's head and body is thrown away from the female (11.23 sec).

Fig. H. The male is just completing tail-slapping and his body is suspended in the water (11.27 sec).

(Taken from a 16mm. movie (22 fps) of one continuous sequence. Total elapsed time is 11.27 seconds).

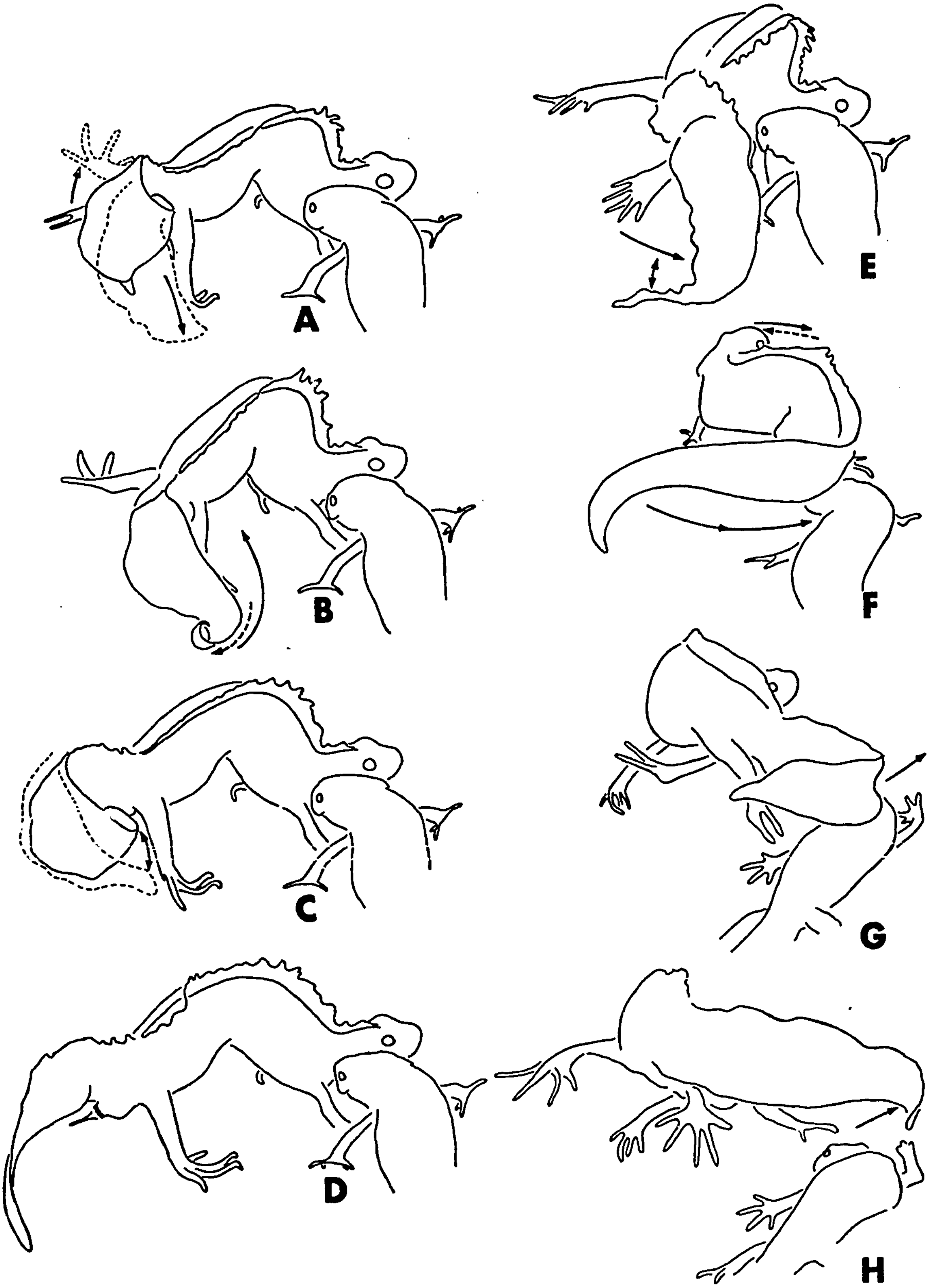
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Table 12. Frequencies of transition between male actions, taken two at a time, during the lateral display of *Triturus cristatus*.

FIRST ACTION	SECOND ACTION E	 F	 G	 H	 I
Motionless with tail curved (E)	0	63	0	0	0
Rock hindbody towards female (F)	0	0	51	73	0
Tail-slap (G)	0	49	0	1	0
Tail-snapping (H)	0	0	1	0	63
Tail undulation with tail reflexed (I)	64	2	0	0	0

Table 13. Frequencies of transition between male actions, taken three at a time, during the lateral display of _Triturus cristatus_.

FIRST ACTION	SECOND ACTION	THIRD ACTION				
		E	F	G	H	I
Motionless with tail curved (E)	E	0	0	0	0	0
	F	0	0	45	17	0
	G	0	0	0	0	0
	H	0	0	0	0	0
	I	0	0	0	0	0
Rock hindbody towards female (F)	E	0	0	0	0	0
	F	0	0	0	0	0
	G	0	48	0	1	0
	H	0	0	1	0	65
	I	0	1	0	0	0
Tail-slap (G)	E	0	0	0	0	0
	F	0	0	0	48	0
	G	0	0	0	0	0
	H	0	0	0	0	1
	I	0	0	0	0	0
Tail-snapping (H)	E	0	0	0	0	0
	F	0	0	0	0	0
	G	0	1	0	0	0
	H	0	0	0	0	0
	I	64	1	0	0	0
Tail undulation with tail reflexed (I)	E	0	60	0	0	0
	F	0	0	1	1	0
	G	0	0	0	0	0
	H	0	0	0	0	0
	I	0	0	0	0	0

(The data on which this and the preceding table are based were taken from motion pictures of a single male _Triturus cristatus_ courting on three separate occasions; 5 March 1970, 12 April 1970 and 22 April 1970). Strictly speaking, the numbers above represent the frequency of joint occurrence of male actions taken three at a time. For example the sequence E, F, G occurred 45 times.

is sometimes followed by G and sometimes by H). But a consideration of the frequencies of actions taken two at a time does not completely specify the temporal sequences which occur. Table 12 specifies a first-order Markov process, but predicts that the sequence F, G, F, G should occur. In fact this sequence does not occur, see Table 13. Instead the sequence G, F is always followed by H.

Tail-snapping occurs in bouts ranging from 1 to 57 successive tail snaps.

When the female has remained continually stationary during the lateral display, the male suddenly terminates the lateral display by turning and moving away from the female with his tail S-shaped (Fig. 51A through C, and Fig. 54A to B). The male then pauses with his vent approximately 1-2 snout-vent lengths in front of the female's snout with his tail S-shaped (action K) (see Fig. 52B for a dorsal view and Fig. 51D and Fig. 54C for lateral views).

If the female does not move forward and nudge the male's tail (as in Fig. 52), the male turns (Fig. 52D) and may reapproach her (Fig. 52D) and perform lateral display again (Fig. 52E). When the male turns back towards the female in such circumstances, the turn is very similar to pivoting, for the male pauses after turning 100° with the tail reflexed on the side facing the female (note reflexion of male's tail in Fig. 52C). In contrast to pivoting, however, the forefoot on the inside of the turn is not held stationary and both forefeet step laterally and forward as the male turns.

If, however, the female does move forward and nudge the male's tail while he is stationary with S-shaped tail (as in Fig. 53A and Fig. 54C), the male immediately lifts his tail 45° and begins spermatophore deposition (Fig. 53B and Fig. 54D). Durations of two filmed spermatophore

Figure 51. Courtship activities in *Triturus cristatus*.

Fig. A. A male in a lateral display in front of the female. The female is behind the male and faces out of the page.

Fig. B. The male has turned away from the female out of lateral display and is now moving forward away from the female. The male's cloacal papillae are whitish and a few of them can be seen on the dorsal posterior margin of the male's vent against the dark background of his tail.

Fig. C. The male continues moving away from the female and begins to flex his tail in an S-shape.

Fig. D. The male is now stationary. He is vibrating his tail slightly with his tail flexed laterally in an S-shape. The male has moved forward until his vent is about two snout-vent lengths in front of the female. The female remains motionless behind him.

A

B

C

D

Figure 52. Courtship activities in Triturus cristatus (dorsal views).

Fig. A. A male in lateral display in front of the female. Notice that only the male's forefeet contact the substrate.

Fig. B. The male has moved out of the lateral display and away from the female (as in Fig.

The male has stopped with his vent one snout-vent length in front of the female's snout. His tail is flexed laterally in an S-shape and vibrates slightly. The female remains stationary.

Fig. C. The female has not contacted the male's lateral tail with her snout. The male is now turning back towards the female.

Fig. D. The male moves rapidly back towards the female.

Fig. E. The male springs again into a lateral display in front of the female.

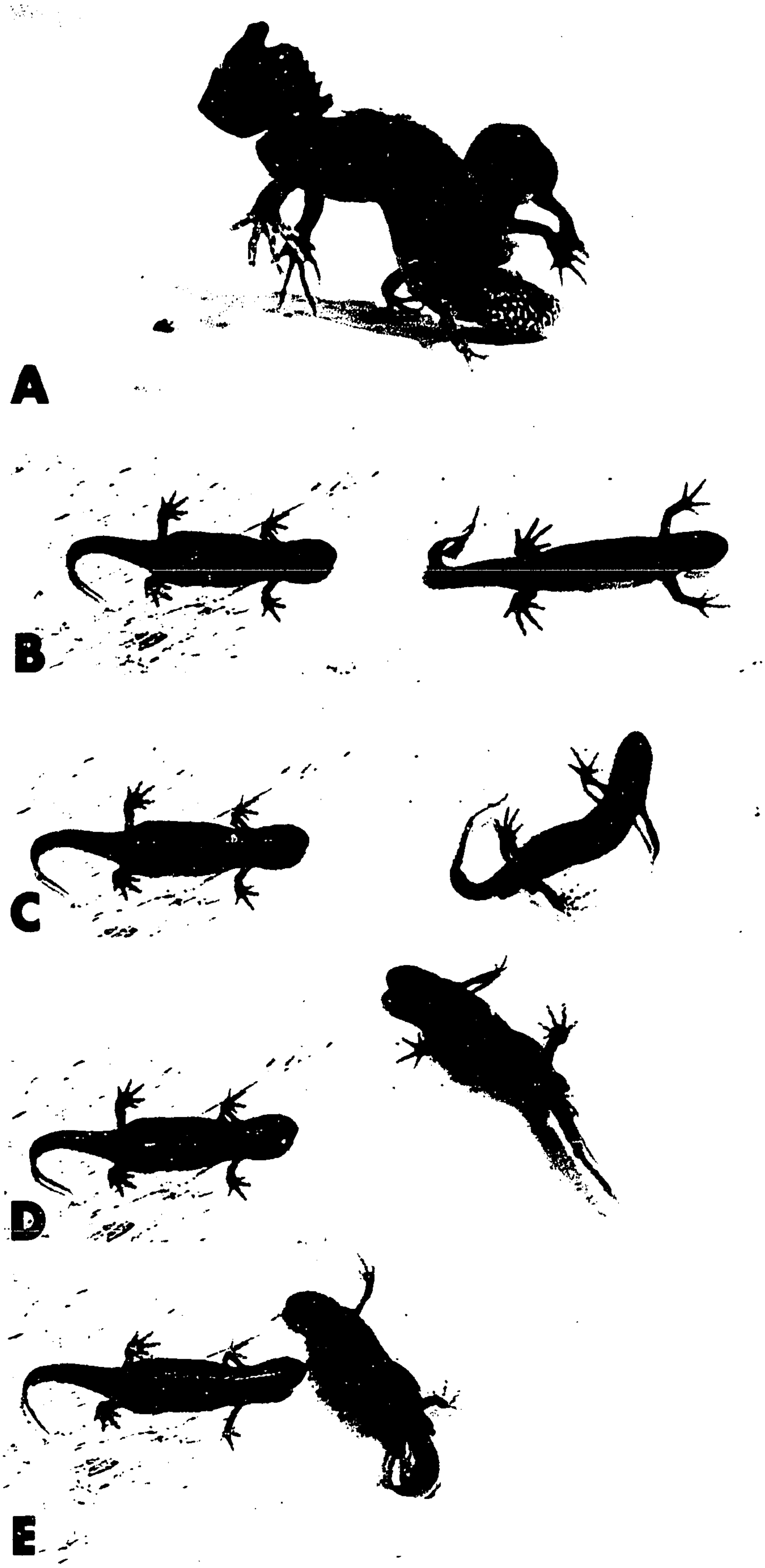
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Figure 53. Spermatophore deposition in Triturus cristatus (dorsal views).

Fig. A. A male has moved out of a lateral display and stopped in front of the female with his tail flexed laterally in an S-shape (as in Figs. 51 and 52). This time, however, the female has moved forward several centimeters towards the male's tail. She has not contacted the male's tail with her snout, and the male's tail is still level.

Fig. B. The female has now contacted the male's tail with her snout. The male has lifted his tail 45° and is now in the process of spermatophore deposition.

Fig. C. The female approaches the male and nudges his cloaca with her snout as the male continues to deposit the spermatophore.

Fig. D. The male is now moving off of the spermatophore by pivoting about his right forelimb (the solid dot provides a fixed point of reference in all figures).

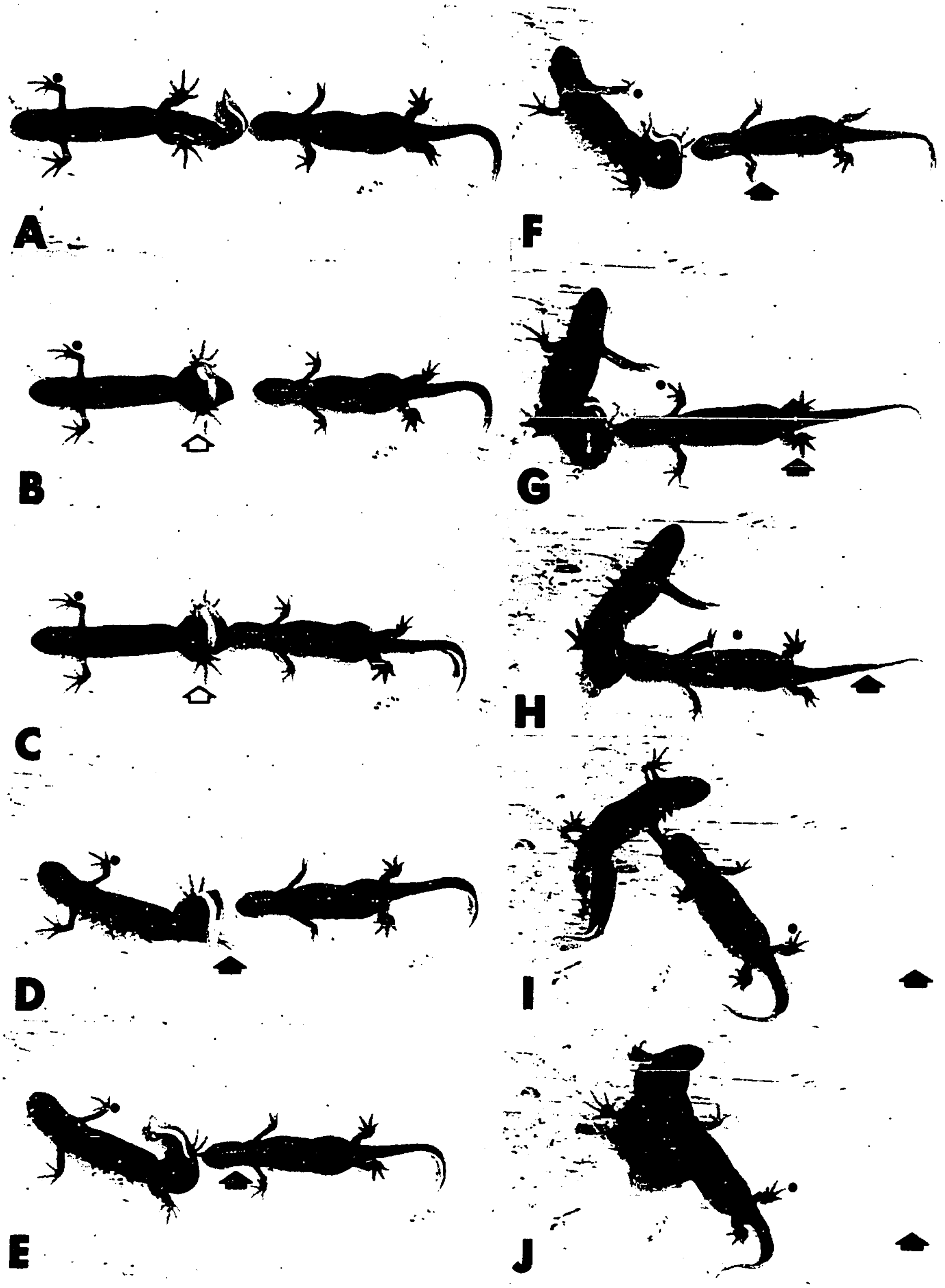
Fig. E. The female moves forward and nudges the male's tail as he continues to pivot. He has now reflexed his tail on the side facing the female. The spermatophore now lies under the female's chin.

Fig. F. The female continues forward on a straight course as the male continues to pivot. The spermatophore lies beneath her anterior body.

Fig. G. The female has stopped with her vent in contact with the spermatophore. The male is stationary in front of her and still undulates his reflexed tail.

Fig. H. The female has now moved forward off of the spermatophore (the solid arrowhead indicates its position).

Figs. I,J. The male now springs into lateral display.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J

Figure 54. Spermatophore deposition and sperm transfer in Triturus cristatus.

Fig. A. A male performing tail-snapping during a lateral display in front of the female.

Fig. B. The male has turned away from the female and is now moving forward. He is beginning to flex his tail laterally in an S-shape.

Fig. C. The male has paused in front of the female and is vibrating his tail with his tail flexed laterally in an S-shape. The female is now approaching the male (0 sec).

Fig. D. The female has contacted her snout to the male's lateral tail. He has raised his tail 45° and is now in the process of depositing a spermatophore (5.3 sec).

(Continued in Fig. 55).

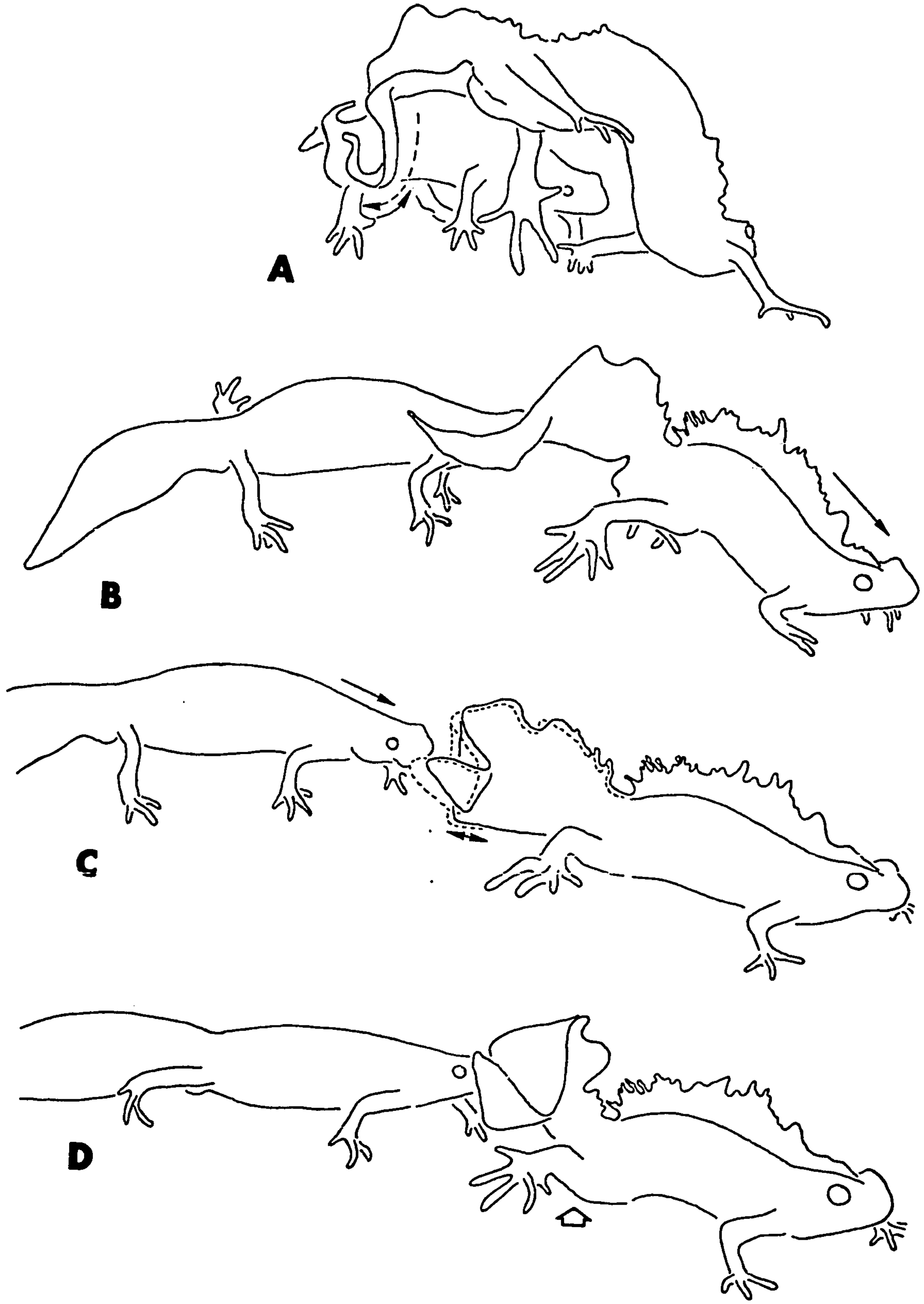
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Figure 55. Spermatophore deposition and sperm transfer in Triturus cristatus. (Continued from Fig. 54).

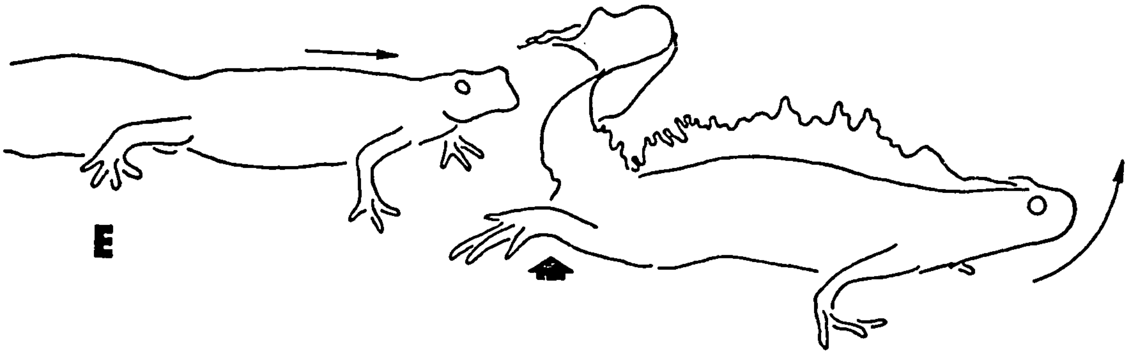
Fig. E. The male has completed spermatophore deposition and is now moving off of the spermatophore by pivoting to the left about his left forelimb. As he pivots he is flexing his tail to the left. The female is now beginning to move forward on a straight course (14.0 sec).

Fig. F. The male continues to pivot about his left forelimb and his tail is now reflexed to the left. The female is moving forward and is contacting her snout to the male's reflexed tail. The spermatophore lies just below her chest. The sperm mass (which lies on the apex of a nearly transparent spermatophore) is visible just above the solid arrow head (18.1 sec).

Fig. G. The spermatophore has contacted the female's vent. She is stationary and the sperm mass has adhered to her cloacal lips. The sperm mass is visible as a small circle just above the solid arrowhead which indicates the position of the spermatophore. The male continues to pivot in front of the female while undulating his reflexed tail (25.2 sec).

Fig. H. The female has successfully removed the sperm mass from the spermatophore. The male has sprung into a lateral display in front of the female and has just executed tail slapping (57.9 sec).

(Taken from a 16mm. movie of one continuous sequence. Total elapsed time from Fig.54 C to 55H is 57.9 seconds).



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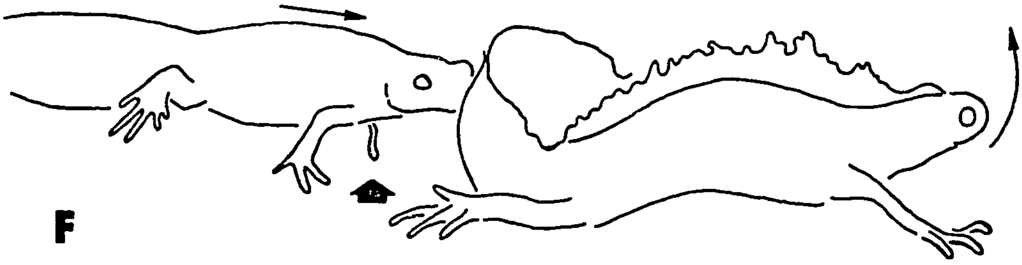

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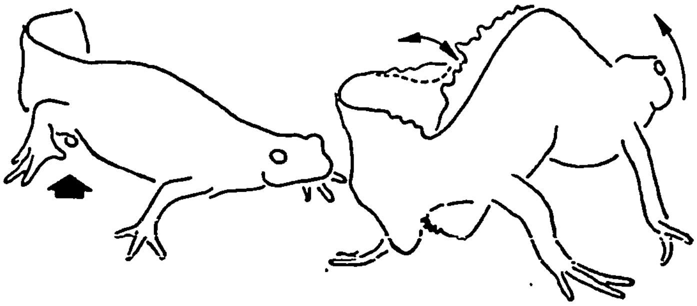

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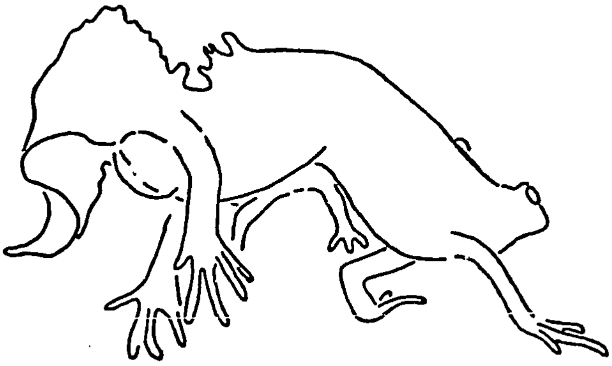


H

depositions, from the time the male lifted his tail 45° until he first began moving off the spermatophore, were 7.7 and 7.8 seconds. During spermatophore deposition the female may contact her snout to the male's tail base or cloaca (see Fig. 53C and Fig. 54D). Spermatophore deposition terminates with the male lifting his cloaca upward and forward off of the spermatophore and pivoting (Fig. 53D and Fig. 55E). During pivoting, lateral stepping by the male with his hindfeet and thus the forward movement of his hindbody in an arc was always preceded by the female touching her snout to the base of the male's reflexed tail. The male pivots forward following each contact, pauses, and pivots forward again with each contact. The male remains stationary, however, after pivoting 100° despite contacts to his tail by the female's snout. At this point the male's cloaca lies approximately one snout-vent length from the spermatophores (see Fig. 53G). The female's snout is now in contact with the male's reflexed tail base, and her cloaca lies in the vicinity of the spermatophore (Fig. 53G). During the female's forward progress (on a straight course while the male pivots in front of her) the spermatophore lies directly in her path, and it may slide along her abdomen as she moves forward (Fig. 55F). If the spermatophore contacts her cloaca (as in Fig. 53G and Fig. 55G), the female lowers her vent upon it with her hindlimbs flexed against the sides of her tail base. The sperm mass on the apex of the spermatophore may then adhere to her cloacal lips and be successfully removed by the female.

Male Triturus cristatus possess a very distinct longitudinal white stripe on the tail (see lateral view in Fig. 51). Notice that in Fig. 53 as the male begins pivoting after spermatophore deposition, his tail is lowered and reflexed on the side facing the female. As he continues to pivot the white stripe on his tail moves forward on a straight course away from the spermatophore and then stops approximately one snout-vent length away from the spermatophore (Fig. 53D to G). It seems very likely that the female orients visually to this white stripe as she moves forward on a straight course over the spermatophore. Triturus cristatus seem to possess a "fail-safe" method for insuring that the female locates the spermatophore. The white stripe of the male's tail marks out the distance and route the female must travel, and in addition the female may orient tactilly to the spermatophore as she passes over the top of it. Artificial obliteration of the male's white tail stripe should lower the probability that the female will locate the spermatophore. Immediately before spermatophore deposition the white tail stripe probably serves an analagous orienting function. When the male moves out of the lateral display and pauses with his vent 1-2 snout-vent lengths from the female's snout, his tail is level and curved in an S. From the female's viewpoint the male appears as a short horizontal white stripe on a dark background. The female may use this visual information when she walks forward and contacts his tail (see Fig. 53A). Therefore obliteration of the male's white tail stripe should reduce the probability that the female will move forward and contact the male's tail, and thereby cause him to initiate spermatophore deposition. To my knowledge these experiments have not been performed.

Regardless of whether the female successfully removes the sperm mass, the male moves immediately into lateral display, with its associated actions, after pausing in the final position of pivoting (Fig. 53I, J and Fig. 55H). If the female remains stationary, the male may deposit a second spermatophore following lateral display, but the deposition of additional spermatophores are subject to the same contingencies outlined above.

Zeller (1890) notes that the lateral display of European Triturus may last for hours. He describes the actions I have called tail undulation with tail reflexed and tail-slapping (Zeller does not note which species of Triturus he observed). Periodically the male may turn away from the female, with his widely gapping cloaca facing towards the female. When the female finally moves towards the male during the lateral display, the male turns away from the female. The female nudges the male's tail, and the male stops, raises his tail and deposits a spermatophore as the female nudges his cloaca with her snout. The male then moves forward again with the female following behind him. The female moves over the top of the spermatophore and lifts the sperm mass out of the gelatinous spermatophore (into which it is loosely inserted) with her cloacal lips. The male may deposit two or three spermatophores in succession, and the female may retrieve more than one sperm mass with her cloacal lips. The male then remains immobile for several minutes (Zeller, 1890).

Zeller (1890) does not describe the characteristic 90° pivoting of the male after spermatophore deposition (see Fig. 53). Neither does Zippelius (1948), Prechtl (1951) or Gauss (1961). Marquenie (1950), however, provides figures of this behavior in Triturus vulgaris (see Thorn, 1968), and I have observed 90° pivoting in Triturus helveticus as well as Triturus cristatus. This male action probably escaped the notice of the workers above because it occurs as the female moves over the spermatophore and because it can be seen clearly only when the animals are observed from above.

Prechtl (1951) performed several experiments which suggest how the lateral display of Triturus males is perceived by the female. During the courtship season females develop a rheotactic response to water currents. The female will turn her head towards an artificially produced water current, and she will orient to it as the direction of the current is changed. On many occasions Prechtl inserted a glass pane between a male and a female as the male performed a lateral display. The female invariably failed to approach the male. Thus tail undulations with the tail reflexed during the lateral display probably enable the female to orient to water currents produced by the male. In addition Prechtl (1951) suggests that the female may respond to visual stimuli, chemical cues in the water current produced by the male, and to the forceful striking of her body during the male action I have called tail slapping.

Prechtl (1951) concluded that the male terminates the lateral display and moves away from the female to initiate spermatophore deposition only when the female approaches the male during the lateral display (see also Grant, 1966). From my observations of Triturus cristatus it was not clear to me that this was the case. Once the male has moved away from the female and paused (as in Fig. 53A), I invariably found that the female must approach and nudge the male's tail before he would deposit a spermatophore.(as in Fig. 53A). Perhaps additional investigations can establish whether a nudging response by the female is required for both the transition from lateral display to moving away from the female and the transition from stationary with tail S-shaped to spermatophore deposition in Triturus cristatus.

Prechtl (1951) observed courtship behavior in three geographic races of Triturus cristatus (T. c. karelini T. c. danubialis and T. c. karnifex) and detected no differences in courtship behavior. My observations are based on the courtships of one male with several different females. From a photograph of this male Thorn (pers. comm.) suggests that he is from Northern Italy (T. c. karnifex). The animals were obtained from a commercial dealer and no locality data was available.

Triturus helveticus

Catalog of male actions.

The following actions are performed by the male while facing towards the female.

A.) SLOW APPROACH The male walks slowly towards the female.

B.) NUDGING The male contacts his snout lightly to the female's lateral body.

C.) SPRINGING FORWARD The male springs towards the female by undulating his tail rapidly, pauses and may then spring forward again.

D.) LATERAL DISPLAY The male faces towards the female with his head a few centimeters from the female's head (see Fig. 56). The orientation of the male's body ranges from facing her head-on to perpendicular to the female's body axis. The following two actions are performed by the male during the lateral display.

E.) TAIL UNDULATION WITH THE TAIL REFLEXED With the tail reflexed on the side facing the female, the male performs very rapid undulations of the distal tail. The male's lateral body on the side facing the female is concave, and the undulating distal tail lies against this concavity (see Fig. 56A, C). All four feet rest on the substrate.

F.) TAIL-SLAPPING The male slowly brings his tail and posterior body towards the female. Fig. 56B shows a male as he begins this action. When the tail is a few centimeters from the female's body, the male rapidly snaps his tail towards the female's head and then rapidly and immediately pulls his tail back and executes tail undulation with his tail reflexed (Fig. 56C). The slapping motion is executed so rapidly that I was unable to see precisely how the action is accomplished. Motion pictures should resolve the action into additional components (as in Triturus cristatus).

The following actions are performed by the male while facing away from the female.

G.) MOVING FORWARD WITH S-SHAPED TAIL The male moves forward away from the female with his tail flexed at the base and curved laterally in an S-shape. The tail shape alternates between a forward and backward S-shape, with the tail level.

H.) SPERMATOPHORE DEPOSITION The male stops and adpresses his vent to the substrate. The tail is directed nearly straight back and held at a 45° angle to the substrate.

I.) PIVOTING The male moves his posterior body away from the spermatophore by pivoting about one forelimb. If the male pivots about the right forelimb, his tail is reflexed on the right side of his body (the side facing the female), and undulates as he moves his posterior body to the left through a 90° arc.

Temporal relations (Triturus helveticus)

This summary is based on one night's observation of one courting pair (from the vicinity of Luxembourg City, Luxembourg).

When first introduced into the same container, the male and female moved about actively. The male then slowly approached the female and nudged her with his snout. As the female continued to move forward, the male moved rapidly along beside her (action C) and then turned in front of her and performed a lateral display. The female then turned and moved away from the male. This sequence was then repeated several times, with the female moving away from the male each time he moved in front of her and began lateral display. Finally the female paused, and the male continued to perform a lateral display in front of her. During the lateral display, the male repeated the sequence, tail undulation with tail reflexed (action E), tail-slapping (action F), tail undulations with tail reflexed (action E), ... many times. During the action (E) called tail undulation with tail reflexed, bouts of very rapid tail undulation (lasting about 10-60 seconds) alternate with shorter periods in which the tail is motionless but still reflexed. The female, meanwhile, remained motionless, but then began to turn her head slowly towards the male. (As the male performed tail undulations with tail reflexed I could clearly see that detritus particles in the water were wafted rapidly along the side of the male's body to the female's head). The male suddenly turned around and paused facing away from the female with his tail curved laterally in an S-shape just in front of the female's snout. The female moved forward and nudged the male's S-shaped tail with her snout. Both animals then moved forward a few centimeters on a straight course with the female nudging her snout to the male's S-shaped tail as the male moved forward in front of her. The male then stopped and deposited a spermatophore. During spermatophore deposition the female paused behind the male with her snout in contact with his tail base. After spermatophore deposition, the male immediately pivoted away from the spermatophore about his right forelimb (see action I). As the male pivoted, the female moved forward on a straight course over the spermatophore with her snout in contact with the male's reflexed and undulating tail. She stopped with her vent over the spermatophore. The male paused in front of her with his body axis now perpendicular to hers and with the female's snout in contact with his reflexed and undulating tail. The female then moved away from the male and the spermatophore, but did not remove the sperm mass from the spermatophore.

The male then repeatedly approached the female and performed lateral display, but the female repeatedly moved away. Finally the female remained stationary. The male continued lateral display and then turned and paused in front of her with his tail S-shaped. The female then nudged his tail and the pair moved forward as described above. The male deposited a second spermatophore and immediately pivoted. The female moved over it and paused (just as described above). She then moved away from the spermatophore, and this time the sperm mass adhered to her cloacal lips. Observations were then terminated, and a few days later the female began laying fertile eggs.

I will make a few comparisons between courtship in _Triturus_ _cristatus_ and _Triturus_ _helveticus_. The lateral display of _T._ _cristatus_ is considerably more complex than that of _T._ _helveticus_ both in terms of the number of elements and temporal structure, but both species share the actions of tail undulation with the tail reflexed and tail slapping. Bouts of tail undulation are much longer in duration than in _T._ _cristatus_, and the male is placed relatively further from the female. In _T._ _helveticus_, males terminate the lateral display by turning around essentially in place so that the male's S-shaped tail lies just in front of the female's snout when the male pauses; whereas _T._ _cristatus_ males move one or more body lengths from the female's snout and then pause. _T._ _helveticus_ males then move forward a few centimeters with S-shaped tail as the female nudges the tail before depositing a spermatophore. _T._ _cristatus_ males deposit a spermatophore without moving forward once the female nudges the male's tail.

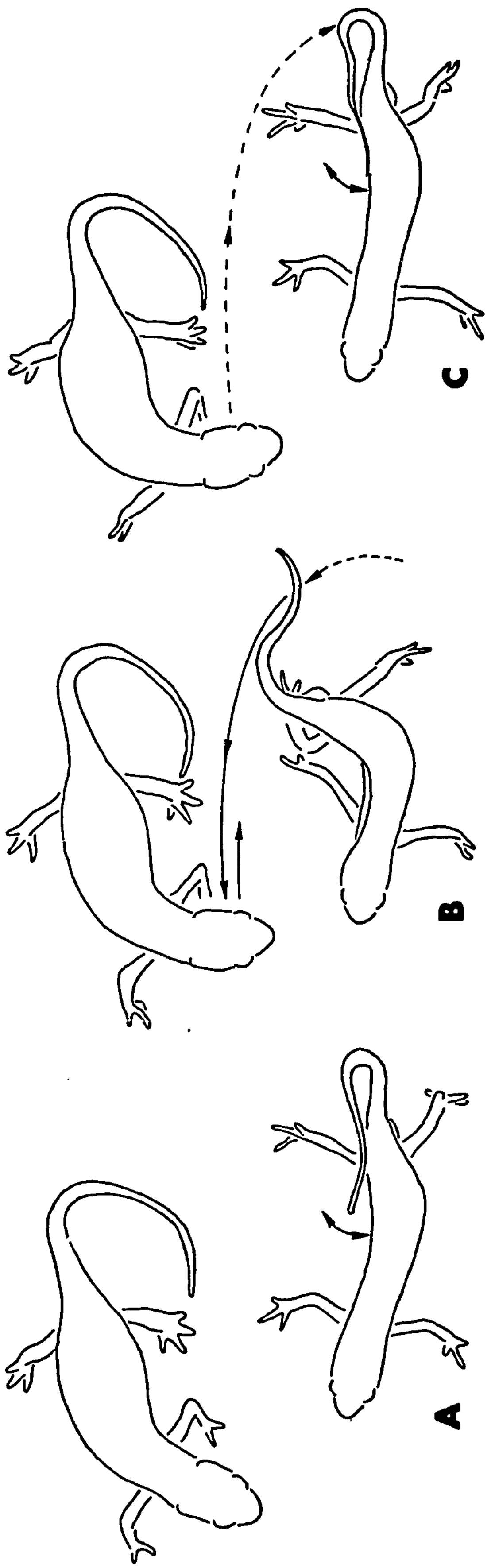
Figure 56. Male actions during the lateral display in *Triturus helveticus* (dorsal views).

Fig. A. The male performs rapid undulations of his distal tail with his tail reflexed towards the female. This tail action produces a water current, and detritus particles in the water were wafted along the right side of the male's body to the female's snout.

Fig. B. The male is slowly bringing his tail and posterior body towards the female. When the male's tail reaches approximately the first arrow head along the solid line, he will rapidly slap his tail towards and against the female's head.

Fig. C. The male has now rapidly moved his tail back along the path indicated with the dotted line and now again performs rapid tail undulations of the distal tail with the tail reflexed towards the female. Notice that from Fig. A to Fig. C the female has gradually turned her head towards the male.

(From a sequence of photographs of a courting pair from the vicinity of Luxembourg City, Luxembourg).


C
B
A

Triturus alpestris

I was able to observe only preliminary courtship interactions in one pair. The male repeatedly approached the female (he may or may not nudge the female's lateral body with his snout), moved rapidly along beside her, and then performed a lateral display in front of the female. During the lateral display the male rested with all four feet on the substrate and intermittently performed rapid undulations of the distal tail with the distal tail reflexed on the side facing the female (see Fig. 57C). The female repeatedly moved away from the male when he performed a lateral display in front of her. The male then reapproached the female and the sequence above began again.

Prechtl (1951) and Eibl-Eibesfeldt (1955) note that during the lateral display in Triturus alpestris the male springs very rapidly upward into a handstand and then quickly resumes tail fanning (ie. tail undulations with the tail reflexed). This very rapid action is executed by a male in a very fine movie of courtship available from the Institut für Wissenshaftlichen Film (Eibl-Eibesfeldt, 1955 is the accompanying literature for this film). As Prechtl (1951) suggests the action is very similar to the first elements in the tail-slapping action of Triturus cristatus (as well as T. helveticus) but the male T. alpestri does not appear to contact the female with his tail.

This same film (see Eibl-Eibesfeldt, 1955) shows a male and female from below during spermatophore deposition and sperm transfer. As the male moves forward with his tail bent laterally in an S-shape, the female nudges the male's tail with her snout, and her snout is then very near the male's everted cloacal papillae. The male's tail also alternates between a forward and backward directed S as he moves forward (as in Triturus helveticus and Cynops pyrrhogaster). It seems likely that the female is orienting to secretions, from the male's cloacal papillae, which are diffused in the water by this alternating tail movement. Unfortunately the film does not show the male's behavior as the female moves over the spermatophore, and it is not clear whether the male pivots about a forelimb after spermatophore deposition as male *Triturus cristatus*, *T. helveticus* and *T. vulgaris* do. The male does move forward with the female following and nudging his tail before spermatophore deposition like *Triturus helveticus* and unlike *Triturus cristatus*.

In 1880 Gasco watched courtship in *Triturus alpestris* through the glass bottom of aquaria and for the first time provided a precise description of how internal fertilization was accomplished in salamanders (see Lataste, 1881 for a translation in French of Gasco, 1880). Gasco does not mention whether the male proceeds forward on a straight course or pivots 90° after spermatophore deposition.

Figure 57. Courtship activities in Triturus alpestris (dorsal views).

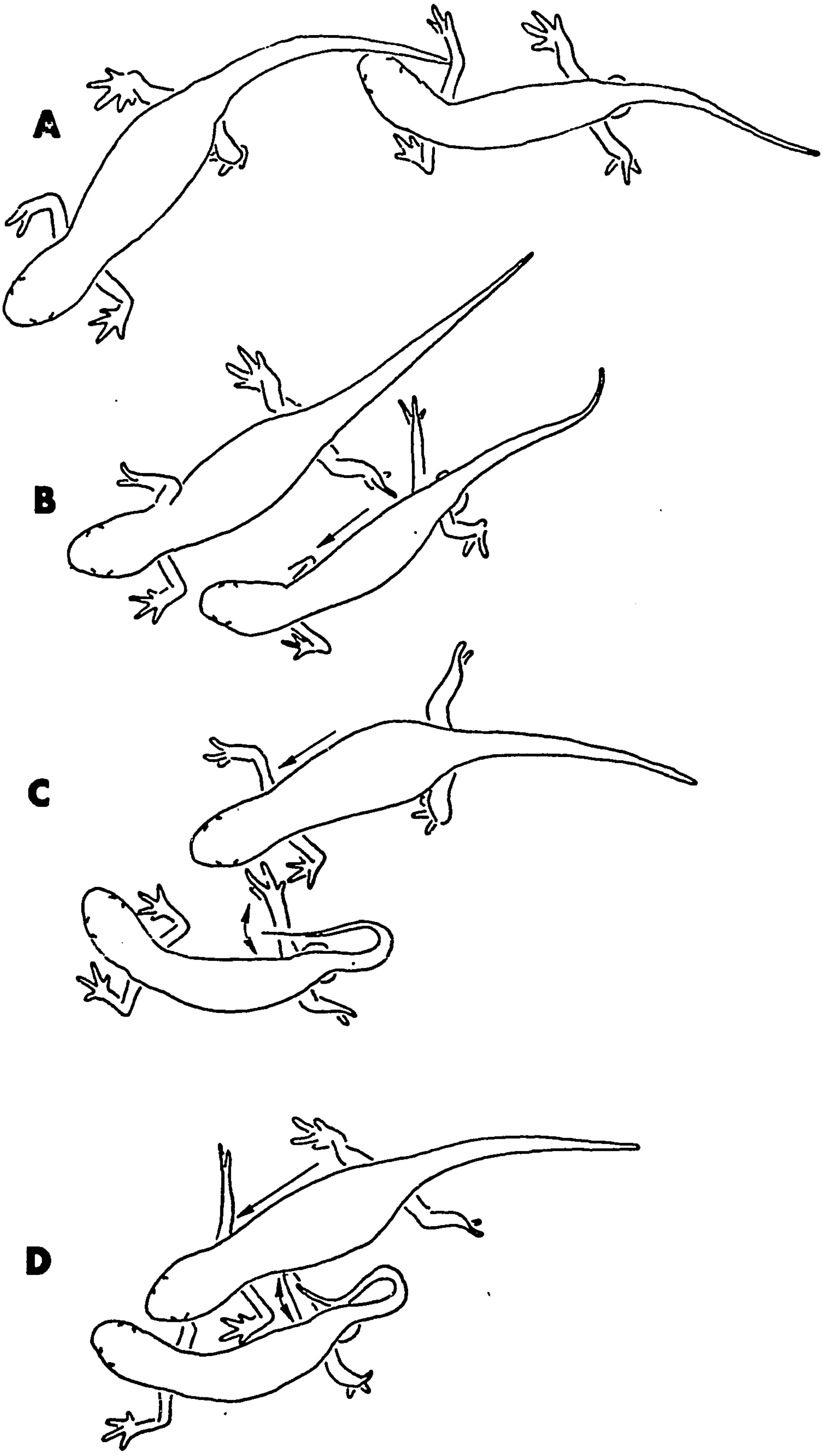
Fig. A. The male (right) has just approached a female and is nudging her tail with his snout.

Fig. B. The male now moves rapidly along beside the female while turning his head towards her.

Fig. C. The male performs a lateral display in front of the female. His tail is reflexed on the side facing the female, and the male is undulating his distal tail rapidly. The female is continuing to move forward.

Fig. D. The female continues to move forward. This female repeatedly moved away from or over the male as he performed lateral display in front of her.

(From photographs of a courting pair from the vicinity of Luxembourg City, Luxembourg. Fig. A and B were taken in sequence. Fig. C and D represent another sequence).


A
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D

Triturus vulgaris

Prechtl (1951) notes tail fanning in *T. vulgaris* is similar to *T. alpestris* and unlike *T. cristatus*. I briefly observed a male *Triturus vulgaris* as he performed tail undulations with his tail reflexed during a lateral display in front of the female (with his body placed some distance from the female as in *T. helveticus* . Bouts of tail undulation were of long duration and the tail undulations were very rapid as in *T. alpestris* and *T. helveticus*.

As in *Triturus alpestris*, male *T. vulgaris* periodically jerk the hindbody upward in the water rather than slap the female with the tail as in *T. cristatus* (Prechtl, 1951).

After spermatophore deposition the male pivots 90° (Marguenie, 1950; see figures in Thorn, 1968).

Triturus boscai

Krefft (1937) describes, in a remarkably confusing way, the courtship behavior of captive Triturus boscai. Krefft notes that the male performs tail-fanning (presumably with the tail recurved towards the female) and delivers blows to the female which may throw her slightly upward in the water. He also describes an unusual position in which the male's tail is raised at approximately a 90° angle with the tail tip undulating.

Prechtl (1951) notes that the male initiates tail-fanning as the male rests next to the female so that his snout nearly reaches the tail base of the female and the female's snout nearly reaches his tail base. The male then reflexes the distal half of his tail along the proximal half of his tail and begins tail-fanning with the tip of his tail directly in front of the female's snout. Bouts of tail undulation are particularly long in this species and last for approximately one minute. The male may also slap the female on the snout or flank with his tail as in Triturus cristatus. The lateral display may last for hours before a spermatophore is deposited.

Triturus vittatus

Oeser (1951) observed courtship behavior in a captive pair of Triturus vittatus. The male approached the female laterally and undulated his tail with the tail recurved towards the female. The male then executed a vertical, vibratory, trembling movement of his head. This head movement produced a water current which struck against the female's head. A few seconds later the male snapped his anterior body against the female, whacking her firmly on the flank. Spermatophore deposition and sperm transfer were not observed.

Cynops pyrrhogaster (Hiroshima samples)

Catalog of male actions.

The following actions are performed by the male while facing towards the female.

A.) NUDGING The male contacts his snout lightly to the female's lateral body.

B.) SLOW APPROACH The male moves slowly forward towards the female.

C.) SPRINGING FORWARD The male springs rapidly forward, undulating his tail rapidly as in swimming, and then lands with all four feet on the substrate.

D.) LATERAL DISPLAY (see Fig. 60A) The hindbody is curved laterally presenting a concave surface towards the female's head. The tail is reflexed with the tail tip against the concave surface of the hindbody. The male extends his hindlimbs, but all four feet rest on the substrate. The head is bent laterally towards the female at a 10°-45° angle. The axis of the male's body lies within 30° on either side of perpendicular to the axis of the female's body with the male's snout within two centimeters of the female's snout.

E.) TAIL UNDULATION WITH TAIL REFLEXED Very rapid undulations of small amplitude are restricted to the distal half of the male's reflexed tail (Fig. 60A). Tail undulations always occur in short bursts of approximately 5-10 seconds in duration.

F.) CHEEK-PRESSING By leaning forward towards the female on the forelimbs during the lateral display, the male may firmly press his cheek against the female's snout.

G.) BACKING UP The male backs up quickly with tail straight or reflexed.

H.) BITING The male grasps the female's lateral head, body or tail firmly with his mouth and may maintain the grasp for a few minutes.

The following actions are performed by the male while facing away from the female.

I.) MOVING FORWARD WITH S-SHAPED TAIL The male moves forward with tail level and curved in an S-shape. As the male moves forward, the tail base slowly undulates laterally so that the tail shape alternates between a forward and a backward facing S (Fig. 58C, 58D, 59A, 59D).

J.) STATIONARY WITH S-SHAPED TAIL This action is the same as the preceding action except the male is stationary.

K.) STATIONARY WITH TAIL EXTENDED The male is stationary with hindlimbs extended laterally (Fig. 58E) and with vent resting on the substrate (Fig. 59B, 59E). The proximal half of the tail is extended straight backward and raised at approximately a 45° angle, while the distal half of the tail is slightly curved (Fig. 58E, 59B, 59E).

L.) SPERMATOPHORE DEPOSITION When spermatophore deposition occurs it follows the action just described (K) with the male maintaining the same posture. All four feet are held motionless during spermatophore deposition. The male lifts off of the spermatophore by extending the hindlimbs and lifting the tail (Fig. 59C, 58G).

M.) PIVOTING While holding the right, for example, forelimb stationary, the male moves the hindbody to the left by stepping laterally with the hindlimbs. Thus the male pivots, in this instance, about the right forelimb.

Temporal relations (*Cynops pyrrhogaster* (Hiroshima))

When a pair is introduced into the same container, the first few reactions of the male to the female is to approach her slowly and nudge the female lightly along her tail, body or head. In all subsequent approaches by the male, however, the male springs forward rapidly behind and then parallel to the female without contacting her as she moves forward. As the male moves anterior to the female's head, he turns his head and body rapidly towards her and performs lateral display (Fig. 58B). If the female remains stationary, the male performs bursts of rapid tail undulations with the tail reflexed which alternate with intervals with the tail motionless. The male may lean towards the female and press his cheek against her snout and then lean away from her again. In these circumstances some females repeatedly move away from the male. If the female turns posteriorad along the male's body axis, the male may back up quickly and then resume lateral display. If she moves away from him either anteriorad or over the top of him, the male springs forward behind and along beside her and again springs into lateral display in front of her. If the female nudges the male's cheek as he performs lateral display (Fig. 58B), the male suddenly turns away from her and moves forward with S-shaped tail (Fig. 58C). If the female does not follow the male and does not nudge his S-shaped tail, the male pauses with S-shaped tail and then turns and reapproaches her. Forward progress by the male with S-shaped tail is dependent upon contact to his tail. If the female gives intermittent contact to his tail, the male moves forward with S-shaped tail and then pauses following each contact as it is broken. If the female moves forward continuously nudging his tail (as in Fig. 58D or 59A), the male too moves forward continuously. After several such contacts to his tail by the female's snout, or a short period of continuous contact, the male suddenly moves forward and pauses while straightening the proximal half of his tail and with his vent two to three

Figure 58. Courtship activities in *Cynops pyrrhogaster* (dorsal views).

Fig. A. A male (left) is just beginning to move in front of the female and into a lateral display.

Fig. B. The male now is performing a lateral display in front of the female with his tail reflexed on the side facing the female. His distal tail is undulating rapidly. Note the complex lateral flexure of his body. The female has turned her head towards the male's head.

Fig. C. The female has nudged the male's cheek with her snout. The male has turned away from the female and is now moving forward with his tail flexed laterally in an S-shape. The female follows behind him and nudges his tail with her snout.

Fig. D. A male moves forward with his tail flexed in an S-shape as the female (left) follows behind him and nudges his tail with her snout.

Fig. E. A male has stopped, extended his tail backward and is now depositing a spermatophore. The female nudges his tail.

Fig. F. The male continues to deposit the spermatophore as the female now nudges his tail base.

Fig. G. The male is lifting his vent off of the spermatophore.

Fig. H. The male moves forward on a straight course away from the spermatophore and again flexs his tail in an S-shape. The female is moving forward behind the male, and the spermatophore lies just below her neck.

Fig. I. The female continues forward behind the male. The spermatophore lies beneath her hindbody. The male has paused, momentarily, in front of the female and continues to undulate his tail with his tail flexed in an S-shape.

Fig. J. The female is now turning and moving away from the male and the spermatophore.

(These animals are from Hiroshima, Japan).

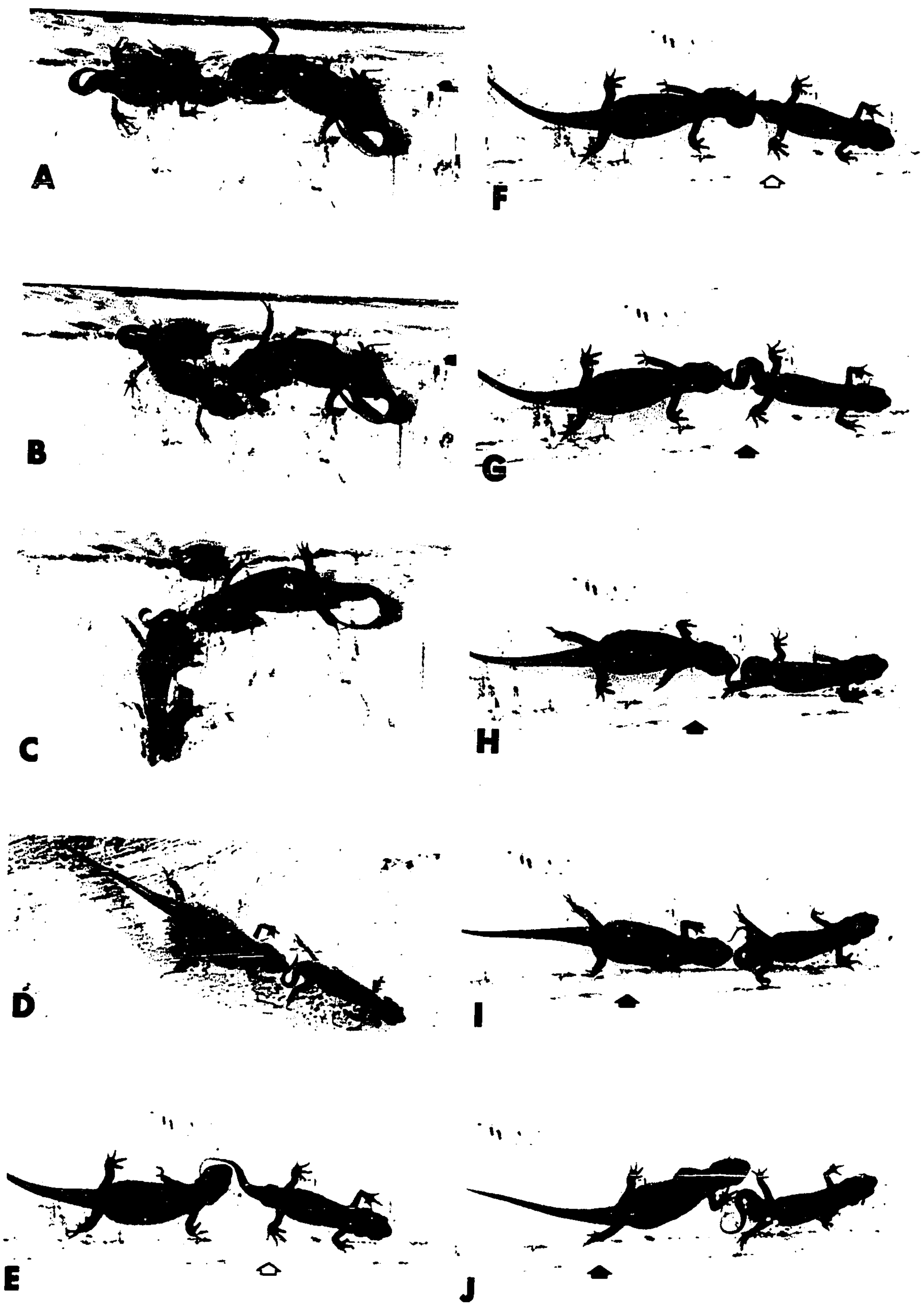
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Figure 59. Successive spermatophore depositions in *Cynops pyrrhogaster*

Fig. A. A male moves forward in front of a female (right) with his tail flexed in an S-shape as the female nudges his tail and follows behind him (0 sec).

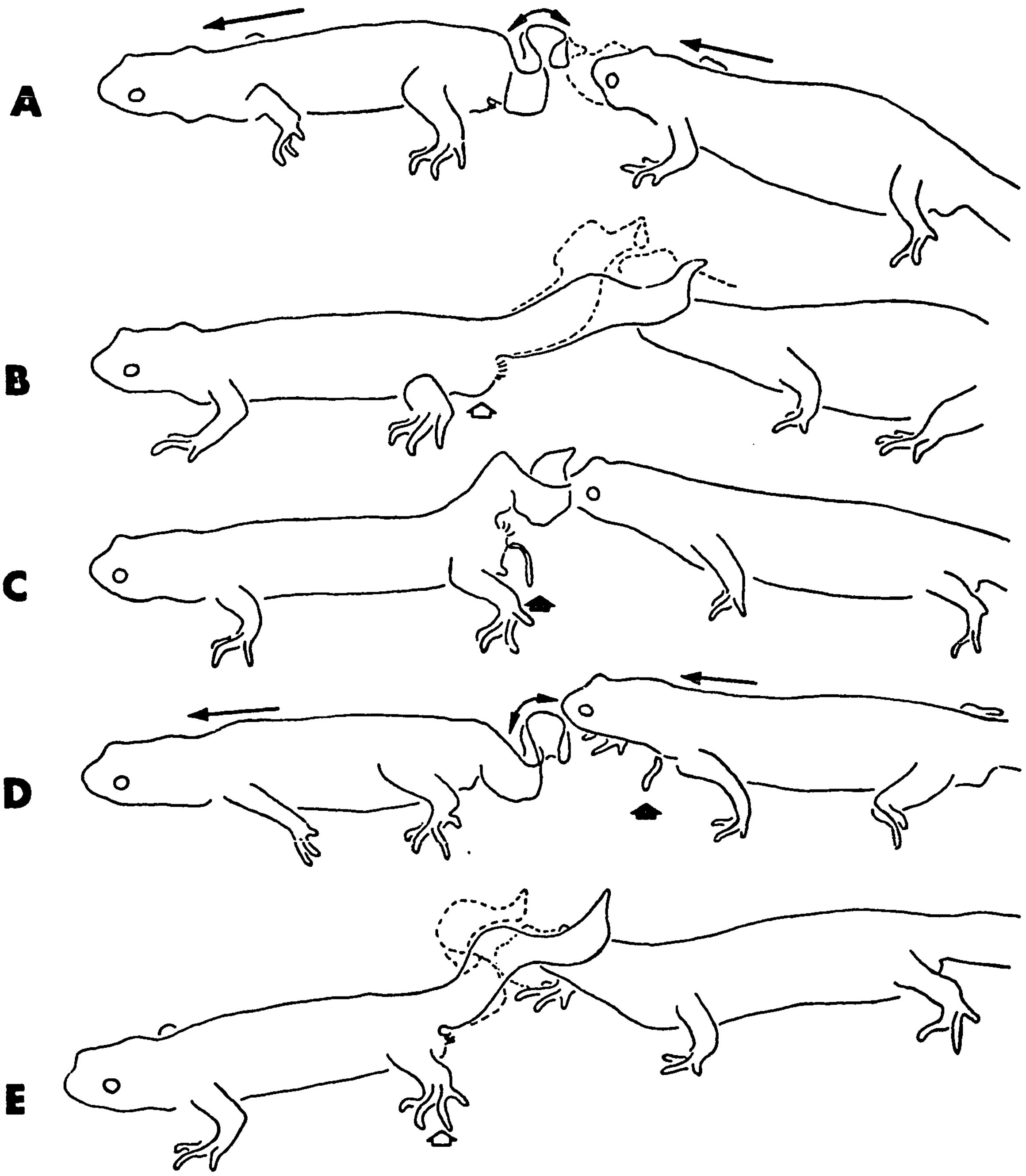
Fig. B. The male has stopped in front of the female, extended his tail backward and raised his tail at a 45° angle. He is now depositing a spermatophore. The female pauses behind the male and nudges his tail with her snout. The male's cloacal papillae are visible on the posterior margin of the male's vent (4.2 sec).

Fig. C. The male is in the process of lifting his vent off of the spermatophore. The sperm mass is visible as an elongate vertical cylinder. The nearly invisible spermatophore lies just above the solid arrow head and is not shown (9.9 sec).

Fig. D. The male moves forward on a straight course away from the spermatophore and again flexes his tail in an S.-shape. The female follows behind him and nudges his tail. The sperm mass lies just below the female's neck as she moves forward (11.2 sec).

Fig. E. The male has again paused and is now depositing a second spermatophore. The female has stopped behind him and nudges his tail with her snout. She has passed beyond the first spermatophore (23.0 sec).

(Taken from a 16mm. movie of one continuous sequence. The total elapsed time is 23.0 seconds. The animals are from Hiroshima, Japan).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E

centimeters in front of the female's snout (Fig. 58E, 59B). If the female's snout contacts his tail (as in Fig. 58E and 59B), he remains stationary and deposits a spermatophore without changing his posture; but if she fails to contact his tail, the male turns and reapproaches her without depositing a spermatophore. During spermatophore deposition, the female remains stationary behind the male nudging his extended tail with her snout (eg. Fig. 58F). After spermatophore deposition the male moves forward on a straight course with S-shaped tail (Fig. 59D and Fig. 58H), and as before he continues forward only if the female contacts his tail with her snout. As the female moves forward behind him, the spermatophore may contact her ventral body (Fig. 59D). I never observed females pausing over the spermatophore, even when it contacted the female's vent. Instead the female moves forward continuously over the spermatophore, and the sperm mass may then adhere to the female's cloacal lips and become detached from the spermatophore base. In other instances, however, the sperm mass adheres to the female's forelimbs, body, hindlimbs or tail or is not detached from the spermatophore base. Two or more spermatophores may be deposited in succession as the male moves forward intermittently on a straight course (eg. Fig. 59), but the deposition of each additional spermatophore is subject to the contingencies outlined above.

If the female moves her snout anterior to the male's vent while he moves forward with S-shaped tail, he pauses with S-shaped tail. If the female then moves away from and behind him, the male may pivot through 90°-180°, pause and then reapproach the female. Pivoting was never observed, however, immediately after spermatophore deposition.

On several occasions males bit females. The male seemed to bite the female only after she persistently moved away from him. Males rapidly approached such fleeing females and seized them with the mouth. Upon release such females quickly darted off away from the male. Approach to the female leading to biting was often repeated several times in sequence, and males did not vacillate between approaches leading to lateral display and approaches leading to biting. Sometimes females were bitten when they repeatedly fled from the male after successfully removing sperm masses from his spermatophores. Klinge (1915) also observed a male biting a female after several spermatophore depositions had occurred. Perhaps this behavior is used by males to chase away females with which further courtship is unprofitable.

The preceding observations were made on animals from Hiroshima, Japan. Kawamura and Sawada (1959) studies courtship behavior of Cynops Pyrrhogaster from three widely separated populations in Japan (Hiroshima, Kagoshima and Sasayama). Courtship behavior was very similar in all three populations, except that males from Sasayama differed markedly from males from Hiroshima and Kagoshima in the position assumed during the lateral display. Sasayama males grasp the female's dorsum by putting one hindlimb on the female's forelimb or scapular region (see Fig. 60C, after Kawamura and Sawada, 1959), while males from Hiroshima and Kagoshima assume a position with the body nearly perpendicular to the female and do not contact her with the hindlimb (Fig. 60A, 60B). In all three populations the male intermittently performs rapid tail undulations with the tail reflexed on the side facing the female, and the male's head is turned sharply towards the female.

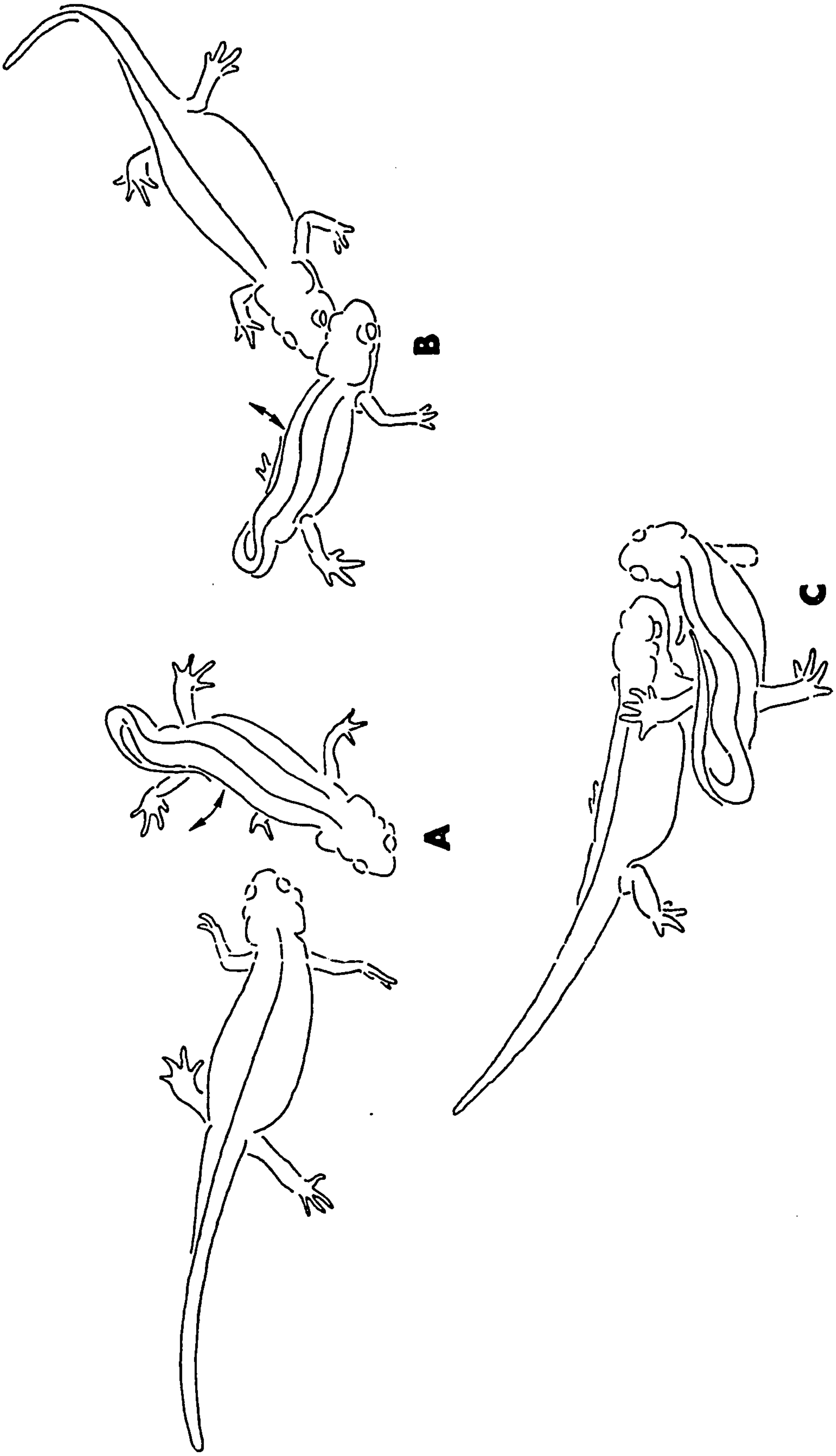
Sawada (1963b) investigated courtship behavior in Cynops pyrrhogaster from seven localities in Japan and found that males from Sasayama frequently placed one hindlimb on the female's scapular region during the lateral display, and so did males from Atsumi. Sawada (1963a) also found geographic variation in a variety of morphological characters (total

Figure 60. The lateral display in Cynops pyrrhogaster from three localities in Japan.

Fig. A. A male from Hiroshima, Japan performs a lateral display in front of a female (left) from the same locality. The male does not contact the female with his forelimbs or hindlimbs. The male is undulating his distal tail.

Fig. B. A male from Kagoshima, Japan performs a lateral display in front of female (right) from the same locality. As in males from Hiroshima, the male does not contact the female with his forelimbs or hindlimbs (after Kawamura and Sawada, 1959).

Fig. C. A male from Sasayama, Japan performs a lateral display in front of a female (left) from the same locality. The male grips the female's scapular region with his left hindfoot (after Kawamura and Sawada, 1959).


B
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C

length, tail length, shape of the male's tail, limb length, head length and width, ventral and dorsal coloration) using specimens from a large number of localities in Japan. He found that the courtship difference above coincided with geographic variation in morphology.

Tsutsui (1931) observed courtship behavior in animals from near Kyoto and thus in animals of the Sasayama geographic race (Kawamura, pers. comm.). Tsutsui describes and figures the male clasping the female's scapular region during the lateral display. He notes that the male may simultaneously place one forelimb on the dorsum of the female's snout. Prechtl (1951) and Klinge (1915) also observed a male holding the female with a forelimb and a hindlimb, but Freytag (1970) found that the male's forelimb was placed on the substrate in front of the female's snout rather than upon her snout. Presumably the observations of Prechtl, Klinge and Freytag were also based on animals of the Sasayama race. The position of the male's forelimb is apparently more variable than the position of the male's hindlimb during the lateral display in this geographic race of _Cynops pyrrhogaster_.

My observations on courtship behavior in animals from Hiroshima are in good agreement with the studies of Kawamura and Sawada (1959) and Sawada (1963b) on this race. With the aid of motion pictures I have provided some clarifications on the positions and actions performed during courtship, and I have provided additional observations on variability in behavioral sequences.

Kawamura and Sawada (1959) and Sawada (1963b) felt that the male turned and moved away from the female and initiated spermatophore deposition if the female nudged his neck or shoulder during the lateral display. I agree that this female behavior is probably used by the male as an index of female receptivity. Females which so nudged the male were also females which followed the male during and after spermatophore deposition. Sawada (1963b) found an interesting instance of geographic variation in this female behavior. Females from Kanto frequently bite the male's neck, although they may also nudge the male's neck with the snout, while females from all other races only nudge the male's neck during the lateral display. In addition Kanto females usually perform biting actions on the male's S-shaped tail while following him in the context of spermatophore deposition, rather than simply nudging his tail as in the other races.

The remarkably elaborate spermatophore of this species is almost completely transparent and so special pains (such as vital staining) are required to see it. This has caused some observers (Tsutsui, 1931; Kawamura and Sawada, 1963 and Sawada, 1963b) to state or imply that only a sperm mass is deposited, despite the fact that Zeller (1905) provided a very fine and accurate illustration of the spermatophore's structure.

Cynops pyrrhogaster ensicauda

Gerlach (1934) observed courtship in captive animals and reports that the male never clasps the female in any way. As the male approaches the female, he performs tail fanning. Presumably tail fanning is executed with the tail recurved, since Gerlach notes that the courtship is very similar to European *Triturus*. The male moves in front of the female as she moves forward and blocks her path. He assumes a position facing towards either her head or tail, either diagonal to her head or parallel to her, and fans constantly with his tail. The female, meanwhile, remains motionless. During spermatophore deposition the male's cloaca faces the female, and the male extends his posterior body upward as he discharges the spermatophore. After spermatophore deposition the male moves forward slowly with the female following behind him. The female's cloaca is everted and cone-shaped, and she removes the sperm mass from the spermatophore as she moves over it.

Paramesotriton hongkongensis

Catalog of male actions.

The following actions are performed by the male while facing towards the female.

A.) SLOW APPROACH The male moves slowly towards the female.

B.) SPRINGING FORWARD The male moves forward in rapid bursts towards the female by springing forward with a short bout of forceful tail undulations.

C.) NUDGING The male contacts his snout lightly to the female's lateral or dorsal body.

D.) LATERAL DISPLAY The male forces towards the female's head with his body axis within a region 45° on either side of perpendicular to the female's long axis. The male's head is 1-3 cm from the female's head, and his hindbody forms a lateral concavity on the side facing the female. The distal half of his tail is reflexed against the side of his body facing the female. The male's cloacal papillae are everted during the lateral display. The following two actions are executed during the lateral display.

E.) TAIL UNDULATION WITH THE TAIL REFLEXED The male performs rapid tail undulations of the distal half of his tail with the tail reflexed and held against the side of his body facing the female. These undulations are given in bouts lasting a few to several seconds and are separated by shorter periods during which the tail is motionless but still reflexed. I was able to see the cloaca of one male as a reflection on the glass substrate of the aquarium during the lateral display. With the onset of each bout of tail undulation, the male's posterior cloaca opens widely so that the cloacal papillae spread out laterally from his vent. The cloacal lips then close slightly at the termination of each bout of tail undulation.

F.) LEANING TOWARDS THE FEMALE During the lateral display the male may lean slightly towards the female on his forelimbs, but he does not appear to contact or rub his cheek on the female's snout.

The following actions are performed by the male while facing away from the female.

G.) MOVING FORWARD WITH S-SHAPED TAIL The male moves forward with his tail curved laterally, at the base, in an S-shaped figure. The tail is level. While curved in an S-shape, the tail is jerked slightly laterally and the S-shape also alternates between a forward and a backward directed S. The cloacal papillae are strongly everted.

H.) STATIONARY WITH S-SHAPED TAIL Same as the preceding action, but the male is stationary.

I.) SPERMATOPHORE DEPOSITION The male pauses and adpresses his vent to the substrate. The tail is extended straight backward with only a slight S-shaped lateral curvature, and the tail is raised at nearly a 45° angle to the substrate. The male's limbs are motionless during spermatophore deposition. The male lifts off of the spermatophore by extending his hindlimbs, lifting his vent upward, and then immediately curving his tail again in an S-shape with the tail level.

Temporal relations (*Paramesotriton hongkongensis*)

When first introduced into a tank with a female, the male approaches her slowly and then nudges her body lightly with his snout. The male may follow behind the female, or beside her, and briefly nudge her with his snout. He then springs forward rapidly along beside her, turns in front of her head and immediately stops and performs a lateral display (see action D together with actions E and F). If the female stops and remains stationary, the male continues to perform bouts of tail undulation during the lateral display. If the female continues moving forward or departs from the male, he turns and follows her by springing forward and then reinitiates lateral display in front of her. If the female actively nudges the male's cheek during the lateral display, or if she contacts his cheek by simply moving forward, the male immediately turns away from her and pauses just in front of her snout with his tail S-shaped (see action H). If the female fails to contact his S-shaped tail, the male turns, reapproaches the female and reinitiates the lateral display.

On one occasion the female nudged the male's S-shaped tail with her snout as he paused facing away from her. The male and female then moved forward for about five centimeters on a straight course with the female nudging the lateral surface of the male's S-shaped tail with her snout as the male moved forward in front of her (see action G). The male then stopped and deposited a spermatophore (see action I). During spermatophore deposition the female paused momentarily behind the male with her snout in contact with his anterior tail. After spermatophore deposition, however, the female moved forward along beside the male and to one side of the spermatophore. The male immediately followed her and reinitiated a lateral display.

The females I observed repeatedly failed to nudge the male's S-shaped tail when the males turned away from them, out of the lateral display, and paused. On one occasion I reached into the tank at this point and gently contacted the male's tail on the posterior facing surface of the S-shape with the eraser of a pencil. The male immediately moved forward several millimeters with S-shaped tail (action G) and paused once again. With each new contact to his tail, the male moved forward a few millimeters and paused. By repeatedly contacting the pencil eraser lightly to his tail, I caused the male to move forward intermittently for about eight centimeters. The male then stopped and deposited a spermatophore. The female was now on the opposite side of the tank. During spermatophore deposition, I held the eraser lightly in contact with his anterior tail. As the male began to lift off of the spermatophore, I again began to lightly "nudge" his S-shaped tail with the eraser. As before, the male moved forward on a straight course with his tail S-shaped. He then paused and I removed the pencil from the tank.

Sperm transfer has not yet been observed in this species. The two observations above, one with a participating female and one with a simulated female, suggest that the male does not pivot and displace his hindbody through an arc of 90° after spermatophore deposition. In this respect Paramesotriton hongkongensis may resemble Cynops pyrrhogaster rather than other newts (eg. Triturus), which pivot after spermatophore deposition, but additional observations are needed to substantiate this point.

The postures assumed during the lateral display (the position of the tail, a lateral turning of the head towards the female and the complex curvature of the body axis of the male) are very similar to Cynops pyrrhogaster. In addition, like Cynops, Paramestotriton hongkongensis males do not perform tail slapping during the lateral display (as Triturus males do). I never observed male Paramesotriton hongkongensis clasping the female with their limbs or tail.

Courtship is probably nocturnal in this species. Males consistently initiated courtship when placed with females at night (in dim light), but they did not initiate courtship during the day.

I sometimes observed males performing tail undulations with the tail reflexed when they were not in the proximity of a female. I am uncertain about the function of this behavior.

Romer (1951) observed courtship on one occasion. He notes that the male's tail was folded and vibrated as in other aquatic salamandrids. This observation probably refers to the action I have called lateral display.

Paramesotriton deloustali

Dao Van Tien (1965) found two pairs of courting animals on January 13. In each case the female's snout was adpressed to the male's cloacal region with the male's body curved in a tight arc in front of the female's head. Dao Van Tien (1965) provides a figure of a pair in this position. It is not clear whether the male is clasping the female or simply curved in front of her head. The animals appeared to remain motionless in this posture for a few hours.

Neurergus strauchii

Schmidtler and Schmidtler (1970) observed courtship behavior when a recently captured pair of animals was placed in an aquarium. The male repeatedly approached the female's head and assumed a position with his body forming an acute angle to her's. In this position the male recurved his tail and fanned his tail vigorously towards the female's flank. Whenever the female swam away, the male reapproached her and again performed tail-fanning with his tail recurved while facing the female. This cycle of events apparently lasted for a few hours. Spermatophore deposition and sperm transfer were not observed. At no time was any body contact (eg. clasping with the limbs) observed.

During the breeding season sexually active males possess a series of silver-blue spots on the sides of the tail, and the cloacal lips are very swollen (Schmidtler and Schmidtler, 1970).

Pleurodeles waltl

Catalog of male actions

The following actions are performed by the male while facing towards the female and not clasping her.

A.) SLOW APPROACH The male moves slowly towards the female. When parallel or at an oblique angle to the female during slow approach, the male turns his head to the side towards the female.

B.) DASHING FORWARD The male dashes forward rapidly. The forelimbs may be widely spread and directed forward and upward (as in Fig. 61C).

C.) NUDGING The male contacts the tip of his snout lightly to the female's body or tail (Fig. 63A). Usually this is accomplished by a slight forward rocking which brings the male's snout in contact with the female's body, and then the male rocks slightly away from her, breaking contact.

D.) STATIONARY WITH HEAD TURNED TOWARDS FEMALE While stationary the male turns his head sharply to one side towards the female (Fig. 63B, C). The male may repeatedly rock towards the female slightly on his forelimbs and contact his lateral snout to her body, head or tail and then rock away breaking contact.

E.) TAIL UNDULATION WITH TAIL REFLEXED While in the position described in the preceding action (D), the male may reflex the distal portion of the tail along or perpendicular to the proximal tail and perform a single, short burst of tail undulation with the distal tail (Fig. 63B).

The following actions are performed by the male while clasping the female with one or both forelimbs.

F.) VENTRAL CLASPING WITH BOTH FORELIMBS The male's body lies parallel to the female's body and directly beneath her body. The male clasps the female's proximal forelimbs by hooking both of his forelimbs over hers.

His proximal forelimb is directed straight upward just posterior to the female's forelimb, while his distal forelimb is perpendicular to his proximal forelimb and hooked over the top of her forelimb (see Fig. 64A, 64F). His forefoot then grasps the female's anterior proximal forelimb (see Fig. 61B). While so clasping the female, the male's body sometimes lies out to one side rather than directly beneath the female's body.

G.) PIVOTING OUT FROM UNDER THE FEMALE When pivoting out from under the female to the right, for example, the male releases the female with his left forelimb and then pivots about his right forelimb as it still clasps the female's right forelimb (see Fig. 64B). Thus the male pivots from body parallel to and beneath the female's body (Fig. 64A) to a position with his body perpendicular to the female's long axis (Fig. 64C), by turning his head to the right and rapidly stepping forward and laterally with his hindlimbs. Fig. 64G shows the male pivoting out from under the female to the left.

H.) STATIONARY WITH INTERLOCKED FORELIMB The male is stationary and motionless with his body curved in a U in front of the female's snout and with one forelimb interlocked with one of the female's forelimbs (Fig. 64C, H and 62A). For example, the male's left forelimb is hooked around the female's left forelimb with the anterior surfaces of their distal forelimbs in contact (as in Fig. 62A). The male's head is turned towards the female's body and his laterally curved body is either perpendicular to the female or parallel to her.

I.) NUDGING WITH INTERLOCKED FORELIMB Beginning in the same position as in the preceding action (H), the male curves his body laterally in a tighter U with the female's snout lying inside the inflexion of his body. During this action the male presses his cheek or lateral snout against the female's lateral forebody while extending on the hindlimb and forelimb on the side away from the female and simultaneously arching the tail base upward. The male's hindbody too is brought nearer the female, and the male's vent or tail base may be pressed against the female's snout. See Fig. 64D and I).

J.) PIVOTING TO UNDERNEATH THE FEMALE From the position in the two preceding actions, ie. curved in front of the female with one forelimb interlocked with one of hers, the male moves forward pivoting around the interlocked forelimb. He pushes his snout under the female's forebody as he pivots around (see Fig. 62B). In the process his tail is frequently wrapped around the female's neck or forebody, and he may lash with his tail as he forces his head and forebody under the female. He then raises his free forelimb as it passes clear of the female's body on the opposite side (Fig. 64E) and hooks it over her free forearm, eg. his left forearm over her left forearm. The action is completed as the male pulls his hindbody under the female and thereby resumes ventral clasping with both forelimbs (see Fig. 64E to F).

K.) TWISTING WITH INTERLOCKED FORELIMB While maintaining a firm grip with one forelimb, the male twists his body vigorously and lashes with his tail while turning his head in the direction of his interlocked forelimb. Thus the male may pivot around with his dorsal body in contact with the female's venter or dorsum. The male's free forelimb is, meanwhile, often extended and directed forward and upward.

L.) MOVING FORWARD DURING VENTRAL CLASPING While clasping the female from below with both forelimbs, the male walks forward with his hindlimbs and may lash his tail laterally as in swimming.

M.) SURFACING FOR AIR DURING VENTRAL CLASPING With the male clasping the female with both forelimbs and beneath her, both animals lash their tails in swimming motions as they rise to the surface, and then both animals gulp air.

N.) PIVOTING WITH INTERLOCKED FORELIMB With his right, for example, forelimb interlocked with the female's right forelimb, the male pivots around his right forelimb by stepping laterally with his hindlimbs. While thus pivoting the male may nudge the female's lateral forebody just posterior to her forelimb with his cheek or lateral snout, or he may press his cheek against hers (see Fig. 65B through E).

O.) VENT PRESSED TO SUBSTRATE WITH INTERLOCKED FORELIMB The male assumes the same posture as in the action described next, spermatophore deposition (P), but he does not deposit a spermatophore.

P.) SPERMATOPHORE DEPOSITION During spermatophore deposition one of the male's forelimbs is interlocked with the female's ipsilateral forelimb, and his body axis lies approximately 180° to the long axis of the female's body. The male presses his vent to the substrate, and his hindlimbs are outstretched perpendicular to his body with the palms resting on the substrate (Fig. 65A). The male does not undulate his body or tail, nor does he move his limbs, during spermatophore deposition.

Temporal relations (Pleurodeles waltl)

Males will approach slowly females which have just moved or are slowly moving forward. If the female remains stationary as the male approaches slowly, the male may nudge the female lightly while continuing his slow approach. If the female continues to remain stationary, the male may pause and repeatedly nudge the female, or he may slowly force his snout and head under the female's tail or body. In the latter instance, the male may turn parallel to the female beneath her, move slowly forward and then clasp her hind or her forelimbs with both of his

Figure 61. Courtship activities in Pleurodeles waltl.

Fig. A. A pair has flipped over as the male clasps the female's forelimbs with his forelimbs. The male now lies upside-down above the female. The male does not possess eversible cloacal papillae in Pleurodeles waltl.

Fig. B. The same pair as in Fig. A in an upright clasping position. The male lies directly beneath the female and his forelimbs are hooked over and clasp the female's forelimbs. Note that the male's right forefoot firmly grips the female's proximal forelimb.

Fig. C. As a male slides under the female from behind, he raises his forelimbs.


B

Figure 62. Courtship activities in Pleurodeles waltl.

Fig. A. A male (below) has pivoted out from underneath the female. His left forelimb is interlocked with the female's left forelimb. The male is nudging the female's lateral forebody with his snout. The female remains stationary and does not nudge the male.

Fig. B. The male (below) begins to pivot back underneath the female. His left forelimb is still interlocked with the female's left forelimb, and he has just shoved his head under the female's chest.

Fig. C. The male (below) continues to pivot underneath the female and now lashes with his tail.


A
C

forelimbs. Almost invariably, however, a female will swim rapidly away from the male as he approaches or contacts her. Such rapid movement of the female causes the male to dash forward. If, as he dashes forward, his outstretched forelimbs contact the female's forelimbs or hindlimbs, the male rapidly hooks his forelimbs downward and so may capture the escaping female. Females captured about the hindlimbs with the male facing either anterior or posterior, or about the forelimbs with the male facing posterior, swim and twist violently through the water and, in all my observations, eventually dislodged the male and escaped. When he has captured the female in any of these positions, the male may release one forelimb and twist around beneath the female with the free forelimb outstretched and with his tail wrapped over and around the dorsum of the female. By such movements males may be able to shift their clasping position from the female's hindlimbs facing posterior, from female's hindlimbs facing anterior, or from the female's forelimb facing posterior to a position with the male clasping the female's forelimbs facing anterior. But this kind of outcome has not yet been observed.

Females usually escape from the male many times before being clasped. Once the female is clasped by both of the male's forelimbs with the male beneath her, however, she may be held in this position for a few hours even though she may twist and struggle.

Sometimes the male captures the female in quite a different fashion from the ways described above. If the female remains stationary as the male approaches her slowly, the male may move towards her head-on, or move parallel to her, and then perform the action stationary with head turned towards the female (D). In this position the male's body may lie from perpendicular to nearly parallel to the female's body but facing in the opposite direction. If the female remains stationary, the male may perform nudging by repeatedly rocking towards the female and contacting his cheek to her snout or cheek. He may also give a single burst of tail undulation with his tail reflexed (Fig. 63B). Usually the female moves off rapidly in these circumstances, and the male may then dash towards her, as she moves away, with outstretched forelimbs. Occasionally, however, the female turns her head towards and actively nudges the male as he performs action D (stationary with head turned towards the female). When the female persists with such a nudging response, her forelimb facing towards the male, is positioned very near the male's forelimb. The male may then rapidly hook his forelimb around hers. With forelimbs thus interlocked, the male rapidly pivots or twists under the female and clasps her free forelimb with his other forelimb.

Ventral clasping can thus be initiated by two very different routes. The male can either grasp the female's forelimb with only one of his forelimbs while facing towards her head on, or he may actively slide underneath her, from posterior to anterior, and grasp both forelimbs of the female simultaneously. The first route is preceded by a very slow approach to a female which remains stationary, while the second route is preceded by a rapid pursuit under a fleeing female.

If the female remains motionless during clasping, the male repeatedly pivots out from under her (as in Fig. 64). After each such pivoting, the male repeatedly alternates between motionless and curved in front of the female (see action H in Fig. 64C) and nudging (see action I in Fig. 64D). If the remale remains motionless and does not nudge the male during these activities (as in Fig. 64), the male pivots back underneath the female and thereby resumes ventral clasping. Thus when the female does not nudge the male when he lies in front of her interlocking her forelimb, the male repeats the sequence F, G, (H, I, H, ...), J, F, ... many times.

Figure 63. Preliminary courtship activities in Pleurodeles waltl.

Fig. A. A male (left) has just approached a female and now nudges her lateral tail with his snout.

Fig. B. A male (right) has just approached a female. The female remained stationary. The male is undulating his distal tail with his tail reflexed towards the female and with his head turned to one side towards the female's head.

Fig. C. A male (left) has just approached a female and is stationary with his head turned towards the female's snout.

(From photographs of courting animals; laboratory stock).

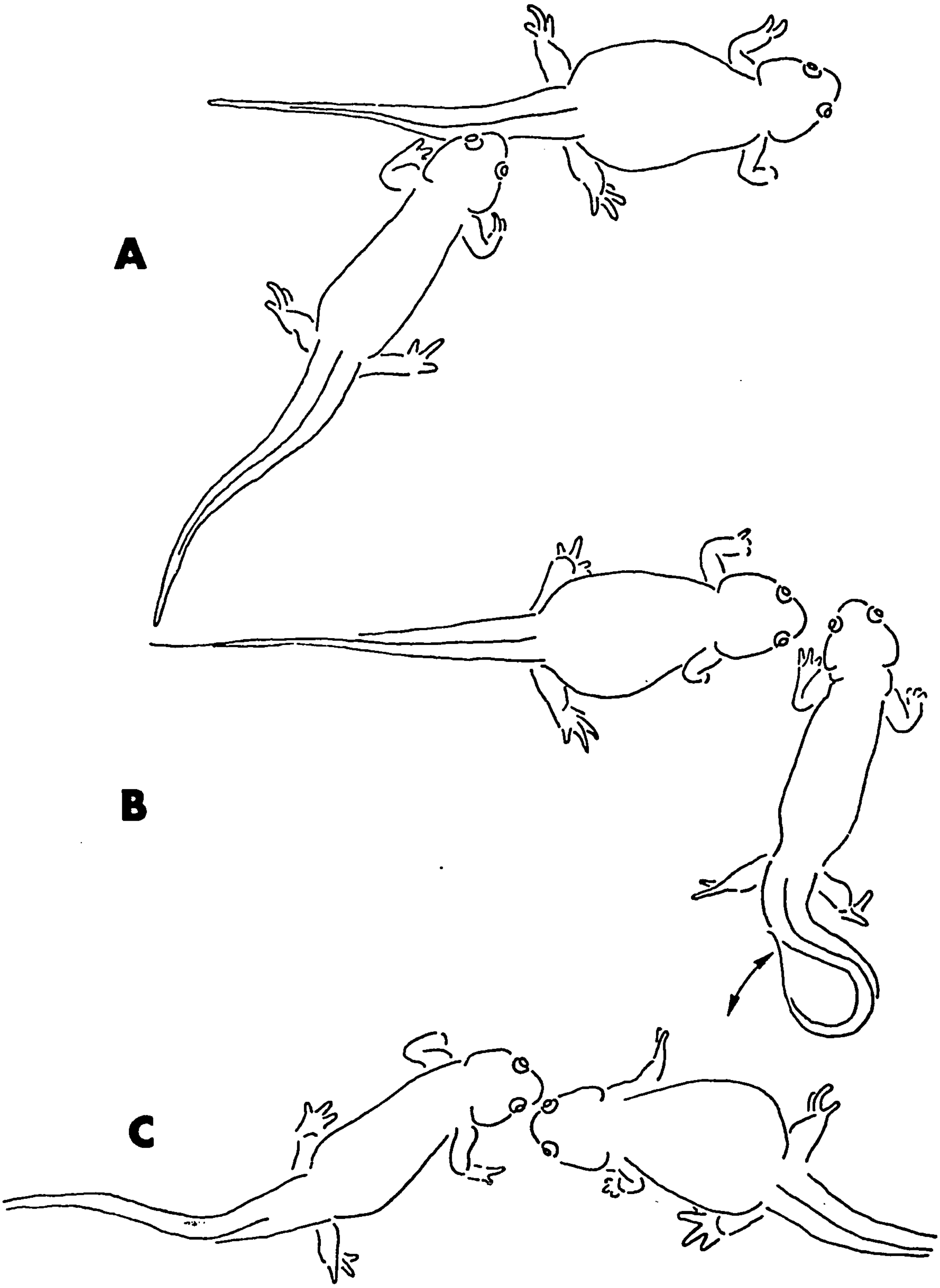

A
B
C

Figure 64. Male actions during forelimb clasping in *Pleurodeles waltl*

Fig. A. A male lies directly beneath the female and clasps her forelimbs with his forelimbs.

Fig. B. The male is just beginning to pivot out from under the female. He has released the female's left forelimb and is pivoting about his right forelimb (out of view) which is still interlocked with the female's right forelimb.

Fig. C. The male now pauses in front of the female. His right forelimb is still interlocked with the female's right forelimb.

Fig. D. The male nudges the female's lateral forebody with his snout and simultaneously presses his cloaca towards the female's snout.

Fig. E. The male has repeatedly nudged the female, paused, and nudged the female. The female has failed to nudge the male. The male now pivots about his right forelimb to back underneath the female. He raises and swings his left forelimb downward as it passes out from under the female's body.

Fig. F. The male has hooked his left forelimb over the female's left forelimb and now again clasps her with both forelimbs as he lies beneath her.

Fig. G. The male is now pivoting out from under the female. Note that his left forelimb is interlocked with the female's left forelimb.

Fig. H. The male now pauses in front of the female with his left forelimb (now out of view) interlocked with the female's left forelimb.

Fig. I. The male nudges the female with an upward stroke of his lateral snout.

Fig. J. The male has repeatedly nudged the female, paused, and nudged the female with his snout. The female has failed to nudge the male. The male is now pivoting back underneath the female with his left forelimb still interlocked with the female's left forelimb.

(Taken from a 16mm. movie of one continuous sequence. These animals are from Northeast Spain).

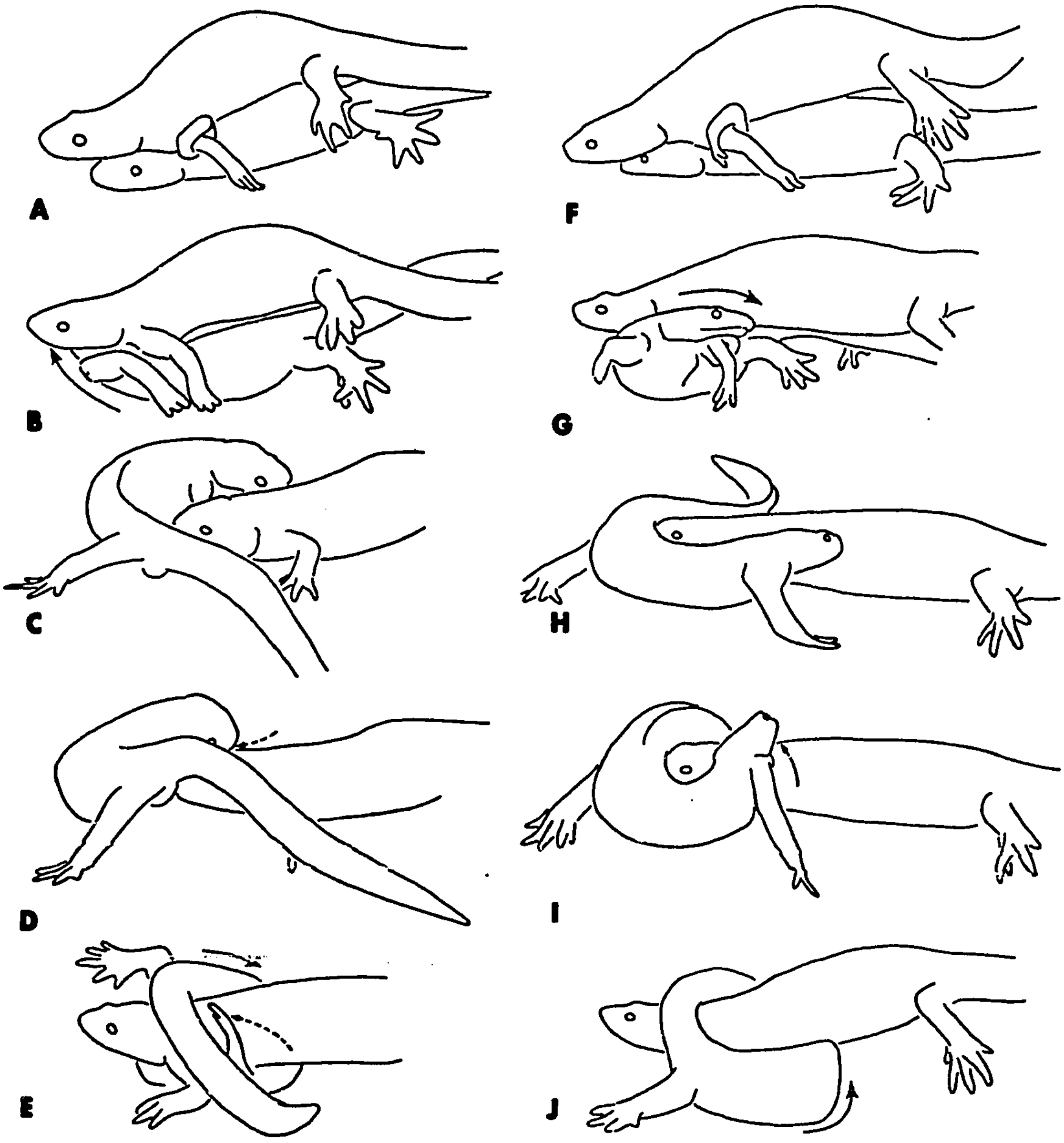

A
B
C
D
E
F
G
H
I
J

Fig. 64 shows part of this sequence, but with iterations of the sequence (H, I, H) left out, or F, G, H, I, J, F, G, H, I, J.

If, however, the female nudges the male when he lies in front of her interlocking her forelimb with his (ie. during male actions H and I), the male initiates an entirely new sequence of activities. Spermatophores are deposited only in this context. The male now begins to pivot with his forelimb interlocked with the female's ipsilateral forelimb. The male continues to pivot only if the female continues to nudge his cheek or lateral forebody, and simultaneously the female also pivots. And so the pair may begin to rotate around with both animals pivoting about their interlocked forelimbs (see Fig. 65). During such rotation the pair may rotate through several complete circles. If the female fails to nudge the male as they rotate, the male pivots back underneath her and resumes ventral clasping.

If the female continues to nudge the male, the pair continues to rotate, and the male may suddenly stop and adpress his vent to the substrate with hindlimbs outstretched. He may then resume pivoting or he may continue in the same posture and deposit a spermatophore (Fig. 65A). Following spermatophore deposition, the male resumes pivoting, as does the female, and so the pair rotates around (Fig. 65B). As the female pivots around, the spermatophore may contact her ventral hindbody. This will occur in multiples of 180° rotation of the male following spermatophore deposition (see Fig. 65). Once the spermatophore has contacted her ventral hindbody, the female may slide forward and laterally, as she pivots, over the top of it (Fig. 65C). If the spermatophore then contacts her vent, she rocks slightly over it and then lowers her vent upon it, thus inserting the apex of the spermatophore into her vent (Fig. 65D shows a dorsal view). She then pauses motionless for about 30 seconds, and the

Figure 65. Spermatophore deposition and sperm transfer in Pleurodeles waltl (dorsal views).

Fig. A. After clasping the female ventrally with both of his forelimbs, the male (below) has pivoted out from under the female. As the male nudged the female with his snout, the female nudged the male with her snout. The pair then rotated along the paths indicated with dotted lines, with the male's right forelimb interlocked with the female's forelimb. The male has stopped and is now in the process of depositing a spermatophore with his right forelimb still interlocked with the female's right forelimb.

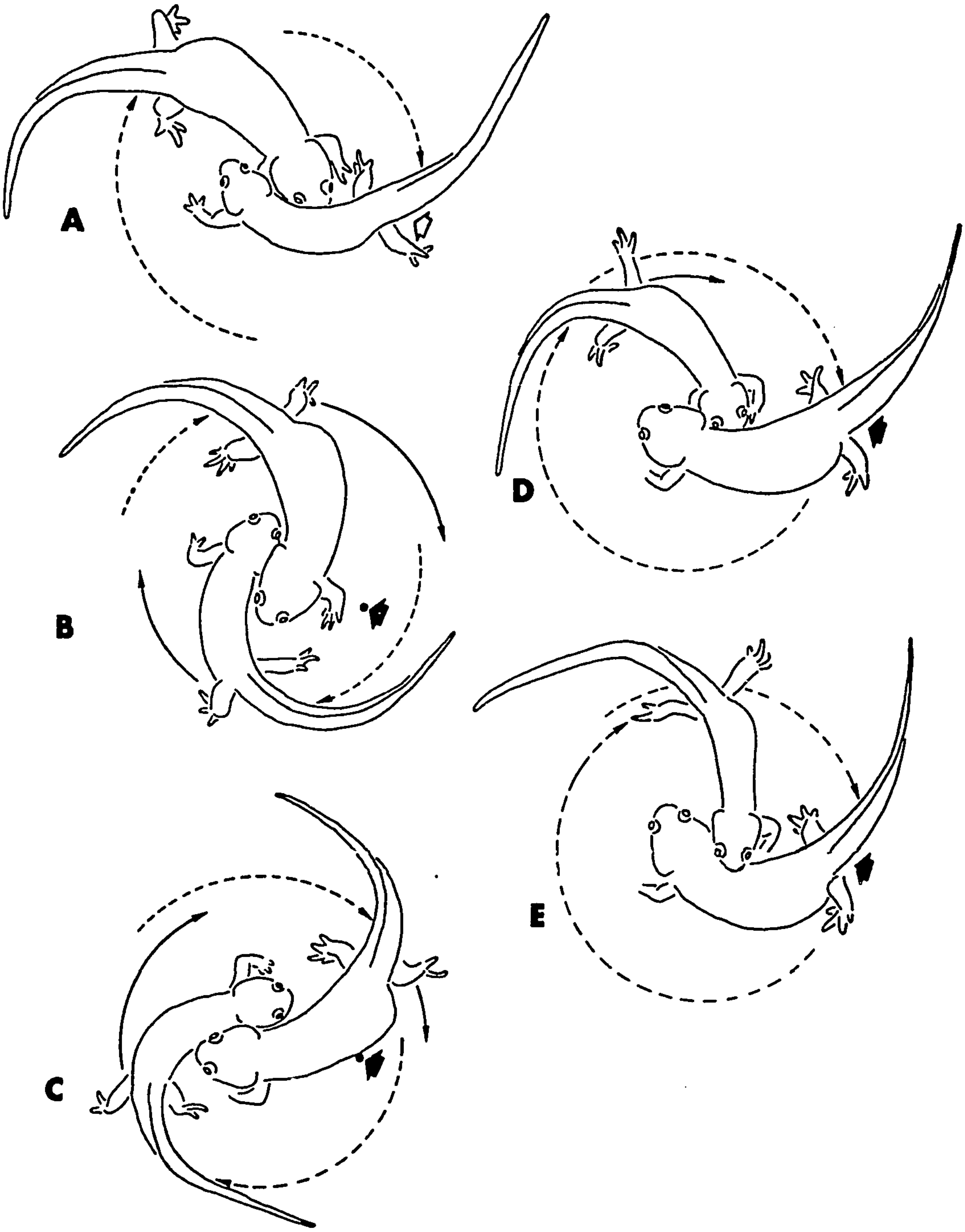
Fig. B. The male moves away from the spermatophore (indicated with a solid dot to the left of the solid arrow head) by continuing to pivot about the forelimb interlocked with the female's forelimb. The female has also resumed and continues to pivot.

Fig. C. As the female continues to pivot, the spermatophore contacts her lateral body.

Fig. D. The female has moved over the top of the spermatophore and now stops with her vent in contact with the spermatophore. Note that the male and female have now exactly reversed positions from the positions during spermatophore deposition (compare with Fig. A). The male continues to pivot.

Fig. E. The male nudges the female's lateral body as the female remains with her vent over the spermatophore. His forelimb is still interlocked with the female's forelimb.

(Taken from a sequence of photographs of one courting pair; laboratory stock).


A
B
C
D
E

male may continue to pivot and nudge the female (Fig. 65E). The female moves off of the spermatophore by resuming pivoting, and the pair then continue to rotate about their interlocked forelimbs.

More than one spermatophore may be deposited during the same rotation bout. Several rotation bouts may occur, however, without the male depositing a spermatophore.

Zeller (1890) found that the male clasped the female for hours at a time while crawling or swimming about. Finally the male releases one of the female's forelimbs, turns his body so that his posterior body is directed against the female's snout and pushes against the side of the female with repeated turnings of his body. The male then deposits a spermatophore in front of the female's snout and then moves in a tight circle, until the female's vent reaches the spermatophore. The female then moves her body back and forth over the spermatophore and takes up the sperm mass with her cloacal lips. I find nothing in this very brief account which is inconsistent with my observations.

Gallien (1952) describes the clasping posture and notes that the male may clasp the female for hours before separating from her. He did not observe spermatophore deposition, but notes that one male may deposit as many as six or seven spermatophores.

Pleurodeles poireti

Bedriaga (1882) observed courtship behavior of captive Pleurodeles poireti. The male pursues the female while holding his forelimbs bent forward, hook-like. If the male succeeds in getting under the female, he seizes the female's forelimbs with his forelimbs. The humerus of the male is stretched upward, while the radius and wrist of the male pass forward and downward over the dorsum of the female's humerus. The male then swims slowly for a long time while still clasping the female with his forelimbs and lying beneath her. The male rubs the chin of the female with his snout and dorsal head. After a while the male releases one of the female's forelimbs and quickly rotates out from under the female, towards the side still being clasped by the male's other forelimb, until his body lies diagonally in front of her snout. The male's body is then curved around in front of the female's snout, and he touches one side of the female's trunk with his snout. Frequently the female's snout contacts the male's cloaca. When it does the male extends on his hindlimbs and thereby lifts and exposes his vent. The male rubs his snout back and forth on the female's lateral trunk. If the female struggles, the male rapidly rotates back under the female and seizes her free forelimb with his free forelimb and so clasps her once again with both forelimbs as the female rests on his dorsum. If the female does escape from the male by struggling, she holds her forelimbs firmly against the sides of her body. In such cases the male's attempts to reclasp the female are unsuccessful, although sometimes the male may clasp her hindlimbs. Females which escape from the male, after having been clasped for hours, repeatedly flee from the male. Usually the female struggles more and more as the male continues to clasp her, and the pair separate after about 12 hours. On two occasions, however, Bedriaga observed successful transfer of sperm. The male rotated out from under the female while still clasping one of her forelimbs, as described above. The female then began to rub the male's axilla with her snout, and the pair began to rotate in a circle. Their posterior bodies rotated around in a circle whose center lay near the female's and male's forelimbs. After a few complete rotations on this circular course, the male stopped and then extended on his hindlimbs and left a spermatophore attached to a small stone. The pair then resumed their circular rotation, until the female's cloaca contacted the spermatophore. The spermatophore was then taken up by the female's cloacal lips and disappeared into her cloaca.

Tylototriton verrucosus

Boulenger (1920) observed courtship in animals at the Zoological Gardens in London. He notes that Tylototriton possess an amplexus similar to Pleurodeles with the male clasping the female's forelimbs with his forelimbs, and that pairs may remain in this position for days.

Khin Mg Gyi (1969) observed courtship in the field and in the laboratory. Courtship occurred under water. The male pursues the female by swimming after her. The male clasps the female's forelimbs with his forelimbs while lying beneath her with his head adpressed to hers. The pair may swim while clasping. Chaudhuri (1966) also notes that the male clasps the female with his forelimbs.

Spermatophore deposition and sperm transfer have not been observed in this genus. Males apparently lack the pads on the anterior portion of the humerus which are present in Pleurodeles males during the courtship season.

Salamandrina terdiqitata

Strötgen (1927) obtained a glimpse of courtship behavior in *Salamandrina*. For approximately one hour, a male continually followed another individual with his snout held constantly in the direction of the other animal's cloaca. The two animals formed an elongate ellipse. Their cloacae were distended, and their bodies apparently undulated laterally. Compared with the non-courting activities of *Salamandrina*, the animals were very animated. Suddenly the male stopped and deposited a spermatophore, but then Strötgen terminated his observations. Strötgen was uncertain about the sex of the other animal, but it was more stocky and had a proportionally shorter tail. In some ways the behavior Strötgen describes resembles the rotating of *Pleurodeles* pairs immediately before and after spermatophore deposition (see Fig. 65), but additional observations of *Salamandrina* courtship are needed before courtship in this genus can be interpreted and compared with other salamanders.

Salamandra salamandra

Catalog of male actions.

The following actions are performed by the male while facing towards the female and not clasping her.

A.) NUDGING The male contacts his snout or lateral snout to the female's dorsal or lateral body.

See the section on temporal relations for descriptions of other actions performed by the male while facing towards the female, including capture of the female.

The following actions are performed by the male while clasping the female.

B.) VENTRAL CLASPING WITH BOTH FORELIMBS The male's body lies directly beneath the female's body with both of his forelimbs hooked over the female's forelimbs from behind (see Fig. 67 and 68A). The male's proximal forelimbs are directed upwards, directly behind the female's forelimbs, while his distal forelimbs are horizontal over the top of her forelimbs. The male's forefeet are directed downward and are pressed against the anterior surface of the female's proximal forelimbs.

C.) BODY-SHIFTING While clasping the female ventrally, the male shifts his hindbody and tail from side to side, thus rubbing his dorsal body and tail on the ventral surfaces of the female's body and tail. Simultaneously the male alternatively raises and lowers his hindlimbs. The male's head is inclined upward slightly (Fig. 67A).

D.) HEAD MOTIONLESS WITH TAIL UNDULATION The head is held motionless and slightly raised under the female's chin. Tail undulations of much smaller amplitude than in the preceding action (C) proceed along the entire length of the tail (Fig. 67B).

E.) HEAD-SWINGING WITH TAIL UNDULATION Tail undulations proceed along the entire length of the tail. While lifting his head upward slightly, the male swings his head back and forth laterally and thereby rubs the dorsum of his head on the female's chin. At the onset of head swinging, the lateral swings have a jerky appearance, for the male swings his head in one direction with two or more short strokes before reversing the direction of swinging. As head-swinging proceeds in time, however, the lateral strokes are continuous, and the action becomes a smooth swinging of the head to the right, to the left, to the right ... During head swinging the head is moved through an arc of about 90° (Fig. 67C).

F.) HEAD-SWINGING WITH NO TAIL UNDULATION The male swings his head in continuous arcs, as in the preceding action (E), but the tail is motionless. When this action terminates, the male moves off of the spermatophore (Fig. 67D).

G.) PARTIAL LATERAL DISPLACEMENT OF THE BODY The male rapidly moves just his hindbody and tail laterally out from under the female's hindbody. The male pauses with his hindbody parallel to the female (see Fig. 67E for a lateral view and Fig. 68C for a dorsal view).

H.) COMPLETE LATERAL BODY DISPLACEMENT The male moves his body laterally until his hindbody rests at a 45° angle to the long axis of the female's body. The male's hindlimbs are widely outstretched, and his head is swung laterally. During both partial and complete lateral body displacement, the male clasps the female's forelimbs with both of his forelimbs. See Fig. 67F for a lateral view and Fig. 68D for a dorsal view.

Figure 66. Initiation of ventral clasping in *Salamandra salamandra*

Fig. A. A male has shoved his head under a female's tail. The male is now turning his head towards the female as she moves forward away from him.

Fig. B. The male moves forward and slides under the female as she continues to move forward.

Fig. C. The male continues to move forward rapidly under the female.

Fig. D. The male is now rapidly swinging both of his forelimbs upward.

Fig. E. The male has hooked his forelimbs over the female's forelimbs. He now pauses with his forelimbs clasping the female's forelimb.

(Fig. A through E taken from a sequence of photographs).

Fig. F. A male lying beneath a female and clasping her hindlimbs with his forelimbs. The male crawled posterior, rather than anterior, under the female and then clasped her.

(From a photograph).

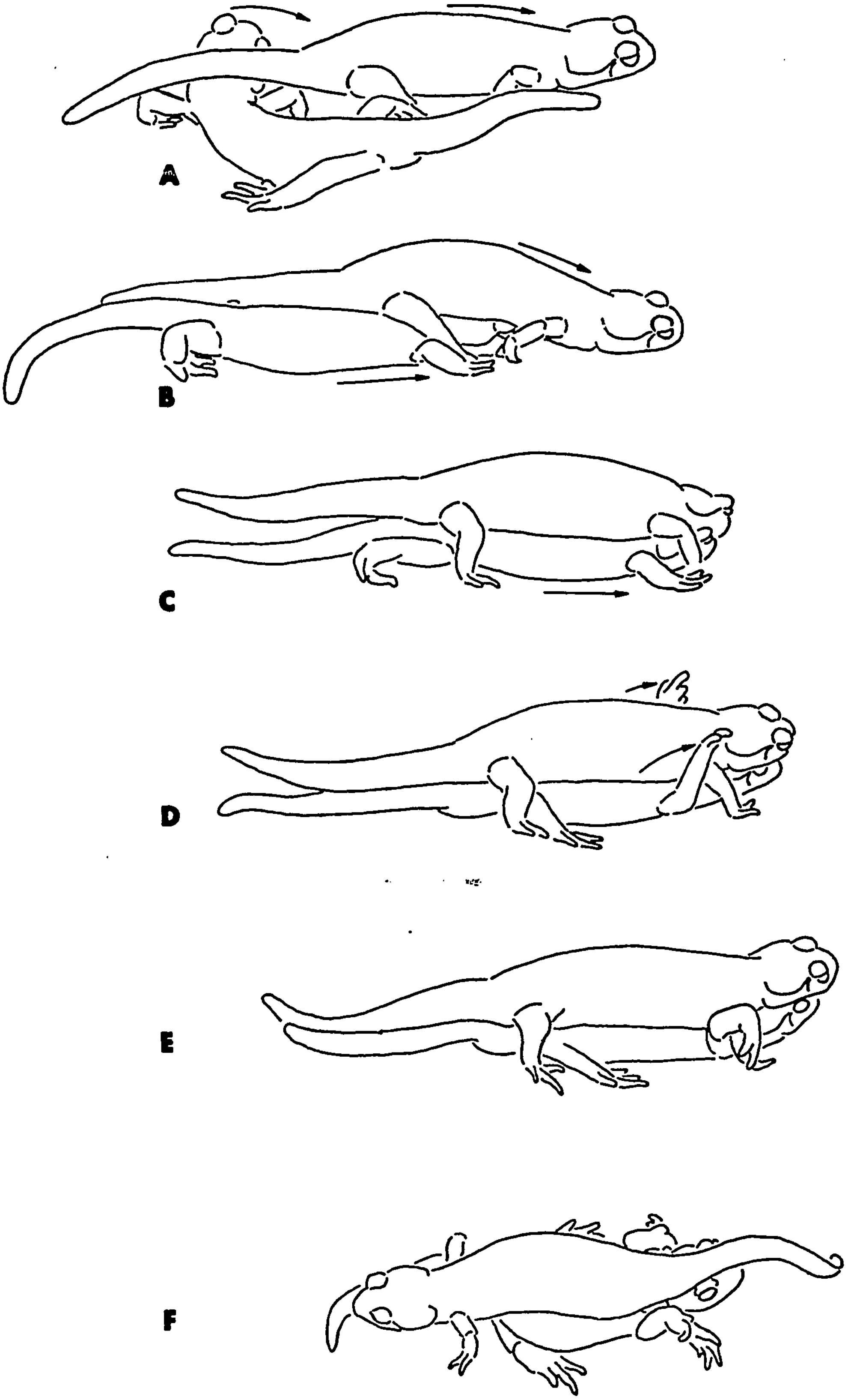

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Figure 67. Spermatophore deposition and sperm transfer in _Salamandra salamandra_.

Fig. A. The male lies beneath the female and is clasping her forelimbs with both of his forelimbs. The male is shifting his posterior body and tail from side to side under the female (0 sec).

Fig. B. The male now holds his vent stationary in contact with the substrate and undulates his tail laterally (79.0 sec).

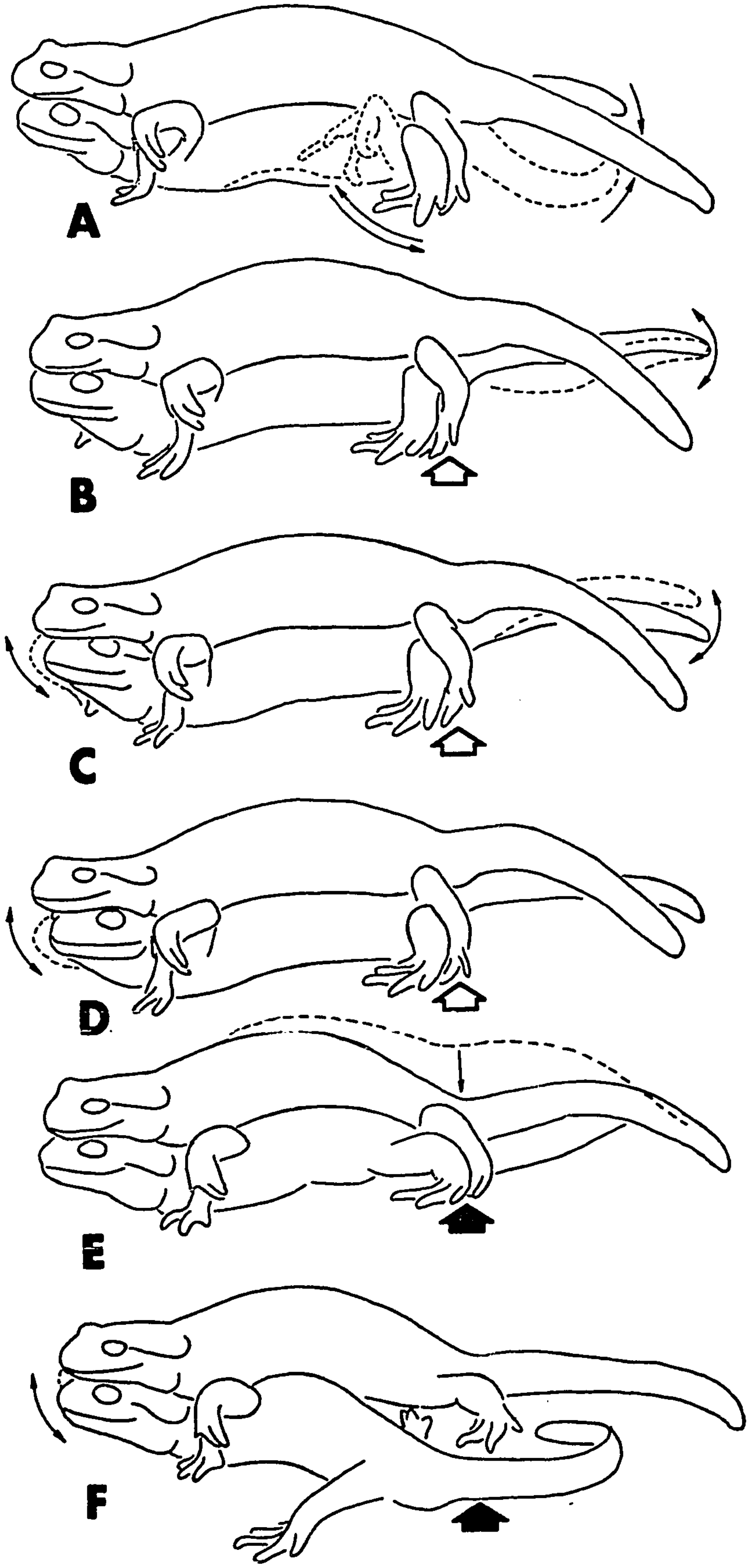
Fig. C. The male now swings his head from side to side under the female's chin and continues to undulate his tail (88.5 sec).

Fig. D. The male continues to swing his head from side to side but no longer undulates his tail (110.1 sec).

Fig. E. The male has displaced his sacrum to the left and a spermatophore under the female's vent. The female's vent has fallen down towards the spermatophore. The male is stationary (118.3 sec).

Fig. F. The male has displaced his posterior body to a 45° angle with the female's body axis. He is now stationary in this position and swings his head from side to side under the female's chin. The female is stationary with the spermatophore inserted into her cloaca (127.9 sec).

(Taken from a 16mm. movie of one continuous sequence. Total elapsed time is 127.9 seconds or 2.13 minutes).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Temporal relations (Salamandra salamandra)

When introduced into a container with a female, the male may markedly increase his locomotor activity. When stationary he rests with his forelimbs extended and buccal pumping increases in rate and amplitude. If the female remains stationary, the male may approach her, or he may contact her in the course of moving about the container. Upon first contact with a stationary female, the male nudges her lateral or dorsal body with his snout, pushing against the female with his snout bent downward. If the female remains stationary, the male may then vigorously force his snout under the female's head, body or tail. Forcing of the head under her body is accomplished by turning the head back and forth and by strong cervical flexure and extention which cause the snout to move up and down as the male pushes against the female. Once the male has forced his head under the stationary female, he turns his head either anterior (as in Fig. 66A) or posterior and moves forward underneath her. If the male turns anterior, he slides forward underneath the female's body (Fig. 66B and C) and then stretches his forelimbs outward and forward (Fig. 66D) as he slides forward beneath her. If his outstretched forelimbs contact the female's forelimbs, the male rapidly hooks his forelimbs simultaneously over hers and thus captures the female (Fig. 66E). If, on the other hand, the male turns posterior and moves forward beneath her, he may clasp her hindlimbs (as in Fig. 66F), or he may proceed on forward out from under her tail.

Females seldom remain stationary after the male contacts them. If the female moves forward as the male forces his way beneath her, the male may dash forward beneath her and seize her hindlimbs or forelimbs as she flees. When the male clasped the female's hindlimbs, while facing either anterior or posterior, the females always freed themselves by vigorously twisting and then running away rapidly. Females may also free themselves in this way when captured by the forelimbs with the male facing anterior.

When the female breaks contact with the male and moves off rapidly, the male rapidly turns towards her and dashes forward behind her. While thus dashing forward behind a fleeing female, the male may force his snout under her body and move rapidly beneath her. He may then clasp her hindlimbs or forelimbs with his forelimbs.

Dorsal clasping of a female was observed on only one occasion. A male approached a stationary female, nudged her dorsal body and then clasped her forebody with his forelimbs just posterior to her forelimbs. After clasping her thus for only a few seconds, with his hindbody at a 45° angle to hers and resting on the substrate, the male released the female and began forcing his snout against her lateral body. The female then ran off.

If the female does not twist and escape from the male once she has been captured by the forelimbs, with the male facing anterior, the male begins body-shifting (Fig. 67A). During body-shifting the male may push forward with his hindlimbs and move the pair forward. Then the lateral shifting of the male's body gradually decreases in amplitude, and with head motionless, the male begins tail undulations with his body directly beneath the female (Fig. 67B). As tail undulation continues, the male begins head-swinging (Fig. 67C). Head-swinging continues and tail undulations cease (Fig. 67D). Then suddenly the male draws his hindbody out from under the female (partial lateral body displacement, G), leaving a spermatophore behind in the former position of his vent (Fig. 67E and Fig. 68C). From the onset of tail undulation with the male's vent stationary (Fig. 67B), the female gradually arches her proximal tail

Figure 68. Spermatophore deposition in *Salamandra salamandra* (dorsal views).

Fig. A. Lateral view of a pair as the male clasps the female during spermatophore deposition. The arrowhead indicates the position of the future spermatophore. Notice that the female's cloaca lies directly above the male's cloaca and hence the spermatophore that he is depositing.

Fig. B. Dorsal view of a pair as the male clasps the female during spermatophore deposition. The male lies directly beneath the female, but his hindfeet are visible just in front of the female's hindfeet.

Fig. C. The male has displaced his hindbody out from under the female and has left a spermatophore directly beneath the female's cloaca. The female's vent has fallen down towards the spermatophore, but her vent lies just to the left of the spermatophore (just at the end of the solid arrow).

Fig. D. The male has now completed the lateral displacement of his body. He still clasps the female's forelimbs with both of his forelimbs. The female has not located the spermatophore with her vent.


A

upward slightly (see Fig. 67B through D). As the male withdraws his sacrum from under her vent, the female's vent immediately falls down towards the spermatophore (Fig. 67E). Her vent may fall directly upon the spermatophore with the spermatophore penetrating between her cloacal lips. If the female's vent falls to one side of the spermatophore (as in Fig. 68C), the female may shift her vent laterally by rocking on her hindlimbs, move her vent up onto the spermatophore and then squat upon it (see Fig. 67F for a female in this last position). The entire spermatophore enters the female's cloaca. Meanwhile the male pauses with his body partially displaced from under the female. The male then displaces his hindbody to a 45° angle to the female's long axis (complete lateral body displacement) and pauses in that position while swinging his head laterally under the female's chin with his raised slightly (Fig. 67F and Fig. 68D).

The male may then shift his hindbody laterally back under the female's body and reinitiate body shifting (Fig.67A). Usually, however, the female twists free of the male and escapes, so that the male must recapture the female between successive spermatophore depositions.

During a single evening with a female, a male usually deposited three or four spermatophores.

Van Leewen (1907) gave the first accurate description of the mode of insemination in Salamandra salamandra and dispelled the earlier notion that insemination was accomplished by direct application of the cloacae.

Himstedt (1965) and Joly (1966) have recently provided excellent descriptions of courtship in Salamandra salamandra, and my observations are in rather precise agreement with theirs.

Joly (1966) concluded that male Salamandra salamandra clasp the female dorsally as well as ventrally. He notes that when a male first contacts a female, the male straddles the female's neck with his forelimbs, while rubbing the female's snout with his chin (see Joly, 1966, Fig. 2). The male then releases his hold, slides beneath her and may clasp her forelimbs with his forelimbs. Himstedt (1965) also found that upon first contact with a female, the male presses his snout down upon her dorsum. Himstedt provides a photograph of a male simultaneously straddling the female with his forelimbs (see Himstedt, 1965, Fig. 1). I have also observed this behavior when the male first contacts the female. On one occasion the male did appear to actually clasp the female's dorsum with his forelimbs. In my observations this dorsal straddling behavior was rather infrequent, compared with ventral clasping, and usually the male began shoving his head under the female's venter after only briefly contacting his snout to her dorsal or ventral body. Joly's (1966) observations are more extensive than mine, however, and I am inclined to accept his view that Salamandra salamandra males possess two distinct modes of actual clasping. The male first employs a dorsal clasping of the female's anterior body with his forelimbs and then clasps the female's forelimbs with his forelimbs with the female resting on his dorsum. Nevertheless, my observations suggest that the first mode of clasping can be deleted.

Joly (1966) found that some females swing their tails counter to the lateral tail movements of the male during ventral clasping. In addition some females are reported to rub their chins laterally on the male's snout, counter to his head swinging. I have not been able to observe either of these female actions. Himstedt (1965) did not mention them. Presumably they are manifested only in some females and are correlated, as Joly (1966) suggested, with the sexual receptivity of the female.

Joly (1966) emphasized that the female does not play a passive role in courtship, despite the fact that the male clasps her firmly and positions her over the spermatophore. I agree that male Salamandra practise courtship rather than rape. The male does not force the female onto the spermatophore. Both Joly and I found that some females actively shift their vents from side to side after spermatophore deposition and then lower the vent upon the spermatophore. In addition, some females actively escape from the male, and in these circumstances the male does not deposit a spermatophore.

With an interesting series of experiments, Joly (1966) established that the "alert" posture of the male (male extended on forelimbs and increased buccal-pharyngeal pumping) is elicited by air-borne substances from the female, which the male perceives via olfaction. Pursuit of the female is elicited by visual stimuli.

I have observed a very distinct whitish secretion from the dorsum of the male's body and tail as he performs body shifting and tail undulation during ventral clasping. This secretion probably serves to lubricate the female's venter, so that when the male's body is displaced following spermatophore deposition, the female's body remains in situ with her vent directly over the spermatophore. Neither Joly (1966) nor Himstedt (1965) mention this secretion. Joly (1966) does note that females frequently release fluid from their cloacae immediately before spermatophore deposition. It may be that fluids from two sources serve the function of lubrication and thereby increase the probability that the female will locate the spermatophore.

Salamandra atra

Häfeli (1971) observed *Salamandra atra* courting in the field on several occasions, and he provides a detailed account of courtship behavior in this species. Males are very active during the courtship season and actively pursue females, other males and juveniles. Since pursuit can be elicited by objects pulled by a string, Häfeli concludes that the behavior is released by visual stimuli.

Once the male overtakes a female, he climbs onto her dorsum from behind or from the side. The male clasps the female's neck with his forelimbs and begins to rub the dorsum of the female's head with his chin. To perform this rubbing action the male bends his head down sharply and swings his head from side to side, pendulum-like. Dorsal clasping of the female together with head swinging may persist for a half hour or more.

The male then releases the female and attempts to shove his head under her trunk. The male raises his head and lifts the female's anterior body off the substrate as she shoves forward beneath her. Once the male's head lies beneath the female's chin, he swings his head from side to side and continues to raise his head. The male then initiates a second type of clasping. He wraps his forelimbs over the female's forelimbs and thereby clasps her just as in *Salamandra salamandra*. If the female struggles, the male continues to carry her about on his dorsum until she no longer attempts to escape. The male also increases the intensity with which he rubs his head against her chin.

Once the female becomes quiescent the male presses his tail base against the female's cloaca and swings his tail in a horizontal plane. As the male's tail base rubs against the female's cloaca, his cloacal lips swell and begin to spread apart. Very soon the male resumes rubbing the female's chin with his head. He then presses his cloaca against the substrate and deposits a spermatophore. Next the male displaces his posterior body to one side and out from under the female. The male continues to clasp the female's forelimbs with his forelimbs, and their bodies now form an acute to right angle.

The female's cloaca falls down towards the spermatophore once the male moves his posterior body to one side. In the ideal case the female's cloaca falls directly upon the spermatophore. The sperm mass is surrounded by her widespread cloacal lips and is removed from the spermatophore. If the female's cloaca does not fall directly upon the spermatophore, she moves her tail from side to side until her cloaca contacts the spermatophore, whereupon she immediately lowers upon it. Thus the female may play an active role in locating the spermatophore.

Courtship elements were very constant from courtship to courtship. In contrast the duration of courtship was quite variable. Courtship lasts 1-4 hours and averages 1.5-2 hours. Häfeli suggests that the duration of courtship is directly related to the sexual receptivity of the female. The male courts and clasps the female longer when she is not receptive. Males deposited three spermatophores in each courtship.

The courtship behavior of Salamandra atra is exceedingly similar to Salamandra salamandra both in terms of the elements which are present and their temporal patterning. The great similarity between these two species can be appreciated by comparing the fine photographs of Joly (1966) and Häfeli (1971). There is one notable difference. In Salamandra atra apparently, the male always clasps the female's dorsum for a rather lengthy period before he initiates ventral clasping. In Salamandra salamandra dorsal clasping is frequently omitted, and it is brief when it does occur.

Häfeli's (1971) report is the first complete account of courtship in Salamandra atra. Other workers have observed one or another aspect of courtship but not the entire courtship process. Schreibers (1833) observed ventral clasping, but he confused the sexes and thought that the female was clasping the male with her forelimbs as she lay beneath him. Boulenger (in a communication transmitted to and published by Lataste, 1881) also observed ventral clasping by a captive male S. atra courting with a female S. salamandra. Schlosser (1925) watched a male pursue and dorsally clasp a female.

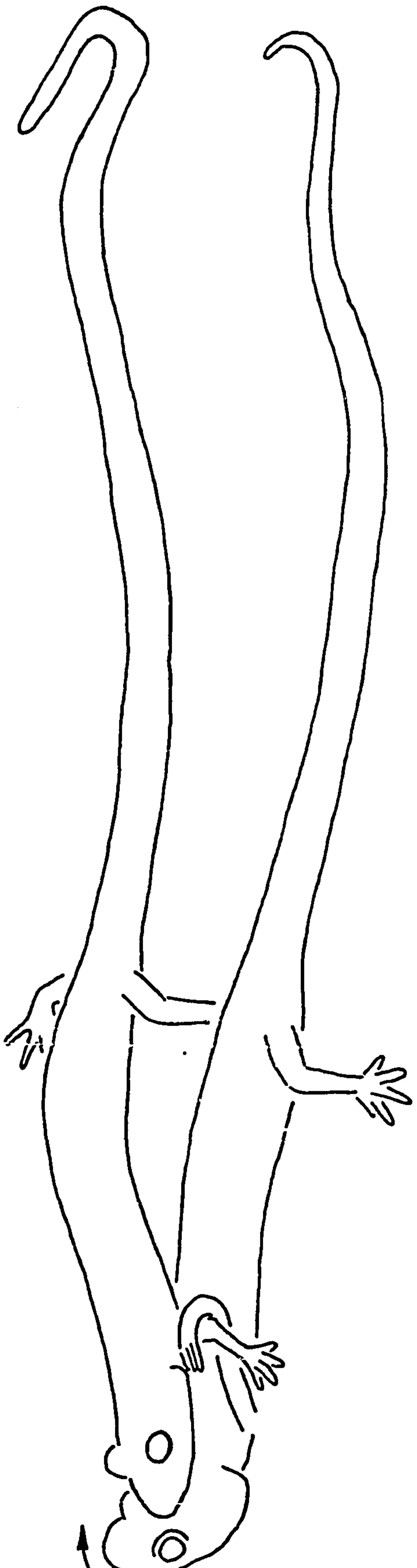
Vilter, Lugan and Reymond (1959) suggest that sperm is passed directly from the male's to the female's cloaca. Pairs were observed in which the female's dorsum rested against the snow with the male on top of the female with his venter against hers and with his feet touching the substrate. The male's cloaca contacted the female's cloaca, and both the male and female undulated their tails laterally. This behavior lasts for 10-20 minutes before the animals separate, and was apparently observed in several pairs. In light of the consistencies between the observations of all other workers who have described courtship behavior in the genus Salamandra, Vilter, Lugan and Reymond's observations are inexplicable.

Chioglossa lusitanica

Thorn (1966) was able to observe courtship behavior for 20 minutes in a pair of Chioglossa courting on land in a terrarium on September 24. Thorn found the male positioned completely underneath the female, facing anterior with his forelimbs hooked over and clasping the forelimbs of the female. In this position the male performed a slow undulatory movement of his trunk, such that the base of his tail rubbed against the female's cloaca. The male then moved his body to the left without releasing the clasp of his forelimbs on the female's forelimbs, so that his trunk and tail lay beside those of the female. In this position (see Fig. 69) the male raised his head and rubbed his inter-ocular region laterally in contact with the female's snout. The male then drew his body back underneath the female's body and again performed the lateral undulatory movement while continuing to rub the female's snout, as before, with his dorsal head. Almost immediately he ceased the lateral head movement and continued the lateral undulatory movement of his posterior trunk. This cycle of lateral undulation of the trunk, lateral body displacement and lateral head movement was repeated several times. The male then released the female and departed from her rapidly without depositing a spermatophore. Thorn (1966) suggests that his departure may have been due to a light used to illuminate the courting pair.

Figure 69. Ventral clasping in *Chioglossa lusitanica* (after Thorn, 1966).

A male has just displaced his posterior body laterally out from under the female. He continues to clasp the female's forelimbs with both of his forelimbs. He is swinging his head from side to side and rubbing the dorsum of his head on the female's chin.



Mertensiella caucasica

Males of Mertensiella caucasica possess a small protrusion on the medial side of the humeral region of each forelimb (Nikolskii, 1918). The male also has a remarkable spike-like protuberance on the dorsum of his tail base.

In late April Cyrén and Lantz observed a male clasping a female under water in the mountains of "Transkaukasien" (Cyren, 1911). The male was directly under the female, facing anterior with his forelimbs hooked upward and over the female's forelimbs. The pair separated as the observers approached them.

Obst and Rotter (1962) reported on a captive pair courting under water. Courtship behavior in the male could be regularly induced with cool water from May until June. A male was observed to pursue a female and hold his forelimbs upward. After a short time the male succeeded in clasping the female's hindlimbs tightly with his forelimbs with his head under her sacrum. The pair remained in this position for a long time, while swimming about. The male rubbed the female's abdomen with undulatory movements of his head while still clasping her hindlimbs with his forelimbs. The male then released the female's hindlimbs and clasped her forelimbs with his forelimbs while facing anterior underneath the female (see Obst and Rotter, 1962 for figures of courtship positions). In this position the male performed lateral undulatory movements of his entire body which rubbed the male's caudal protuberance sideways against the female's cloaca. Both animals rotated around their long axes, entwining their tails. Sometimes the male clasped the female with only one forelimb. These elements of courtship behavior apparently occurred on a number of occasions, but spermatophore deposition and sperm transfer were never observed.

Perhaps courtship behavior can occur on land as well as under water, for Lantz found a male clasping a female in a collecting container with only moist moss (Wolterstorff, Lantz and Herre, 1936).

Spermatophore deposition and sperm transfer have not yet been observed in the genus Mertensiella. Consequently the function of the very peculiar protuberance on the male's tail base is poorly understood. It is known that the structure is rubbed against the female's vent as the male clasps the female ventrally (Obst and Rotter, 1962). Wake and Özeti (1969) concluded that Mertensiella and Salamandra are closely related and place them both in the genus Salamandra. Mertensiella males may deposit spermatophores directly beneath the females' cloaca just as Salamandra salamandra do. If this is so, then the male Mertensiella may insert his caudal protuberance into the female's cloaca just before he deposits a spermatophore and thereby align and stabilize the female's cloaca directly over the site of the spermatophore. Eiselt (1966) has recently provided a very fine photograph of the caudal protuberance in a male Mertensiella luschani. The protuberance is in precisely the right position to effectively align the male and the female cloacae just before spermatophore deposition. Furthermore, the caudal protuberance is remarkably similar to a Salamandra spermatophore! It is the same size, the same shape, and it even possesses an apical knob which resembles closely the apical sperm mass of a Salamandra spermatophore. The caudal protuberance of Mertensiella may very well be a "dildo", or false spermatophore, which simulates the insertion of real spermatophore into the female's cloaca and distends her cloaca. The false spermatophore is then rapidly withdrawn from the female's cloaca (as the male displaces his hindbody as in Salamandra, see Fig. 68) and the female's cloaca falls upon the real spermatophore. Further observations of Mertensiella courtship could easily test these hypotheses.

In the light of recent re-evaluations of the relationships of the families Salamandridae and Plethodontidae, the caudal protuberance of male *Mertensiella* is certainly not homologous to the glandular hump on the dorsum of the male's tail base in the plethodontid genus *Eurycea* (*E. bislineata* and *E. multiplicata*) as Noble (1931) suggested. The structure of male *Eurycea* serves a very different function in courtship (see account of *E. bislineata* courtship).

Euproctus asper

Bedriaga (1882) describes the process of spermatophore deposition. The male holds the female tightly with his tail. It is wrapped around her posterior body just anterior to her hindlimbs. The male lies diagonally under the female with her venter in contact with his dorsum with the male facing anterior. Their cloacae lie tightly against each other, in contact laterally or with the male's cloaca under the female's cloaca (see Fig.70A). (The cloaca of female Euproctus asper is cone-shaped). With one of his forelimbs, the male grasps the female or supports himself on her shoulder. In this position the male performs remarkably dexterous movements with his hindfeet and thus rubs and presses the tail base and cloacal lips of the female. The male also rubs the female with his anterior head and snout by either turning posterior and stroking her legs and tail or by rubbing his dorsal head against her chin. The male then executes 90-100 (or more) convulsive movements, and a spermatophore is discharged as the male continues to grasp the female. The females observed by Bedriaga did not retrieve the spermatophores deposited by the males. One spermatophore clung to the cloacal lips of the female. In another instance a spermatophore clung to the female's hindlimbs. In the course of two and a half hours, four spermatophores were deposited in an interval of 30-50 minutes.

Despax (1923) observed a pair in which at least three spermatophores were deposited as the male clasped the female. During spermatophore deposition the male's body trembled spasmodically. Immediately after spermatophore discharge, the male began moving his hindfeet, and the spermatophore disappeared from view. The spermatophores initially adhered to the sides of the female's cone-like cloaca but were later dislodged.

Dähne (1926) found that clasping pairs were very unresponsive to external stimuli, and he was able to position pairs so that he could obtain an unobstructed view of sperm transfer. Dähne notes that the female is completely passive during clasping. Her posterior body is strongly constricted by the grip of the male's tail. The cloacae lie on a straight line, with their anterior-posterior axes aligned, with the male's cloaca anterior to and abutting against the female's cloaca. The cloacae lie in a cavity bounded laterally by the male's hindlimbs. Soon after clasping is initiated, the male begins to vigorously grasp the female's cloacal lips with the toes of his hindfeet which are bent, hook-like. This activity persists for an hour or more, and then suddenly the male begins to gently rub the female's cloacal lips by moving his hindlimbs in an anterior-posterior direction. The male's cloaca is now everted, and a sperm mass protrudes from his cloacal aperture. The rubbing movements of the male's hindlimbs continue and the sperm mass is directed out into the cavity which surrounds the male's and female's cloacae. The male's hindlimb movements prevent the sperm mass from slipping laterally, and it is directed towards and reaches the female's cloaca without ever touching the substrate. The clasping lasts for 1-5 hours, or more, and two or more sperm masses may be extruded during this time. When clasping is terminated, the female retreats immediately.

Ahrenfeldt (1960) observed clasping bouts lasting one (on two occasions), five, eight, twenty-one and twenty-eight hours.

Bedriaga (1895), Wolterstorff (1925), Dähne (1926) and Ahrenfeldt (1960) provide figures of clasping pairs.

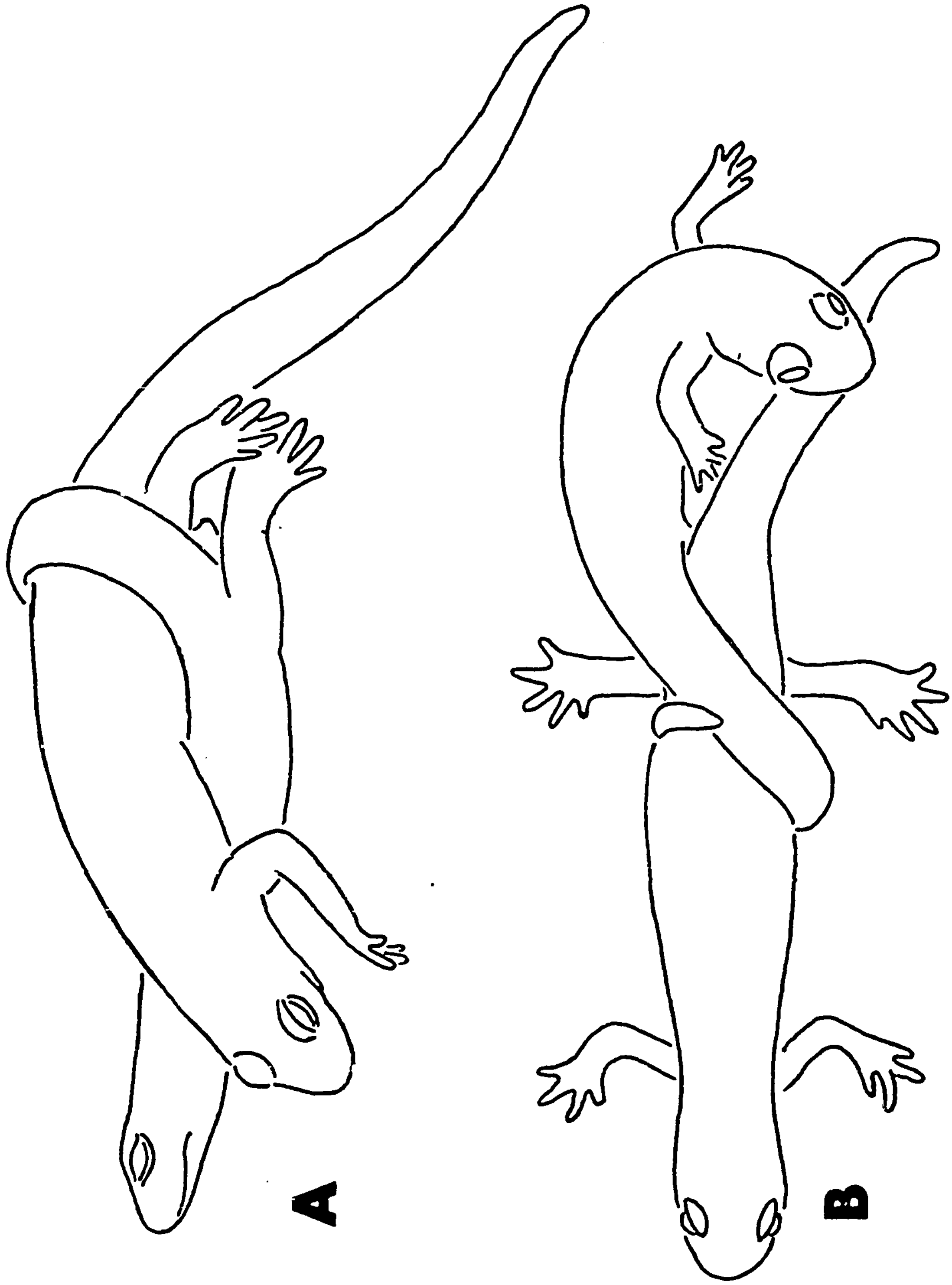
I was able to observe only preliminary courtship activities in one pair. On one occasion the male approached the female as she climbed vertically up the side of the container so that only her tail lay in the water. After nudging her tail several times, the male crawled beneath it.

He then threw his tail forcefully to one side several times and finally curled his tail around the female's tail. The female crawled upward away from the male, and he remained in the water. On another occasion the male faced towards the female and repeatedly threw his tail and posterior body rapidly to one side towards the female. Perhaps the male captures the female with this rapid tail action.

Figure 70. Clasping postures in Euproctus asper and Euproctus montanus.

Fig. A. A clasping pair of Euproctus asper, viewed laterally. The male's body lies under the female's body with his cloaca close to hers, and the male grips the female tightly with his tail (after Bedriaga, 1895).

Fig. B. A clasping pair of Euproctus montanus, viewed from above. The female faces to the left. The male grips the female's body with his tail and holds her tail in his mouth. The male's hindlimbs (out of view) grasp the female's hindlimbs, and his cloaca lies next to hers (after Bedriaga, 1883).


A
B

Euproctus platycephalus

Bedriaga (1897) provides the following account of courtship in captive Euproctus platycephalus. Sexually active males swim around actively with their mouths agape, or they rest under stones. The male grabs the female's body with his mouth when she comes near. The male then holds the female's body tightly in his jaws and gradually shifts his grip posteriorly so that he grasps the female's posterior body diagonally in his jaws. The male bends his posterior body towards the female. The male's elongate, cone-like cloacal protuberance is brought under the female's cloaca, while his proximal tail is raised high and held over the dorsum of the female's tail base. The male's distal tail is directed anterior and is pressed against the female's body opposite the male's jaws. While so grasping the female with his jaws and tail, the male holds the female's hindlimbs with his hindlimbs. The male presses the plantar surfaces of his hindfeet against his cloaca, and with an anterior to posterior motion be rubs his plantar surfaces against the sides of his cloacal proturberance. The male also employs the spur-like processes on the posterior edge of his tibia. During this rubbing action of the male's hindlimbs, the female's tail quivers. Small masses of sperm-bearing material are then taken into the female's cloaca. The gelatinous mass which transports the sperm mass clings to the female's vent for a long time before falling off. Some females are not receptive to the male's courtship, however. Such females have poorly developed tail fins.

Euproctus montanus

Bedriaga (1882a, 1883) was able to observe courtship behavior in three pairs of E. montanus on March 16. When first observed the male was grasping the female in each case. The male grasps the female with his tail, hindlimbs and mouth. While facing posterior, the male holds the female's distal tail in his mouth. His distal tail girdles the female's abdomen just anterior to her hindlimbs by wrapping over her dorsal back and then under her abdomen (see Fig. 70B). The male possess disc-like protuberances (a bony process of the tibia) on his hindlimbs. The male press these protuberances against the female's tail base. The male's cone-like cloaca therefore lies next to the female's cloaca. While thus grasping the female, the male rubs her cloaca (presumably with his hindlimbs). The female's cloacal lips swell gradually, and her cloacal aperture increases in diameter. The male then deposits a spermatophore while still grasping the female and with his cloaca next to hers. Due to the male's position, their cloaca lie in a cavity formed by the male's tail on one side and by his hindlimbs on the other. The spermatophore may be transferred directly from the male's cloaca to the female's cloaca within the cavity formed by their bodies. The spermatophore, frequently only a portion of it, is then gradually taken into the female's cloaca. Alternatively the female may take the spermatophore off of the male's hindlimbs with her cloacal lips. This entire procedure lasts 10-20 minutes. Following sperm transfer the female becomes very active, and she may discharge the spermatophore from her cloaca.

Family PLETHODONTIDAE

Pseudotriton ruber

Catalog of male actions.

The following actions are performed by the male while facing towards the female.

A.) NUDGING The male contacts the female's lateral body with his snout or lateral snout.

B.) RUBBING Rubbing of the female may take a variety of forms. The male may slide his chin along the dorsum of the female's body with head level and without lateral movements of his head (head sliding). By bending his head down the male may force his mentum against the dorsum of the female's body and may also repeatedly swing his head laterally (head swinging).

C.) LIFTING The male lifts his head under the female's chin, forcing her head upward, while turning his head to the side towards the female. The male may simultaneously swing his head laterally in short arcs thereby rubbing the dorsum of his head on the female's chin. Occasionally the male lifts his head under the female's tail.

The following actions are performed by the male while facing away from the female.

D.) FORWARD WITH TAIL UNDULATING The male moves forward undulating his tail laterally. The vent is raised above the substrate and the proximal tail may be arched upwards slightly.

E.) STATIONARY WITH TAIL UNDULATING Same as the preceding action (D), but with the male stationary.

F.) SLIDING VENT AGAINST SUBSTRATE The male moves forward sliding his vent in contact with the substrate. The tail is undulated laterally and the tail is level.

G.) STATIONARY WITH VENT ADPRESSED TO SUBSTRATE The male is stationary with his vent adpressed to the substrate. The tail is undulated laterally and the tail may be either level or slightly arched.

H.) SPERMATOPHORE DEPOSITION The male is stationary with his vent adpressed to the substrate. The hindlimbs are aligned with the femurs perpendicular to the body axis and parallel to the substrate. The tail is held level and is undulated laterally, and during the course of spermatophore deposition the tail undulations increase in both frequency and amplitude. Spermatophore deposition terminates with the male ceasing tail undulations and lifting his vent clear of the spermatophore.

I.) MOVING FORWARD WITH FLEXED TAIL The male moves forward on a straight course with the proximal tail arched upward and with the distal tail flexed slightly to one side.

J.) STATIONARY WITH FLEXED TAIL The male is stationary with hindlimbs extended and with the proximal tail arched upward. The distal tail is flexed slightly to one side. The tail may be undulated slightly. The male gradually shifts backward from an initial posture of hindlimbs extended vertical to extended backward at an angle of 45° to the substrate. During the backward shifting the male may extend and flex his hindlimbs, but the action is not performed rhythmically. See Fig. 71D for a male in this position.

Temporal relations (*Pseudotriton ruber*)

Initial encounters between a male and a female are characterized by the male actively pursuing and rubbing the female. Whenever the male recontacts the female after she has moved away from him, the male moves

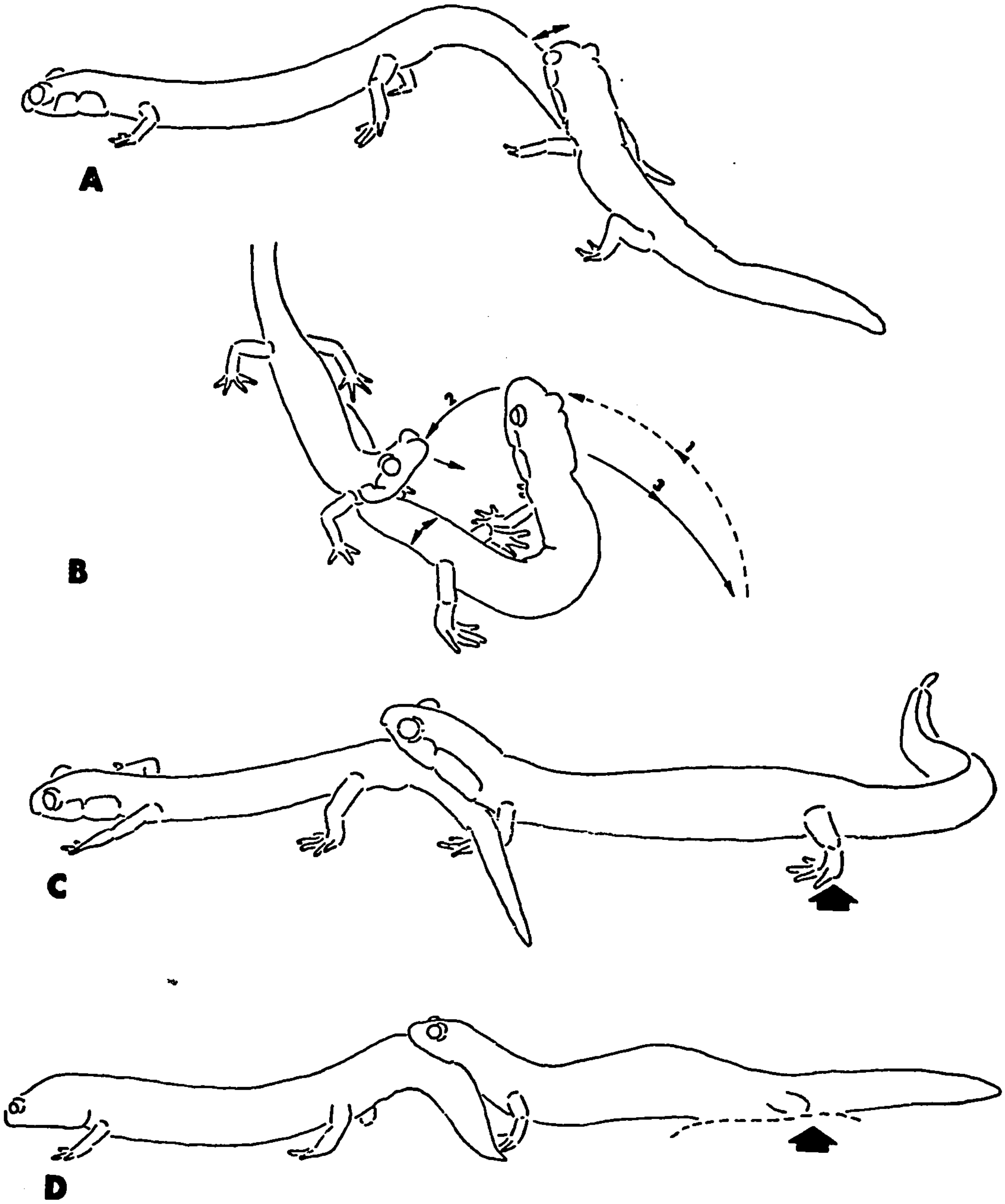
Figure 71 Courtship activities in Plethodon welleri, Plethodon jordani and Pseudotriton ruber

Fig. A. A male Plethodon welleri is stationary as he undulates his tail with his tail arched upward in contact with the female's chin. The male has just crawled under the female's chin and the female is not astride the male's tail.(From a photograph of animals from Mount Rodgers, Virginia).

Fig. B. A male Plethodon jordani has just turned back towards the female during a tail straddling walk (along arrow 1.). The male is pausing with his body axis forming a U. Next the male will turn further towards the female and pause with his head directly above the female's head. He will then slap his mental gland downward on the female's head (arrow 2.), and then immediately open to a U again. He will then turn away from the female (along arrow 3) and then again move forward in a tail straddling walk.(From a photograph of animals from Standing Indian Rec. Area, Macon Co., N.Carolina).

Fig. C. A male Plethodon jordani leans backward on his hindlimbs with his tail arched upward under the female's chin as the female rests with her vent over the spermatophore (From a photograph of animals from Standing Indian Rec. Area, Macon Co., N.Carolina).

Fig. D. A male Pseudotriton ruber leans backward on his hindlimbs with his tail arched upward under the female's chin as the female rests with her vent over the spermatophore. (From a photograph of animals from Highlands, Macon Co., N. Carolina).


A
B
1
2
3
C
D

anteriorly or posteriorly along the length of the female, rubbing and nudging her. When the male then contacts the female's head with his snout, he may turn his head laterally and lift his head under the female's chin, forcing her head upward. The female may then depart from the male, in which case the male may reapproach her, or simply recontact her in the course of moving about the container, and resume rubbing and nudging. If, however, the female remains stationary as the male lifts his head under her chin he may either contunue under the female's chin and move posterior along the opposite side of her body, or he may turn and move away from her and then arch and undulate his tail if it contacts her chin.

In three courtships which lead to spermatophore deposition these activities persisted for approximately 15, 60 and 60 minutes, and in each case pursuit of the female and rubbing of the female were in progress when the observations were begun. During these initial periods, the female repeatedly moved away from the male while he contacted her.

Then suddenly in each of the three courtships, the female began a new activity. As the male lifted his head under the female's chin and rubbed the dorsum of his head against her chin, the female began swinging her head laterally with her chin in contact with the dorsum of the male's head. The male then turned away from the female and moved forward so that the contact with the female's chin slipped posterior along his dorsum. The male arched and undulated his tail as the female's chin contacted his dorsal tail. The female continued to swing her head laterally in contact with his tail, and both animals moved forward with the male arching his tail slightly and undulating his tail. As they moved forward the female stepped astride the male's tail and continuously swung her head laterally with her chin in contact with the dorsal surface of the male's anterior tail.

At the beginning of this tail straddling walk, the male holds his vent above the substrate and alternatively pauses and moves forward. While stationary the male accentuates the upward arch of his proximal tail. Forward progress seemed to be associated with the female's snout over the male's tail base or proximal tail. The male seemed to pause whenever the female's snout slipped posterior to about one and one half vent lengths posterior to the rear margin of his vent. As the tail straddling walk progresses, the male lowers his vent to the substrate and alternates between sliding his vent in contact with the substrate and pausing with his vent in contact with the substrate. He undulates his tail laterally with the tail level or slightly arched above the substrate.

Throughout the tail straddling walk, the female continues to swing her head laterally over the dorsal surface of the male's undulating tail. With her chin in contact with the male's dorsal tail, her snout remains posterior to the insertion of the male's hindlimbs and over the male's anterior tail. As the male turns during the course of the tail straddling walk, when the sides of the container are encountered for example, the female maintains her chin axial over the male's tail by turning her head laterally.

While sliding his vent in contact with the substrate, the male suddenly stops, aligns his hindlimbs and begins spermatophore deposition. During spermatophore deposition the female may or may not continue to swing her head laterally over the male's undulating tail. She remains astride the male's tail with her snout posterior to the insertion of the male's hindlimbs over his anterior tail.

At the termination of spermatophore deposition, the male extends on his hindlimbs, arches his proximal tail upward, lifts his vent free of the spermatophore and moves forward. The male and female move forward together on a straight course with the male arching his tail and undulating it slightly and with the female's chin resting on the dorsum of the male's arched anterior tail. As they move forward the female's ventral body may slide over the spermatophore. If the spermatophore contacts her vent, she stops and lowers her vent upon it. With the spermatophore inserted into her cloaca and with her vent pressed against the substrate, the female undulates her tail base slightly.

As the female stops with her vent over the spermatophore, the male stops in front of her with his tail still arched upward in contact with her chin. He may now flex his tail to one side, or it was drawn out from under the female's forelimbs soon after the male moved forward from the spermatophore. In either case, the distal tail is only slightly flexed to one side and lies just outside of the female's forelimb. The male pauses momentarily in front of the female undulating his arched tail and then intermittently backs up by extending backward on his hindlimbs and thereby forces his arched and undulating anterior tail up under the female's chin as she rests over the spermatophore. Then the non-rhythmic movements cease and the male becomes motionless while extended backward at a 45° angle on his hindlimbs with his tail arched in contact with the female's chin and not undulating (Fig. 71D).

In two courtships the female then turned and moved away from the male and successfully removed the sperm mass. The male remained motionless after the female departed. He then reapproached her and began nudging and rubbing her. In both cases the female repeatedly moved away from the male, and only one spermatophore was deposited.

In a third courtship, the female moved on past the first spermatophore without locating it. The female continued to swing her head from side to side and moved up the dorsum of the male's back as he paused in one corner of the container. The female then turned and moved away from the male. The male then reapproached her, moved directly to her chin, and rubbed the dorsum of his head under her chin. The female began swinging her head from side to side. The male then turned away from the female and they moved forward in a tail straddling walk as the female's chin slid posterior to his dorsal tail. The male then deposited a second spermatophore, and the female successfully removed the sperm mass. The female then departed from the male as in the first two courtships. The male reapproached her and nudged and rubbed her. She repeatedly moved away from him, and no additional spermatophores were deposited.

Organ and Organ (1968) observed courtship behavior in captive animals from Whitetop Mtn., Virginia in late June. My observations are essentially in agreement with theirs. As they point out, the courtship behavior of male Pseudotriton is quite rapid compared with other plethodontids. They observed one complete tail straddling walk (with a male and a female), and, as in my observations, the male did not turn back towards the female.

Organ and Organ (1968) suggest that Pseudotriton might deposit spermatophores exclusively on terrestrial sites. My animals courted in containers tilted so that a third of the substrate was submerged in water. In the deepest portion of the container the bodies of the animals were just submerged. Initial encounters between the male and female occurred in either the submerged or terrestrial portion of the container. Tail straddling walks occurred in the terrestrial portion. Spermatophore depositions occurred either on the terrestrial portion or in water less than two milimeters deep.

One male observed by Organ and Organ deposited two spermatophores in a single evening. One was deposited during a homosexual courtship, and subsequently a second spermatophore was deposited with a female. The female did not successfully locate this spermatophore.

Organ and Organ (1968) also briefly observed a captive male and female from New Jersey in a tail straddling walk in early May. Thorn (1959) observed a captive male *P. ruber shcenki* pursuing a female *P. r. ruber* and rubbing his snout against her snout in a continuous up and down motion.

James Organ and I observed male *Pseudotriton* from Whitetop Mtn., pursuing and biting other males when they were housed in containers with females. Earlier Organ and Organ (1968) suggested that aggressive interactions did not occur between male *Pseudotriton*.

Eurycea bislineata

Catalog of male actions.

The following actions are performed by the male while facing towards the female.

A.) NUDGING The male contacts his snout or lateral snout to the female's lateral body.

B.) PULLING The male slides his snout forward a short distance in contact with the female's dorsal body with his head level. The male then arches his neck, bending his head down, so that the snout is pressed against the female's body. The male then draws his snout backward, pulling his snout in contact with the female's dorsal body. When the male lies on top of the female or parallel to her, several such pulls may be given in rapid succession. When the male's body lies perpendicular to the female, the male may fall off of the female with each backward pulling motion. The male then replaces his snout on the female's body to reinitiate pulling.

C.) SNAPPING The initial motions are just as in pulling. The male contacts his snout to the female's dorsal body, slides his snout slightly forward and then arches his neck downward strongly. But then, instead of drawing the snout back slowly, the male vigorously snaps (or flexes) his body, and his snout is consequently drawn backward very rapidly in contact with the female's dorsum. The action is performed so rapidly that I could not detect whether the snapping of the body occurred in a horizontal or vertical plane. In any case, the snapping action is so vigorous that the male's whole body is thrown backward a few centimeters.

D.) TAPPING The male rapidly lowers and then raises his head, tapping his naso-labial cirri to the substrate or on the female's body.

E.) LIFTING The male lifts his head under the female's chin and forces her head upward. The action is usually performed as the male turns his head to one side, towards and under the female's chin as the male lies parallel to her and faces anterior. The male may also rub his cheek on the female's chin while in this position.

The following actions are performed by the male while facing away from the female.

F.) <u>STATIONARY WITH TAIL ARCHED AND UNDULATING</u> While stationary the male arches his proximal tail upward and undulates his tail laterally. The vent is raised above the substrate.

G.) <u>MOVING FORWARD WITH TAIL ARCHED</u> The male moves forward slowly with the proximal tail slightly arched or essentially level. The tail may be undulated slightly laterally.

H.) <u>TURNING BACK TOWARDS THE FEMALE</u> As the female's chin rests on the dorsum of the male's tail, the male turns his head back towards the female, while continuing to arch and undulate his tail. Thus from an initial position with the male's body axis straight, the male turns until his body axis forms nearly a complete circle with his head opposite or above the female's body posterior to her head. In this position the male extends his hindlimbs, accentuating the upward arch of his proximal tail, while continuing to undulate his tail under the female's chin. The male may remain stationary on all four limbs, or he may walk forward with the hindlimbs so that the pair makes a few spiral revolutions about the initial point. In this position the male performs snapping.

I.) <u>SLIDING VENT AGAINST SUBSTRATE</u> The male moves forward sliding his vent in contact with the substrate with his tail level. The tail may be undulated slightly.

J.) <u>STATIONARY WITH VENT ADPRESSED TO SUBSTRATE</u> The male pauses with vent in contact with substrate and with tail level. The tail may undulate slightly.

K.) SPERMATOPHORE DEPOSITION The male remains stationary with vent adpressed to the substrate and aligns his hindlimbs with his femurs perpendicular to his long body axis. The tail is level, and tail undulations of large amplitude proceed along the entire length of the tail. Tail undulations appear to increase in frequency as spermatophore deposition proceeds. After spermatophore deposition begins the male may initiate slight lateral rocking on his hindlimbs. Spermatophore deposition terminates with the male ceasing tail undulations and hindlimb rocking, and then pulling the tail to one side at its base to nearly a 90° angle to his body axis, and lifting the vent free of the spermatophore.

L.) MOVING FORWARD WITH TAIL FLEXED The male moves forward with the tail flexed to one side at the base at a 45° to nearly a 90° angle. The vent is held above the substrate and the midbody is curved in a sigmoid lateral flexure. As the male moves forward the tail is repeatedly flexed laterally as if to maintain the lateral displacement of the tail as the distal tail drags on the substrate.

M.) STATIONARY WITH FLEXED TAIL The following series of actions is executed as the female stops with her vent over the spermatophore. The male stops with his tail still flexed to one side. The male then straightens his tail, so that with the female's chin resting on the dorsum of his tail base, the male's tail proceeds around the outside of one of the female's forelimbs and then straight backward, parallel to and in contact with the female's lateral and ventral midbody. The male then produces strong sinuous undulations of the distal tail as it contacts the female's ventral or lateral midbody, and the tail appears to massage the female's body. His distal tail follows the contours of her body as it undulates. As the sinuous, massaging tail undulations continue, the male initiates rapid and rhythmic extentions and flexions of the hindlimbs, which cause the female's head to move up and down rapidly as her chin rests on his proximal tail. Then as the repeated extentions and flexions of the hindlimbs continue, the sinuous tail undulations cease. Finally the hindlimb extentions and flexions decrease in amplitude and frequency and then stop altogether. The male then pauses motionless with his proximal tail slightly arched and with the female's chin resting on the dorsum of his proximal tail.

As the male begins the hindlimb extentions and flexions, he leans backward on his hindlimbs so that they form now a 45° angle with the substrate, and the sigmoid lateral flexure of his body straightens.

Temporal relations (_Eurycea bislineata_)

A male initiates or reinitiates contact with a female in one of two ways. The male may either move parallel to the female and directly towards her head without contacting her, or the male may intermittently contact her with his head (via tapping, nudging, pulling or head sliding) as he moves anterior or posterior along her length. Since in the latter case the female frequently moves forward away from the male when she experiences any of these modes of head contact, initial interactions are characterized by the female repeatedly moving away from the male with the male approaching her from behind each time she moves off.

If, however, the female remains stationary and the male reaches her head, he turns his head to the side towards the female and lifts his head under her chin. Or the male may turn his head to the side and press his cheek against the female's snout and then, if the female remains stationary, lift under her chin. The female may then move off, in which case the male follows rapidly each time she moves forward and eventually reinitiates contact with her.

If the female's chin contacts the male's dorsal fore or hindbody as he lifts beneath her chin, the male turns and moves away from the female in front of her. As the contact with her chin slides posterior to the male's anterior dorsal tail, he arches and undulates his tail in contact with her chin and pauses.

If the female slides forward along the male's tail and steps astride it, the male and female move forward in a tail straddling walk with the female's chin resting on the male's anterior tail and with his tail in contact with the female's ventral body; but otherwise the male reapproaches the female. The tail straddling walk may also be initiated by the female actively approaching the male and contacting her chin to his dorsal midbody or anterior tail. In such cases the male does not lift under the female's chin before moving forward and arching and undulating his tail.

Initially during the tail straddling walk the male moves forward slowly on a straight course. When the male pauses, he arches his tail upwards and undulates it in contact with the female's chin. When he is moving forward, his tail may be nearly level, and the tail undulations are much less pronounced. Forward progress by the male is associated with more anterior contact of the female's chin to the male's tail (eg. female's snout just above the posterior margin of the male's vent), and the male pauses whenever the female's snout slips posterior. During forward progress by the male, the female's snout frequently rests just posterior to the male's caudal hump (a glandular thickening on the dorsum of the tail base which is present only in males during the breeding season). Whether the male is moving forward or stationary during the tail straddling walk, the female's snout invariably lies on the dorsal tail region posterior to the insertion of the male's hindlimbs and anterior to a point about two vent lengths posterior to the rear margin of the male's vent. During the tail straddling walk the female swings her head back and forth in short arcs over the dorsum of the male's tail.

After initiation of a tail straddling walk and having moved forward on a straight course for a few centimeters, the male invariably turned back towards the female (H). With his body curved in nearly a complete circle, the male snaps on the dorsum of the female's forebody, hindbody or, less frequently, her anterior tail. The male may first tap the dorsum of the female's body before snapping.

In some instances the female rapidly moved away from the male following snapping. The male then reapproaches her.

The backward motion of the male's body produced by snapping may throw the male's body away from the female. Frequently then the tail straddling walk was immediately reinitiated by the female approaching the male and placing her chin on his anterior tail, or by the male turning, lifting under the female's chin and then crawling forward without any intervening tapping, nudging or pulling.

If, however, the female's chin remains on the dorsum of the male's tail following snapping, the male simply turns away from the female and moves forward on a straight course with the female straddling his tail. During uninterrupted bouts of tail straddling walk, snapping was executed by the male one to three times before spermatophore deposition.

After tail straddling walk with the male's vent raised above the substrate and after snapping has occurred, the male may begin sliding his vent in contact with the substrate while moving forward on a straight course. If then the female's snout slips posterior along his tail, the male pauses and raises his vent above the substrate, and remains in this position until the female again slides forward along his tail.

While sliding his vent against the substrate, the male suddenly stops and begins spermatophore deposition, During spermatophore deposition, the female remains astride the male's tail with her snout resting on the male's anterior tail. The male's tail undulates in contact with her ventral body as she rests upon it. During spermatophore deposition the female may or may not swing her head laterally in short arcs in contact with the male's undulating tail.

As the male pulls his tail out to the side and moves forward following spermatophore deposition, the female follows behind him with her chin resting on his anterior tail anterior to the lateral flexure. As she moves forward the spermatophore contacts her ventral body, and she slides over it, or contacts it intermittently, while moving forward. If the spermatophore contacts her vent, she lowers her vent upon it, and so inserts the sperm mass into her cloaca. The female then remains motionless, squatting upon the spermatophore, for a few minutes, while the male executes the complex series of actions described previously (action M) including massaging of her ventral and lateral body with his tail.

Finally the female turns and moves away from the male and the spermatophore. The male remains motionless as she departs, but may then turn and reapproach her. In each of four observed spermatophore depositions, the female successfully removed the sperm mass. The females repeatedly moved off away from the male after sperm pickup, and no additional spermatophores were deposited by the male. Thus in each of four cases one spermatophore was deposited per courtship.

In one instance the female moved off and away from the male as he began spermatophore deposition. The male ceased tail undulations and reapproached her without depositing a spermatophore.

Noble (1929) observed preliminary courtship behavior in captive animals. He observed males nudging females and pressing their cheeks against the female's snouts. Tail straddling walks were observed, which Noble notes may last for over an hour. Spermatophore deposition and sperm transfer were not observed.

Noble's observations were made on animals courting under water, while my observations were made on animals courting in terrestrial containers. I have also observed animals courting while completely submerged, although in these situations I never observed spermatophore deposition. Tail straddling walks of animals courting under water were much prolonged compared with animals courting out of water.

Noble (1929) noticed that in contrast to females, males possess during the breeding season a very pronounced swelling of the temporal region and a distinct lump on the dorsum of the tail base. Histological examinations showed a distinctive type of gland on the male's mentum, posterior portion of the upper eyelid, jaws, temporal region and on the dorsum of the male's tail base. Since it is precisely these regions which the male applies to the female's body, particularly her anterior head, during courtship, Noble suggested that the glands functioned during courtship and that they be called hedonic glands. In addition,as Noble noted, the male, unlike the female, possesses elongate teeth in both jaws and the premaxillary teeth are directed slightly forward. Situated just beneath the premaxillary teeth, on the mentum is a circular concentration of glands called collectively the mental gland. From the postures assumed by males during courtship, Noble discerned clear functions for the various hedonic glands and protruding premaxillary teeth. But since males were never observed to bite either females or males, Noble was unable to suggest a function for the elongate maxillary teeth of the male.

I was able to observe several behavioral actions, not observed by Noble, which further clarify the functions of this remarkable suite of sexually dimorphic characters. Hedonic glands situated on the male's lateral head are rubbed on the female's lateral body as the male nudges the female, but in addition they are applied to the female's snout, in the vicinity of her nares, just before the male turns his head under the female's chin. The glands situated on the male's dorsal tail base, lie precisely in the site contacted by the female's snout and nares during the tail straddling walk. The male's elongate premaxillary teeth and his mental gland are employed by the male during the action of snapping, which occurs in Eurycea bislineata during the tail straddling walk, and during the action of pulling. Both of these actions, snapping and pulling, occur in Desmognathus, and I will discuss more fully the relationship between these actions and the male characters' mental gland and premaxillary teeth in the section on Desmognathus courtship. On many occasions I observed males pursuing and biting other males. This only occurred during the courtship season in containers which also contained females. For some reason Noble did not observe interactions of this kind between males. I found that a male courting a female would suddenly pursue and bite another male if he contacted a male with his snout. If, for example, a male contacts the body of another male as he leads the female forward in a tail straddling walk, the courting male will depart from the female and pursue and bite the other male. The pursued male then swims off rapidly (these observations were made on animals under water), while the pursuing male then circles rapidly about the container, recontacts the female and immediately reinitiates the tail straddling walk. The enlarged maxillary teeth of male Eurycea bislineata are therefore employed during agonistic encounters between sexually active males. Such encounters between males probably insure the reproductive monopoly of a female by a male once he initiates courtship with her.

In some geographic races of Eurycea bislineata, males possess remarkably elongate naso-labial cirri. I observed courtship behavior of males from Mt. Rodgers, Virginia, with very elongate naso-labial cirri and courtship of males from Loudonville, Ohio where the naso-labial cirri of males are not nearly so well developed. I found no differences in courtship behavior between males from these two localities. Nevertheless, sexual dimorphism in naso-labial cirri, however well developed, seems to be clearly related to male behavior during courtship. The naso-labial cirri of plethodontids represent elongations of the naso-labial groove. During courtship behavior in all the plethodontids I have observed, the male periodically performs a distinctive action, tapping, during which the tips of the naso-labial cirri are momentarily and lightly contacted to the substrate or to the dorsum of the female's body. When tapping the substrate, male plethodontids frequently swing the head from side to side as they move forward. Several authors have suggested that the naso-labial groove of plethodontids serves to drain water off the surface of the animals' heads, and particularly from the nares (Whipple, 1906; Brow and Martot, 1966; Brown, 1968). At the same time the groove is capable of drawing fluids up and into the nares, apparently by capillary action. The water draining function of the groove may very well be real, but it does not explain why the naso-labial groove is extended on an elongate cirrus in only the male of plethodontids. Elongate naso-labial grooves are probably used by male plethodontids, during the courtship action tapping, to transport chemical substances from other animals, and from the substrate, into the nares. Obliteration of the groove, or its cirrus, in male plethodontids should therefore interfere with the male's ability to locate the female before and during courtship or with his ability to identify the sex of conspecifics. Critical experiments of this kind have not been performed.

Grant (1955) observed agonistic interactions between captive specimens of *Eurycea bislineata*. When several individuals were housed in the same terrarium, each animal used a separate retreat. Two kinds of interactions were observed. When one animal approached the retreat of another animal, the resident approached the intruder and then paused with its snout in contact with the snout of the intruder. The intruder then always retreated from the resident. On some occasions the resident bit the intruder and the intruder fled. Captive *Hemidactylium scutatum* also established individual retreats but intruders always withdrew from an approaching resident and no biting interactions were observed.

Eurycea lucifuga

Organ (1963b) observed courtship in a pair of animals on July 19 and on July 22. On July 19 Organ found a female straddling the male's tail with her forelimbs while facing anterior with her chin in contact with his dorsal proximal tail. The male undulated his tail laterally in contact with the female's chin. The male was extended on his hindlimbs and so held his sacrum and tail base high above the substrate. The tail undulations near the tail base were rotatory and became more lateral in motion as the waves passed posteriad along his tail. Both animals remained stationary, until after a few minutes the female backed up posteriorly along the male's tail. The male then increased the amplitude of his tail undulations and initiated repeated extentions and flexions of his hindlimbs. The female moved away from the male, and he reapproached her. He moved directly towards the female's head and contacted his cheek to her lateral snout. He then crawled under her chin with his dorsum in contact with her chin. He stopped with his dorsal tail in contact with her chin and began extentions and flexions of his hindlimbs which forced his pelvis and tail base up under her chin as he undulated his tail. The female stepped astride the male's tail and the pair moved forward a short distance in a tail-straddling walk. The female then departed from the male.

On the evening of July 22, the same pair was again observed in courtship. The male rubbed the dorsum of his head under the female's chin and lifted his head contacting his cheek to the female's lateral snout for a period of four minutes. Observations were then discontinued, but 90 minutes later a spermatophore was found in the container. The animals were no longer courting, and a sperm mass was found between the female's cloacal lips.

Spermatophore deposition and sperm transfer have not yet been observed in this species.

Hemidactylium scutatum

Branin (1935) observed the behavior of *Hemidactylium* courting in the laboratory. 21 sexually mature adults were housed in a 10 inch crystallizing dish with a substrate of moist moss. These animals were collected on November 2, and over 100 spermatophores were deposited between November 4 and December 2. Branin notes that the behavior he observed was similar to the observations of Noble (1929) on *Eurycea bislineata.* Aggregations of courting animals were common in the rather small container. Nudging of other animals was frequently observed. And "... on several occasions males were seen to move briskly about with the tail turned sharply at an angle of 90° from the body." Branin also found that the "Female straddles the tail of the male and presses her chin against the dorsal surface of the base of his tail. As he moves forward, she keeps the same relative position. As the tail of the male undulates from side to side, the chin of the female closely follows its every bend. If the pair is unmolested this straddle walk may continue for a considerable period of time. On several occasions it was observed for 20 or more minutes."

Branin (1935) did not provide detailed observations of either spermatophore deposition or sperm transfer. He did note that the female pauses over the spermatophore and then gradually moves away from it. One such female was preserved and sectioned. She held a portion of both the sperm mass and the spermatophore base between her cloacal lips.

Desmognathus fuscus

Catalog of male actions.

The following actions are performed by the male while facing towards the female.

A.) TAPPING The male rapidly lowers and raises his head thereby tapping his mentum and nasolabial cirri to the substrate or to the dorsum of the female's body.

B.) NUDGING The male contacts his snout or lateral snout to the female's lateral body.

C.) BUTTERFLYING The male raises both forelimbs simultaneously and swings them forward and upward and then downward in a smooth arc. The forelimb action is very similar to the arm action during the butterfly swimming stroke (but the male does not undulate his body in a vertical plane).

D.) PULLING The male presses his mentum down in contact with the female's body by bending his neck downward. The male then draws his head backward axially by pulling his mentum in contact with the female's body in a short stroke.

E.) SNAPPING The mentum is pressed down against the female's body and then drawn rapidly backward with the head still bent down by a sudden, vigorous snapping of the body.

F.) RUBBING The male swings his head laterally in one or a few short arcs, back and forth, with the mentum in contact with the female's dorsum.

G.) LIFTING The male lifts his head under the female's chin thereby raising her head upward. Usually the action is performed with the male parallel to the female and facing in the same direction with his head turned towards the female and under her chin.

The following actions are performed by the male while facing away from the female.

H.) MOVING FORWARD WITH TAIL ARCHED AND UNDULATING The male moves forward with his proximal tail arched upward and with his tail undulating laterally. The vent is raised above the substrate.

I.) STATIONARY WITH TAIL ARCHED AND UNDULATING The male is stationary with his proximal tail arched upward and with his tail undulating laterally. The vent is raised above the substrate.

J.) SLIDING VENT IN CONTACT WITH SUBSTRATE The male moves forward sliding his vent in contact with the substrate. His tail is essentially level, and there is little or no lateral undulation of the tail.

K.) STATIONARY WITH VENT ADPRESSED TO SUBSTRATE This action is the same as the preceding action (J) except that the male is stationary.

L.) TURNING BACK TOWARDS THE FEMALE From a position with the male straight forward in front of the female, with their body axes aligned, the male turns his head and forebody back towards the female. While turning back the male continues to arch and undulate his tail under the female's chin and accentuates the upward arch of his tail by extending on his hindlimbs. As a consequence of this turning action, the male forms a U and finally a nearly complete circle with his snout opposite or above the female's body, and with the female's chin resting on his dorsal proximal tail.

M.) SPERMATOPHORE DEPOSITION The male pauses with his vent adpressed to the substrate and with his tail level. Lateral tail undulations of large amplitude proceed along the entire length of the male's tail. The male's hindlimbs are aligned with femurs perpendicular to the long axis of his body and with hindfeet firmly planted on the substrate. The male does not appear to rock laterally on his hindlimbs. Spermatophore deposition terminates with the male ceasing tail undulations and lifting the vent upward free from the spermatophore and then flexing the tail to one side out from under the female's body. The male then moves forward.

N.) MOVING FORWARD WITH FLEXED TAIL The male moves forward with the midbody in a lateral sigmoid flexure and with the tail flexed laterally at the base at approximately a 45° angle. The tail therefore proceeds outside one of the female's forelimbs, as the female's chin rests on the male's tail base.

O.) STATIONARY WITH FLEXED TAIL The following series of actions is executed by the male as the female rests with her vent over the spermatophore. The male stops with the female's chin resting on his dorsal tail base. The male extends his hindlimbs and gradually leans backward without raising his hindfeet from the substrate, so that the angle formed by his hindlimbs with the substrate changes from 90° to 45°. As a consequence of this backward leaning, his body axis changes from sigmoid flexure to straight. Simultaneously the male undulates his tail slightly, but the tail remains flexed to one side, and the only point of contact with the female is the male's dorsal tail base in contact with her chin. The female's head is moved slightly up and down, but despite close examination I was unable to find out how this motion was produced by the male. It is either produced by very subtle extentions and flexions of the male's hindlimbs or by the male's tail undulations. Finally the male ceases all movement and remains stationary.

Temporal relations (Desmognathus fuscus)

If the female moves away from the male at any time during courtship, the male turns and follows her, moving forward rapidly each time the female moves forward.

Frequently when the male has come within a few centimeters of a female which has fled from him, the male changes his rate of approach dramatically. He lowers his forebody and moves slowly forward parallel to the female and one to a few centimeters away from her. While moving forward slowly the male may repeatedly jerk forward in short bursts. The male may perform butterflying and may simultaneously arch his proximal tail upward and undulate his tail. Tail undulation and/or tail arching may also occur without butterflying as the male creeps slowly forward or pauses parallel to the female without contacting her. During slow approaches with any of these elements, the female usually remains stationary.

Alternatively, the male may slowly approach the female and tap, pull, rub, nudge, or slide his mentum forward in contact with the female's body. Eventually the female almost invariably dashes or moves off from the male when any of these actions are performed (ie. when the male contacts the female with his head while approaching her).

When the male reaches the female's head, he turns his head to the side and towards the female, and lifts his head under her chin. If the female's chin contacts his dorsal forebody, the male turns and crawls forward away from the female, causing her chin to slide posterior along his hindbody to his dorsal anterior tail. If the female's chin contacts his dorsal anterior tail, the male stops, arches his proximal tail upward and undulates his tail laterally (action I).

If the female then turns and moves away from the male, he ceases tail undulation, lowers his tail and reapproaches her.

If, on the other hand, the female moves forward, sliding her chin anterior along his tail and stepping astride his tail with her forelimbs, the male then moves forward, arching and undulating his tail (action H) with his tail directed posterior under and in contact with the female's ventral body.

During this tail straddling walk the male may turn back towards the female (action L). With his body axis then in nearly a complete circle, with the female's chin resting on his anterior tail, and with his head opposite and nearly contacting her forebody, the male rests his mental gland on the female's lateral or dorsal forebody and then snaps. In both instances in which snapping was observed in this context, the female immediately moved away from the male, and the male then turned and reapproached her.

When not turning back towards the female during the tail straddling walk, the male moves forward on a straight course and alternates between pausing and moving forward (ie. between actions I and H). Forward progress appears to be associated with the female's snout more anterior on the male's proximal tail, while the male stops whenever the female's snout slips posterior. During the tail straddling walk, the female's snout is always in the region from above the posterior margin of the male's vent to one vent length posterior to this point.

After moving forward on a straight course with the female straddling his tail, the male begins sliding his vent in contact with the substrate. He may pause momentarily with vent adpressed to substrate and then continue forward.

Finally the male stops with vent adpressed to substrate and begins spermatophore deposition. During spermatophore deposition the female remains motionless astride the male's tail and does not move her head actively in a lateral plane over the male's tail. Her snout rests just above the posterior limit of the male's vent.

Following spermatophore deposition the male flexes his tail to one side and moves forward with tail flexed and with his body in a sigmoid flexure. The female follows behind him with her chin resting on the male's tail base. As she moves forward her forebody and then hindbody slide over the spermatophore. As the spermatophore contacts her vent, she stops and lowers her vent upon it, inserting the spermatophore into her cloaca. While squatting on the spermatophore, the female undulates her proximal tail slightly, and the male executes the complex series of actions previously described (see action O). The female then ceases tail undulations and remains stationary.

Finally the male turns and moves away from the female. After the male departs the female moves off of the spermatophore. Only one spermatophore deposition was observed, and the female successfully removed the sperm mass. Afterward no additional courtship interaction occurred.

Organ (1961a and 1961b) observed courtship behavior of captive *Desmognathus fuscus*, *D. ochrophaeus*, *D. monticola* and *D. wrighti*, all from Southwest Virginia. Organ found that the courtship actions and behavioral sequences were basically similar in these four species. My observations on *D. fuscus* and less complete observations on *D. ochrophaeus*, *D. monticola* and *D. quadramaculatus* also suggest that *Desmognathus* species are remarkably similar to one another in courtship behavior.

Of the *Desmognathus* species I observed, only in *D. fuscus* was I able to see courtship behavior spanning the whole range of courtship activities. The behavioral actions which I call tapping, butterflying, snapping, lifting, as well as the actions H, I, J, K, M, (which are associated with the tail straddling walk and spermatophore deposition) are also described by Organ. The following are the most notable new additions to our knowledge of Desmognathus courtship. First, the mental gland and premaxillary teeth of the male are applied to the female's dorsum during pulling as well as during the more vigorous action of snapping. Second, the male may turn back towards the female during the tail straddling walk and perform snapping in this context. Third, the male assumes a characteristic posture and performs a characteristic set of actions with the female stationary with her vent near or over the spermatophore. Fourth, the sequences of actions performed during courtship encounters are more variable than Organ's description might indicate. I have outlined some of this variability above.

Organ (1961a) made two novel proposals concerning the functions of male secondary sexual characters during courtship. In light of my observations on this genus, I find Organ's proposals very compelling. Organ notes that during the male action of snapping, the male presses his mental gland and enlarged premaxillary teeth firmly against the female's dorsum and then vigorously snaps backward. Organ notes that the female's skin is well vascularized and proposed that the male might deliver secretions from his mental gland directly into the female's circulation by producing superficial lacerations with his premaxillary teeth. I found that indeed the male presses his snout firmly enough to the female's dorsum and snaps backward violently enough to make this interpretation feasible. In addition, the male's mental gland is situated, in Desmognathus, on a slight anterior projection of the mentum itself (see Fig. 72C for a view of the mental gland of Desmognathus, as well as the remarkably premaxillary (and maxillary) teeth present in male Desmognathus ochrophaeus (Fig. 72A and B), all after Noble, 1927). Therefore when the male bends his head down both the premaxillary teeth and mental gland are pressed against the female's dorsum. Furthermore, during the backward stroke during either pulling or snapping, the mental gland moves against the female's surface followed by the projecting premaxillary teeth.

Organ (1961a) also notes that the male produces a clear secretion from his tail during the tail-straddling walk. He suggests that his secretion serves to lubricate the female's venter prior to spermatophore deposition, so that the female will not dislodge the sperm mass before it reaches her vent as she slides forward over the top of it.

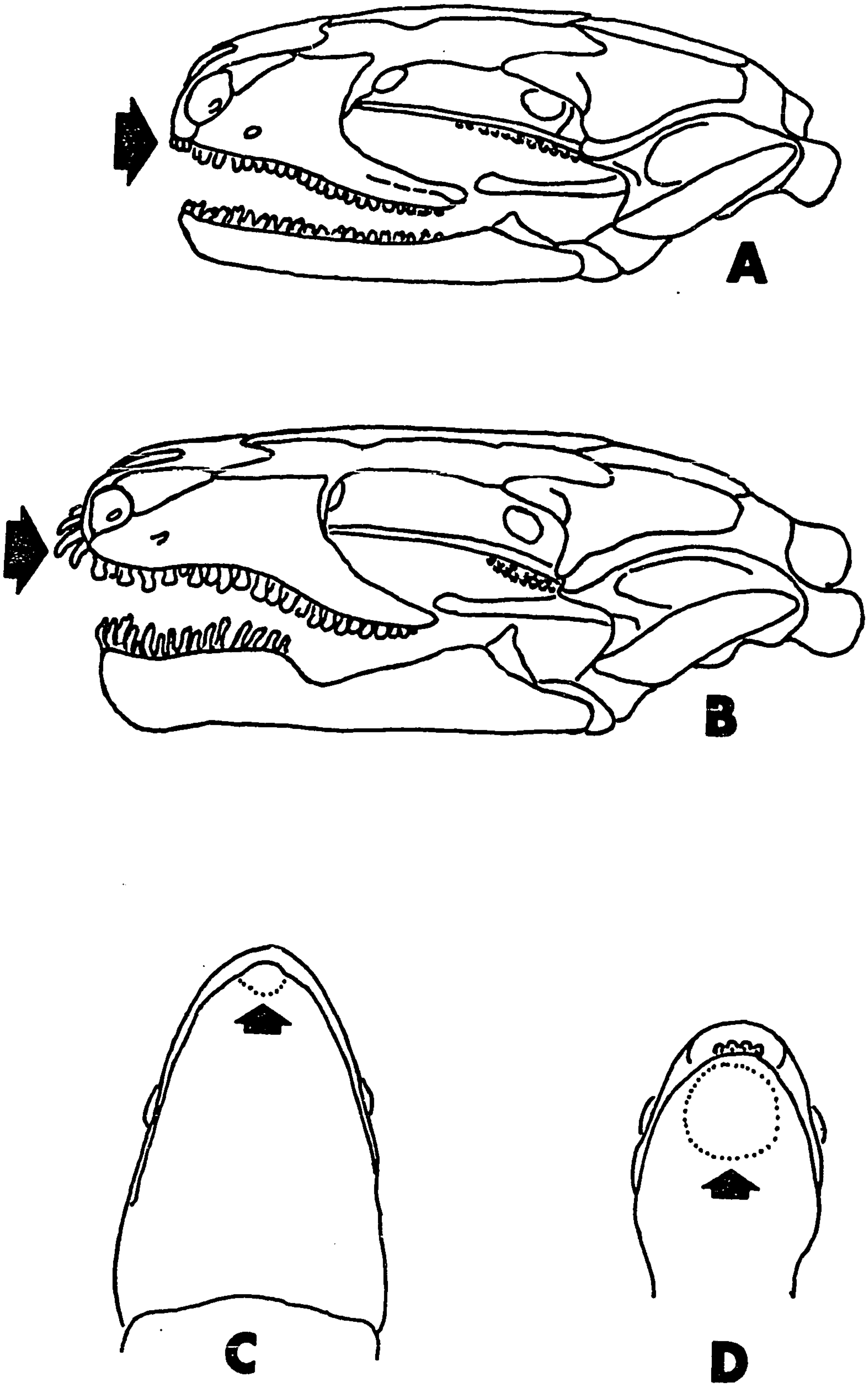
Figure 72. Sexual dimorphisms in plethodontid salamanders (after Noble, 1927).

Fig. A. A lateral view of the skull of a female Desmognathus ochrophaeus (after Noble, 1927).

Fig. B. Lateral view of the skull of a male Desmognathus ochrophaeus. Notice the very elongate, protruding premaxillary teeth (arrow) as well as the elongate teeth on the dentary (after Noble, 1927).

Fig. C. Ventral view of the head of a Desmognathus fuscus male. The mental gland lies on a slight forward projection of the mentum (after Noble, 1927).

Fig. D. Ventral view of the head of a Bolitoglossa adspersa male. Arrow indicates the position of the large mental gland. Premaxillary teeth protrude from the upper jaw just anterior to the mental gland (after Noble, 1927).


A
B
C
D

Desmognathus ochrophaeus

Catalog of male actions.

I was able to observe only the processes of spermatophore deposition and sperm transfer. The following actions are performed by the male while facing away from the female.

A.) SPERMATOPHORE DEPOSITION The male is stationary with his vent adpressed to the substrate. His hindlimbs are aligned with the femurs perpendicular to the long axis of his body. The tail is level and undulations of large amplitude proceed along the entire length of the tail. The male does not appear to rock laterally on his hindlimbs. Spermatophore deposition terminates with the male ceasing tail undulations, lifting his vent free of the spermatophore and flexing his tail to one side outside of one of the female's forelimbs.

B.) MOVING FORWARD WITH TAIL FLEXED The male moves forward with the tail flexed to one side at a 45° to 90° angle to his body axis. The male's body axis is sigmoid in shape due to lateral body flexure.

C.) STATIONARY WITH TAIL FLEXED The following actions are executed by the male as the female rests with her vent over the spermatophore. The male leans backward on his hindlimbs, arching his proximal tail upward under the female's chin. Consequently the male's body axis straightens. The male then begins rhythmic extentions and flexions of the hindlimbs with the hindlimbs slanted backward at a 45° angle to the substrate, and with the hindfeet and forefeet firmly planted on the substrate. The resultant backward and upward motion rhythmically raises and lowers the female's head as her chin rests on the dorsum of the male's tail base and may even lift the female's forelimbs off the substrate. Finally the extentions and flexions of the male's hindlimbs cease and he remains motionless with his proximal tail still arched upward in contact with the female's chin, and with his distal tail still flexed to one side outside of one of the female's forelimbs.

Temporal relations (<u>Desmognathus ochrophaeus</u>)

During spermatophore deposition the female rests astride the male's undulating tail with her snout just above the posterior margin of the male's vent. She does not appear to swing her head laterally over the male's tail.

As the male moves forward away from the spermatophore with reflexed tail (action B), the female follows with her chin resting on the male's tail base. As she moves forward the spermatophore slides posterior in contact with her ventral body. When her vent contacts the spermatophore, she stops and lowers her vent upon it, inserting the spermatophore into her cloaca.

The male then stops in front of the female and performs the series of actions previously described (see action C) with the female's chin resting on his tail base and with her snout above the insertion of his hindlimbs. While squatting on the spermatophore the female does not appear to undulate her tail.

Finally, the female turns her head off of the male's tail and moves away from him. Four spermatophore depositions were observed and in each case the female successfully removed the sperm mass.

The male remains motionless after the female moves off and then moves off tapping the substrate. Two males contacted the spermatophore base with their snouts while moving about the tank. One male then repeatedly grasped the spermatophore base with his mouth and ate the entire structure. Alternatively, after the female departs, the male may swing around rapidly and bite the female.

In each of the four observed courtships, courtship behavior ceased after only one spermatophore was deposited.

Desmognathus monticola

Catalog of male actions.

I was able to observe only initial courtship actions between the male and female. The following actions are performed by the male while facing towards the female.

A.) NUDGING The male contacts his snout or lateral snout to the female's lateral body.

B.) BUTTERFLYING The male raises both forelimbs simultaneously and swings them forward and upward and then downward in a smooth forward arc.

C.) PULLING The male presses his mentum down against the female's dorsum by arching his head downward slightly, and then draws the head backward axially, pulling the mentum in contact with the female's dorsum.

D.) SNAPPING The mentum is pressed down against the female's body and then drawn rapidly backward with the head bent downward by a sudden, vigorous snapping of the body. The action may fling the male backward a few centimeters from the female.

E.) HEAD SLIDING The male moves forward sliding his mentum in contact with the female's dorsum.

F.) JERKING While moving forward slowly, the male's whole body jerks forward very slightly and repeatedly.

G.) LIFTING The male turns his head to the side and towards the female and lifts his head under her chin while rubbing his snout on her chin.

Temporal relations (Desmognathus monticola)

A sexually active male repeatedly approaches the female and, if she remains stationary, contacts her with his head by performing nudging, pulling, snapping and head sliding. Frequently the female moves off rapidly away from the male as he contacts her with his head in these ways. The male then rapidly pursues the female by moving forward in rapid bursts each time the female moves forward. When the male approaches to within a few centimeters of the female, he moves forward very slowly towards her. He may move directly towards her chin and then perform lifting, if the female remains stationary. In one instance in which the male lifted under the female's chin, he then crawled forward under her chin with his dorsum in contact with her chin. The female then departed from the male rapidly, and he reapproached her and resumed head contact. Alternatively the male may approach the female more posteriorly and then move along beside her while performing the various modes of head contact described above. In close proximity to the female, the male may perform jerking.

Snapping was observed on only one occasion. The male reapproached the female laterally and moved directly towards her chin. He then lifted under her chin and rubbed her chin for approximately five minutes with a jerking forward and backward movement of his head. The male then moved slightly posterior along the female, on the same side as the approach. The male slid his snout slowly up onto the dorsum of the female above the insertion of her forelimbs and then slid his snout forward and backward (pulling) a few times. The male then snapped violently, flinging his body backward three centimeters from the female. The female remained motionless, and the male slowly moved towards her while performing butterflying and nudged the female. Butterflying ceased, and the male continued to nudge the female. The female then moved rapidly away from the male, and the male reapproached her.

Two gravid females were housed with one sexually active male, and during the course of an hour's observation (4.20 - 5.20 pm, 5 May 1970) the male approached both of them repeatedly. Both females repeatedly ran away from the male as soon as, or shortly after, the male would initiate head contact. The next morning a single spermatophore base was found in the container, and one of the females held a sperm mass inside her cloaca.

Plethodon cinereus

Catalog of male actions.

The following actions are performed by the male while facing towards the female.

A.) TAPPING The male lowers and raises his head thereby tapping his naso-labial cirri to the substrate.

B.) NUDGING The male contacts his snout or lateral snout to the female's lateral body.

C.) HEAD SLIDING The male moves forward with his head level and sliding his chin, and mental gland, in contact with the female's dorsal body.

D.) HEAD SWINGING The male rhythmically swings his head slowly from side to side in short arcs with his mentum in contact with the female's dorsum. Sometimes the head is arched downward so that only the mentum contacts the female's dorsum during head swinging. Frequently the male undulates his tail laterally during head swinging, but the tail is held level.

E.) SNAPPING The male arches his head downward strongly, sometimes lifting the forelimbs off of the substrate, and pauses momentarily in this position. The male then draws the head backward very rapidly in a snapping motion. This backward snapping action is so forceful that it frequently throws the male's whole body backward two to three centimeters. Always before snapping the male performs lateral tail undulations which increase dramatically in frequency and amplitude just before the backward snapping action is executed. The tail undulations cease immediately as the backward snapping motion is completed.

F.) LIFTING The male lifts his head with his head turned slightly to one side under the female's chin and with his dorsal head, eye, snout or lateral snout contacting her chin.

The following actions are performed by the male while facing away from the female.

G.) STATIONARY WITH TAIL ARCHED AND UNDULATING While stationary the male arches his proximal tail upward and undulates his tail laterally.

Temporal relations (Plethodon cinereus)

My observations are limited to initial courtship interactions and do not include spermatophore deposition or sperm transfer.

Upon initiating contact with a female, the male moves parallel to her, generally from posterior to anterior, contacting the female's body with his head in a variety of ways. As he moves forward along beside the female, or axially on top of her, the male may perform tapping, nudging, head swinging, head sliding or snapping. Lateral tail undulations may occur simultaneously with any of these actions. These various modes of head contact may also be performed with the male perpendicular to or at an oblique angle to the female. Head swinging and head sliding are the most frequent actions. Snapping occurs only sporadically and always follows one of these two actions.

When the female moves away from the male, the male approaches her each time she moves forward. When the female moves far away from the male and stops, the male may move forward swinging his head in large arcs while tapping the substrate.

Tail undulations, with the tail level, occur only when the male is contacting the female with his head or when his head is in close proximity to the female. Tail undulations cease abruptly when the female moves away from the male.

When the male reaches the female's head, he may nudge the female's cheek and lift (action F) under the female's chin. In each instance the female then moved away from the male.

In a few instances the female walked over or paused with her ventral body on the male's tail. The male then arched and undulated his tail and remained stationary.

I observed preliminary courtship behavior in pairs from Mt. Rodgers, Virginia and in pairs from Ann Arbor, Michigan. The same actions and the same temporal patterning of actions (as described above) are present in males from both localities. In particular, males from both localities undulate the tail rapidly in a lateral plane during any of the modes of head contact described above.

Plethodon richmondi

Catalog of male actions.

The following actions are performed by the male while facing towards the female.

A.) TAPPING The male lowers and raises his head thereby tapping his nasolabial cirri to the substrate or to the dorsum of the female.

B.) NUDGING The male contacts his snout or lateral snout to the female's lateral body.

C.) HEAD SLIDING The male moves forward sliding his mentum in contact with the female's dorsal body. The head is level and not moved laterally.

D.) HEAD SWINGING The male rhythmically swings his head from side to side in short arcs with his mentum in contact with the female's dorsal body. The action may be performed with the head level or with the head bent downward.

E.) SNAPPING The male undulates his tail and then bends his neck down, arching his back upward, and pressing his mentum against the female's dorsum. The male then rapidly snaps his body backward. Tail undulations cease abruptly as the snapping action is performed.

F.) LIFTING The male turns his head to one side and under the female's chin and lifts his head, contacting his lateral snout to the female's chin or swinging his head laterally with the dorsum of his head in contact with her chin.

The following action is performed by the male while facing away from the female.

G.) STATIONARY WITH TAIL ARCHED AND UNDULATING While stationary the male arches his proximal tail upward and undulates his tail laterally.

Temporal relations (Plethodon richmondi)

My observations are limited to initial courtship interactions. Spermatophore deposition has not been observed in this species.

Upon contacting a female, a sexually active male moves parallel to her while contacting her body with his head in a variety of ways. The male usually moves anteriad along the female, but he may move posteriad along her length. While stationary or moving forward, the male may perform tapping, nudging, head swinging, head sliding or snapping on the female's body.

Head swinging and head sliding are the most frequent of these actions with the male usually crawling axially along the female's dorsum as they are performed. Snapping is the least common mode of head contact.

Lateral tail undulations are performed only before and as snapping is initiated. Tail undulations never occur during any other mode of head contact.

As the male contacts the female, she may move away and break contact with him. The male then follows behind her, and he moves forward each time she does and then reinitiates contact. When the female has moved far off, the male may rapidly tap his snout to the substrate as he moves forward swinging his head in large lateral arcs.

When the male reaches the female's head, in the process of moving along beside or on top of her, he may lift under her chin. In the two instances in which this was observed, the male then crawled posterior along the opposite side of the female and her chin did not contact his dorsal tail. In one instance the female then moved away from him, walking over his tail. The male then arched and undulated his tail while remaining stationary, and then lowered his tail and ceased tail undulations when the female broke contact with his tail.

Plethodon welleri

Catalog of male actions.

The following actions are performed by the male while facing towards the female.

A.) TAPPING The male rapidly lowers and raises his head and thereby taps his nasolabial cirri on the substrate or on the female's dorsum.

B.) NUDGING The male contacts his snout or lateral snout to the female's lateral body.

C.) HEAD SLIDING The male moves forward with his head level, sliding his mentum in contact with the female's dorsum without moving his head laterally.

D.) LIFTING The male turns his head to one side towards the female and lifts his head under the female's chin, contacting his cheek, eye or the dorsum of his head to her chin.

The following actions are performed by the male while facing away from the male.

E.) STATIONARY WITH TAIL ARCHED AND UNDULATING While stationary the male arches his proximal tail upward and undulates his tail laterally. He may extend on his hindlimbs and at irregular intervals raise and lower a hindlimb without moving forward. The vent is raised above the substrate (see Fig. 71A).

F.) MOVING FORWARD WITH TAIL ARCHED AND UNDULATING The male moves forward while arching his proximal tail upward and undulating his tail laterally. The vent is raised above the substrate.

G.) SPERMATOPHORE DEPOSITION The male is stationary with his vent adpressed to the substrate. The hindlimbs are aligned with the femurs perpendicular to the long body axis. The tail is level, and lateral undulations proceed along the entire length of the tail. The male does not appear to rock laterally on his hindlimbs. Spermatophore deposition terminates with the male ceasing tail undulations and then flexing his tail to one side as he lifts his vent free of the spermatophore.

H.) <u>MOVING FORWARD WITH TAIL FLEXED</u> The male moves forward with his tail flexed to one side at the base at approximately a 90° angle. The body is curved in a sigmoid lateral flexure.

I.) <u>STATIONARY WITH TAIL FLEXED</u> The male performs the following series of actions as the female rests with her vent over the spermatophore. The male stops and extends upward on his hindlimbs, pressing the dorsum of his tail base up under the female's chin. The male then leans backward on his hindlimbs and thereby straightens the sigmoid flexure of his body. There is no rhythmic extention and flexion of the hindlimbs, and the forelimbs are motionless. The tail is not undulated and remains flexed to one side at the base. Following the backward leaning on the hindlimbs, the male remains completely motionless.

Temporal relations (<u>Plethodon welleri</u>)

After initiating or reinitiating contact with a female, the male moves along beside her, either anteriad or posteriad, contacting her with his head. Head contacts take the form of tapping, nudging and head sliding. Rapid lateral tail undulations occur simultaneously with any of these three modes of head contact. Rapid lateral tail undulations also may occur when the male is in close proximity to the female but not contacting her with his head (or body).

If the female moves away from the male as he contacts her, he moves rapidly towards her each time she moves forward and may then reinitiate contact with her.

When the male reaches the female's head (as he moves along beside her), he may lift under her chin (see action D). If the female's chin fails to contact his dorsum posterior to his neck after he has performed lifting, the male continues forward under her chin and then posterior along the opposite side of her body. If the female's chin does contact his dorsal fore or hindbody, he turns away from her and moves forward and then stops and arches and undulates his tail when her chin slides posterior to his dorsal proximal tail. In every such instance, the female remained stationary, and after a few minutes (of action E) the male lowered his tail, ceased tail undulations and turned and reapproached the female.

In one instance a male and a female were observed moving forward in a tail-straddling walk. The male moved forward arching and undulating his tail with the female astride his tail and moving forward with her snout half a vent length posterior to the rear margin of the male's vent. The female then moved off of the male's tail and away from him. The male lowered his tail, ceased tail undulations and reapproached her.

Spermatophore deposition was observed on one occasion. Spermatophore deposition was already in progress when observations began. The female was motionless astride the male's tail with her snout above the rear margin of the male's vent. The female did not swing her head laterally over the male's tail as his tail undulated in contact with her ventral body.

The male then withdrew his tail from under the female's body by flexing it to one side. As the male moved forward with his tail flexed, the female moved forward behind him with her chin resting on the dorsum of his proximal tail. As she moved forward, the spermatophore slid posterior along her venter. When the spermatophore contacted her vent, she stopped and lowered her vent, inserting the spermatophore into her cloaca. She then rested motionless over the spermatophore with her vent pressed to the substrate. As the female stopped over the spermatophore, the male stopped in front of her and performed the series of actions previously described (see action I) with the female's chin resting on the dorsum of his proximal tail.

Finally the male turned and, while tapping the substrate, moved back towards the female as she remained motionless with her vent over the spermatophore. As the male walked over the top of her, nudging her, the female suddenly moved rapidly away from the spermatophore and the male. The female successfully removed the sperm cap from the spermatophore, and no additional courtship activities were observed.

Organ (1960) also observed courtship behavior in Plethodon welleri from southwestern Virginia. My observations are in good agreement with his. I have provided some additional observations on variability in courtship sequences. Organ did not describe the posture and actions performed by the male, as the female rests with her vent over the spermatophore. I agree with Organ (1960) that male P. welleri frequently perform a rapid tail "wagging" when approaching the female and that they lack a foot dance. The absence of a foot dance in this species is not simply a consequence of reduction in limb length as Organ (1960) suggests. Plethodon caddoensis, a salamander of very comparable proportions, does possess a foot dance.

Plethodon glutinosus

Catalog of male actions.

The following actions are performed with the male facing towards the female.

A.) TAPPING The male rapidly lowers and raises his head thereby tapping his nasolabial cirri to the female's dorsum or to the substrate.

B.) NUDGING The male contacts his snout or lateral snout to the female's lateral body.

C.) HEAD SLIDING The male moves forward sliding his mentum in contact with the female's dorsal body.

D.) MOUTH GRASPING The male bends his head down sharply, opens his mouth and grasps the female's body loosely in his mouth. He then opens his mouth and releases his grasp. (Mouth grasping was observed only on two occasions and in males from Whitetop Mtn., Virginia. Mouth grasping was not observed in males from Mountain Lake, Giles Co., Virginia, but it is quite possible that my observations were not extensive enough to record its presence).

E.) FOOT DANCE The male raises and lowers his forefeet and hindfeet while stationary or moving forward slowly. One limb only is raised at a time. There is no obvious sequence of limb movement.

F.) LIFTING While turning his head to one side towards the female, the male lifts his head and thereby contacts his snout, lateral snout or the dorsum of his head to the female's chin.

The following actions are performed by the male while facing away from the female.

G.) STATIONARY WITH TAIL ARCHED AND UNDULATING While stationary the male arches his proximal tail upward and undulates his tail laterally.

The vent is held above the substrate. The male may, or may not, perform a foot dance.

H.) MOVING FORWARD WITH TAIL ARCHED The male moves forward on a straight course while arching his proximal tail upward slightly and with the vent raised above the substrate. The male may or may not undulate his tail laterally.

I.) TURNING BACK TOWARDS THE FEMALE This is actually a complex series of actions. After moving forward with arched tail on a straight course (action H) with the female straddling his tail, the male turns his head and forebody back towards the female. This is accomplished by stepping laterally with the forelimbs, while the hindlimbs either remain stationary or step forward slowly. The female remains astride the male's tail, facing anterior with her snout resting on the dorsum of his proximal tail. The male continues turning back towards the female until his body axis forms a U and then nearly a complete circle. As his head approaches the female's head, he raises and holds his head high. In this position he may perform any, or all, of the following components; (1) increase the amplitude and frequency of tail undulation under the female's chin, (2) extend upward on his hindlimbs thereby accentuating the tail arch under the female's chin, (3) foot dance. Then with a rapid downward stroke, the male slaps his mental gland on the female's snout (and nares), upper eyelid or dorsal head. The male then turns immediately away from the female, so that his body axis again forms a shallow U, rather than a circle. He pauses in this position and then straightens his body axis, by stepping laterally away from the female, and moves forward once again on a straight course. Occasionally this series of actions is executed with the deletion of the downward slapping of the male's mental gland on the female's head. Very rarely a male may lean forward towards the female's head, when she is not straddling his tail, hold his head high, and then slap his mental gland on the female's head with a rapid, downward and backward stroke.

J.) SLIDING VENT AGAINST SUBSTRATE The male moves forward sliding his vent and midbody in contact with the substrate. The tail is level and may undulate laterally slightly.

K.) STATIONARY WITH VENT IN CONTACT WITH SUBSTRATE The male pauses with his vent and midbody in contact with the substrate. The tail is level and is undulated laterally.

L.) SPERMATOPHORE DEPOSITION The male pauses with his vent and midbody in contact with the substrate. The hindlimbs are aligned with femurs perpendicular to the body axis and tibias perpendicular to the substrate. The male may or may not rock laterally on his hindlimbs. The tail is level and undulations of large amplitude proceed posteriorly along the entire length of the tail. Undulations increase in frequency and amplitude as spermatophore deposition proceeds. Spermatophore deposition terminates with the male ceasing tail undulations and then flexing his proximal tail to one side as he moves forward off of the spermatophore.

M.) FORWARD WITH TAIL FLEXED After spermatophore deposition the male moves forward with his proximal tail flexed to one side at a 45°-90° angle to his body. The male moves forward with his body in a sigmoid lateral flexure and with the vent held above the substrate. As he moves forward he repeatedly jerks his proximal tail laterally.

N.) STATIONARY WITH TAIL FLEXED The following series of actions is executed by the male as the female stops with her vent near or over the spermatophore. The male stops and extends upward, while leaning backward, on his hindlimbs and thereby straightens the sigmoid flexure of his body. His proximal tail is forced up underneath the female's chin. The male may remain motionless in this posture, or he may repeatedly extend and flex on his hindlimbs and then remain motionless with his hindlimbs extended. Throughout, the male's proximal tail remains flexed to one side at a 45°-90° angle to his body.

Temporal relations (Plethodon glutinosus)

These observations are based on the courtships of pairs from Giles Co., and from Grayson Co., Virginia; I found no differences in courtship behavior between these two localities.

Upon contacting or recontacting a female, the male moves slowly along her length while contacting her intermittently with his head via nudging, tapping, head sliding and mouth grasping. The male may perform foot dance simultaneously with any of these modes of head contact, or when close to but not contacting the female with his snout. The male usually moves along beside the female, but he may crawl along her dorsum.

If the male reaches the end of the female's tail when moving posterior along the female, he turns while tapping the substrate and then moves anterior along the female, if he recontacts her.

Whenever the female moves away from the male, he reapproaches her by moving forward in rapid bursts each time she moves forward. In close proximity to the female, the male approaches her very slowly.

The male may reach the female's head by approaching her head on, by moving slowly along beside her and directly towards her head without contacting her, or by moving along beside her while contacting her intermittently with his head. If the female remains stationary when the male reaches her head, the male turns his head towards the female and lifts his head under her chin (action F). The male then crawls forward under the female's chin. If the female's chin fails to contact his dorsal proximal tail, the male moves posteriad along the female and resumes tapping, nudging, and head sliding. If the female's chin does contact his dorsal proximal tail, the male arches his proximal tail upward and undulates it in contact with the female's chin. If the female then remains stationary for several minutes, or if she departs from the male, the male lowers his tail, ceases tail undulations, reapproaches the female and resumes head contact with her. Alternatively, the female may turn her head axial to the male's tail and slide her chin forward along it while stepping astride the male's tail with her forelimbs. The male and female then move forward, intermittently, in a tail-straddling walk with the female's chin resting on the dorsum of the male's proximal tail as the male arches and undulates his tail.

During the tail-straddling walk, forward progress by the male is related to the position of the female's snout on his dorsal tail. When the female's snout slips posterior to about one and a half vent lengths posterior to the rear margin of the male's vent, he pauses (action G). The male moves forward (action H) when the female slides her snout anterior to this point on his tail.

During some tail-straddling walks the male repeatedly performs turning back towards the female (see action I) which includes a slapping of the male's mental gland on the female's head. Tail-straddling walks which included repetitions of this action seemed to be of much longer duration (see example below) than tail-straddling walks in which the male never turned back towards the female.

Initially the male holds his vent high above the substrate during the tail-straddling walk. If the female departs from the male, he lowers his tail and reapproaches her. If she remains astride his tail, the male eventually begins to slide his vent in contact with the substrate (action J). He may then alternate between holding the vent above the substrate (actions G and H) and contacting his vent to the substrate (actions J and K). Finally the male pauses with his vent adpressed to the substrate, aligns his hindlimbs and begins spermatophore deposition (action L)., which, as in *P. jordani*, *P. ouachitae* and *P. yonahlossee*, requires three to four minutes. During this time the female remains essentially motionless astride the male's tail with her snout over, or within one vent length of the rear margin of the male's vent, as the male's tail undulates in contact with her venter. The females I observed did not move the head counter to the male's tail undulations during spermatophore deposition.

After spermatophore deposition, the male flexes his tail to one side, thereby withdrawing his tail from beneath the female's venter, and moves forward (see action M). The female follows behind him with her chin resting on the dorsum of his proximal tail, and the spermatophore slides posterior in contact with her venter. When the spermatophore contacts her vent, the female stops and lowers her vent upon it. The male stops in front of her, and with the female's chin still resting on the dorsum of his proximal tail, executes the sequence of actions described above (see action N). After a few minutes the female turns and departs from the male. She may, or may not, remove the sperm cap from the spermatophore and hold it in her cloaca. In either case the male usually remains stationary after the female departs and does not reinitiate courtship that evening.

On one occasion, however, a male deposited two spermatophores in the same evening with the same female. When first observed the male was depositing a spermatophore with the female astride his tail. When the female moved forward behind the male after spermatophore deposition, she stopped with her vent in the vicinity of the spermatophore but failed to locate it. The male, meanwhile, performed action N. The female then slid forward along the male's tail, again stepping astride it. The pair then moved forward, intermittently, in a tail-straddling walk for three hours! During the tail-straddling walk the male repeatedly turned back towards the female and slapped his mental gland on her head (action I). Finally the male stopped and deposited a second spermatophore. This time the female successfully removed the sperm cap with her cloaca.

For some reason I was able to observe only the process of spermatophore deposition in pairs from Arkansas, Oklahoma and North Carolina, and not any of the other activities of courtship (except that I observed a male from Arkansas performing a foot dance). I could see no differences in behavior during spermatophore deposition between animals from these localities and two localities in Virginia (Grayson and Giles counties).

Pope (1950) reports that two P. glutinosus were observed in a tail-straddling walk on the evening of August 19 in Giles Co., Virginia. Organ (1968c) observed tail-straddling walks in captive pairs from New Jersey in September and October. Organ (1960a) and I observed courtship in August and September in pairs from southwestern Virginia (Giles, Smyth and Grayson counties).

My observations are in good agreement with Organ's (1960a) descriptions of courtship behavior, but I make the following qualifications. (1) Mouth grasping appeared to me to be rather infrequent male behavior. Nevertheless, I have observed it only in Plethodon glutinosus and not in any other species of large eastern Plethodon. (2) Organ (1960a) notes that the male occasionally raises his head and, as the adhesion between his mental gland and the female's dorsum breaks, the male's head snaps upward.

I observed this behavior, but only rarely, in P. glutinosus (as well as in P. jordani and P. ouachitae). I think the behavior is simply a rare consequence of adhesion between the male's mental gland and the female's body, and not, as Organ suggests, a behavior specifically designed to stimulate the female during courtship. (3) Turning back towards the female (see action I for a complete description) occurs only in some tail-straddling walks in P. glutinosus (and likewise in P. jordani and P. yonahlossee). When it does occur, the male repeats the action many times, and the tail-straddling walk is of much longer duration than tail-straddling walks in which the action is never performed. I am unclear about the functional (and adaptive) significance of these two types of tail-straddling walks in large eastern Plethodon. Perhaps tail-straddling walks of long duration, with periodic slapping of the male's mental gland on the female's head, are used when the female is non-receptive. (4) Tail-straddling walks of long duration are not simply a consequence of small containers. I observed long tail-straddling walks in containers considerably larger than the eight inch bowls used by Organ (1960a) to house courting pairs. (5) Organ notes that the superficial blood vessels dialate in males during courtship and produce a reddening of the male's chin, feet and spots. I illuminated the male described above at the termination of a three hour courtship and found the same phenomenon. Like all other plethodontids, Plethodon glutinosus are lungless. Perhaps dialation of superficial blood vessels in the skin is a respiratory compensation for oxygen stresses incurred during courtship.

Organ (1960a) observed aggressive interactions between males when they were housed with females during the courtship season. When one sexually active male approaches another male, the approached male usually attacked him (ie. lunged and bit him). Alternatively the approached male may flee or remain passive, as a female would. If the approached male remains passive, the approaching male initiates the preliminary activities of courtship. The approached male then begins tail undulations. When he does, the approaching male bites and pursues him. Organ (1960a) suggests that sex recognition is accomplished by olfactory perception of skin secretions and by the behavioral devices outlined above.

On three occasions I observed homosexual courtship between male Plethodon glutinosus when more than one male was housed with a female. These interactions took the same course as in P. jordani and P. ouachitae. In each case two P. glutinosus males were found in a tail-straddling walk, with the following male behaving very much like a female. The leading male eventually stops and deposits a spermatophore. The following male remains stationary during spermatophore deposition, just as a female would, but then walks past the spermatophore as the other male leads him forward (action M). In each case the following male then departed as the other male performed action N after spermatophore deposition.

Plethodon caddoensis

Catalog of male actions.

The following actions are performed by the male while facing towards the female.

A.) TAPPING The male rapidly lowers and raises his head thereby tapping his nasolabial cirri to the substrate or to the female's dorsum.

B.) NUDGING The male contacts his snout or lateral snout to the female's lateral body.

C.) HEAD SLIDING The male moves forward sliding his mentum in contact with the female's dorsum. The head is usually level, but it may be arched down slightly.

D.) HEAD SWINGING The male swings his head slowly from side to side in short arcs with his mentum in contact with the female's dorsum. The head may be arched downward slightly.

E.) FOOT DANCE The forelimbs and hindlimbs are individually raised from and lowered to the substrate. Two limbs are never raised simultaneously. There is no obvious patterning to the foot movements.

F.) LIFTING The male turns his head to the side under the female's chin and raises his head contacting his lateral head to the female's chin.

The following actions are performed by the male while facing away from the female.

G.) STATIONARY WITH TAIL ARCHED AND UNDULATING While stationary the male arches his proximal tail upward and undulates his tail laterally.

Temporal relations (Plethodon caddoensis)

After contacting or recontacting the female with his head, the male moves along her length, anteriad or posteriad, performing tapping, nudging, head sliding and head swinging. Head sliding is the most frequent mode of head contact with the male frequently crawling axially on top of the female as he performs this action.

Lateral tail undulations with the tail level are usually associated with the performance of foot dance. The male may intermittently undulate his tail and perform foot dance while engaged in any of the five modes of head contact above.

When the female moves away from the male, he moves forward after her each time she moves forward and may reinitiate contact with her. When she has moved away from him, the male may also tap the substrate while moving forward and swinging his head laterally in large arcs.

When the male reaches the female's head, he may perform head swinging on the dorsum of her head, or he may contact his snout or cheek to her cheek. The male may then lift under the female's chin. The female may raise her head upward as the male contacts his head to her chin. If the female remains stationary, the male may then crawl forward under her chin. If the female's chin contacts the male's dorsal anterior tail, he pauses and arches and undulates his tail. If nothing contacts the dorsum of the male's tail, however, he continues moving posteriad along the female while contacting her with his snout. In both instances in which the male paused arching and undulating his tail under the female's chin, the female remained motionless. After a few minutes the male turned and reapproached her. In two instances as the male contacted the female's body with his snout, I picked up the female and placed her in contact with the male's dorsal anterior tail. The male remained stationary and immediately arched and undulated his tail. The female remained motionless and after a few minutes the male ceased tail undulations, lowered his tail and reapproached her.

Spermatophore deposition and sperm transfer were not observed.

Courtship behavior was observed in a terrarium containing several males and females. Although several of the males had well developed mental glands (suggesting that they were otherwise capable of courtship), most of the courtship activities were performed by only one male. This male repeatedly bit and pursued other males when he contacted them with his snout. A pursued male would dash off and climb up the sides of the terrarium. The one male alternated between approaching and courting females and pursuing and biting other males. On a few occasions spermatophores were found in this terrarium.

Plethodon ouachitae

Catalog of male actions.

The following actions are performed by the male while facing towards the female.

A.) TAPPING The male rapidly lowers and raises his head, tapping his nasolabial cirri to the substrate or on the female's dorsum.

B.) NUDGING The male contacts his snout or lateral snout to the female's lateral body.

C.) HEAD SLIDING The male moves forward with his head level and sliding his mentum in contact with the female's dorsal body.

D.) HEAD SWINGING The male swings his head from side to side in short arcs with his mentum in contact with the female's dorsum.

E.) FOOT DANCE The male raises and lowers his forefeet and hindfeet individually and not in any obvious sequential pattern. Two feet are never raised simultaneously.

F.) LIFTING The male turns his head to the side towards the female and under her chin and raises his head contacting his cheek or lateral snout to the female's chin. The male may rub his cheek or lateral snout against the female's chin with a back and forth axial motion of his head.

The following actions are performed by the male while facing away from the female.

G.) STATIONARY WITH TAIL ARCHED AND UNDULATING While stationary the male arches his proximal tail upward and undulates his tail laterally.

H.) MOVING FORWARD WITH TAIL ARCHED The male moves forward arching his proximal tail upward slightly. The vent is held above the substrate, and the male may, or may not, undulate his tail laterally.

I.) SLIDING VENT IN CONTACT WITH SUBSTRATE The male moves forward with tail level, sliding his vent in contact with the substrate. The tail may be undulated slightly laterally.

J.) STATIONARY WITH VENT ADPRESSED TO SUBSTRATE The male pauses with his tail level and with his vent in contact with the substrate. The tail is undulated laterally.

K.) SPERMATOPHORE DEPOSITION While stationary the male aligns his hindlimbs with femurs perpendicular to his body and with tibia perpendicular to the substrate. The tail is level and lateral undulations of large amplitude proceed posterior along the entire length of his tail. During the course of spermatophore deposition, these undulations appear to increase both in frequency and amplitude. The male rocks rhythmically and laterally on his hindlimbs without lifting his hindfeet from the substrate. Spermatophore deposition terminates with the male ceasing tail undulations and then lifting his vent free of the spermatophore and then flexing his proximal tail to one side at a 45°-90° angle to his body.

L.) MOVING FORWARD WITH FLEXED TAIL The male moves forward, away from the spermatophore, with his proximal tail flexed to one side at a 45°-90° angle. The male's long axis is held in a sigmoid lateral flexure and his proximal tail is repeatedly jerked laterally as he moves forward. The vent is raised above the substrate.

M.) STATIONARY WITH TAIL FLEXED The male executes the following series of actions as the female stops with her vent over or near the spermatophore. The male stops in front of the female with the female's chin resting on the dorsum of his proximal tail. The male leans backward on his hindlimbs and consequently straightens the sigmoid flexure of his body. The male now executes rapid, rhythmic extentions and flexions of his hindlimbs which force the female's head up and down rhythmically as her chin rests on the male's dorsal tail base. Finally the rhythmic extentions and flexions of his hindlimbs cease, and the male remains motionless while extended upward and backward on his hindlimbs with his tail base forced upward under the female's chin. Throughout, the male's tail remains flexed to one side, nearly perpendicular to his body axis.

Temporal relations (Plethodon ouachitae)

Upon initiating or reinitiating contact with the female, the male moves along her length while performing tapping, nudging, head sliding and head swinging. Foot dance may be executed simultaneously with any of these actions. Forward progress along the length of the female is intermittent. Foot dance is performed when the male pauses or is moving forward very slowly. Usually the male moves along beside the female as he contacts her with his head, but less frequently the male crawls along axially on top of the female. He may move anteriad or posteriad along the length of the female.

If the male reaches the end of the female's tail when moving posteriad, he usually moves a short distance beyond, and then, while tapping the substrate, he turns back towards her and reinitiates contact. He then moves anteriad along her length.

Whenever the female moves away from the male as he contacts her, the male reapproaches the female by moving forward in rapid bursts each time the female moves forward. In close proximity to the female, he may crouch low to the substrate and approach her very slowly. He may simultaneously perform foot dance.

When reapproaching the female, the male may move towards the closest region of her body. This is usually the tail or hindlimbs, if the female has just moved away from him. The male then moves anteriad along her.

Alternatively, the male may approach the female by moving directly towards her head by moving along parallel to her without contacting her body.

When the male reaches the female's head, by either of these ways, the male may turn his head towards the female and perform lifting under her chin. If the female remains stationary, the male crawls forward then under her chin. If the female's body (eg. her chin) fails to contact his dorsal tail, the male continues forward and moves posteriad along the opposite side of the female and resumes nudging, head sliding and head swinging. If the female's chin does contact his dorsal tail as he crawls under her chin, the male arches his proximal tail upward in contact with her chin and pauses while arching and undulating his tail. If the female departs from the male, or if she remains motionless for a few minutes, the male lowers his tail, ceases tail undulations and reapproaches the female. Alternatively, the female may step astride the male's tail with her forelimbs and slide forward axially along the male's tail with her chin in contact with it. In this case the male moves forward, arching and undulating his tail, and the pair moves forward in a tail-straddling walk with the female astride the male's tail with both fore and hindlimbs, facing anteriad, and with her snout over the dorsum of the male's proximal tail.

The tail-straddling walk may also be initiated if the female actively approaches the male's tail and places her chin upon it as the male crawls along beside her. In such cases, the male does not lift under the female's chin, but instead immediately arches and undulates his tail under her chin.

During the tail-straddling walk, forward progress by the male appears to be determined by the anterior point of contact of the female's chin on the male's tail. The male tends to move forward when the female's snout is anterior to a point approximately half to one vent length posterior to the rear margin of the male's vent. The male pauses and undulates his tail, while accentuating the upward arch of his proximal tail, whenever the female's snout slips posterior to this region. Thus during the tail-straddling walk, the pair makes intermittent forward progress on a straight course.

After moving forward in the tail-straddling walk with the vent raised above the substrate, the male lowers his vent to the substrate and alternates between sliding forward and pausing with vent in contact with substrate. The male may then revert to raising his vent from the substrate, or he may begin spermatophore deposition.

During spermatophore deposition the female remains essentially motionless astride the male's tail with her snout over the male's tail base. She may slide anteriad or posteriad a few millimeters, but she does not swing her head actively from side to side. The male's tail undulates rhythmically with its dorsal surface in contact with the female's venter from her chin to her vent.

Finally the male ceases tail undulations and lifts his vent free of the spermatophore while withdrawing his entire tail from underneath the female's venter by flexing his proximal tail to one side. The male then moves forward on a straight course with his tail flexed. The female moves forward behind him with her chin resting on the dorsum of his proximal tail. As the female moves forward, the spermatophore contacts her venter. She lifts her body slightly as she moves forward and the spermatophore slides posteriorly with the sperm cap in contact with her venter. If the spermatophore contacts her vent, she stops and lowers her vent upon it, inserting the entire spermatophore into her cloaca.

She pauses motionless, except for slight lateral undulations of her proximal tail, with her chin still resting on the male's dorsal proximal tail.

As the female pauses with her vent on or near the spermatophore, the male stops in front of her with his tail still flexed to one side and performs the series of actions previously described (see action M).

The female may then depart from the male and the spermatophore, or she may remain motionless. The male may remain motionless after the female departs, or he may swing around suddenly, back towards the female. He may then remain motionless, or he may reapproach the female. In the latter case he may lunge at the female and bite her, or he may simply tap the female briefly. The male may also tap the substrate and circle about the site of spermatophore deposition. If he contacts the spermatophore with his nasolabial cirri, he may repeatedly grasp the spermatophore with his mouth and eat it.

Almost invariably courtship activities cease abruptly after the male and female depart from the site of spermatophore deposition. The female repeatedly moves away from the male when he approaches her whether or not she has removed the sperm cap successfully. Even if the male contacts her, he only taps and nudges her briefly, or bites the female, before moving away. Thus only one spermatophore is deposited during an evening's courtship with a female.

On one occasion, however, a male deposited two spermatophores during a single courtship with the same female. When I began observations the male was in the process of spermatophore deposition with the female astride his tail. As I approached the tank, the female moved off of the male's tail and paused two centimeters from and parallel to the male and not in contact with him in any way. The male continued just as before in spermatophore deposition with his vent adpressed to the substrate, hindlimbs aligned and with his tail undulating. Finally the tail undulations ceased, and the male moved forward leaving a complete spermatophore attached to the substrate. The male did not flex his tail to one side as he moved forward, and the sperm cap adhered to his tail and was detached from the spermatophore. The male very slowly reapproached the female. He performed a foot dance as he approached her. The male crawled anteriad along beside the female while nudging her and sliding his mental gland along her dorsum. Upon reaching the female's head, the male turned his head under the female's chin, lifted and then crawled forward beneath her chin. The male's tail contacted the female's chin, and he arched and unulated his proximal tail under her chin. After a pause in this position, the female turned her head axial to the male's tail. When the female's snout was half a vent length posterior to the rear margin of the male's vent, the male moved forward, still arching and undulating his tail, and both animals moved forward in a tail-straddling walk with the female's snout at this same point on the dorsum of the male's tail. The male then lowered his vent to the substrate and slid his vent forward a short distance. He then stopped and began spermatophore deposition. During spermatophore deposition the female remained motionless astride his tail with her snout over the midpoint of the male's vent. The male had moved forward six centimeters from the onset of the tail-straddling walk. Both animals moved forward after spermatophore deposition with the male's tail characteristically flexed to one side and with the female's chin resting on his proximal tail. The female stopped with her hindfoot, rather than her vent, on top of the spermatophore, and she did not remove her sperm cap. The female then departed from the male. Later the male reapproached her, nudged her and then lunged at her.

The male then ate the second spermatophore and the sperm cap of the first spermatophore. No additional courtship activity occurred that evening.

These observations are based on the courtships of pairs from Kiamichi Mountain and pairs from Winding Stair Mountain, LeFlore Co., Oklahoma. Animals from these two localities differ in dorsal colorations (see Blair and Lindsay, 1964), but I could see no difference in courtship behavior.

On one occasion I observed a homosexual courtship between two males from Kiamichi Mtn. The two males were engaged in a tail-straddling walk, except for one feature. The leading male had only a regenerated tail stump (such that his tail terminated just beyond his vent), and so there was no tail for the following male to straddle. Instead the male followed the leading male while touching his chin to the leading male's tail stump. Then after three minutes, the leading male stopped and began depositing a spermatophore. During the four minutes required for spermatophore deposition, the following male was stationary with his chin resting over the undulating tail stump of the leading male. After spermatophore deposition the following male again moved forward with his chin resting on the leading male's tail stump. The following male moved past the spermatophore and then departed from the leading male. A few minutes later, the leading male approached the following male and lunged at him. The following male ran off, and the leading male pursued him and bit his tail. Later that evening the following male was observed initiating courtship with two females. Before the homosexual interaction was observed, the leading male was observed in courtship with a female. The evening before the following male was observed courting a female.

Plethodon yonahlossee

Catalog of male actions.

The following actions are performed by the male while facing towards the female.

A.) TAPPING The male lowers and raises his head, tapping his nasolabial cirri to the dorsum of the female or to the substrate.

B.) NUDGING The male contacts his snout or lateral snout to the female's lateral body.

C.) HEAD SLIDING The male moves forward sliding his mentum in contact with the female's dorsum with his head level.

D.) LIFTING The male turns his head towards the female and under her chin and then raises his head contacting his snout, upper eyelid or the dorsum of his head to the female's chin.

The following actions are performed by the male while facing away from the female.

E.) STATIONARY WITH TAIL ARCHED AND UNDULATING While stationary the male arches his proximal tail upward and undulates his tail laterally. The vent is raised above the substrate.

F.) MOVING FORWARD WITH TAIL ARCHED The male moves forward with the proximal tail arched upward slightly and with the vent raised above the substrate. The tail may be undulated laterally.

G.) TURNING BACK TOWARDS THE FEMALE From a position facing straight away from the female with the female straddling the male's tail and facing anteriad, the male turns his head and anterior body back towards the female's head, by stepping laterally with his forelimbs, so that his body axis now forms a U. As he turns back towards the female, the male accentuates the upward arch of his tail, increases the frequency of tail undulations, and holds his head high. The male continues to circle by stepping laterally towards the female with his forelimbs while stepping forward with his hindlimbs. The male then pauses, with his body axis now in a circle, holding his head high above the female's head while the female's chin rests on his arched and undulating proximal tail. Then suddenly the male lowers his head rapidly and with a downward and backward stroke slaps his mental gland on the dorsum of the female's head. The male immediately opens the curve of his body to a U again and then pauses in this position. Finally the male opens to the original position with his body axis straight and facing straight away from the female.

H.) <u>SLIDING VENT IN CONTACT WITH THE SUBSTRATE</u> The male moves forward sliding his vent in contact with the substrate. The tail is level and may undulate slightly laterally. The midbody is in contact with the substrate.

I.) <u>STATIONARY WITH VENT ADPRESSED TO SUBSTRATE</u> The male pauses with his vent in contact with the substrate. The tail is level and undulates laterally.

J.) <u>SPERMATOPHORE DEPOSITION</u> The male pauses with vent and midbody in contact with the substrate. The male aligns his hindlimbs with femurs perpendicular to his body and with tibia perpendicular to the substrate. The tail is level and tail undulations of large amplitude proceed posteriad along the entire length of the tail. During the course of spermatophore deposition the undulations appear to increase both in frequency and amplitude. The male may rock slightly laterally on his hindlimbs without raising his hindfeet from the substrate. Spermatophore deposition terminates with the male ceasing tail undulations and lifting his vent free of the spermatophore while withdrawing his tail from underneath the female's body by flexing his proximal tail to one side.

K.) MOVING FORWARD WITH TAIL FLEXED The male moves forward with his tail flexed to one side at a 45° - 90° angle. The proximal tail is arched upward, and the vent is held above the substrate. As the male moves forward he holds his body in a sigmoid lateral flexure.

L.) STATIONARY WITH TAIL FLEXED The male executes the following series of actions as the female stops with her vent over or near the spermatophore. The male stops and extends upward and backward on his hindlimbs and thereby straightens the sigmoid lateral flexure of his body. The male then rapidly and rhythmically extends and flexes on both his hindlimbs and forelimbs. These rapid extentions and flexions force the male's proximal tail up and down rhythmically under the female's chin. Finally the extentions and flexions cease, and the male pauses motionless, extended upward and backward on his hindlimbs. Throughout the male's proximal tail is flexed 45° - 90° to one side, and his vent is held high above the substrate.

Temporal relations (Plethodon yonahlossee)

Upon initiating or reinitiating contact with a female, the male moves along the length of the female while contacting her intermittently with his head. These contacts by the male take the form of tapping, head sliding and nudging. The male usually moves along beside the female, but he may also crawl along her dorsum. The male moves either anteriad or posteriad along the female's length.

The female may remain motionless, or actively approach the male, or she may move away from the male as he contacts her with his head. Whenever the female departs from the male, he reapproaches her by moving forward in rapid bursts each time the female moves forward. When in close proximity to the female, the male approaches her slowly. As, or just after, the male reinitiates contact with the female, he may undulate his tail laterally with or without arching his proximal tail upward.

When the male reaches the end of the female's tail while moving posteriad along her length, he either turns and moves anteriad without breaking contact with her, or he moves beyond the tip of her tail. In the latter case the male taps the substrate while turning his head from side to side and then moves anteriad along the female's tail if he recontacts it.

When the male reaches the head of a stationary female, he turns his head towards the female and under her chin and performs lifting. If the female then departs, the male reapproaches her. If she remains stationary, the male crawls forward under her chin. If the female's chin fails to contact his dorsal tail as he crawls forward under her chin, the male continues forward and moves posteriad along the opposite side of the female and resumes head contact with her. If the female's chin does contact his dorsal tail, the male arches his proximal tail upward and undulates his tail laterally, in contact with the female's chin. Once the female's chin contacts his tail, the male continues forward while arching and undulating his tail until the point of contact slips posterior to about one vent length posterior to the rear margin of the male's vent. The male then stops and continues to undulate his arched tail. If the female departs, the male lowers his tail, ceases tail undulations and reapproaches her. If she remains motionless for several minutes, the male lowers his tail, ceases tail undulations and reapproaches her. If, however, the female turns her head axial on the male's tail and slides anteriad with her chin in contact with his dorsal tail while stepping astride the male's tail with her forelimbs, the male moves forward arching and undulating his tail in contact with the female's chin. Both animals may then move forward intermittently in a tail-straddling walk.

This tail-straddling walk may be initiated in another way. The female may actively approach the male, as he crawls beside her, and place her chin on the dorsum of the male's body or tail. In such instances the male does not lift under the female's chin but instead crawls forward immediately and then arches and undulates his tail, if the female's chin contacts his dorsal tail. The female may then step astride the male's tail and slide anteriad along his tail.

During the tail-straddling walk, the female's snout usually rests on the dorsum of the male's tail within a region one to two vent lengths posterior to the insertion of the male's hindlimbs. The male tends to move forward whenever the female's snout is anterior to a point approximately one vent length posterior to the rear margin of the male's vent. The male stops whenever the female's snout slips posterior to this point and accentuates the upward arch of his tail while undulating his tail laterally in contact with the female's chin. The female maintains an axial orientation of her chin on the male's tail by actively turning her head towards the male's tail when the male's tail slips laterally off the midline of her chin (eg. when the male turns to avoid obstacles in his path).

In some courtships the male moves forward on a straight course following the initiation of the tail-straddling walk and then stops and deposits a spermatophore after moving forward a few centimeters. In other courtships, however, the male pauses intermittently during the tail-straddling walk and turns back towards the female (see action G) and then resumes forward progress on a straight course. In this way the male alternates between moving forward and turning back towards the female (and slapping her anterior head with his mental gland) before stopping and depositing a spermatophore.

If the female departs from the male during the tail straddling walk, he lowers his tail, ceases tail undulations and reapproaches the female.

If, however, the female remains astride the male's tail and continues to move actively forward, the male begins sliding his vent in contact with the substrate and pauses intermittently with his vent in contact with the substrate. Finally, after pausing with vent in contact with substrate, the male aligns his hindlimbs and begins spermatophore deposition with the female straddling his tail and with her snout directly above, or within a few millimeters of, his vent.

During spermatophore deposition the female remains essentially motionless astride the male's tail while his tail undulates in contact with her venter from her chin to her vent. She may slide her snout anterior or posterior a few millimeters, but she does not actively swing her head from side to side.

Following spermatophore deposition the male withdraws his tail from underneath the female by flexing his proximal tail to one side. The male then moves forward on a straight course with his tail still flexed to one side. The female moves forward behind him with her chin resting on the dorsum of his proximal tail. As she moves forward the spermatophore lies directly in her path, and it slides posteriad in contact with her ventral midline. If the spermatophore contacts her vent, she stops and lowers her vent upon it and thereby inserts the spermatophore into her cloaca. She may undulate her proximal tail slowly as her vent rests over the spermatophore. Almost simultaneously the male stops in front of her and with rhythmic extentions and flexions of his forelimbs and hindlimbs forces the female's head upward.

Three spermatophore depositions were observed. Each one with a different pair of animals. In each pair the female successfully located the spermatophore with her vent but then failed to successfully remove the sperm mass. In two pairs the female departed from the male after pausing with her vent in contact with the spermatophore. In both cases the male at first remained motionless after the female departed and then moved forward tapping the substrate, but no additional courtship interactions occurred.

In the third pair the female moved forward slowly and intermittently over the spermatophore, rather than moving forward rapidly and continuously as in the other two courtships. The female eventually paused with her cloacal lips in contact with the sperm cap, and the male executed the series of actions described above (see action L) with his tail flexed to one side. Both animals then moved forward in a tail-straddling walk with the female astride the male's tail. The male then turned back towards the female (action G) and slapped his mental gland on the female's hindhead. The female then departed from the male, and no additional spermatophores were deposited that evening.

Aneides lugubris

Catalog of male actions.

The following actions are performed by the male while facing towards the female.

A.) TAPPING The head is rapidly lowered and raised, tapping the nasolabial cirri to the substrate or to the female's body.

B.) NUDGING The male contacts his snout or lateral snout to the female's lateral body.

C.) PULLING The male slides his head forward a short distance with his head level and with his mentum in contact with the female's dorsal or lateral body. The head is then arched down, pressing the mentum against the female's body. The head is then immediately drawn backward with the head arched down with the mentum in contact with the female's body.

D.) JERKING The male's whole body jerks very slightly forward without raising fore or hindfeet from the substrate.

E.) LIFTING The male raises his head while turning his head under the female's chin and contacting his lateral snout to her chin.

The following actions are performed by the male while facing away from the female.

F.) STATIONARY WITH TAIL ARCHED AND UNDULATING While stationary the male arches his proximal tail upward and undulates his tail laterally. The male may rock laterally on his hindlimbs without raising his hindfeet from the substrate. At rather infrequent intervals the male may raise and lower a hindlimb without moving forward. The vent is held above the substrate.

G.) MOVING FORWARD WITH TAIL ARCHED AND UNDULATING The male moves forward arching the proximal tail upward and undulating his tail laterally.

The vent is raised above the substrate.

H.) <u>SLIDING VENT IN CONTACT WITH SUBSTRATE</u> The male moves forward sliding his vent in contact with the substrate with his tail essentially level and undulating laterally.

I.) <u>STATIONARY WITH VENT ADPRESSED TO SUBSTRATE</u> The male pauses with his vent in contact with the substrate. His tail is level and undulating laterally.

J.) <u>SPERMATOPHORE DEPOSITION</u> While stationary with his vent adpressed to the substrate, the male aligns his hindlimbs with femurs perpendicular to his long body axis. The tail is level and lateral undulations proceed along the entire length of his tail. During the course of spermatophore deposition the tail undulations appear to increase in amplitude and frequency. The male does not appear to rock laterally on his hindlimbs. Spermatophore deposition terminates as the male ceases tail undulations and lifts his vent free of the spermatophore.

K.) <u>MOVING FORWARD WITH FLEXED TAIL</u> The male moves forward with his tail flexed to one side and with his body axis in a sigmoid lateral flexure.

L.) <u>STATIONARY WITH TAIL FLEXED</u> The male performs the following series of actions as the female rests with her vent over the spermatophore. The male stops with his tail flexed to one side and with the female's chin resting on his proximal tail. The male then backs up under the female's chin, so that his venter is flush with the substrate with his forelimbs stretched out perpendicular to his body. The male then straightens his tail backward and with vigorous undulations massages the dorsal hindbody and sacrum of the female with the distal half of his tail. As his tail undulates, it follows the contours of the female's body. In this position the long axes of the two animals lie on the same line, the female's snout rests on the male's dorsal hindbody and her forelimbs lie just posterior to the male's hindlimbs. The male's tail base lies beneath the female's chest, with the massaging distal tail curving backward and upward onto her dorsal hindbody and sacrum. During tail massaging, all four limbs of the male are motionless. Finally the tail massaging ceases, and the pair remain in the same position as before.

Temporal relations (Aneides lugubris)

When the male initiates or reinitiates contact with a female, he moves along her length, usually from posterior to anterior, while performing tapping, nudging, pulling or sliding his mental gland in contact with her dorsum. The male may crawl axially along the dorsum of the female, or he may crawl along beside her. Pulling is a very common action, and almost all contacts of the male's head to the female are followed by pulling. Pulling may occur as a single stroke, or it may be performed several times in rapid succession.

Whenever the female moves away from the male during such encounters, the male follows behind her and then reinitiates contact. When moving forward and not in contact with the female, the male may perform tapping on the substrate. When moving forward slowly close to the female, but not in contact with her, the male may perform jerking.

The male may reach the female's head either by moving directly towards her head without contacting her or by moving along her length while contacting her with his head in the ways described above. When he reaches the female's head, the male may contact his lateral snout to the female's lateral snout or he may perform pulling on the dorsum of her anterior head. The male may then turn his head under the female's chin and perform lifting. The female may then move away from the male, in which case the male follows her and reinitiates contact. Alternatively the female may turn her head posterior over the male's dorsal hindbody as he performs lifting. The male then turns and moves forward parallel to the female and then arches and undulates his tail in contact with the female's chin. The male stops with the female's snout resting one vent length posterior to the rear margin of his vent on the dorsum of his tail, while arching and undulating his tail in contact with her chin. If the female moves forward sliding her chin anterior along the dorsum of the male's tail, stepping astride his tail, both animals move forward in a tail-straddling walk. If, however, the female stops for several minutes or moves away from the male at this point, or once the tail-straddling walk is in progress, the male lowers his tail, ceases tail undulations and reapproaches her.

The tail-straddling walk may be also initiated by the female turning and placing her chin on the male's dorsal hindbody as he crawls parallel to her before he lifts under her chin.

During the tail-straddling walk, the female's snout lies in the region on the male's dorsal tail posterior to the insertion of the male's hindlimbs and anterior to a point about one and a half vent lengths posterior to the rear margin of the male's vent. Forward progress by the male is associated with the female's snout being anterior in this region, and the male stops when the female's snout slips posterior along his tail. During the tail-straddling walk the female may slowly and non-rhythmically swing her head laterally over the male's tail.

After moving forward in the tail-straddling walk with his vent raised above the substrate (action G), the male may briefly slide his vent in contact with the substrate (action H), stop (I) and begin spermatophore deposition (action J).

During spermatophore deposition the female remains stationary astride the male's tail with her snout about one and a half vent lengths posterior to the rear margin of the male's vent, and with the male's tail undulating laterally in contact with her chin and ventral body. The female occasionally swings her head laterally over the male's tail but the action is not rhythmic.

As the male (action K) and the female move forward on a straight course after spermatophore deposition, the female's chin rests on the male's proximal tail just anterior to its lateral flexure. The spermatophore contacts the female's venter as she moves forward, and she lifts her body and slides over the top of it. When the spermatophore contacts her vent, she stops and lowers her vent upon it, thereby inserting the spermatophore into her cloaca. While resting on the spermatophore, the female undulates her tail base slightly. As the female rests on the spermatophore, the male performs the complex series of actions (action L) previously described including a very remarkable massaging of her hindbody and sacrum with his distal tail.

Only one spermatophore deposition was observed and the female did not successfully remove the sperm mass, although she dislodged it from the spermatophore.

The female then turned her head away from the male and he remained stationary and motionless. She paused and then moved back towards the male sliding her vent against the substrate. As she approached the male, they both raised their heads high and mutually rubbed their lateral snouts. The female then turned and walked over the top of the male and away from him. The male remained motionless and did not reapproach her.

Spermatophores were deposited on numerous occasions when I was not present to observe the process. Always a male deposited only a single spermatophore in an evening.

Aneides aeneus

Cupp (1971) observed courtship behavior in this species in a crevice in a sandstone outcrop in Kentucky. The observations were made from 12.10 to 12.35 on the afternoon of October 17. When first observed the male and female were moving in a circle and appeared to have their chins resting on each other's tails. In this position the male is reported to have occasionally bitten and nudged the female. The female was straddling the male's tail and occasionally the male stopped and undulated his tail laterally. After circling in the position just described, and occasionally crawling over each other and mutually rubbing snouts, the pair apparently moved forward on a straight course in a tail-straddling walk for a distance of 15 centimeters or less. The male then stopped and undulated his tail laterally with the female still astride the male's tail. After four minutes the male arched his tail and moved forward leaving a spermatophore behind. Both animals moved forward and the female stopped with her vent over the spermatophore. She then lowered her vent onto the spermatophore and slowly undulated her posterior body. With the female still straddling the male's tail and with her vent over the spermatophore, the male "exhibited jerking movements of the body and lateral undulations of the tail".

The circling movements that Cupp describes during the tail-straddling walk of Aneides aeneus probably represents the behavior I have called "turning back towards the female" in Eurycea, Desmognathus, and Plethodon. I did not observe this behavior in the one tail-straddling walk I observed in Aneides lugubris, but in Plethodon the behavior occurs only in some tail-straddling walks.

Brooks (1948) observed a pair of animals "clasping" at night in West Virginia on June 13. He provides so little detail however, that one cannot be sure that the animals were actually courting, or indeed whether they were a male and a female.

Ensatina eschscholtzia

Catalog of male actions.

The following actions are performed by the male while facing towards the female.

A.) TAPPING The male rapidly lowers and raises his head, tapping his snout to the substrate or to the dorsum of the female.

B.) NUDGING The male contacts his lateral snout to the female's lateral body.

C.) LIFTING The male turns his head under the female's chin and raises his head contacting the dorsum of his eye, snout, lateral snout or, less frequently, the dorsum of his head to the female's chin.

The following actions are performed by the male while facing away from the female.

D.) MALE STATIONARY WITH TAIL ARCHED While stationary the male extends on his hindlimbs and arches the proximal tail upward. The male may rock laterally on his hindlimbs without raising his hindfeet from the substrate, and he may undulate his tail laterally. Alternatively, the male may walk laterally with his forelimbs wihtout moving forward on his hindlimbs and while keeping his body axis straight. The male walks laterally with his forelimbs 40° to 80° and then reverses to walk 40° to 80° in the opposite direction.

E.) MOVING FORWARD WITH TAIL ARCHED The male moves forward with the sacrum arched upward only slightly. The male walks laterally with the forelimbs while walking forward on the hindlimbs, so that the sacrum moves forward on a straight course while the forebody and head move slowly from side to side like a pendulum.

F.) SLIDING VENT IN CONTACT WITH SUBSTRATE The male moves forward on a straight course sliding the vent in contact with the substrate. The tail is level.

G.) <u>STATIONARY WITH VENT ADPRESSED TO SUBSTRATE</u> The male pauses with the vent adpressed to the substrate and with the tail level.

H.) <u>SPERMATOPHORE DEPOSITION</u> The male is stationary with the vent adpressed to the substrate. The hindlimbs are aligned with femurs perpendicular to the long axis of his body and parallel to the substrate. The tail is level and undulations proceed along the entire length of the tail. The male is initially motionless on his hindlimbs, but then begins rocking laterally on his hindlimbs without raising his hindfeet from the substrate. Finally the hindlimb rocking ceases and the male remains stationary and motionless, with vent still adpressed to the substrate. The male then vibrates the tip of his tail very rapidly two or three times along the female's flank. Each burst of tail tip vibration lasts one or two seconds. After another short pause, the male flexes his tail to one side and lifts his vent off of the spermatophore.

I.) <u>MOVING FORWARD WITH TAIL FLEXED</u> The male moves forward away from the spermatophore on a straight course with the proximal tail flexed to one side and with his body axis in a sigmoid lateral flexure. As the male moves forward he throws his distal tail over the dorsum of the female's hindbody and sacrum and begins tail massaging.

J.) <u>STATIONARY WITH TAIL FLEXED</u> The following series of actions is executed by the male as the female rests with her vent in the vicinity of the spermatophore. The male is stationary with the female's forelimbs abutting against the posterior surfaces of, or just anterior to, the male's hindlimbs and with her chest resting on the male's sacrum and with her chin resting on the male's dorsal hindbody. The male's tail proceeds out from under the female's chest, up and over her dorsal hindbody.

The distal third or fourth of the male's tail undulates vigorously over the dorsum of the female's sacrum while conforming to and following the contours of her body. Simultaneously with this tail massaging, the male rapidly rocks laterally on his hindlimbs and repeatedly extends and flexes on his forelimbs. The female's head vibrates rapidly as a consequence of these male actions, as if resting on a vibrator. Finally the male's tail massaging, hindlimb rockings and forelimb extendings cease, and the male remains motionless.

Temporal relations (Ensatina eschscholtzia)

A sexually active male follows the female each time she moves away from him. The male moves forward rapidly in bursts each time the female moves forward. In close proximity to the female, the male moves slowly while crouching low to the ground with his forelimbs, and moves parallel to her towards her head. He usually moves posterior to anterior and two to five centimeters away from her while crouching low, but he may also approach her head-on.

While thus approaching the female and moving along parallel to her, the male does not contact the female with any part of his body. Infrequently the male may tap the dorsum of the female's tail or body or momentarily nudge her. Occasionally he may step on the female's tail or a limb while moving parallel to her. There is no rubbing or sliding of the male's snout on the female's body.

When the male reaches the female's head, he turns his head under her chin and lifts beneath her chin. Frequently the female raises her head when the male contacts his head to her chin and thereby breaks contact with him. The female may turn and move away from the male when he contacts her chin, in which case the male reapproaches her. If, however, the female remains stationary as the male lifts under her chin, the male then crawls forward under the female's chin. If the female's chin then contacts his dorsal midbody, he changes direction and continues forward away from the female, so that he makes an S-shaped path under the female's chin. The male arches his sacrum upward by extending on his hindlimbs as it passes in contact under the female's chin.

The female may immediately move forward and step astride the male's tail with her chin resting on the dorsum of the male's tail and with her snout over the male's sacrum or tail base. If she does, the pair moves forward in a tail-straddling walk. If the female remains stationary, however, the male moves forward until his dorsal proximal tail contacts the female's chin and then he stops. He then rocks on his hindlimbs and undulates his tail laterally. If the female then moves forward, stepping astride the male's tail, he moves forward arching his tail. If the female remains stationary for several minutes, or if she turns and moves away from the male, he lowers his tail and reapproaches her.

Once a tail-straddling walk begins, the male continually walks laterally back and forth, pendulum style, on his forelimbs. While moving forward during the tail-straddling walk, the female's snout usually rests immediately above the male's sacrum or vent. The male's tail contacts her venter along its entire length with the tip of his tail proceeding to just posterior to the female's hindlimbs. The female maintains her chin axial on the male's tail by actively turning her head laterally towards the male's tail each time it moves off the midline of her chin.

If the female's chin slips posterior to the male's vent along his tail, the male stops, then arches his tail upward and finally undulates his tail laterally. The male remains stationary until the female slides anterior along his tail to a position with her snout just over his vent or sacrum. He then moves forward. Subject to these conventions, the male alternates between moving forward and pausing with his vent raised above the substrate during the tail-straddling walk.

Finally, the male moves forward sliding his vent in contact with the substrate and pauses with the female's snout in the same position as before. Spermatophore deposition then begins with the female's snout resting over the male's sacrum and with the female still astride the male's tail. As the male rocks laterally on his hindlimbs during spermatophore deposition, the female actively swings her head counter to the movement of the male's sacrum.

As the male moves forward following spermatophore deposition with his tail now withdrawn from under the female, the female moves forward behind him with her snout resting on his sacrum. As she moves forward the spermatophore slides posterior in contact with her venter. She stops with the spermatophore in the vicinity of her vent. If it contacts her vent, she lowers upon it thereby inserting the spermatophore into her cloaca while undulating her tail slightly. Meanwhile the male has stopped in front of her and executes the complex series of actions (action J) previously described.

Three spermatophore depositions were observed. In the first case the female departed from the male during spermatophore deposition. The male moved forward off of the spermatophore 50 seconds later, but he did not flex his tail to one side. The male then reapproached the female and successfully reinitiated a tail-straddling walk. The female later moved away from the male, and no additional spermatophores were deposited.

In the second case the female successfully removed the sperm cap from the spermatophore and moved away from the male. He remained stationary and did not reapproach her. No additional spermatophores were deposited.

In the third case the female stopped with the spermatophore to one side of her vent. She remained stationary and did not remove the sperm cap as the male performed tail massaging, hindlimb rocking and forelimb extention (all of these constitute action J). The male then moved forward and arched his sacrum upward under her chin, and they moved forward again in a tail-straddling walk. The female moved away from the male two minutes later. He reapproached her and reinitiated tail-straddling walk at least three times, but no additional spermatophores were deposited.

Stebbins (1949) provides a very fine, detailed account of courtship behavior in this species, and his figures should be consulted to visualize the actions performed during courtship (particularly the amazing posture assumed by the male as the female rests over the spermatophore). I am essentially in agreement with Stebbins's observations, but I can make a few additions to the catalog of actions present in this species. First, I observed males vibrating their tail tips intermittently along the female's flanks after lateral tail undulations had ceased and just before the male moves forward off of the spermatophore. Second, I found that the male flexes his tail to one side and then begins tail massaging as he moves forward away from the spermatophore. Thus the tail-straddling walk immediately before and immediately after spermatophore deposition are not identical. Finally, the male may perform rhythmic extentions and flexions of the forelimbs while the female pauses behind him with her vent over the spermatophore.

Stebbins found that the tail-straddling walk which precedes spermatophore deposition is of exceedingly long duration in Ensatina. He observed tail-straddling walks lasting five hours and one hour, fifty-five minutes and both terminating with spermatophore deposition. The latter tail-straddling walk resulted in successful sperm transfer and less than an hour later the pair resumed a tail straddling walk lasting for three hours and ten minutes. In all instances the animals were performing tail-straddling walk when first observed. I observed two tail-straddling walks lasting five hours and fifty-five minutes and two hours, eight minutes respectively, from onset of the tail-straddling walk to spermatophore deposition. In another case the animals were first observed while in a tail-straddling walk and this behavior persisted for four hours and three minutes before spermatophore deposition occurred. In duration the tail-straddling walk of Ensatina far exceeds that of any other plethodontid species I have observed. In other plethodontids the tail straddling walk usually proceeds for only several minutes (occasionally for half an hour or more) before spermatophore deposition occurs or the female departs. The adaptive significance of Ensatina's remarkably lengthy tail-straddling walk remains a mystery.

Pseudoeurycea belli

Salthe and Salthe (1964) observed courtship behavior in a pair of Pseudoeurycea belli which had been injected with Rana pipiens pituitaries. The male received an intraperitoneal injection of five ground frog pituitaries 32 days after the pair was collected in Oaxaca, Mexico. Three days later the male was injected intraperitoneally with 200 units of pregnant mare serum, and the female received two frog pituitaries. Courtship behavior was observed intermittently for 15 days, beginning two days after the male's first injection.

With only his head in contact with the female, the male was observed to rub his chin in contact with the female's back with a slow up and down motion. While so rubbing the female, the male moved anteriad along the female. Sometimes the male pressed his chin down against the female's back or head by arching his back. The male then "violently drew his chin down over her flanks with a snap".

The male sometimes rubbed the dorsum of his head on the female's chin while she rubbed her chin on his head. The male then crawled out from under her chin with his body in contact with her chin. He then turned back towards the female's flank and resumed the rubbing and snapping motions. Occasionally the male undulated his tail.

On a subsequent day the male repeatedly ran in front of the female as she moved away from him, such that the female's chin contacted his body. The male then turned away from the female while keeping his body in contact with her chin.

During this day's observation session, the male also straddled the female's dorsum, as he had on previous days, and was carried along by the female as she moved away.

A few days later Salthe and Salthe (1964) observed the following sequence. The male moved after the female, moved his head under the female's chin and then moved his head slowly back and forth in contact with her chin. Both animals then moved forward with the female's chin continually in contact with the dorsum of his head. The male then turned to one side and moved forward under her chin so that the contact with the female's chin slipped posterior to his dorsal tail base. With the female's chin resting on his tail base, the male turned back towards the female and touched her dorsal pelvic region with his chin while undulating his pelvic region laterally. Frequently the male then executed a rapid downward motion of his head, usually beginning with his head held high and not in contact with the female. Immediately after the male performed this action, the female moved away from the male. The male then moved towards her chin again, and the sequence above was repeated. Later the female's chin position shifted posterior, and the pair moved forward in a tail-straddling walk with the female's chin resting on the male's anterior tail for a short time.

The next day the male moved towards the female's chin and both animals moved forward, as before, with the female's chin resting on his dorsal head. Soon, however, the female's chin slipped posterior to the male's dorsal tail base, and the pair moved forward in this position for the next eight hours. The male raised his pelvic region under the female's chin when moving forward. The male stopped intermittently, and frequently he turned his head back towards the female's pelvic region. Finally, the male lowered his pelvic region suddenly, breaking contact with the female's chin. The female departed from the male, and he remained motionless. No additional courtship behavior was observed during the next three weeks.

Bolitoglossa subpalmata

Catalog of male actions.

The following actions are performed by the male while facing towards the female.

A.) TAPPING The male rapidly lowers and raises his head, tapping his nasolabial cirri to the substrate or to the dorsum of the female.

B.) NUDGING The male contacts his snout or lateral snout to the female's lateral body.

C.) HEAD SLIDING The male moves forward with head level sliding his mentum in contact with the female's dorsum and without swinging his head laterally.

D.) PULLING The male slides his head forward slightly with his mentum in contact with the female's dorsum and then draws his head backward with his head bent down slightly. This action is distinguished from snapping only by a less pronounced backward movement of the head.

E.) SNAPPING The male slides his head forward slightly with his mentum in contact with the female's dorsum. The male then arches his head down and rapidly his head backward with his mentum still pressed against the female's dorsum. The backward movement may move the male's head clear of the female's body. Frequently rapid lateral tail undulations are initiated just before snapping begins and cease with the backward motion of snapping.

F.) JERKING While moving forward the male intermittently jerks his whole body forward very slightly.

G.) LIFTING The male turns his head to the side towards the female and raises his head contacting his lateral snout to the female's chin.

The following action is performed by the male while facing away from the female.

H.) STATIONARY WITH TAIL ARCHED AND UNDULATING While stationary the male arches his proximal tail upward and may undulate his tail laterally.

Temporal relations (*Bolitoglossa subpalmata*)

My observations are limited to initial interactions between the male and female during courtship. Spermatophore deposition and the events which immediately precede it have not been observed. On many occasions spermatophores were however, deposited when I was not present.

When the male initiates or reinitiates contact with the female, he moves forward intermittently along her length while performing tapping, nudging, head sliding, pulling and snapping. Generally the male moves anterior along beside the female, but he may move posterior along her length.

Whenever the female moves away from the male, he moves forward after her each time she moves forward and then reinitiates contact with her. When in close proximity to the female, or during head sliding, the male may perform jerking. Head sliding and nudging are the most frequent modes of head contact with the female. Infrequently during nudging and head sliding the male may momentarily undulate his tail laterally. Pulling was always followed by snapping (ie. a repetition of slow backward drawings of the mentum against the female's dorsum was always followed by one forceful, backward drawing of the mentum). When the male reaches the female's head during head sliding, he frequently presses his mentum down on the dorsum of the female's head.

In one instance, the male lifted under the female's chin, while undulating his tail momentarily, as he crawled parallel to her. The female turned and crawled over the male's tail. The male remained stationary and arched and undulated his tail as the female crawled over it. When the female broke contact with his tail, the male ceased tail arching and undulation and reapproached her.

Bolitoglossa flavimembris

Catalog of male actions.

The following actions are performed by the male while facing towards the female.

A.) TAPPING The male rapidly lowers and raises his head thereby tapping his nasolabial cirri to the substrate or to the female's dorsum.

B.) NUDGING The male contacts his snout or lateral snout to the female's lateral body.

C.) HEAD SLIDING The male moves forward with head level, sliding his mentum in contact with the female's dorsal body.

D.) SNAPPING The male pulls his head backward rapidly with his head level and with his mentum in contact with the female's dorsum. The backward motion causes the male's head to break contact with the female's body.

E.) JERKING While moving forward slowly, the male's whole body is intermittently jerked forward slightly without raising the feet from the substrate as the action is accomplished.

F.) LIFTING The male turns his head to the side towards and under the female's chin and raises his head contacting his snout to the female's chin.

Temporal relations (Bolitoglossa flavimembris)

My observations are limited to the initial courtship interactions of one pair. Spermatophore deposition and sperm transfer have not been observed.

After initiating or reinitiating contact with the female, the male moves anterior or posterior along her length while performing tapping, nudging, or head sliding. The male did not undulate his tail.

When the female moves away from the male, he moves forward after her each time she moves forward. When approaching the female and in close proximity to her the male may perform jerking.

The male may move parallel to the female and directly towards her head and perform lifting under her chin. The female then repeatedly raised her head breaking contact with the male's snout, and the male crawled posterior along the opposite side of the female while nudging her.

Hydromantes genei

Mertens (1923) observed courtship in a captive pair of animals for 15 minutes on April 10. The male rubbed his snout on the tail and head of the female, and the female performed writhing tail movements. The male then moved onto the dorsum of the female, with his forelimbs just behind hers, and both animals undulated their tails vigorously. The female moved forward a short distance carrying the male, and the pair separated. The male later reapproached the female and moved onto her dorsum with his forelimbs anterior to hers. Again the pair separated. The male followed the female up the wall of the terrarium, but the female then crept under a stone.

Noble and Brady (1930) note that male's were observed astride the females for extended periods, pressing their mental glands over the female's nares. Noble (1931) provides a figure of a male in this position.

On the evening of January 10, Rehberg (1960) observed courtship interactions in a pair of captives. The male rested astride the female's dorsum with his head bent downward so that his mental gland contacted the female's snout. In this position the male performed sinuous tail undulations. The female moved forward with the male on her dorsum. The male was dislodged from the female after fifteen minutes, and he immediately reapproached her. Finally the male ceased following the female. The following evening both animals were observed briefly, presumably with the male astride the female. Both animals performed sinuous tail undulations. Later no spermatophores were found in the container.

Hydromantes italicus

Durand (1970) observed a captive male standing erect with his tail slightly raised in front of the female as the male rubbed his snout along the female's lateral body.

Spermatophore deposition and sperm transfer have not been observed in the genus Hydromantes.

Family PROTEIDAE

Proteus anguineus

Chauvin (1883) watched a captive female move actively around a container one evening. She contacted the male and repeatedly rubbed her snout on his body and moved her tail actively back and forth. The male at first moved away from the female, but then began to rub the female with his snout and performed the same tail movements. The pair then retreated into a concealing cavity.

Kammerer (1912) found that the male approached the female and rubbed her with his snout, frequently on the female's venter. The male moved in front of the female, obstructed her path and performed wave-like undulations of his tail with his tail recurved. On some occasions the female nudged the male's cloacal region while the male jerked or vibrated his tail. On at least one occasion a pair was observed with only their heads in contact, the male's head under the female's head, and with their bodies forming an acute angle. The male's tail was flexed to one side and vibrated periodically. The male then departed rapidly from the female. The female moved slowly to one side and then paused for a few minutes. Kammerer (1912) suggests that the male had deposited a spermatophore, and the female was positioning her vent over it, but Kammerer was unable to observe the spermatophore. Kammerer (1912) notes that the male never clasps the female.

Briegleb (1961, 1962) reports that at the onset of courtship the male circles around the female while fanning his tail with the tail recurved. As the male circles the female, facing towards her, jerkings of the male's tail base alternate with this fanning movement. The male contacts the female's body with his snout and then faces towards the female while directing the fanning movements of his recurved tail towards her head. The amplitude of the tail movements then increase to 180°. The female may then nudge the male's cloaca with her snout, and both animals move forward for 5-10 centimeters with the female behind and contacting the male's lateral and dorsal tail base with her snout. As they move forward, the male shoves his body forward intermittently while increasing the fanning movements of his tail. The male then stops and deposits a spermatophore while jerking or vibrating his tail base from side to side. The male and female then move forward. As the female moves forward, the spermatophore contacts her venter. When the spermatophore contacts her vent, she stops and remains over it for approximately one minute. The sperm mass is not actively removed by the female. Instead the sperm adhere to the female's vent and then gradually move into her cloaca. This entire sequence of events can be repeated several times during an interval of a few hours. Frequently the above sequence is repeated three times, such that three spermatophores are deposited.

Necturus maculosus

Bishop (1926) describes some observations made by Paul A. Webb. A pair of animals was maintained in a large aquarium. "The male swam and crawled around the female and frequently passed over her tail and between the legs." This behavior apparently continued for a considerable period of time, and the female remained stationary. These observations may represent courtship behavior, but no spermatophore depositions were observed, and no spermatophores were found in the aquarium.

Kingsbury (1895) found that female Necturus maculosus possess spermathecae which contain spermatozoa in the fall and winter. Bishop(1932) found sperm masses in the vents of female's collected in October. Males injected with sheep pituitary extract later extruded gelatinous masses, each with a whitish sperm mass.

At present we know only that fertilization is internal in the genus Necturus, and no detailed accounts of courtship behavior are available.

Family AMPHIUMIDAE

Amphiuma tridactylum

This is an elongate animal with exceedingly small limbs. Baker and Caldwell (1947) observed what may have been courtship and insemination in this species in an outdoor, aquatic enclosure in Tennessee. On a few successive nights in June, two females and a male were observed swimming rapidly about together. In addition the two females were observed nudging the male's lateral anterior body. These activities continued regularly early each evening for four nights. On the fifth evening one female slowly glided anterior under the body of the male as he lay in shallow water, so that their bodies formed an acute angle. The female then rolled over and moved into a position with her cloaca in contact with the male's cloaca. They remained in this position for twenty minutes and then moved to deeper water. The following morning spermatozoa were found in the female's cloaca. Baker and Caldwell (1947) concluded that sperm were transferred directly from the male's to the female's cloaca, but in fact the process of sperm transfer has never been observed at close range.

B. Construction of an evolutionary hypothesis

The purpose of this section is to reconstruct the phylogeny of salamanders from the courtship behavior of living species. Estabrook (1968) has recently referred to estimates or reconstructions of true phylogenies as evolutionary hypotheses. This is much more than a simple addition to the unwieldy jargon of numerical taxonomy, for Estabrook's terminology focuses attention on the hypothetical and provisional nature of the evolutionary trees produced by systematists. I have attempted to reconstruct the phylogeny of salamanders in this spirit. My principle aim is to formulate specific hypotheses about the evolutionary history of courtship behavior, so that these hypotheses can serve as departure points for future research.

Obviously from this standpoint some hypotheses are more useful than others. In general the simplest explanation of an observed phenomenon is the one most liely to encourage future research. When the aim of an investigation is to reconstruct the phylogeny of a group of organisms, the use of this principle (Occam's Razor) becomes a search for the most parsimonious evolutionary tree which explains the evolution of the characters under study. The "most parsimonious evolutionary tree" is taken to mean that tree, or evolutionary hypothesis, with the fewest total number of evolutionary changes in characters. In this sense I have constantly tried to apply the principle of parsimony in the discussions which follow. I do not imply that parsimony is necessarily a feature of evolving biological systems. I have simply applied the principle of parsimony in an effort to find the simplest (and hence the most useful) hypothesis about the evolution of courtship behavior. In addition, hypotheses about evolution are most useful when they can be falsified.

Wilson (1965) has expressed this outlook with characteristic clarity. Hypotheses about evolution "... should make concrete predictions that are capable of being negated if the hypothesis is false; and they should point the way to deeper, more meaningful investigations if they are momentarily upheld." (Wilson, 1965). In this spirit I have tried to employ a methodology which allows one to specify precisely how the evolutionary hypothesis can be falsified.

In Table 14 I have listed several methodologies which can be used to approximate (or in one case to find) the most parsimonious evolutionary hypothesis for a group of organisms. For each methodology I have listed the assumptions which must be made and the principle characteristics of the evolutionary hypothesis which will be produced. This list is by no means exhaustive. The papers listed may be consulted for specific applications or for earlier, less specific formulations of the methodology in question. The states of each character may be arrayed on a separate network or character state tree. Ideally one might wish to assume only the form of the character state tree for each character (undirected character state trees) or perhaps only that certain chracter states can be distinguished (character state lists) and then be guaranteed of finding the most parsimonious tree(s). At present no such methodology exists. If one can specify the character state tree for each character, and one assumes that evolution is irreversible, Estabrook's (1968) methodology is guaranteed to find the most parsimonious tree. The other methodologies may relax one or both of these assumptions, but they are not guaranteed to find the most parsimonious tree.

For the majority of courtship characters I have considered in salamanders, I am unwilling to make the a priori assumption that evolution has been irreversible. After first discussing the selection and coding of

Table 14. A comparison of several methods for deducing branching patterns in phylogeny

	ASSUMPTIONS		CHARACTERISTICS OF THE EVOLUTIONARY HYPOTHESIS PRODUCED			
	1. Directed character state trees	2. Evolution is irreversible	Direction of evolution specified	Evolutionary reversals occur on the tree	Constructs hypothetical intermediate organisms	Approach to a most parsimonious solution(s)
Prim Network (Farris, 1970)	NO	NO	NO	YES	NO	In general finds a less parsimonious solution than next method
Wagner Network (Farris, 1970; rootless Wagner method)	NO	NO	NO	YES	NO	Finds a rather parsimonious solution
Wagner Tree (Farris, 1970; Wagner method)	YES	NO	YES	YES	YES	Finds a rather parsimonious solution
Camin & Sokal (1965)	YES	YES	YES	NO	YES	Finds a rather parsimonious solution
Estabrook (1968)	YES	YES	YES	NO	YES	3. Finds the most parsimonious solution(s)

1. The states of each character must be arrayed on a tree with the direction of evolution specified, or, in the case of binary characters, the ancestor of all OTUs in the study must be specified.
2. Once a character state, A, gives rise to a descendant state, B, then B cannot give rise to A.
3. This method yields a set of solutions guaranteed to contain the most parsimonious solution(s). This solution(s) must then be found by exhaustive search in this restricted set.

courtship characters in salamanders, I will discuss an approach, although not a fully satisfactory one, for generating a most parsimonious evolutionary hypothesis which does not make the *a priori* assumption that evolution has been irreversible and which readily suggests ways to falsify the hypothesis.

1. Selection and coding of characters.

In the analysis which follows I have included only those species for which observations are available for all phases of courtship behavior. These species include (i) species for which I have made observations on all aspects of courtship behavior; (ii) species for which my incomplete observations together with accounts in the literature give an unambiguous picture of the behavioral characters present in courtship (eg. Taricha granulosa, T. torosa and T. rivularis); and (iii) species whose courtship behavior I have not observed when literature descriptions together with my own observations on a congeneric species yielded an unambiguous picture of courtship behavior (eg. Ambystoma dumerelli, Aneides aeneus, Cynops pyrrhogaster (sasayama race)). I did not include several species for which rather complete behavioral observations are given in the literature, simply because I could not be sure that some behavioral traits not mentioned by the authors were actually absent. I have also excluded several species for which I have not been able to observe the process of spermatophore deposition.

Selection of characters is necessarily a subjective process. To proceed I seized upon a similarity of courtship in two or more species and provisionally defined this similarity as a character. I then examined every other species and asked myself if the character was unambiguously present or absent. Many characters were ambiguous in this sense, and I discarded them. For example, male Taricha and Salamandra swing the head from side to side while clasping the female's dorsum. In these two genera the swinging motion is rhythmic. Many other salamanders swing their heads from side to side on the female's dorsum, but in some cases the action is not rhythmic (eg. plethodontids) and in other cases the male does not clasp the female while he swings his head (eg. some Ambystoma and plethodontids). Should head-swinging be scored as present regardless of whether the action is rhythmic or not, and regardless of whether the male simultaneously clasps the female or not? I could not decide, and so I discarded this character. I discarded many such characters. I was left with 25 characters which presented no difficulties or ambiguities when I scored each of the species. These characters are described below. In most cases these characters are unambiguous because they consist of many individual attributes (eg. see the character "tail-straddling walk"). The names of each character correspond to usage in the preceeding accounts of courtship behavior. The reader should refer to these accounts for additional information about each character.

Courtship characters

1) DORSAL CLASPING The male firmly clasps the female's dorsum with either, or both, the forelimbs and the hindlimbs.

2) VENTRAL CLASPING The male clasps the female by hooking his forelimbs over the female's forelimbs while lying beneath her.

3) FORELIMB CLASPING The male clasps some region of the female's body with his forelimbs.

4) HINDLIMB CLASPING The male clasps the female's dorsum firmly with his hindlimb(s).

5) HINDLIMB-TREADING The male treads repeatedly with his hindlimbs by moving alternate hindlimbs forward and backward while clasping the female's dorsum with his forelimbs.

6) TAIL UNDULATION WITH TAIL REFLEXED The male undulates his distal tail rapidly with his distal tail reflexed towards the female.

7) TAIL UNDULATION WITH TAIL REFLEXED AND HEAD TURNED TOWARDS THE FEMALE

The male undulates his distal tail rapidly with the distal tail reflexed towards the female, while the male turns his head sharply to one side towards the female.

8) LATERAL DISPLACEMENT OF HINDBODY AFTER SPERMATOPHORE DEPOSITION The male moves his hindbody laterally through an arc of 45° - 90° immediately after spermatophore deposition.

9) SPECIFICITY IN LOCATION OF SPERMATOPHORE DEPOSITION 0 = the male deposits spermatophores in a wide variety of locations in relation to the female's body.

1 = spermatophores are consistently deposited in a specific location in relation to the female's body (eg. directly in front of her head).

10) PROLONGED NUDGING AND RUBBING OF THE FEMALE For a prolonged period the male nudges or rubs the female's lateral or dorsal body with his snout while moving along beside the female.

11) LIFTING AND TURNING HEAD UNDER THE FEMALE'S CHIN The male lifts his head while turning his head laterally under the female's chin.

12) TAIL-STRADDLING WALK The male and female move forward with intermittent progress in a tail-straddling walk. The female straddles the male's tail with her forelimbs and rests her chin on the male's dorsal proximal tail. Periodically the male arches and undulates his tail.

13) LATERAL STEPPING DURING THE TAIL-STRADDLING WALK During the tail-straddling walk, the male steps laterally with his forelimbs (includes pendulum side stepping and turning back towards the female).

14) RAPID DOWNWARD AND BACKWARD APPLICATION OF MALE'S MENTUM TO THE FEMALE The male performs a rapid downward and backward motion of his snout which has the effect of first contacting his mentum to the female's dorsum and then drawing his head backward off of the female's dorsum,

(includes both snapping and slapping of the mental gland).

15) BODY-SNAPPING The male presses his snout and mentum downward on the female's dorsum and performs a rapid lateral snapping of his body which flings the male backward away from the female.

16) PULLING While pressing his snout down on the dorsum of the female's body, the male repeatedly pulls his head backward in short strokes.

17) TAIL MASSAGE As the female pauses with her vent over or near the spermatophore, the male massages her dorsal or ventral hindbody and her sacrum with his tail.

18) FOOT DANCE The male arhythmically raises and lowers the forelimbs and hindlimbs while stationary or moving forward slowly and while facing towards the female.

19) RAPID BODY FLEXING UNDER THE FEMALE'S CHIN The male performs rapid lateral flexing of the body with his body curved under the female's chin.

20) SHOVING The male swims rapidly with his snout in contact with the female's lateral or ventral body and thereby shoves her rapidly through the water.

21) TAIL-SLAPPING The male swings his hindbody and tail rapidly towards the female and, frequently, strikes her body or head forcefully with his lateral tail.

22) SPERMATOPHORE DEPOSITED UNDER FEMALE'S VENT The spermatophore is consistently deposited on the substrate under the female's vent.

23) BUTTERFLY MOVEMENT OF FORELIMBS The male repeatedly swings both forelimbs upwards and forwards as he faces towards the female.

24) PENDULUM SIDE-STEPPING DURING THE TAIL-STRADDLING WALK During the tail-straddling walk, the male repeatedly steps to one side on his forelimbs and then reverses direction and steps to the other side.

25) MOUTH-GRASPING The male loosely grasps the female's body with his mouth.

The distribution of these characters among the species under study is shown in Table 15. I have employed the convention of denoting the presence of a character with a 1 and absence of a character with a 0. Note that several species cannot be distinguished on the basis of the 25 characters under study (eg. Ambystoma maculatum and Ambystoma texanum). For simplicity I have grouped such species and will consider them as one entity in the analysis which follows. Since some of the taxonomic entities in Table 15 are species, some are groups of species, and some are geographic races of a single species, I will henceforth use the convenient notation of referring to these entities as operational taxonomic units (OTU s).

2. LeQuesne's theorem and the concept of incompatability.

LeQuesne (1969) has provided an extremely powerful test for the occurrence of evolutionary convergence.[1] Consider a pair of characters (A and B), each of which exists in two states (0 and 1). Considering just this pair of characters, there are four distinguishable organisms (A_0B_0, A_1B_0, A_0B_1, and A_1B_1; where, for example, A_1B_0 represents the organism with character state 1 for character A and character state 0 for character B). Lequesne notes that if all four conceivable organisms (that is all four possible combinations of character states) occur among the organisms under study, then one can state categorically that at least one evolutionary convergence has occurred in the phylogeny of these organisms. You can satisfy yourself that this strong statement is so by attempting to represent the phylogeny of four such organisms without invoking an evolutionary convergence in at least one of the two characters (see appendix III). It is simply impossible.

LeQuesne's test may then be stated as a theorem (LeQuesne's Theorem):

i) Consider two binary characters. If all four combinations of character states occur,

ii) then every branching sequence representing the phylogeny of the four combinations will include at least one evolutionary convergence in character state.

iii) Consequently during evolution there has been at least one evolutionary convergence in character state.

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[1] In the discussions which follow I use convergence in a somewhat broad sense. If the states of a character are not convergent, I mean that the character is unique and unreversed in the sense of Wilson (1965). If the states of a character are convergent, I mean that either a character state has arisen more than once during evolution or that the character has undergone an evolutionary reversal.

Note that LeQuesne's Theorem requires no a priori assumptions about the direction of evolution in either of the two characters. Therefore the theorem also applies if one does make a priori assumptions about the direction of evolution (eg. that character state 1 was derived from character state 0).

The theorem applies only to the characters as they are currently coded. This point will be clarified later.

If the condition of LeQuesne's Theorem is satisfied, we know only that at least one evolutionary convergence has occurred during evolution. Furthermore the theorem does not specify the character in which the evolutionary convergence has occurred. If the condition of the theorem is not satisfied, convergence may, or may not, have occurred during evolution.

Farris (1970) has shown that the compatibility relationship between characters proposed by Camin and Sokal (1965) is based upon LeQuesne's Theorem. Furthermore the inconsistency test of Wilson (1965) is actually a less general statement of LeQuesne's Theorem (see Appendix IV).

When all pairs of binary characters are compatible (ie. no pair of characters show all four combinations of character state), there exists a most parsimonious (or a set of equally parsimonious) evolutionary hypothesis(ses) for the organisms under study (Farris, 1971). Since most studies include incompatible pairs of characters, Farris (1969, 1971) has made the following novel proposal. The character states in one of the characters in an incompatible pair can be recoded in a way which will render the original pair of characters compatible. The character state change(s) can then be recorded by creating a new binary character which, together with the recoded pair of characters, preserves the distribution of character states in the original character pair. In this way all incompatibilities among original and new characters can be systematically removed. If all characters are binary and there are n characters, the most parsimonious branching sequence will contain n evolutionary steps (ie. n changes in character state). If all characters are compatible, we know that a most parsimonious solution(s) exists, and that it contains n evolutionary steps. This most parsimonious solution(s) can then be obtained in a variety of ways. The important point is that we can recognize a most parsimonious solution when it is obtained.

A note of caution should now be introduced. The solution obtained will be a most parsimonious solution with regard to the original set of characters only if a minimum number of new characters are created. At present there exists no methodology for finding the minimum number of new characters required to remove the incompatibilities among all characters (Farris, pers. comm.). Nevertheless the application of LeQuesne's Theorem and Farris's proposal provides many heuristic insights into the evolution of characters, as I hope to demonstrate.

Table 15. Distributions of characters and recodings of incompatible characters

OTUs	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	1'	6'	8'	3'	4'	7'	5'	1''	4''	4'''	1'''	17'	14'	15'	16'	16''
Ambystoma maculatum/texanum										1	1																														
A. opacum										1	1								1																						
A. tigrinum/mexicanum/dumerilii									1	1	1									1																					
A. laterale	1		1		1				1		1																														
Taricha	1		1	1	1	1		1	1																																
Notophthalmus	1		1̲	1	1̲	1	1	1	1																				1			1									
Cynops pyrrhogaster (Sasayama)	1		1̲	1	1̲	1	1	1̲	1																	1̲		1	1	1̲		1			1	1					
C. pyrrhogaster (Hiroshima)	1̲		1̲	1̲	1̲	1	1	1̲	1																	1		1	1	1		1									
Triturus cristatus/helveticus	1̲		1	1̲	1̲	1	1	1	1												1					1			1	1		1									
Pleurodeles	1̲	1	1	1̲	1̲	1	1	1	1																	0̲				0̲		1	1	1							
Salamandra	1	1	1	1̲	1̲	1̲	1̲	1	1													1					1			0̲	1	1		1							
Pseudotriton									1	1	1	1																													
Desmognathus									1	1	1	1	1	1	1	1							1																		
Eurycea bislineata									1	1	1	1	1	1	1	1	1																								
Aneides lugubris/aeneus									1	1	1	1	1	1̲	1̲	1	1																					1	1		
Ensatina									1	1	1	1	1	1̲	1̲	1̲	1							1														1	1		
Plethodon yonahlossee									1	1	1	1	1	1	1̲	1̲	1̲																				1		1	0	1
P. jordani/ouachitae									1	1	1	1	1	1	1̲	1̲	1̲	1																			1		1	1	
P. glutinosus									1	1	1	1	1	1	1̲	1̲	1̲	1							1												1		1	1	

1̲ indicates that a character state was recoded from 0 to 1

0̲ indicates that a character state was recoded from 1 to 0

Table 16. Incompatibilities among pairs of characters

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	Total number of incompatibilities
1		X	X			X	X	X			X								6
2						X													2
3				X		X		X											4
4					X		X												3
5						X		X											3
6								X											5
7								X											3
8																			5
9																			0
10																			0
11																			1
12																			0
13																			0
14																X	X		2
15																	X		1
16																	X		1
17																			3
18																			0

X indicates that a pair of characters is incompatible. Only the upper right triangular matrix is shown. Characters 19 through 25 have one character state manifested in only one OTU. These characters cannot be incompatible with other characters and are not included in the matrix.

3. Recoding of characters

By applying LeQuesne's Theorem to the characters in Table 15 we can test for evolutionary convergences among the characters. For example, if we examine character 1 (dorsal clasping) and character 2 (ventral clasping), we find all four combinations of these two characters. As a consequence of LeQuesne's Theorem we can state that one (or both) of these characters has undergone at least one evolutionary convergence. In other words, we have disproved the hypothesis that all similarities in character states of these two characters are due to homology. (All such pairs of incompatible characters are shown in Table 16). With regard to characters 1 and 2, four simple hypotheses are possible;

(1) dorsal clasping has evolved independently at least once,
(2) dorsal clasping has been lost during evolution at least once,
(3) ventral clasping has evolved independently at least once, or
(4) ventral clasping has been lost during evolution at least once.

We know that at least one of these hypotheses is true. How can we choose among them?

I have employed two operating procedures to chose between such alternative hypotheses. First, I have tried to explain the incompatibilities between characters with a minimum number of hypotheses about evolutionary reversals. Second, when it is necessary to decide between secondary loss of a character (ie. convergence in absence) and independent origin of a character (ie. convergence in presence), I have assumed that secondary loss of a character occurred during evolution. I have employed this second operating procedure simply because when a character is absent in 2 OTUs, due to primitive absence in one OTU and secondary loss in another OTU, the character itself provides no evidence for distinguishing between these two different bases for absence. On the other hand, when a character is present in two OTUs, there are many individual components of the character which can be compared, since when selecting characters I endeavoured to choose characters composed of many components. Consequently when two OTUs agree in many descriptive details of a character, I think it unlikely that the similarity is due to convergence. This is simply an operating procedure and not an axiom about evolutionary processes. In particular cases I have deviated from this operating procedure and chosen the hypothesis of secondary origin of a character, rather than the hypothesis of secondary loss, when examination of the OTUs possessing the character showed marked differences in details of the character when it was present (see example below).

These two operating procedures were applied to the characters in Table 15, and the results are shown in the same table. New characters are denoted with primes to indicate which of the original characters was recoded (eg. character 6' is a new character which records that the character state of character 6 was changed from 0 to 1 in Salamandra). I have recoded incompatible characters in order of total number of incompatibilities beginning with the character involved in the highest number of initial incompatibilities with other characters (ie. character 1). The order of creation of new characters is shown in Table 15 (ie. 1', 6', 8', 3', 4', ...).

Since character 1 is a rather special case, I will use character 6 (tail undulation with tail reflexed) as an example of the recoding process. Character 6 was initially incompatible with five other characters (see Table 16), or with four other characters after the recoding of character 1. Note that if the character state of character 6 is changed in Salamandra from 0 (absent) to 1 (present), then character 6 is compatible with all other characters. This change is recorded by creating a new character, 6', which has character state 1 only for Salamandra. If we assume, for a moment, that tail undulation with the tail reflexed was primitively absent in the OTUs under study, then these changes have the following interpretation. Salamandra is in a lineage which evolved tail undulation with the tail reflexed, but Salamandra has secondarily lost this character (character 6' represents this secondary loss of tail undulation with the tail reflexed). Similar interpretations apply to all other recodings of characters.

The recodings of characters 1 and 4 are rather complex, and I will discuss the recodings of these characters as a second example. In order to render character 1 compatible with the other original characters, the state of character 1 was changed from 0 to 1 in Cynops pyrrhogaster (Hiroshima race), Triturus cristatus/T. helveticus and Pleurodeles. The new character, 1', was created to record these changes, with a character state of 1 for each of these 3 OTUs. Character 1' was then incompatible with character 2. The character state of character 1" was then changed from 1 to 0 in Pleurodeles to remove this incompatibility, and the new character 1'' was created to record this change. These recodings are equivalent to saying that dorsal clasping (character 1) was lost independently in a lineage containing Cynops pyrrhogaster (Hiroshima race) Triturus cristatus and T. helveticus (character 1') and in a lineage containing Pleurodeles (character 1''). Character 1' (loss of dorsal clasping) is, however, still incompatible with character 8' (character 8' represents loss of a right angle turn by the male after spermatophore deposition in Cynops pyrrhogaster). A re-examination of dorsal clasping (character 1) shows that only the sasayama race of Cynops pyrrhogaster clasps the female with only one hindlimb, whereas all other OTUs with dorsal clasping with the hindlimbs straddle the female and clasp with both hindlimbs. This suggests (together with the incompatibilities of character 1' and 4' with 8') that the sasayama race of Cynops pyrrhogaster has independently evolved dorsal clasping with the hindlimb. Under this hypothesis I recoded character 1' and 4' from state 0 to 1 in the sasayama race of Cynops pyrrhogaster has independently evolved dorsal clasping with the hindlimb. Under this hypothesis I recoded character 1' to 4' from state 0 to 1 in the sasayama race of Cynops pyrrhogaster, thus placing it in a lineage which has lost dorsal clasping with the hindlimbs, and I created characters 1''' and 4''' which together state that dorsal clasping was re-evolved (1'''), but with only one hindlimb employed (4'''), in one geographic race of Cynops pyrrhogaster. Character 4' (loss of hindlimb clasping) is still incompatible with character 2 (ventral clasping). Since ventral clasping consists of many components (see descriptions of this mode of clasping in the courtship accounts for Pleurodeles waltl and Salamandra salamandra), I assumed that loss of hindlimb clasping occurred independently in the lineage containing Pleurodeles and Salamandra and in the lineage containing Cynops and Triturus. Thus character states of character 4' were changed from 1 to 0 in Pleurodeles and Salamandra, and the new character 4'''' was created to record these changes. Character 4' is now compatible with character 2.

4. Polarity of evolution and the reconstruction of the phylogeny of salamanders

I required 16 new characters to render all pairs of characters compatible (Table 15). Since all character pairs are compatible and there are 41 binary characters (25 original characters and 16 new characters), we know that a most parsimonious evolutionary tree(s) exist, and that it contains 41 character changes.

The search for this particular tree will be simplified if we can determine which of the OTUs in the study is most primitive (ie. most like the most recent common ancestor of the OTUs in the study). Hynobiids are considered to be more primitive than the OTUs included in this study by many systematists (eg. Noble, 1931; Tihen, 1958; Regal, 1966). In my opinion the most compelling evidence is the presence of external fertilization in hynobiids and the presence of internal fertilization in all OTUs in this study (ie. ambystomatids, salamandrids and plethodontids). I propose that species in the genus Ambystoma are the most primitive OTUs in the study because they share several aspects of courtship behavior with hynobiids (ie. Hynobius) which are not shared between other OTUs and hynobiids. (1) Only Hynobius and Ambystoma clasp with the hindlimbs during spermiation. Hynobius males clasp the egg sacs with their hindlimbs while shedding sperm, and Ambystoma males clasp available objects with their hindlimbs during spermatophore deposition. (2) Only Hynobius and Ambystoma males arch the back upward during spermiation. (3) The jerking, lateral pelvic movement of Hynobius nebulosus males (and H. naevis males (R. Thorn, pers. comm.)) is very similar to the male action I have called vent shuffling in various Ambystoma species. Among Ambystoma species, A. maculatum and A. texanum are the most likely ancestor candidates, since they share more characters with Hynobius than the other *Ambystoma* species (ie. absence of characters 1,3,5,9,19,20).

The branching sequence shown in Fig. 73 was constructed using *Ambystoma maculatum* and *A. texanum* as the ancestors (ie. most like the ancestor) of the other OTUs in the study by using the Wagner method described by Farris (1970). This tree contains 41 evolutionary steps and is therefore a most parsimonious solution. Much of the structure of the tree is apparent from the distributions of character states in Table 15, and the same solution could be found by simple trial and error. Other equally parsimonious solutions may exist (ie. other trees with 41 evolutionary steps). In the discussions which follow I refer only to the solution shown in Fig. 73.

Changes in character states are described in Fig. 73. With the direction of evolution specified on the tree (by assuming that *A. maculatum* and *A. texanum* are most like the recent common ancestor of all OTUs), I have given interpretations to the new characters (1', 3', 4', etc.).

DISCUSSION

A). The evolution of salamander courtship behavior

The evolutionary hypothesis shown in Fig. 73 suggests the following interpretations (I will discuss how this hypothesis can be falsified in the next section). Notice first that the families Ambystomatidae, Salamandridae and Plethodontidae are each monophyletic. Estes (1970) has recently reviewed the fossil information on salamanders. From Estes'(1970) re-evaluations I have indicated the minimum time of origin of these three families in Fig. 73. These very conservative estimates indicate that many aspects of courtship behavior, such as the 90° turn of the male after spermatophore deposition in salamandrids and the tail-straddling walk of plethodontids, are exceedingly old.

The most primitive salamanders with internal fertilization, Ambystoma maculatum and A. texanum, deposit many (mean of 40 in A.maculatum) spermatophores per courtship, and the spermatophores are deposited in a wide variety of sites in relation to the female's body. Males spend a very short period of time courting between spermatophore depositions. In the preceding chapter I suggested that the brevity of interactions between the male and female between spermatophore depositions and the correspondingly large variability in the site of spermatophore deposition result in a low probability that the female will locate any given spermatophore with her vent. The fast rate of spermatophore deposition and the tendency to deposit many spermatophores are probably adaptive responses to high densities of courting males.

From courtship behavior of this kind there evolved a courtship system in which the male tended to deposit spermatophores in front of the female's head. In this site the spermatophore lies directly in the

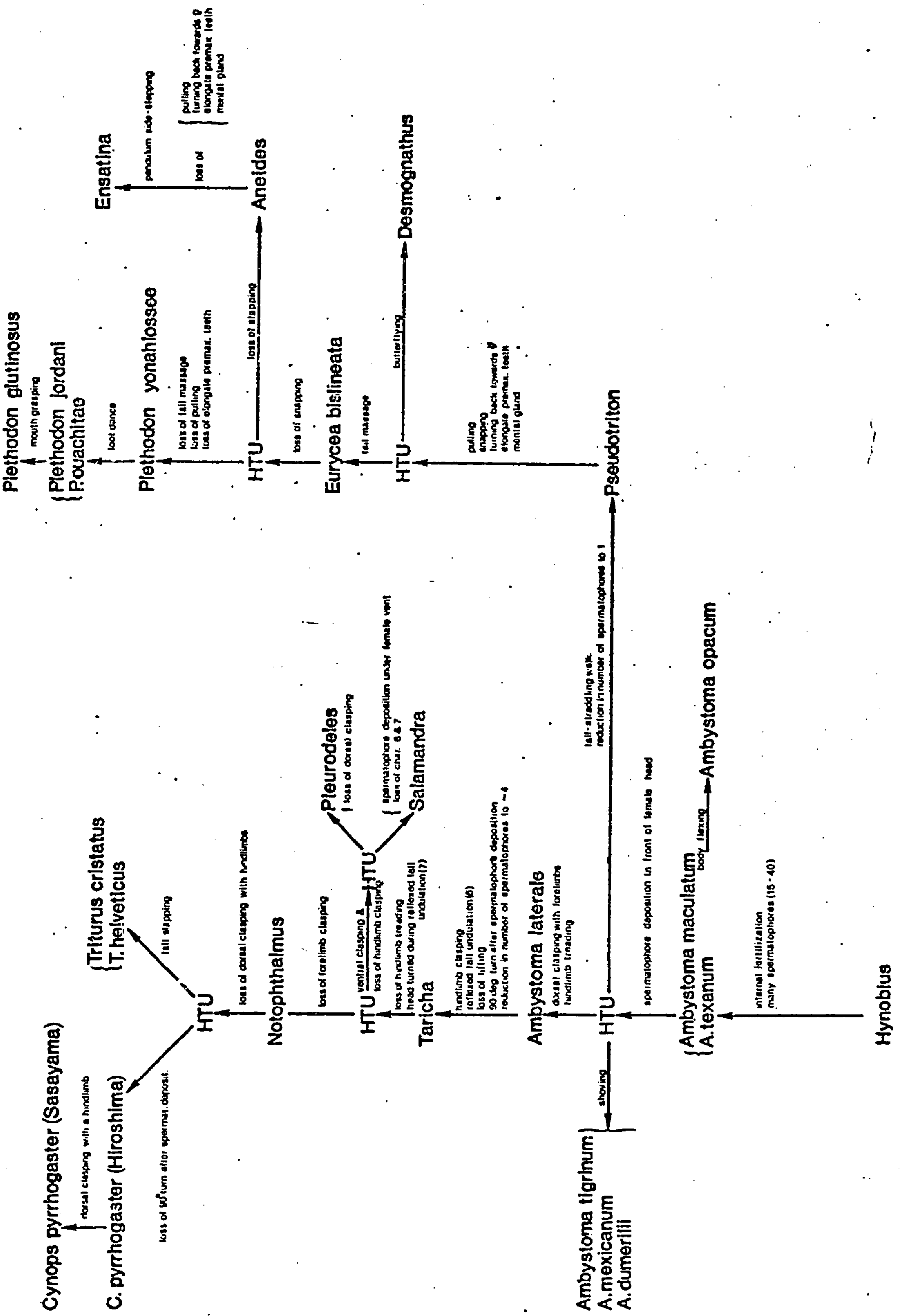
Figure 73. An evolutionary hypothesis; a phylogeny of salamanders based on 25 courtship characters.

HTU represents a hypothetical intermediate organism (a hypothetical taxonomic unit).

Some morphological characters are shown on the figure, but they were not used to construct the phylogeny.

The cluster of characters directly below Taricha are at least as old as the Oligocene (26-40 million years). The small cluster of characters just below Ambystoma maculatum and A. texanum are at least as old as the Oligocene (26-40 million years). The small cluster of characters on the arrow leading to Pseudotriton are at least as old as the Pliocene (1-13 million years).

This branching sequence, or cladogram, contains 41 steps. It is a most parsimonious solution for the phylogeny of the 41 characters shown in Table 15


Plethodon glutinosus
mouth grasping
Plethodon jordani
P.ouachitae
foot dance
Plethodon yonahlossee
loss of tail massage
loss of pulling
loss of elongate premax. teeth
Ensatina
pendulum side-slapping
loss of
pulling
turning back towards ♀
elongate premax teeth
mental gland
HTU
loss of slapping
Aneides
loss of snapping
Eurycea bislineata
tail massage
HTU
butterflying
Desmognathus
pulling
snapping
turning back towards ♀
elongate premax. teeth
mental gland
Pseudotriton
Cynops pyrrhogaster (Sasayama)
dorsal clasping with a hindlimb
C. pyrrhogaster (Hiroshima)
loss of 90° turn after spermat. deposit.
HTU
tail slapping
Triturus cristatus
T. helveticus
loss of dorsal clasping with hindlimbs
Notophthalmus
loss of forelimb clasping
HTU
ventral clasping &
loss of hindlimb clasping
HTU
Pleurodeles
loss of dorsal clasping
spermatophore deposition under female vent
loss of char. 6 & 7
Salamandra
loss of hindlimb treading
head turned during reflexed tail
undulation(7)
Taricha
hindlimb clasping
reflexed tail undulation(6)
loss of lifting
90 deg turn after spermatophore deposition
reduction in number of spermatophores to ~4
Ambystoma laterale
dorsal clasping with forelimbs
hindlimb treading
HTU
tail-straddling walk
reduction in number of spermatophores to 1
showing
Ambystoma tigrinum
A.mexicanum
A.dumerilii
spermatophore deposition in front of female head
Ambystoma maculatum
A.texanum
body flexing
Ambystoma opacum
internal fertilization
many spermatophores (15 - 40)
Hynobius

female's path, rather than in a less predictable variety of sites, and consequently she is more likely to locate it. Furthermore, the probability of spermatophore locations was further increased by the evolution of a behavioral algorithm which coordinates the position of the male and the female before, during and after spermatophore deposition (as in Ambystoma tigrinum, A. mexicanum, A. dumerilli and A. laterale). The male moves in front of the female and monitors her position with his backward directed tail. Contact to his anterior tail or cloaca causes the male to move forward and eventually deposit a spermatophore, while lack of contact causes the male to stop until the female again moves forward behind him and contacts his tail. In A. tigrinum we find a marked sexual dimorphism in tail length, which is lacking in A. maculatum (Fig. 6). The longer tail of male A. tigrinum no doubt facilitates monitoring of the female's position as she follows him between spermatophore depositions (the spatulate tail tip of male A. tigrinum probably also evolved to function in this context during courtship). In addition the males of A. tigrinum, A. mexicanum, A. dumerilli (and probably A. laterale) possess a cluster of cloacal papillae which are everted and exposed by the male's raised tail during this portion of courtship (these papillae are lacking in A. maculatum, A, texanum and the terrestrial courting A. opacum). These papillae are actively brushed across the female's snout, and secretions from these papillae are probably wafted posteriad by the male's tail undulations, and thereby enable the female to locate the male's cloaca and tail base as she follows behind him in the context of spermatophore depositions. In Ambystoma maculatum the male may occasionally shuffle forward and deposit a spermatophore as the female nudges his tail base. The complex behavioral algorithm, and then the facilitating morphological structures, of A. tigrinum, A. mexicanum, A. dumerilli and A. laterale probably evolved from such a tendency.

Much additional field and experimental work is required before the selective pressures responsible for these evolutionary modifications in the genus *Ambystoma* will be clearly understood. The following arguments suggest some new lines of inquiry, however. I have argued in the preceding chapter that rapid rate of spermatophore deposition and the deposition of many spermatophores per courtship is an adaptive strategy for a species, such as *A. maculatum*, which courts in crowded circumstances. How did one lineage of *Ambystoma* evolve a more lengthy period of interaction between spermatophore deposition? Frequent intrusions by other males would make such selection unfeasible. Two possibilities are that either *A. tigrinum*, *A. mexicanum*, *A. dumerilli* and *A. laterale* court in less crowded breeding sites than *A. maculatum*, *A. opacum* and *A. texanum*, or this first group of species evolved behavioral means for rendering intrusions by other males less likely. Since much additional data on breeding densities are required to test the first possibility, I will consider only the second alternative. Unlike *A. maculatum*, *A. opacum* and *A. texanum*, males of *A. tigrinum*, *A. mexicanum*, *A. dumerilli* and *A. laterale* possess means of transporting the female during courtship. Males of *A. tigrinum*, *A. mexicanum* and *A. dumerilli* periodically shove the female through the water; they can move her a meter or more very rapidly. Male *A. laterale* can actively transport the female, or increase her speed movement, by firmly clasping her dorsum and lashing with his tail. Storez (1969) has suggested that by this means *A. laterale* might be able to remove the female from other courting males. I think this suggestion applies equally well to *A. tigrinum*, *A. mexicanum* and *A. dumerilli*. The crucial experiments have not yet been performed. Does the frequency of transportation of the female increase in the presence of other males, and does this effect increase the fitness of the transporting male? If experiments substantiate these points then transportation of the female (via shoving or swimming while clasping) probably evolved to allow individual males to monopolize a single female (and hence her gametes). As a consequence of this ability males might have been able to increase the complexity and duration of interactions between spermatophore depositions and thereby increase the probability that each of their spermatophores will inseminate the female. One consequence would be that selection should then favor males which deposit fewer spermatophores per courtship, and are thereby capable of courting and inseminating more females each season. *A. tigrinum* does appear to deposit fewer spermatophores per courtship than *A. maculatum* (see preceding chapter), and so should *A. mexicanum*, *A. dumerilli* and *A. laterale*, as well as other clasping *Ambystoma* species such as *A. macrodactylum* and *A. gracile*, *A. jeffersonianum*.

Plethodontids apparently evolved from an ambystomatid population in which males consistently deposited spermatophores near the female's head by employing the leading/following algorithm described above. Males continued to rely on contact by the female to the anterior tail to elicit forward progress during the interval just before spermatophore deposition. In plethodontids, however, the female straddles the male's tail with her chin resting on the male's dorsal anterior tail. The switch in female position in plethodontids is probably correlated with the switch in plethodontids from underwater to terrestrial courtship. Most *Ambystoma* court under water, and the female orients to the male via secretions wafted from his cloacal papillae by tail undulations. She probably also orients to tactile contact to her snout and to water currents produced by the male. In terrestrial courting plethodontids, the female probably orients to the male via tactile input to her venter from the male's tail and perhaps via secretions from the male's dorsal tail which are transported into the female's nares via her nasolabial cirri. But in addition the plethodontid innovation of the tail-straddling walk is probably a response to selection for a higher probability of spermatophore location by the female. By means of a rather complex algorithm, plethodontid males are able to regulate the position of the female in relation to the male's vent (see description of this behavior in Plethodon jordani in the preceding chapter). The regulating algorithm is basically the same as in some Ambystoma species. Contact to the male's anterior tail (the dorsal anterior tail in plethodontids, and the lateral tail base or cloaca in Ambystoma) by the female's snout causes the male to move forward, and lack of this contact causes the male to stop. In plethodontids, spermatophore deposition is then initiated with the female's snout directly behind the spermatophore. This site is invariant within and between the species of plethodontids I have observed (Eurycea, Desmognathus, Aneides, Ensatina and Plethodon), and the site is much more restricted than in Ambystoma species. In the one species of plethodontid for which data are available, Plethodon jordani, the probability of spermatophore location by the female is very high, 0.9. As one might predict, all plethodontids observed thus far deposit very few spermatophores per courtship (usually only one and occasionally two). I argued in the preceding chapter that this constellation of characteristics (lengthy and complex interactions between the male and female, and the deposition of very few spermatophores per courtship) was possible in Plethodon jordani due to the low probability of male intrusions during courtship. The same arguments apply to plethodontids as a whole. First, even in such semi-aquatic genera as Pseudotriton, Eurycea and Desmognathus courtship occurs on land and not in restricted aquatic sites (such as temporary ponds) where crowding results as in *Ambystoma*. Consequently males are less dense during the courtship season, and male intrusions are less likely during courtship than in *Ambystoma*. Second aggression between courting males appears to have evolved early in the history of plethodontids. It occurs in *Pseudotriton*, *Eurycea*, *Desmognathus*, *Plethodon* and probably *Aneides*. By attacking and causing other males to flee during the courtship season, males are probably able to increase their reproductive monopoly of females. Thus early in the history of plethodontids selection for rapid rates of spermatophore deposition and the deposition of many spermatophores per courtship was relaxed.

After the origin of *Pseudotriton*, plethodontids evolved a remarkable behavior for forcefully applying the male's snout to the female's body. The evolution of two peculiar plethodontid morphological structures is tied to the evolution of this behavior. The snout is applied to the female's dorsum in two distinct ways. The male may either draw the mentum backward and forward in a series of short strokes with the head bent down sharply on each backward stroke (pulling), or after first sliding the mentum forward slightly, the male bends his head downward, pressing his mentum against the female's dorsum, and then snaps the body backward rapidly. The latter action sometimes flings the male backward away from the female (snapping). Pulling is present in *Eurycea bislineata*, *Desmognathus*, *Plethodon cinereus* and *P. richmondi*, and *Aneides*. Snapping is also present in these taxa with the exception of *Aneides* (additional observations may show that it is present in *Aneides* as well). Snapping differs from pulling only in the additional component of a violent snapping of the body, and frequently snapping is preceded by a bout of pulling. I suspect, therefore, that snapping evolved from pulling by the addition of a snapping component. Pulling was, in turn, probably derived from the behavior of sliding the head along the female's dorsum, a behavior which is present in all Ambystoma species as well as all plethodontids (including Pseudotriton which lack pulling and snapping). Two unique morphological characters, both present only in male plethodontids and best developed during the courtship season, evolved at the same time, or perhaps shortly after, the origin of pulling and snapping. These are elongate pre-maxillary teeth (which are directed forward and downward), and a small glandular mass on the male's mentum, the mental gland. Both sets of structures are forcefully applied to the female's dorsum during snapping and pulling, and together they clearly represent a functional complex of structure and behavior. During snapping, for example, the mental gland is first rubbed on the female's dorsum, and then the male's premaxillary teeth are rasped over this site as the male snaps his body backward.

Snapping is performed in two contexts in Desmognathus, either with the male facing towards the female and contacting her only with his head, or during the tail-straddling walk. In Eurycea bislineata it has been observed only in the latter context, while in Plethodon cinereus and P. richmondi I have seen it only in the former context (for the last two species, tail-straddling walks have not yet been observed). I suspect that snapping occurs in both of these contexts in all of these taxa. Additional observations are needed. Snapping during the tail-straddling walk is accomplished by stepping laterally with the forelimbs until the male's body is turned in a tight circle. The male then applies his mentum to the female's dorsum and performs snapping. The origin of the behavioral trait of stepping laterally with the forefeet and turning back towards the female during the tail-straddling walk is then closely associated with the evolutionary origin of snapping, the mental gland and elongate premaxillary teeth.

It is not clear what effect snapping has on the female's behavior. Perhaps as Organ (1960) has suggested for Desmognathus, secretions from the male's mental gland are introduced into the female's circulation via lacerations produced by the male's premaxillary teeth, much as in medical vaccinations. Snapping is clearly perceived by the female. In Plethodon cinereus and Eurycea bislineata the female often arches her back upward or bolts away from the male immediately after he performs snapping. It seems possible that snapping might serve the joint functions of increasing the probability that the female will later retrieve sperm from the male's spermatophore (an aphrodaisiac effect) and also cause nonreceptive females to flee from courtship before the male deposits a spermatophore. Perhaps experiments can be designed to test between these possibilities.

In the large species of the genus Plethodon (P. yonahlossee, P. jordani and P. glutinosus) some of the essential elements of snapping are still present (a rapid, downward and backward stroke of the male's head). But instead of snapping,the body backward after first pressing the mental gland against the female's forsum, the male slaps his mental gland on the female's head (often on her snout). This behavior, which I have called slapping, is performed during the tail-straddling walk as the male turns in a tight circle back towards the female (see Fig. 71). Very rarely it is performed as the male faces towards the female, when the pair is not in a tail-straddling walk. Slapping was probably derived from snapping. Elongate premaxillary teeth, which are no longer employed in a rasping action, are absent in these species. The mental gland, however, is remarkably large, probably to provide a larger surface for a slapping delivery of secretions to the female's nares.

Ensatina males also lack the rasping associated with snapping and pulling just as the large Plethodon species do. Correspondingly elongate premaxillary teeth are absent. The loss of elongate premaxillary teeth and the rasping action by which they are employed apparently occurred independently in Ensatina and in the large species of the genus Plethodon (see Fig. 73). Ensatina has also lost the behavioral complex of turning in a circle back towards the female during the tail-straddling walk and then applying the mentum to the female's dorsum with a rapid downward stroke, as in snapping and slapping. Correspondingly, the mental gland has been lost in Ensatina. The peculiar pendulum side-stepping which Ensatina males perform during the tail-straddling walk was probably derived from the behavior of side-stepping with the forelimbs and then turning in a tight circle towards the female. Ensatina males simply initiate, again and again, the first element of stepping laterally with the forelimbs. The last elements of turning in a tight circle and then rapidly applying the mentum to the female have been lost together with the two structures, mental gland and elongate premaxillary teeth, which are usually employed in this context.

Unlike Ambystoma species, in which the male's behavior is the same immediately before and after spermatophore deposition, early plethodontids (before the origin of Pseudotriton) evolved a special means for positioning the female after spermatophore deposition. Immediately after spermatophore deposition, plethodontid males move forward with the female still straddling the tail, but the tail is flexed to one side, out from under the female, rather than directed straight backward under the female as in the tail-straddling walk which precedes spermatophore deposition. The spermatophore is thereby exposed to the female's venter as she moves forward. Once the female stops with her vent near the spermatophore (plethodontid females, like ambystomatid and salamandrid females, appear to orient tactilely to the spermatophore as it contacts the venter of the abdomen), the male stops in front of her, arches his tail upward under her chin and begins rhythmic extentions and flexions of the hindlimbs. This special behavior tends to block forward progress by the female and causes her to remain with her vent near the spermatophore. At least as early as the divergence of Eurycea bislineata, plethodontids evolved the additional component of tail massage. As the female rests near or over the spermatophore, the male massages her hindbody and sacrum with sinuous tail undulations. This tail massage was later lost by the large eastern species of the genus Plethodon (P. yonahlossee, P. ouachitae, P. jordani and P. glutinosus), but it is still retained by modern Ensatina and Aneides. Desmognathines apparently diverged from other plethodontids before the evolutionary origin of tail massage.

Salamandrids were derived from an Ambystoma population (like Ambystoma laterale) in which the male very briefly rubbed and nudged the female with his snout and then clasped her from above with his forelimbs just behind or anterior to her forelimbs. Males of the salamandrid genus Taricha clasp the female in just this way, and in addition they rub the chin on the female's snout by swinging the head from side to side and sometimes tread with the hindlimbs. All of these traits are also shown by Ambystoma laterale.

Early in the history of salamandrids, a special mechanism evolved which no doubt increased the likelihood that the female would locate the spermatophore with her vent. In Ambystoma, females frequently pass beyond the spermatophore. In salamandrids however, the male pivots 90° about one forelimb after spermatophore deposition and thereby blocks the forward path of the female. Furthermore, his body lies approximately one snout-vent length in front of the spermatophore. When the female walks forward until her snout contacts the male's body, her vent is positioned over the spermatophore. If she loses tactile contact with the spermatophore as she moves forward, the female need only step laterally with her hindlimbs to find the spermatophore with her vent. Taricha females do just that. The male feature of turning the body 90° after spermatophore deposition is present today in Taricha, Notophthalmus, Triturus, Pleurodeles and Salamandra. It has been lost in Cynops pyrrhogaster. In Notophthalmus and Triturus the positioning effect of this 90° rotation works just as it does in Taricha.

In Taricha, males sometimes undulate the tail with the tail reflexed forward as they clasp the female. In Notophthalmus the same action is performed by the male while clasping the female. The tail undulations are exceedingly rapid, however, and undoubtedly serve to waft secretions from the male's cloacal papillae to the female's nares. The clasping position has been shifted forward, so that in Notophthalmus the male's vent, with everted papillae, lies over the female's anterior body, close to her head, rather than over her sacrum as in Taricha. This forward shifting of clasping posture probably evolved to facilitate wafting of cloacal secretions with rapid tail undulations. As a consequence of this forward shifting, Notophthalmus males have lost the ability to clasp the female with the forelimbs as their Taricha-like ancestor did, but Notophthalmus males do retain the hindlimb clasping of Taricha.

Dorsal clasping of the female is an obligatory precursor to spermatophore deposition in Taricha, as well as in clasping Ambystoma species such as A. laterale and A. macrodactylum. In Notophthalmus, however, clasping is facultative. Notophthalmus males will delete clasping and immediately initiate spermatophore deposition if the female approaches and nudges the male. The salamandrid lineage leading to modern Triturus and Cynops, in which clasping was lost altogether, probably incorporated this aspect of behavior from a Notophthalmus-like ancestor. In this lineage, several actions performed by Notophthalmus males while clasping (rapid tail undulating with the tail reflexed and the head turned sharply towards the female) were transplanted to a lateral display in front of the female. This lateral display, rather than dorsal clasping, then became the temporal precursor to spermatophore deposition. During the lateral display of Triturus and Cynops secretions from the male's cloacal papillae are wafted towards the female's nares by rapid tail undulations with the tail reflexed just as in Notophthalmus.

In the lineage leading to Triturus cristatus and T. helveticus an additional component was added to the lateral display, tail slapping. This remarkable action (see Fig. 50) may have evolved from the Notophthalmus action of thrashing (see Fig. 46). Both actions share the common feature of rapidly throwing the pelvis first to one side and then to the other via powerful lashings of the tail.

In one geographic race of Cynops pyrrhogaster the male places one hindlimb, and sometimes one forelimb, on the female's shoulder during the lateral display. This is apparently a rather recent innovation and it was not derived from the dorsal clasping of Notophthalmus and Taricha (in which both hindlimbs are employed). Salthe (1967) suggested that hindlimb clasping in Cynops was derived from Notophthalmus, and subsequently Triturus was derived from Cynops with a loss of dorsal clasping. Noble (1931) made a similar suggestion. To derive these lineages in this way one must either assume that the 90° pivoting of the male after spermatophore deposition was lost in Cynops and then re-evolved in Triturus, or that the loss of 90° pivoting occurred independently in at least two races of Cynops pyrrhogaster. Since dorsal clasping in the Sasayama race of Cynops pyrrhogaster differs in several respects from dorsal clasping in Notophthalmus and Taricha, I think my evolutionary interpretation is more likely.

Pleurodeles and Salamandra evolved a unique mode of clasping in which the male hooks his forelimbs over those of the female while lying beneath her. One set of behavioral traits present in modern Salamandra and one set of traits present in modern Pleurodeles suggest how this mode of clasping evolved. Before clasping the female's forelimbs from below, male Salamandra sometimes clasp the female from above with their forelimbs just behind the female's forelimbs, and rub the chin on the female's snout. This suggests that the ancestor of Pleurodeles and Salamandra clasped the female dorsally with the forelimbs, and rubbed the female's snout with his chin, just as Taricha does. But the ancestor of Pleurodeles and Salamandra also clasped the female's forelimbs with his forelimbs while lying underneath the female. A trait in Pleurodeles suggests how this came about. Pleurodeles males sometimes capture the female by approaching her slowly and then hooking one forelimb around her forelimb. This may occur before or immediately after spermatophore deposition. Courtship in the ancestor of Pleurodeles and Salamandra may have taken the following form. The male first captured the female dorsally with his forelimbs and rubbed his chin on the female's snout (as in modern Taricha and Salamandra). The male then slid forward over the dorsum of the female and deposited a spermatophore in front of her, and then pivoted 90° (as in modern Taricha). The female then crawled forward towards the male and located the spermatophore with her vent, while the male blocked her forward path by lying perpendicular to her (as in modern Taricha). The male then hooked the forelimb facing the female around the female's forelimb, while still curved in front of her. From this point on courtship proceeded as in modern Pleurodeles. If the female continued to nudge the male, he continued to pivot about the forelimb interlocked with the female's forelimb and deposited additional spermatophores. If, however, the female failed to nudge the male, or attempted to depart from him, the male rapidly swung beneath the female and clasped her other forelimb with his free forelimb. Additional bouts of spermatophore deposition were then initiated by releasing one forelimb and pivoting out from under the female. Thus in the ancestor of Pleurodeles and Salamandra, courtship behavior began as in Taricha with the male clasping the female dorsally and then dismounting over her head to initiate spermatophore deposition. But then courtship proceeded as in Pleurodeles with the male hooking one forelimb around the female's forelimb as the male continued to pivot and deposit spermatophores. In modern Taricha the female frequently departs from the male immediately after or during spermatophore deposition. Clasping of the female's forelimb with one of the male's forelimbs probably evolved in the ancestor of Pleurodeles and Salamandra to prevent such departure.

Pleurodeles has lost the first stages in this mode of courtship by deleting dorsal clasping of the female, Pleurodeles still retains the ancestral mode of capturing the female's forelimb with one of his forelimbs. A more recent ancestor of Pleurodeles and Salamandra evolved a capture mode by which the male slips rapidly under the female and moves forward to clasp her forelimbs with both of his forelimbs simultaneously. This is the capture mode most frequently employed by males of modern Pleurodeles and Salamandra.

Salamandra still retains the early ancestral mode of first clasping the female dorsally with the forelimbs. During the evolution of Salamandra the occurrence of spermatophore deposition was moved backward in time during courtship encounters. Rather than first pivoting out from under the female and then depositing a spermatophore to one side of the female (as in Pleurodeles), Salamandra males delete the initial pivoting. The spermatophore is deposited directly beneath the female's cloaca, before the male pivots out from under her. The male then turns his body 90° to one side, and the female's cloaca falls downward a few millimeters towards the spermatophore. Presumably spermatophores deposited in this new context were more frequently located by the female (since they lay just below her vent) than spermatophores deposited to one side of her body. If this was so, one would predict that the probability of spermatophore location per spermatophore is higher in Salamandra than in Pleurodeles, and that consequently Salamandra males deposit fewer spermatophores per courtship. These prediction remain to be tested.

In ambystomatids, plethodontids, and in Taricha, Pleurodeles and Salamandra among salamandrids the male's tail is directed straight backward immediately before spermatophore deposition. In one lineage of salamandrids, however, the male evolved a peculiar lateral flexure of the tail in this context. In Notophthalmus the distal tail is bent at a 90° angle before and during spermatophore deposition. In males of Paramesotriton hongkongensis, Cynops pyrrhogaster and Triturus the female follows closely behind the male with her snout close to the male's everted cloacal papillae. The evolution of a lateral tail flexure in these genera probably allowed the female to approach closely and orient to secretions from the male's cloacal papillae. In addition with the male's tail flexed laterally, the female can bring her snout right up to the male's cloaca immediately before spermatophore deposition, and the path to and over the spermatophore is thereby shortened. The S-shaped tail flexure of Paramesotriton, Cynops and Triturus was probably derived from the L-shaped tail flexure of Notophthalmus.

In Paramesotriton hongkongensis, Cynops and some species of Triturus (eg. Triturus cristatus, T. marmoratus, T. vittatus and T. alpestris) males possess a whitish or whitish-blue longitudinal stripe on the otherwise dark tail. As the male moves away from the female and assumes an S-shaped tail flexure just before spermatophore deposition, this light tail stripe is prominently exposed to the female. From the female's viewpoint the male appears visually as a dark rectangle with a contrasting whitish stripe. Presumably a whitish tail stripe evolved in the Paramesotriton, Cynops, Triturus lineage to facilitate visual orientation to the male by the female just before spermatophore deposition (see the account of Triturus cristatus courtship for a further discussion). At the same time this lineage probably retained chemoreceptive orientation to the male. As the male moves forward away from the female, the tail is not held in a stationary flexure, instead the tail is alternatively curled in a forward and backward S-shaped figure. This tail movement probably wafts secretions from the male's cloacal papillae straight backward, thus giving the female olfactory information about the male's position.

In several species of Triturus (eg. T. vulgaris, T. vittatus, T. montandoni, T. alpestris and T. helveticus) and in Cynops pyrrhogaster males possess a series of vertical black bars along the lower margin of the tail, which are very distinct against a reddish-orange or brown background. These markings probably serve the same function as longitudinal white tail stripes in making the location of the male conspicuous to the female when the male assumes the S-shaped tail flexure, while facing away from the female, just before spermatophore deposition.

Salamandrid males (Taricha, Pleurodeles, Salamandra, Notophthalmus, Cynops and Triturus) deposit fewer spermatophores per courtship (usually about four) than Ambystoma (and Dicamptodon, R. Nussbaum, pers. comm.) males (usually about 20 or more). I suspect that this reduction in the number of spermatophores deposited per courtship was accomplished by selection for devices which increased the chances of reproductive success with each spermatophore, followed by selection for the ability to inseminate more females each season by depositing fewer spermatophores with each female. Dorsal clasping in Taricha which permitted males to transport the female away from intruding males and 90° pivoting after spermatophore deposition are probably two devices in salamandrids which increased the chances of insemination with each spermatophore, and thereby permitted selection for fewer spermatophores per courtship. The hypotheses that dorsal clasping in salamandrids such as Taricha increases the male's fitness in the presence of other male's, and that the probability of sperm transfer per spermatophore is higher in Taricha than in ambystomatids (such as A. laterale) which clasp dorsally but lack 90° pivoting remain to be tested.

For many species of salamanders our knowledge of courtship behavior is still quite incomplete. Nevertheless knowledge of the few details that are known can allow us to predict what courtship will look like in these species and to suggest hypotheses about the evolution of courtship behavior.

Ambystoma annulatum apparently lacks dorsal clasping, and males rapidly depart from the female to deposit spermatophores. In these respects A. annulatum courtship appears quite similar to A. maculatum and A. texanum. Perhaps like these two species, A. annulatum also deposits many spermatophores per courtship.

Ambystoma talpoideum also lacks dorsal clasping, and females apparently follow the male immediately before and after spermatophore deposition. If this latter behavior is consistently present during courtship, as it is in A. tigrinum, A. mexicanum and A. dumerilli, then A. talpoideum might be a close relative of this group of species.

Ambystoma macrodactylum agrees in almost all respects with courtship behavior in A. laterale, except that hindlimb treading is apparently absent, and Anderson (1961) does not note turning of the male's head with lifting under the female's chin.

The courtship behavior of Ambystoma gracile is incompletely known, since spermatophore deposition and sperm retrieval have not yet been adequately described. The male is known to clasp the female dorsally with his forelimbs and to rub his chin on the female's snout like other clasping Ambystoma species, as well as Taricha. But in addition the male grips the female firmly with his hindlimbs, performs jerking movements with his hindlimbs, his cloaca is markedly distended during clasping, and the male remains astride the female for long periods of time. All of these traits are found in Taricha, but not in other clasping species of Ambystoma. I doubt that such a large constellation of similarities could arise independently in ambystomatids and salamandrids. If male A. gracile pivot 90° about one forelimb immediately after spermatophore deposition, as only salamandrids do, then Ambystoma gracile is surely closely related to the ambystomatid ancestor of salamandrids.

If one groups Ambystoma species simply on the basis of courtship behavior, one can obtain the following species groups:

(1) A. maculatum, A. texanum, A. annulatum;

(2) A. opacum (closely related to the first group);

(3) A. tigrinum, A. mexicanum, A. dumerelli;

(4) A. talpoideum (closely related to group 3);

(5) A. laterale, A. macrodactylum, A. gracile, A. jeffersonianum.

On the basis of females consistently following the male during the process of spermatophore deposition, groups 3, 4 and 5 shared an ancestor more recent than the divergence of groups 1 and 2. These groupings show a number of apparent conflicts with the Ambystoma species groups proposed by Tihen (1958) on the basis of osteological characters. For example, for my species groups to be consistent with Tihen's groups, his groups might be related in the following way. The subgenus Linguaelapsus must be derived from the maculatum group (Tihen) via A. maculatum, the opacum species group (Tihen) is derived from A. maculatum, and the mexicanum and tigrinum species groups (Tihen) are derived from A. talpoideum of the opacum species group. But then my groups 3-4 and 5 must have independently evolved female-following of the male during spermatophore deposition. Perhaps these conflicts between behavioral and osteological characters will be resolved when the phylogeny of Ambystoma species is better understood.

The courtship behavior of Rhyacotriton is still incompletely known, since spermatophore deposition and sperm transfer have not been observed. Tail undulation with the tail curled above the back during courtship (Fig. 27) is unique to Rhyacotriton. Male Rhyacotriton share with ambystomatids and plethodontids the trait of moving along the length of the female while continuously nudging her with the snout (a trait not present in salamandrids). Rhyacotriton shares a remarkable number of traits with plethodontids which are not present in Ambystoma The male crawls under the female's chin and then pauses arching and undulating his tail in contact with her chin. Aside from Rhyacotriton this trait is found only in plethodontids. Courting Rhyacotriton males may pursue and bite one another. This trait is widespread in plethodontids (including Pseudotriton), but absent in Ambystoma. Spermatophores are deposited on land. This feature occurs in only one Ambystoma species (A. opacum), but in all plethodontids (with the exception of paedogenic forms which never leave the water). Rhyacotriton deposit very few spermatophores per courtship (usually one, and on one occasion three), like plethodontids (in which usually one and occasionally two spermatophores are deposited), and unlike Dicamptodon (R. Nussbaum, pers. comm.) and Ambystoma (in which many spermatophores are deposited per courtship). In addition, the spermatophore of Rhyacotriton is strikingly similar to the spermatophores of plethodontids (in Rhyacotriton and plethodontids the spermatophore base inserts into a large cap-like mass of sperm) and unlike Ambystoma spermatophores (in which a rather incoherent mass of sperm is perched on a four-pronged platform at the apex of the spermatophore). Finally, Rhyacotriton is lungless, unlike Ambystoma, while all plethodontids are lungless. The conclusion that Rhyacotriton is rather closely related to plethodontids seems inescapable. It seems likely that plethodontids diverged from ambystomatids via a Rhyacotriton-like ancestor. Regal(1966) reached the same conclusion on morphological grounds and notes that the palatal dentition and premaxillary morphology of Rhyacotriton resembles plethodontids more than ambystomatids. Additional study of Rhyacotriton courtship behavior should clarify the relationships of plethodontids, ambystomatids and Rhyacotriton considerably.

Regal (1966) points out that ambystomatids and hynobiids are very similar morphologically and that the separations of these two families on the basis of mode of fertilization may be unfounded. We now know that in all ambystomatids (Rhyacotriton, Dicamptodon (R. Nussbaum, pers. comm) as well as Ambystoma) fertilization is internal via spermatophores attached to the substrate. These three ambystomatid genera probably shared an ancestor (with internal fertilization via conical spermatophores attached to the substrate) which was more recent than hynobiids (in which fertilization is external). However, it is still not clear how ambystomatids evolved internal fertilization from external fertilization. Additional study of reproductive behavior in hynobiids and cryptobranchids should make this transition more understandable. Reproductive behavior in forms with external fertilization has been observed only in the genus Hynobius and in the cryptobranchid genera Andrias and Cryptobranchus. Reproductive behavior has not been observed in the hynobiid genera Ranodon, Onychodactylus, Batrachuperus and Pachypalaminus. In Ranodon the sperm are packaged, but the sperm bearing structure is quite unlike the spermatophores of ambystomatids, salamandrids and plethodontids.

Wake (1966) has recently reviewed the morphological work which bears on the origin of plethodontids. Recent investigations on vertebral morphology, dentition, cranial morphology and the distribution of costal grooves suggest that plethodontids were derived from ambystomatids, rather than from salamandrids as Dunn (1922) had suggested (Regal, 1966 reached the same conclusion. Courtship behavior also suggests an ambystomatid origin for plethodontids.

Wake (1966) further suggests that the ambystomatid, plethodontid and the salamandrid lineages were derived independently from hynobiid-like ancestors. The many similarities in the courtship behavior of ambystomatids, plethodontids and salamandrids (eg. internal fertilization via spermatophores with an apical sperm mass, as well as spermatophore deposition in front of the female's head) suggest instead that these three families shared a common ancestor more recent than hynobiids.

Salthe (1967) suggested that in the common ancestor of plethodontids, ambystomatids and salamandrids the male captured and clasped the female dorsally during courtship. Subsequently dorsal clasping was lost independently in three lineages (ambystomatids, salamandrids, plethodontids). My analysis of courtship behavior (see Fig. 73) suggests instead that the most recent common ancestor of these three families did not clasp the female dorsally, that only salamandrids have secondarily lost dorsal clasping, and that plethodontids never possessed dorsal clasping. Salthe (1967) notes that in some plethodontids (Hydromantes and Pseudoeurycea) the male goes astride the female's dorsum. This behavior, which also occurs in Plethodon and Aneides, is quite unlike the dorsal clasping of ambystomatids and salamandrids. In these plethodontids the male simply crawls along the female's orsum. He does not actually grip or clasp the female with his forelimbs. Furthermore the male does not clasp the female dorsally in hynobiids (Hynobius) or in cryptobranchids (Andrias and Cryptobranchus).

Within the family Plethodontidae, my evolutionary hypotheses derived from courtship behavior agrees with branching sequences proposed by Wake (1966) on morphological grounds.

The process of spermatophore deposition and sperm transfer has not yet been observed in the plethodontid genera Hydromantes, Pseudoeurycea and Bolitoglossa, and we have no complete information on the courtship behavior of any bolitoglossine species. As a consequence courtship behavior along gives little basis for speculation about the origin of and the relationships within this lineage. Since pulling has been observed in Bolitoglossa, and snapping has been observed in both Bolitoglossa and Pseudoeurycea, bolitoglossines probably diverged from other plethodontids after the origin of Pseudotriton.

The salamandrid genus Neurergus shares with Cynops, Paramesotriton *hongkongensis* and *Triturus* the features of performing tail undulations with the tail recurved with the male positioned in front of the female, and clasping of the female has not been observed. *Neurergus* is therefore probably closely related to the *Cynops-Paramesotriton-Triturus* lineage. Since *Neurergus* males will also be found to reflex the tail in an S-shape just before spermatophore deposition.

Herre (1935) concluded that *Neurergus*, *Triturus*, *Cynops* and *Paramesotriton* (all included by Herre in the genus *Triturus*) and *Notophthalmus* shared an ancestor more recent than *Taricha* and more recent than *Salamandra*, *Mertensiella*, *Chioglossa*, *Pleurodeles* and *Tylototriton*. My phylogenetic interpretations based on courtship behavior are in harmony with this view (see Fig. 73).

Males of *Mertensiella*, *Chioglossa* and *Tylototriton* are known to clasp the female's forelimbs from below with both forelimbs, as in *Salamandra* and *Pleurodeles*, but little else is known about courtship in these first three genera. On the basis of this unique clasping mode, these five genera are clearly a monophyletic salamandrid lineage (a monophyletic lineage in the sense that these five genera shared a common ancestor more recent than the ancestor of all salamandrids). Herre (1935) and Wake and Özeti (1969) concluded, principally on morphological grounds, that the common ancestor of these genera was also the ancestor of salamandrids as a whole. Perhaps additional behavioral and morphological work will help resolve this disparity in phylogenetic interpretation. *Chioglossa* is probably most closely related to Salamandra, since, like *Salamandra*, the male is known to displace the hindbody out from under the female while still gripping her with both forelimbs, to undulate his body from side to side while clasping the female, and to rub his dorsal head on her chin while clasping. On the basis of morphological studies, Herre (1935) and Wake and Özeti (1969) also concluded that *Chioglossa* and *Salamandra* are closely related. In addition, *Chioglossa* and *Salamandra* are the only salamandrids known in which courtship occurs on land.

Courtship behavior in the salamandrid genus *Euproctus* is very different from other salamandrids, as well as ambystomatids and plethodontids. Spermatophores are deposited on or near the female's cloaca, rather than on the substrate as in all other salamandrids, ambystomatids and plethodontids. Additional observations are needed (particularly on the male and female interactions before the male captures the female) before the evolutionary origin of *Euproctus* courtship behavior can be understood in any clear way. Like *Taricha*, *Euproctus* males clasp the female with the hindlimbs and perform stroking movements with the hindlimbs while gripping her. Perhaps *Euproctus* evolved from a *Taricha*-like ancestor by shifting the site of hindlimb clasping from the female's dorsal sacrum to her ventral sacrum, and my moving the occurrence of spermatophore deposition back in time so that the spermatophore was deposited while the male still clasped the female, rather than after first dismounting from the female, as in *Taricha*. These speculations are not inconsistent with the conclusions of Herre (1935) and Wake and Özeti (1969) about the origin of *Euproctus*.

Male *Proteus* are known to undulate the tail with the tail reflexed, while the male faces towards the female, and the male never clasps the female. This constellation of traits occurs only in *Paramesotriton*, *Cynops*, *Triturus* and *Neurergus*. *Proteus* was, therefore, probably derived from this salamandrid lineage. Herre (1935) reached the same conclusion on morphological grounds. The courtship behavior of *Necturus* is so poorly known that no comparisons with *Proteus*, or with other salamanders, are possible, despite Salthe's (1967) attempt to suggest "vague similarities" between the courtship of Proteus and Necturus.

Sperm may be transferred directly from the male's cloaca to the female's cloaca in Amphiuma. Here again, courtship behavior is so poorly known, that no real comparisons are possible with other salamanders.

B.) Evidence that would falsify the evolutionary hypothesis

How might the evolutionary hypothesis that I have presented in Fig. 73 be falsified with additional courtship data? Below I discuss three conceivable types of courtship behavior which, if discovered, would drastically alter hypotheses about the relationships of three salamander families.

Discovery of an ambystomatid species in which the male does not clasp the female dorsally and in which the male pivots 90° after spermatophore deposition would suggest that salamandrids were derived from a non-clasping ambystomatid, and that dorsal clasping evolved independently in salamandrids and ambystomatids. This would disprove my hypothesis that the dorsal clasping of salamandrids was derived from dorsal clasping of ambystomatids and completely reorder the direction of evolution of courtship within salamandrids.

Discovery of an ambystomatid in which the male clasps the female's forelimbs with his forelimbs would suggest that salamandrids were derived from ambystomatids via a _Pleurodeles_, _Salamandra_, _Mertensiella_, _Chioglossa_ or _Tylototriton_ like ancestor rather than from a _Taricha_-like ancestor.

Discovery of a plethodontid with a tail-straddling walk but with a 90° pivoting of the male after spermatophore deposition would suggest that plethodontids evolved from a salamandrid rather than an ambystomatid ancestor.

C.) Species recognition, sex recognition, female receptivity and the complexity of courtship.

One of the most striking features of salamander courtship behavior is the great complexity of the behavior shown by each species. What is the adaptive significance of this complexity? Evidence from a variety of sources suggests that complex courtship behavior in salamanders is the result of selection for male ability to assay and change the sexual receptivity of the female rather than the result of selection for the ability to avoid errors in species or sex recognition.

In most salamanders, species recognition is apparently accomplished by the male before courtship is even initiated. With an elegant series of experiments, Twitty (1955) established that male _Taricha rivularis_, a stream courting species, locate females via skin secretions carried downstream from the female. Twitty (1955) also found that male _Taricha rivularis_ are attracted upstream to a tethered conspecific female, and tend to ignore females of a sympatric species, _T. granulosa_, which are tethered nearby. Noble and Brady (1930) tried substituting heterospecific females for conspecific females with actively courting plethodontid males. Some of these substitutions were made with sympatric pairs of species. Males uniformly terminated courtship during preliminary stages. Noble and Brady (1930) concluded that species recognition was accomplished by the male's use of olfactory perception of female skin secretions. I placed pairs of _Plethodon jordani_, _P. glutinosus_ and _P. yonahlossee_ together in all possible combinations (9). The animals were collected on the south side of Whitetop Mtn., Virginia where all three species are sympatric in the strictest sense and during late September when from previous years I knew that all three species were courting. I observed <u>no</u> courtship interactions among heterospecific pairs, and no spermatophores were deposited. I observed courtship behavior among conspecific pairs of <u>P. jordani</u> and <u>P. glutinosus</u>, and spermatophores were deposited. No courtship interactions were observed and no spermatophores were deposited among conspecific pairs of <u>P. yonahlossee</u>, but they did deposit spermatophores in the collecting containers in the field. Since the number of pairs in some combinations was very small (eg. 2), I consider this experiment to be a mere suggestion that species recognition is accomplished before or during the very early stages of courtship in sympatric <u>Plethodon</u> species.

While species identification appears to be accomplished near the onset of courtship, the precise mechanisms are, in nearly all instances, poorly understood. In the Mtn. Rodgers/Whitetop area of southwestern Virginia there are six species in the genus <u>Plethodon</u>. I collected at two specific localities in this area. At one locality (4000 ft. on the south side of Whitetop Mtn.,) there are five species of <u>Plethodon</u> which are sympatric in the strictest sense. Any pair of these five species can be taken under the same surface object. At the second locality (4800 ft. on the west side of Mt. Rodgers) there are four species of <u>Plethodon</u> which are sympatric in this strict sense. <u>Every</u> pair of species differs in the courtship actions shown by the male when he first approaches a conspecific female (see Table 17). There is considerable overlap among these species in courtship season. In late September <u>P. jordani</u>, <u>P. glutinosus</u> and <u>P. yonahlossee</u> (all large species) are engaged in courtship. In October <u>P. richmondi</u>, <u>P. cinereus</u> and <u>P. welleri</u> (all small species) are courting.

Table 17. Courtship actions performed by male's during initial interactions with females in each of six sympatric species in the genus <u>Plethodon</u>

	Low elev.	High elev.	RAPID TAIL UNDULATION	SNAPPING	FOOT DANCE	MOUTH GRASPING
Plethodon welleri		x	+	0	0	0
P. cinereus	x	x	+	+	0	0
P. richmondi	x		0	+	0	0
P. yonahlossee	x	x	0	0	0	0
P. jordani	x	x	0	0	+	0
P. glutinosus	x		0	0	+	+

(+ indicates that an action is performed by the male, and 0 indicates that it is not)

No interspecific hybrids were found at these two localities. The adaptive significance of these differences in constellation of male actions is unknown. The differences may be used by females to identify conspecific males. Alternatively these differences may be used by males during the courtship season to identify conspecific males, such that agonistic interactions are initiated only between conspecific males. Agonistic interactions have been observed between conspecific males of P. jordani, P. glutinosus and P. yonahlossee. Experiments with courting Plethodon species from this area (eg. Observations of interactions within heterospecific pairs and between heterospecific males) would contribute much to our understanding of how reproductive isolation is accomplished in salamanders, and to our understanding of the relation between agonistic male-male interactions and courtship behavior. In this same area there are five sympatric species of Desmognathus (as well as the closely related genus Leurognathus). As in Plethodon, the courtship seasons of the Desmognathus species overlap considerably. Organ (1961a, and pers. comm.) found no, or only subtle, differences in courtship behavior between these Desmognathus species. Why should sympatric Plethodon species show discrete differences in male courtship behavior, when sympatric Desmognathus species do not?

In all species of salamanders in which I have observed courtship behavior, the first response of the male to a female is to approach her and contact his snout to her body. The probable function of this initial behavior is to detect, via olfaction, whether the animal is a conspecific female and then terminate courtship behavior if it is not.

Similarly, sex identification appears to be accomplished during the initial encounters of a male with a conspecific. Courtship behavior simply doesn't occur in a container with only males, until a female is introduced. When males and females are present, a male approaches one animal after another and contacts its body with his snout. When another male is encountered, the male simply moves on. He initiates courtship behavior only when a female is encountered. As in species identification, sex identification is accomplished before courtship behavior, in the strictest sense, is initiated, and it is probably accomplished via olfaction.

Since species recognition and sex recognition are accomplished before the complexities of courtship behavior come into play, complexity of courtship behavior apparently serves some other function(s). Complexity of courtship behavior probably serves the functions of (1) allowing the male to assay the female's sexual receptivity and then to take appropriate action during courtship, (2) allowing the male to change the sexual receptivity of the female, and (3) coordinating the activities of the male and female during the process of sperm transfer. All three functions represent adaptive designs for increasing the probability of sperm transfer with each spermatophore deposited.

For several species I view courtship behavior as a complex filter which allows the male to sort females on the basis of sexual receptivity. Only females which are likely to retrieve sperm from spermatophores pass through the filter, and the male deposits spermatophores only with these females. Consider Notophthalmus viridescens, a species with remarkably complex courtship behavior. In the presence of females, males undulate the pelvis and tail with their cloacal papillae everted. These behaviors probably serve to waft secretions from the male's cloaca into the water, and thereby advertise the male's presence. Some females actively approach the male under these circumstances, and nudge him with the snout. The male then turns away from the female and, if she nudges his cloaca, he deposits a spermatophore. Some females, however, do not approach the male. Instead they remain stationary or flee from the male. Such females are pursued, and sometimes captured, by the male. If a captured female bends her head down sharply, the male releases her and terminates courtship. I interpret this programming convention to be an adaptive design for terminating courtship with females which are unlikely to retrieve spermatophores (eg. females which have already laid eggs or have already been inseminated). Some females do not bend the head down sharply, and with such females the male initiates a complex series of actions which lasts for 45 minutes or more. During this time the male repeatedly applies glands on his cheek to the female's nares, wafts secretions from his cloacal papillae to the female's nares with tail undulations, rubs his forearm on the female's snout, and thrashes the female from side to side. These male actions are performed with a temporal complexity approaching a musical symphony (see account of <u>Notophthalmus viridescens</u> courtship). These behaviors probably serve to increase the probability that the female will later follow the male and retrieve sperm from the spermatophores he deposits (ie. these behaviors probably change the female's sexual receptivity). Finally the male dismounts from the female and pauses in front of her while undulating his tail with his cloacal papillae everted. Some females then depart from the male, while other females actively nudge the male's cloaca and follow him. The male deposits spermatophores only with the latter class of females. Thus male <u>Notophthalmus</u> deposit spermatophores with only two classes of females; with very receptive females which actively approach him and nudge his cloaca, and with females which give these same responses after a lengthy period of clasping (during which the male may be able to change the female's sexual receptivity).

In many other species of salamanders the male repeats a sequence of behaviors until the female gives a specific response. Then and only then is a spermatophore deposited. In many species these behavioral iterations of the male can be interpreted as iterations of the question, "Is this female likely to retrieve sperm from a spermatophore?", while the male simultaneously bombards the female with stimuli (eg. glandular secretions) which tend to change the female's answer to "yes". For example in Triturus, Cynops and Paramesotriton the male repeats the sequence; lateral display, turning away from the female, lateral display,... until the female nudges the male's tail when he turns away from her. Only then is a spermatophore deposited. But in addition, during the lateral display the male wafts secretions from his cloacal papillae to the female's nares. The repeated presentation of these secretions to the female probably increases the probability that the female will follow the male and retrieve sperm from his spermatophores. An analagous behavioral iteration is used by male plethodontids. The male repeats the sequence, move along the length of the female while contacting her with the head, crawl under the female's chin and arch and undulate tail, move along the length of the female while contacting her with the head, ... until the female slides forward along the male's tail as he arches and undulates his tail under her chin. The pair then moves forward in a tail-straddling walk, and only then is a spermatophore deposited. The repeated applications of secretions from the male's dorsal tail and his mental gland probably increase the probability that the female will later retrieve sperm from the spermatophore.

The complex algorithms employed by ambystomatids, salamandrids and plethodontids in the immediate context of spermatophore deposition undoubtedly serve to align the male's and female's bodies, so that the female is most likely to contact the spermatophore with her vent.

Thus, complex courtship behavior in salamanders appears to represent adaptations for assaying and changing the female's receptivity and for coordinating activities associated with the transfer of sperm.

Why do female salamanders commonly appear to be "unresponsive" to male courtship activities? I think two explanations are likely. First, female salamanders come to courtship encounters with differing sexual receptivities. Some females have already been inseminated, or have already laid eggs, and are therefore unresponsive to courtship. Second, selection probably favors low receptivity to courtship in gravid females which have not been inseminated. Females which tend to be sexually unreceptive will be inseminated only by males with high perseverance during courtship and with high ability to change female receptivity. Selection will favor such males by virtue of their ability to inseminate non-receptive as well as receptive females. Selection will also favor non-receptive females (compared with ever-receptive females) because they will be inseminated only by males with high courtship perseverance and therefore leave sons with high sexual fitness. Selection for persevering males therefore feeds back on selection for non-receptive females and vice versa.

D.) Programs for future research

Surprisingly little is known about many aspects of courtship behavior in salamanders. In some of the preceding sections I have mentioned specific problems which deserve attention. The following problems also deserve additional research:

a) The courtship behavior of many species is wholly unknown or incompletely known. Courtship behavior in salamandrids is particularly diverse, and we know little or nothing about the courtships of Chioglossa, Hypselotriton, Neurergus, Pachytriton, Salamandrina and Tylototriton. There is every reason to believe that our understanding of salamander phylogeny will be reordered considerably when we know what courtship is like in these and other genera of salamanders.

b) At the same time there is great need for additional work on species which have already been studied. American workers have taken a desultory approach to courtship behavior in salamanders. It is unusual to find two papers on the same species no matter how common that species might be. This state of affairs is probably a consequence of the view that once the behavior of a species has been described there is nothing new to see, describe or puzzle over (when I mention that I have just seen courtship in a particular species, I am frequently asked "Has the behavior of that species been described?"). The result is a literature characterized by superficial surveys and notes rather than by in-depth studies. This criticism is not so true of European workers, but the same general points still apply. The courtship behavior of some salamander taxa has been described in some detail, eg. Ambystoma, Notophthalmus, Taricha, Plethodon, but we do not know everything. We do know enough to begin asking specific questions and to begin answering those questions with experiments. Future studies should explore these "better known" taxa as well as the unknown taxa.

c) For experimental work some taxa are better than others. Plethodontids are very difficult to work with. They court at night, and usually a male courts just once a week. I obtained data on plethodontid species by maintaining many pairs of each species and patiently waiting until some of the pairs courted. Often they never did court, and my list of failures is longer than my list of successes. Experimental work with this family is probably impractical. In contrast, many salamandrids court during the day and are easy to watch. If males are separated from females, they will court as soon as females are introduced. It is relatively easy to stage experiments. Ambystoma are also good subjects for courtship experiments. Males court as soon as they are placed with females.

d) The study of courtship behavior provides unique opportunities for analyzing evolutionary processes. Most studies of reproductive strategies deal with female reproduction and behavior (number of eggs, size of eggs, brooding behavior, etc.). It is important to realize that male behaviors can also be related to reproductive success, and that they can be interpreted as reproductive strategies. Salamanders are especially ideal in this respect. The number of spermatophores deposited per courtship can be taken as an index of the male's reproductive effort per female. In many species the process of insemination can be observed and scored. Consequently the male's reproductive effort can be related to his probability of reproductive success. It is tedious to observe and score each attempt by the female to find a spermatophore and retrieve sperm from it, but we can obtain an index of the male's success by a more simple route. The variability in site of spermatophore deposition is easy to measure (see Fig. 11), and it is directly related to the probability that the female will find a spermatophore. The number of spermatophores deposited per courtship and the variability in site of spermatophore have important evolutionary consequences since they can determine how many offspring a male will leave. How do these variables evolve in relation to the male survivorship, population density, female survivorship and fecundity, and variability in reproductive success from year to year?

e) Male salamanders probably adjust their courtship effort to the likelihood that the female will cooperate and be inseminated, but we have little direct evidence that this is so. I have presented some indirect evidence to support this view in <u>Notophthalmus</u> and a few other genera. I have recently completed a series of experiments with <u>Taricha</u> which confirm this hypothesis (Arnold, 1972). Davis and Twitty (1964) found that female <u>Taricha</u> raise the head just before the male dismounts and deposits a spermatophore. When I anesthesized females and positioned them with the head raised, males deposited more spermatophores than with unrestrained females. When anesthesized females are positioned with the head down, the male clasps them only briefly and does not deposit spermatophores. These results suggest that male <u>Taricha</u> use the position of the female's head as an index of her sexual receptivity. When the female bends her head down, she is saying in effect "No, I will not cooperate and be inseminated". The male then quickly terminates his courtship. When the female raises her head, she says "Yes, I will cooperate and be inseminated". The male then prolongs his courtship and deposits spermatophores. Additional experiments should be performed in which there is an independent assay of female receptivity. For example, how does the male vary his courtship effort with gravid versus spent females? Do males adjust their courtship effort to the number of eggs a female will lay? For example, do males deposit more spermatophores with larger females?

f) Salamander males do not ignore other males which intrude during courtship. Ambystoma males cover the spermatophores of other males with their own spermatopjores. Plethodontid males attack one another. These, and many other behaviors may have evolved to deal with intrusions by other males and thereby enhance the fitness of individual males. These phenomena are very amenable to experimentation, and should be explored.

g. How is reproductive isolation accomplished in salamanders? We know very little about the precise mechanisms. It is common to find several Ambystoma species breeding in the same pond at the same time. How do Ambystoma species recognize conspecifics? In Taricha, males find conspecific females by orienting to pheremones released by the female (Twitty, 1955), but is this the complete story? It probably is not, since males may be found in the field clasping females of other species. Taricha may possess additional mechanisms which prevent insemination once the male clasps the wrong female.

h. Do courtship behaviors in salamanders evolve from non-courtship activities? In some groups of animals courtship behaviors do evolve from non-courtship behaviors (see Tinbergen, 1952 and Hinde, 1966 for reviews), but apparently this is seldom the case in salamanders. In most cases the special behaviors which occur during courtship are clearly derived from the courtships of ancestral salamanders rather than from non-courtship activities. I can think of one possible exception. The peculiar position of the forelimbs which is assumed by male Pleurodeles and Salamandra while clasping the female is identical with the position of the forelimbs during skin-shedding in many other salamandrid genera (Cynops, Notophthalmus, Taricha and Triturus). It is possible that the unique clasping action of

Pleurodeles and Salamandra evolved from the tendency to hook the forelimbs during skin-shedding. A thorough survey of non-courtship activities (eg. fright responses) and detailed comparisons with courtship behavior may yield additional examples of this kind.

i) Very little is known about either the fine structure or the function of the glands employed during courtship. Noble (1929, 1931) referred to these glands as "hedonic", but we still do not know exactly what effect the male's glands have on the female's behavior.

j) Salamander systematists should pay more attention to sexual differences in morphology, since in most cases we know how the males use their special glands and other morphological structures during courtship. It would be profitable to measure the extent and variance of sexual dimorphisms and relate these metrics to other aspects of the life history. For example, are sexual dimorphisms more pronounced in species with short life expectancies (eg. small species)?

APPENDIX I. The mode of fertilization, site of courtship and geographic distribution of Salamander Genera

	Mode of fertilization	Site of courtship	Time of courtship	Larvae	Distribution
Cryptobranchidae					
Cryptobranchus	external	water	?	aquatic	Eastern North America
Andrias	external	water	?	aquatic	China, Japan
Hynobiidae					
Hynobius	external	water	night	aquatic	Asia
Ranodon	external	water	?	aquatic	U.S.S.R.
Ambystomatidae					
Rhyacotriton	internal	terrestrial	night	aquatic	Western North America
Dicamptodon	internal	water	night	aquatic	Western North America
Ambystoma species	internal	water	night	aquatic	North America
Ambystoma opacum	internal	water	night	aquatic*	Eastern North America
Salamandridae					
Taricha	internal	water	day/night	aquatic	Western North America
Notophthalmus	internal	water	day/night	aquatic	Eastern North America
Triturus	internal	water	day/night	aquatic	Europe, Middle East, USSR
Cynops	internal	water	day/night	aquatic	China, Japan, Ryukyu Islands
Paramesotriton	internal	water	day/night	aquatic	China, Dem. Rep. of Vietnam
Neurergus	internal	water	?	aquatic	Turkey, Iran, Iraq
Pleurodeles	internal	water	day/night	aquatic	North Africa, Spain, Portugal
Tylototriton	internal	water	?	aquatic	China, S.E. Asia, Ryukyu Islands
Salamandrina	internal	terrestrial(?)	?	aquatic	Italy
Salamandra	internal	terrestrial	day/night	aquatic**	Europe, N. Africa, Middle East
Chioglossa	internal	terrestrial	night(?)	aquatic	Spain, Portugal
Mertensiella	internal	water	?	aquatic	Turkey, USSR
Euproctus	internal	water	day/night	aquatic	France, Spain, Corsica, Sardinia

* Although the larvae are aquatic, the eggs are laid on land and brooded by the female. In the case of Ambystoma opacum the eggs are later inundated by water as the ponds fill with rain.

** Salamandra salamandra gives birth to aquatic larvae, and S. atra gives birth to transformed young.

Cont/....

APPENDIX I. The mode of fertilization, site of courtship and geographic distribution of Salamander Genera.

Continued

	Mode of fertilization	Site of courtship	Time of courtship	Larvae	Distribution
Plethodontidae					
Pseudotriton	internal	terrestrial	night	aquatic	Eastern North America
Eurycea	internal	terrestrial	night	aquatic	Eastern North America
Hemidactylium	internal	terrestrial	night	aquatic	Eastern North America
Desmognathus	internal	terrestrial	night	aquatic***	Eastern North America
Plethodon	internal	terrestrial	night	terrestrial	North America
Aneides	internal	terrestrial	night	terrestrial	North America
Ensatina	internal	terrestrial	night	terrestrial	Western North America
Pseudoeurycea	internal	terrestrial	night	terrestrial	Mexico, Central America
Bolitoglossa	internal	terrestrial	night	terrestrial	Mexico, Central & S.America
Hydromantes	internal	terrestrial	night	terrestrial	Western N.America, Europe
Proteidae					
Proteus	internal	water	?	aquatic	Europe
Necturus	internal	water	?	aquatic	Eastern North America
Amphiumidae					
Amphiuma	internal	water	night	aquatic*	Eastern North America

* Although the larvae are aquatic, the eggs are laid on land and brooded by the female. In the case of *Ambystoma opacum* the eggs are later inundated by water as the ponds fill with rain.

*** The larvae of one species, *D. wrighti*, transform before hatching from the eggs.

APPENDIX II. Localities for specimens and dates of courtship

Species	Locality	Dates of courtship
Cryptobranchus bishopi	Blair's Bridge, north fork of White River, Ozark Co., Missouri	October
Rhyacotriton olympicus	13 miles up Quinault River from Quinault, Jefferson Co., Washington	April
	Wahkeena Falls State Park, Multnomah Co., Oregon	April
	4 - 4.5 miles up Fall Creek from Highway 34, Lincoln Co., Oregon	April
Ambystoma maculatum	Goss Pond, near Dixboro, Washtenaw Co., Michigan	April
	Edwin S. George Reserve (Univ. Michigan), 4.5 mi. W. Pinckney, Livingston Co., Michigan	April
Ambystoma texanum	Junction Liberty and Zeeb roads, W. Ann Arbor, Washtenaw Co., Michigan	April
Ambystoma opacum	Dickson, Franklin and Humphreys Co. Tennessee	Sept/Oct.
	Colbert Co., Alabama	October
Ambystoma tigrinum	Edwin S. George Reserve (Univ. Michigan), 4.5 mi. W.Pinckney, Livingston Co., Michigan	March/April
Ambystoma mexicanum	Laboratory stock of the Amphibian Facility (G. Nace) University of Michigan	March/April
Ambystoma laterale	Near Whitmore Lake, Livingston Co., Michigan	April
Taricha granulosa	Soap Creek, 10 miles N. Corvallis, Benton Co.,Oregon	March
Taricha torosa	Bollinger Creek, Contra Costa Co., California	March
Notophthalmus viridescens	Goss Pond, near Dixboro, Washtenaw Co., Michigan	April
	Mountain Lake, Giles Co., Virginia	May/June/Sept/Oct/Dec.
Triturus cristatus	Locality unknown, probably southern Europe	March/April/May

Cont/.....

APPENDIX II. Localities for specimens and dates of courtship; continued (i)

Species	Locality	Dates of courtship
Triturus helveticus	Near Luxembourg City, Luxembourg	May
Triturus alpestris	Near Luxembourg City, Luxembourg	May
Triturus vulgaris	Eindhoven, Holland	April
Cynops pyrrhogaster	Hiroshima, Japan	March/April
Paramesotriton hongkongensis	Hong Kong	Oct/November
Pleurodeles waltl	Laboratory stock of the Amphibian Facility (G.Nace), University of Michigan & Wayne State University (J. Taylor). Derived from the stocks of Bagnara and Gallien	January/May
	Northeast Spain	June
Salamandra salamandra	Krefeld, West Germany	April/Sept/May
	Rummelburger Forst, Unterharz, East Germany	April/Sept/May
Euproctus asper	Lescun, Basses-Pyrenées, 1000 m., France	May
Pseudotriton ruber	Highlands, Macon Co., North Carolina	July/September
	Mud Creek, S. side of Whitetop Mtn., 3600-3700ft. Grayson Co., Virginia	July
Eurycea bislineata	Mohigan State Park, Ashland Co., Ohio	October
	West side of Mt. Rodgers, 4800 ft., Grayson and Smyth Co., Virginia	September/October
Desmognathus fuscus	Mohigan State Park, Ashland Co., Ohio	October
Desmognathus ochrophaeus	West side of Mt. Rodgers, 4800 ft., Grayson and Smyth Co., Virginia	October
	Giles Co., Virginia	May
Desmognathus monticola	Giles Co., Virginia	May/September
Desmognathus quadramaculatus	Giles Co., Virginia	August/September

Cont/.....

APPENDIX II. Localities for specimens and dates of courtship; continued (ii)

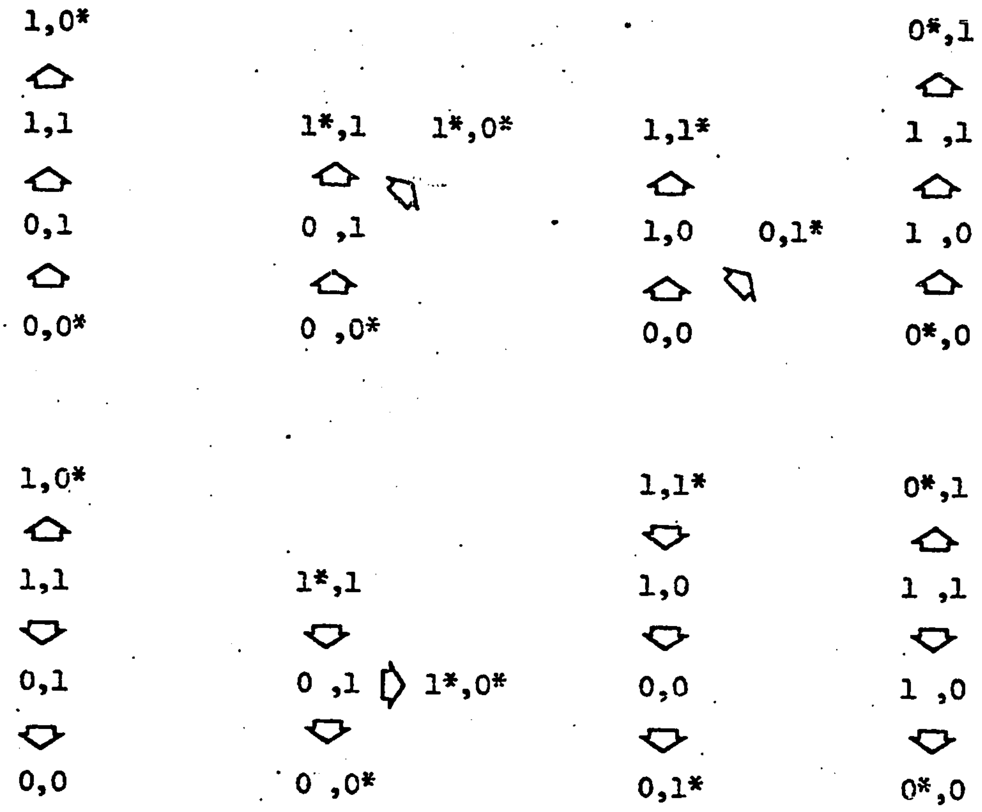
Species	Locality	Dates of courtship
Plethodon cinereus	West side of Mt. Rodgers, 4800 ft., Grayson and Smyth Co., Virginia	October
	Armbrewster's Woods, Ann Arbor, Washtenaw Co., Michigan	October
Plethodon richmondi	South side of Whitetop Mtn., 4000±200 ft., Grayson Co., Virginia	October
Plethodon welleri	West side of Mt. Rodgers, 4800 ft., Grayson and Smyth Co., Virginia	September/October
Plethodon jordani	South side of Whitetop Mtn., 4000±200 ft., Grayson Co., Virginia	August/september
	Standing Indian Recreation Area, 7.0 miles from Hwy 64, Macon Co., North Carolina	August/September
	Highlands, Macon Co., North Carolina	August/September
	Junction Hwy 441 and road to Clingman's Dome Swain Co., North Carolina	August
Plethodon glutinosus	South side of Whitetop Mtn., 4000±200 ft., Grayson Co., Virginia	Aug/Sept/Oct.
	Mountain Lake Biological Station, Giles Co., Virginia	September/October
	Devil's Den State Park, Washington Co., Arkansas	May
	3.0 miles W. junction of Hwy 271 and Hwy 1 on Hwy 1, Winding Stair Mtn., LeFlore Co., Oklahoma	June
Plethodon ouachitae	3.0 miles W. junction of Hwy 271 and Hwy 1 on Hwy 1, Winding Stair Mtn., LeFlore Co., Oklahoma	April/May/June/Aug.
	Junction Hwy 259 and Kiamichi Mtn., Kiamichi Mtn., 2050 ft., LeFlore Co., Oklahoma	April/May
Plethodon yonahlossee	South side of Whitetop Mtn., 4000±200 ft. Grayson Co., Virginia	August/September

Cont/.....

APPENDIX II. Localities for specimens and dates of courtship; continued (iii)

Species	Locality	Dates of courtship
Aneides lugubris	Siesta Valley, Contra Costa Co., California	Jan/Feb/March/April/ Aug/September
Ensatina eschscholtzia	Siesta Valley, Contra Costa Co., California	February
	1.0 miles N. and 1.0 miles E. of Brock Mtn., Shasta Co., California	February
Bolitoglossa subpalmata	Villa Mills and La Georgina, Cerro de la Muerte, Province San Jose, Costa Rica	April/May/June
Bolitglossa flavimembris	Finca Insula, 7.5 km. W and 1.5 km. S. of San Marcos, 2100±50 m., Dept. San Marcos, Duatemala	February

APPENDIX III. Demonstrations of LeQuesne's Theorem



Eight of the many possible hypotheses for the evolution of 4 OTUs with two binary characters (eg. 1,0 represents the OTU with character state 1 for character A and character state 0 for character B). Note that in each case at least one character state had undergone an evolutionary convergence. This will be true of every network which connects these four OTUs. (Convergent similatities in character state are indicated with asterisks in each case. Arrows indicate the direction of evolutionary change).

APPENDIX IV. Wilson's inconsistency test as a special case of LeQuesne's Theorem.

The point of this appendix is to show that Wilson's inconsistency test and LeQuesne's theorem say essentially the same thing, but in different language.

A character's state is considered to be unique and unreversed if it has originated only once during evolution and has not undergone an evolutionary reversal (Wilson, 1965). Wilson considers a character with m character states. In the examples below the character has four states. Each set (A_0, A_1, A_2 and A_3) represents one or more OTUs with a particular combination of character states. For example, in case I the set A_1 represents the OTU with character state 1, and in case II, the intersection of sets A_1 and A_2 represents the OTU with states 1 and 2. Wilson's inconsistency test (Wilson, 1965), states that if the sets overlap and are not completely enclosed in one another, as in case II, the character states are not unique and reversed. If the sets are wholly enclosed in one another, as in case II, the character states are unique and unreversed. If the sets do not overlap or enclose one another, as in case I, the test is inapplicable.

I find Wilson's examples rather confusing because usually characters are not coded so that an organism can simultaneously manifest two or more character states of the same character. Usually characters are coded so that the states of a character are mutually exclusive. If we code Wilson's four-state character as four binary characters, we lose no information, and we find that we can apply LeQuesne's theorem to each of Wilson's three cases. These character transformations and the consequences of LeQuesne's theorem are shown below.

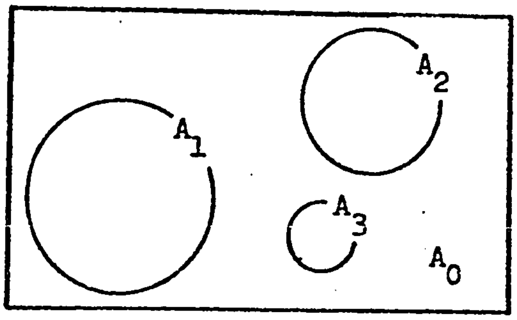
LeQuesne's theorem yields the same results as Wilson's inconsistency test. In cases I and III there are four distinguishable OTUs. All pairs of characters are compatible and consequently LeQuesne's theorem states that there is no evidence for character convergence (ie. the character states are unique and unreversed). In case II there are six distinguishable OTUs. Two character pairs are incompatible. Consequently LeQuesne's theorem states that at least one convergence has occurred during evolution (ie. the character states are not unique and unreversed).

Wilson's inconsistency test may then be regarded as a special case of LeQuesne's theorem for the following reasons. First, a character with more than two states can be recoded as a series of characters, each with two states. Therefore LeQuesne's theorem can be applied in any situation where Wilson's inconsistency test is applicable. Second, Wilson's test deals with an unconventional definition of a character in which character states are not mutually exclusive. Third, LeQuesne's theorem contains a more restricted test for evolutionary convergence. LeQuesne's theorem can tell us that one character of a pair has undergone an evolutionary convergence, whereas Wilson's inconsistency test tells us that somewhere in a multistate character there is a convergent character state. In other words only one pair of characters need be incompatible to demonstrate that character states are not unique and unreversed (ie. in case II only two of Wilson's sets need overlap).

Wilson's inconsistency test as a special case of LeQuesne's Theorem

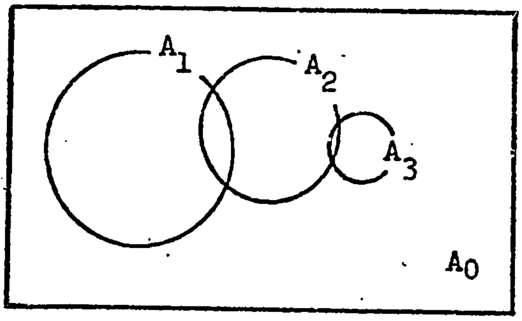
Wilson's inconsistency test:

Case I.



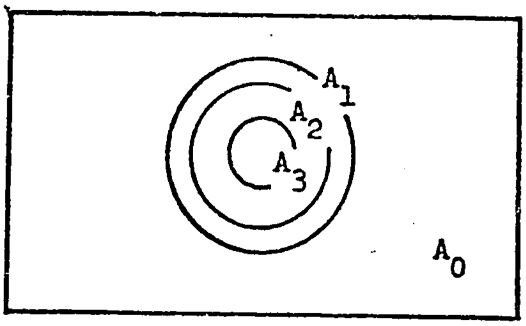
Result: Test not applicable.

Case II.



Result: Character states are not unique and unreversed.

Case III.



Result: The character states are unique and unreversed.

Application of LeQuesne's Theorem:

	character			
OTU	0	1	2	3
a	0	0	0	0
b	0	1	0	0
c	0	0	1	0
d	0	0	0	1

Result: All character pairs are compatible.

	character			
OTU	0	1	2	3
a	0	0	0	0
b	0	1	0	0
c	0	1	1	0
d	0	0	1	0
e	0	0	1	1
f	0	0	0	1

Result: Two character pairs are incompatible (1 with 2, and 2 with 3).

	character			
OTU	0	1	2	3
a	0	0	0	0
b	0	1	1	1
c	0	0	1	1
d	0	0	0	1

Result: All pairs of characters are compatible.

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