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THE EVOLUTION OF COURTSHIP BEHAVIOR IN NEW WORLD SALAMANDERS
WITH SOME COMMENTS ON OLD WORLD SALAMANDRIDS

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Salamander courtship has been the subject of several recent reviews (Joly 1966; Organ and Organ 1968; Salthe 1967; Salthe and Mecham 1974). These reviews introduce the reader to the extensive descriptive literature on salamander courtship and provide some interesting speculations about the phylogeny of sexual behavior. Since macroevolution of salamander courtship has been reviewed recently, I will focus, instead, on the sexual dynamics of populations and on the selective pressures that stabilize and direct the course of behavioral evolution.

Innovation in techniques for sperm transfer and female persuasion are two major themes in the evolution of salamander courtship. Salamanders show a great diversity in modes of sperm transfer and an even greater diversity of behaviors which seem to represent tactics for female persuasion. At least two families (cryptobranchids and hynobiids) practice external fertilization while the remaining families, accounting for about 90% of the extant species, transfer sperm indirectly via spermatophores attached to the substrate. In these species fertilization is internal. Internal fertilization evolved from external fertilization in salamanders (Dunn 1923; Salthe 1967) but the details of this crucial transition are still poorly understood. The present review makes no contribution to this interesting problem. Instead, this paper focuses on species with indirect sperm transfer. Perhaps the most important realization in resolving sexual diversity in these salamanders is that indirect sperm transfer is intrinsically difficult. The failure rate of spermatophores in particular species ranges from about 50-70%. Part of the difficulty is the problem of finding a small sperm-bearing structure placed at some distance from the female. Many

solutions are possible to this intrinsic problem, and the variety of sperm transfer modes in salamanders probably represents a suite of alternative solutions to the problem of spermatophore failure. Other groups with indirect sperm transfer, e.g., terrestrial arthropods, show comparable diversity in modes of transfer (Schaller 1971). The significance of tactics for female persuasion will be discussed in later sections.

Although the major features of courtship evolution in salamanders are known, we are still struggling to understand why this evolution has occurred. We can arrange salamander behaviors in evolutionary series, but the transitions remain a mystery. In most instances we have reached an impasse because we do not understand the function of particular behaviors. While there is a great need for experimental analysis of function, such work is time consuming and only a few taxa will ever be thoroughly analyzed. We need to know where this work should be focused. Comparative studies serve this role by revealing dramatic evolutionary transitions. One of the goals of this review is to point out promising areas for experimental work. Experimental studies can also guide comparative work since important evolutionary transitions may have subtle causes.

There is a considerable body of descriptive work on the courtship of New World salamanders but the record is very incomplete. Courtship behavior for most species has been described only once and often only fragments of courtship are reported. The available reports often lack the detail necessary for comparative purposes; additionally, little attention has been given to temporal and sequential variability in courtship. For many taxa there is no information. We know nothing about courtship in the following genera: Phaeognathus, Leurognathus, Batrachoseps, Lineatriton, Oedipina, Thorius, Parvimolge, Gyrinophilus, Stereochilus, Typhlomolge, Typhlotriton, Haideotriton, Rhyacosiredon, Pseudobranchus and Siren. The published accounts of courtship in Amphiuma (Baker et al. 1947) and Necturus (Bishop 1926) are so incomplete that no meaningful interpretations are possible. In addition, there is still much to be learned about the best known species.

In this review I will focus on a few topics that have yielded promising results and neglect many equally important issues. In particular, I will consider relative rates of behavioral evolution, the use of courtship glands, the sexual resources of males and interactions between sexual rivals, since they raise important evolutionary questions. Consideration of evolutionary rates provides a useful focus. Some aspects of courtship are relatively ancient and conservative. For these aspects long term preservation is the salient issue. Other aspects of courtship evolve rapidly and our attention is directed to the causes of behavioral diversity. The study of courtship glands, a second topic, promises an interpretation of many sexual dimorphisms in morphology as well as of many

otherwise inexplicable courtship activities. Finally, we may be able to generate testable hypotheses for courtship evolution by considering the sexual resources of males and contests between sexual rivals.

RATES OF BEHAVIORAL EVOLUTION

The phyletic distribution of courtship behaviors suggests that some behaviors have had a very conservative evolutionary history, while other behaviors have evolved relatively rapidly. In particular, behaviors directly concerned with sperm transfer seem to evolve slowly, whereas behaviors that occur at the onset of courtship seem prone to relatively rapid evolution. The following sections survey courtship at various taxonomic levels. The supposition guiding this survey is that characters which are constant at a particular taxonomic level have evolved slower than characters which are variable at the same taxonomic level.

Geographic Variation within Species

The only thorough investigations of geographic variation in salamander courtship are Kawamura and Sawada's (1959) and Sawada's (1963) studies of the Asiatic newt Cynops pyrrhogaster. F₁ hybrids among the geographic races of this newt are completely viable (Sawada 1963). Nevertheless, there are sufficient geographic differences in male and female sexual behavior to cause partial or complete sexual isolation between most pairs of races. Males execute a tail-fanning display in front of the female as a precursor to spermatophore deposition. The position assumed by the male during his display and the duration of the display vary geographically. Females show geographic variation in the kind of response given to the male's display (some populations bite the male, while others simply nudge him) and in propensity to respond to various kinds of male display. Matings between newts from different populations fail for a variety of reasons: the female does not respond to the male's display; the male fails to recognize critical cues from the female; the tail-nudging walk, during which sperm transfer is accomplished, is uncoordinated because the partners walk at different speeds; or the female fails to accompany the male during the tail-nudging walk. Sexual coordination within populations of Cynops pyrrhogaster is apparently a consequence of strong selection for male behavior suited to local female behavior and selection for female behavior suited to local male behavior.

Although these preliminary courtship activities show geographic variation in Cynops pyrrhogaster, postures used during sperm transfer do not vary (Sawada 1963).

There are no comparable studies for North American salamanders. Arnold (1976) did not find differences in courtship behavior among four of the geographic isolates of Plethodon jordani recognized by Highton (1970). Geographic variation in courtship has been proposed in each of two Ambystoma species, but both cases are suspect. Licht (1969) observed a clasping behavior in Ambystoma gracile from British Columbia that was not reported in Knudsen's (1960) account of Washington animals and proposed geographic variation as one possible explanation. I recently observed courtship behavior in animals from Knudsen's population and found that individual males used both the clasping posture described by Knudsen and the one described by Licht. Courtship behavior in Ambystoma texanum has been described for animals from Michigan (Arnold 1972); Jackson Co., Illinois (Garton 1972) and McLean Co., Illinois (Wyman 1971). Male clasping of females was observed in the last population but not in the other two. Possible hybridization between A. texanum and A. jeffersonianum is currently being investigated (F. Downs pers. comm.). Since A. jeffersonianum consistently clasps (Uzzell 1964, 1969), while at least some populations of A. texanum do not, the systematics of these two forms must be resolved before a case can be made for geographic variation in A. texanum courtship.

Variation among Congeneric Species

Courtship behavior has been observed in eight species of the genus Plethodon (Arnold 1972, 1976; Organ 1958, 1960a, 1960b): P. caddoensis, P. cinereus, P. glutinosus, P. jordani, P. richmondi, P. ouachitae, P. welleri, and P. yonahlossee. Males of each species execute a unique combination of actions during the initial stages of courtship. These actions include tail undulations, rasping motions with the premaxillary teeth, and a peculiar action of the limbs called "foot dance" (Organ 1958). The process of sperm transfer has been observed in only five of these species (P. jordani, P. glutinosus, P. ouachitae, P. welleri, and P. yonahlossee). In contrast to the diversity of behaviors in the early stages of courtship, sperm transfer is strikingly uniform. Male P. yonahlossee execute a slightly different action while the female retrieves sperm, but the five species seem otherwise identical.

The most pronounced differences among species in the genus Ambystoma are in the presence and mode of clasping. Clasping may be absent (A. annulatum, A. dumerili, A. maculatum, A. opacum, A. talpoideum), males may clasp the female's pectoral region with the forelimbs (A. jeffersonianum, A. laterale, A. macrodactylum), or males may use this same clasping mode and then shuffle forward and clasp with the hindlimbs as in A. gracile (Anderson 1961; Arnold 1972, 1976; Brandon 1970; Noble and Brady 1933; Shoop 1960; Spotila and Beumer 1970; Storez 1969; Uzzell 1969). This genus also shows

modest variation in the mode of sperm transfer. In species with clasping, the female generally follows the male closely during spermatophore deposition and sperm transfer, whereas the female finds spermatophores without closely following the male in some nonclasping species (e.g., A. maculatum, A. opacum).

The genus Triturus shows species differences in the preliminary courtship display (Halliday, this volume). The form of execution of apparently homologous display actions differs among species and, in addition, some species incorporate unique actions into their displays. The nature of transitions between display actions also varies in the genus. Some species revert to the preliminary display between successive spermatophore depositions, but other species do not. In contrast, the postures and actions related to sperm transfer are remarkably constant.

Behaviors Unique to Particular Genera

A peculiar tail-wagging display (Fig. 1) is unique to the monotypic ambystomatid genus Rhyacotriton. The display is performed by sexually active males prior to spermatophore deposition. It may be executed in close proximity to the female or at a distance of several centimeters from her. The function of the display is unknown.

Male Desmognathus execute a unique forelimb action while approaching females during courtship (Organ 1961a, 1961b). Both forelimbs are simultaneously swung forward in an action that resembles the dolphin or butterfly swimming stroke. The action is performed repeatedly as the male creeps towards the female prior to the tail-straddling walk. This forelimb action has been observed in each of the four species of Desmognathus for which

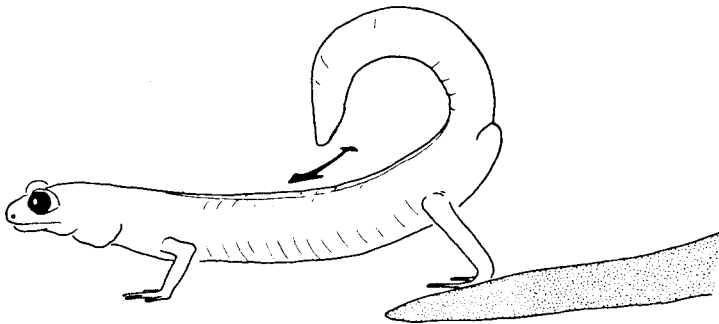


Fig. 1. The tail-wagging display of Rhyacotriton olympicus. The male wags just the tip of his tail. A female is facing away from the male, and only her tail (stippled) is indicated. From a photograph.

courtship observations are available but not in any other plethodontid genus.

Behaviors Unique to Particular Families

Plethodontids engage in a tail-straddling walk (Fig. 2) immediately before spermatophore deposition. This behavior was first observed in *Eurycea bislineata* (Noble 1929) and later reported in a variety of plethodontids (Noble and Brady 1930). Subsequently, tail-straddling walks have been observed in nine genera distributed in both subfamilies and all recognized tribes (Wake 1966) of the family. The behavior is apparently an obligatory precursor to sperm transfer in plethodontids and is not found in any other family. In the one plethodontid for which quantitative information is available, the constancy of male and female positions during the walk is the result of regulatory behavior by the male (Arnold 1976). As a consequence of this behavior, spermatophores are invariably deposited immediately in front of the female's head. The positions assumed by the male and female during sperm pick-up are likewise very uniform in the family Plethodontidae (Fig. 3). A minor variation on this posture is seen in three genera (*Eurycea*, *Ensatina* and *Aneides*). In these genera the male massages the female's sacrum with his tail as she picks up the sperm mass (Stebbins 1949; Arnold 1972).

The wide distribution of the tail-straddling walk among the diverse tribes of plethodontids, and its absence in all other families, indicates that the behavior arose very early in the history of the family. Wake (1966) argued that the divergence of two subfamilies (desmognathines and Plethodontines) occurred in the Mesozoic. Since the tail-straddling walk is found in both subfamilies, this behavioral trait is probably at least 70 million years old.

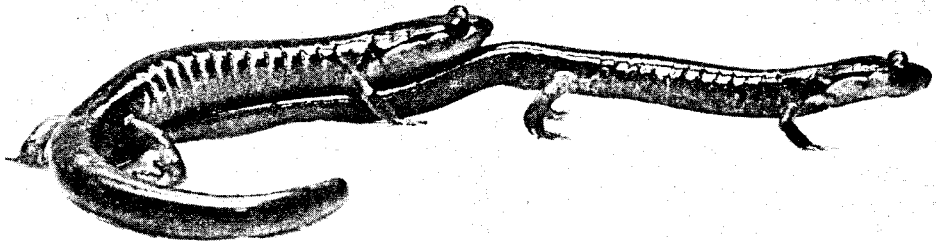


Fig. 2. The tail-straddling walk of *Plethodon jordani*. The female (left) is straddling the male's tail. (From Arnold 1976.) Reproduced with permission of Verlag Paul Parey, Berlin and Hamburg; copyright 1976.

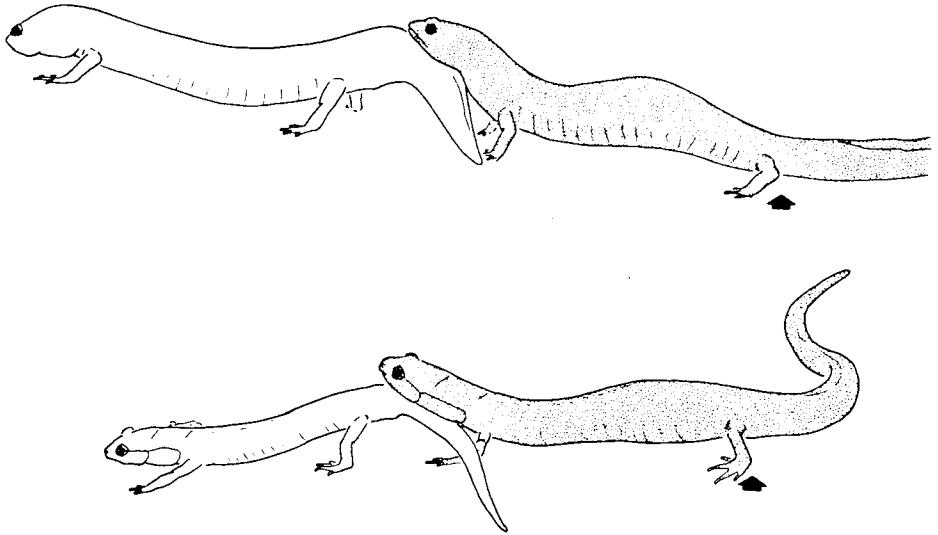


Fig. 3. The postures assumed during sperm pick-up in Pseudotriton ruber (above) and Plethodon jordani (below). In each case the female (stippled) has inserted the male's spermatophore into her cloaca. From photographs.

Salamandrids show a unique behavior during sperm transfer. Males in five genera displace the sacrum laterally in an arc by pivoting about the contralateral forelimb. The action is executed immediately after spermatophore deposition. In Notophthalmus, Taricha and Triturus, the male displaces his sacrum through a 90° arc. The behavior apparently helps the female find the spermatophore, since the male blocks her path at a distance of one body length in front of the spermatophore (Arnold 1972; Halliday 1974b). Male Pleurodeles and Salamandra also displace the sacrum laterally after spermatophore deposition, but the extent of the movement differs from that in the first three genera. In Pleurodeles, the male swings his sacrum through an arc of 180° or more by pivoting about the contralateral forelimb. In Salamandra, the male swings only 45°, and this is accomplished simply by flexing the vertebral column laterally. The effect of lateral displacement of the sacrum is not to block the female's path in these two genera. The Salamandra male holds the female on his dorsum during spermatophore deposition by clasping her forelimbs with his. Lateral displacement of the sacrum allows the female's vent to drop down onto the spermatophore. In Pleurodeles, sperm transfer is accomplished as the pair pivots about interlocked forelimbs while facing each other head to head. Lateral displacement of the sacrum is absent in Cynops and Euproctus. Cynops males march forward on a straight path after spermatophore deposition. Euproctus males embrace the

female during deposition and transfer and pass the spermatophore directly to the female with the hindfeet. Thus lateral displacement of the sacrum after spermatophore deposition is unique to salamandrids but found in only five of the seven genera so far observed.

The peculiar sacral movement of salamandrids is probably very old. Modern Taricha show little osteological modification from their Oligocene ancestor, Paleotaricha (Wake and Özeti 1969). If Triturus and Notophthalmus diverged from Taricha during or before the Oligocene, then the sperm transfer behavior shared by these genera is at least 25 million years old.

Behaviors Shared by Families

Salamanders in four families (ambystomatids, Plethodontids, salamandrids, and the proteid genus Proteus) characteristically deposit spermatophores just in front of the female's snout. In these families the female finds and orients to the spermatophore by touch as she crawls over the spermatophore and it contacts her ventral surface. Spermatophore deposition in front of the female's snout probably represents an adaptive optimum dictated by female behavior. An unrestrained female is most likely to find a spermatophore that is close to her and in her line of travel. Departures from the typical site of spermatophore deposition are of two kinds: (1) In species that restrain the female during spermatophore deposition (Euproctus, Pleurodeles and Salamandra), the site of deposition is stereotyped in each genus but the site varies according to the type of restraint imposed on the female. Euproctus, Pleurodeles and Salamandra have apparently achieved new adaptive optima in deposition site as a consequence of innovations in the ability of the males to restrain females during deposition and sperm transfer; (2) In species that court and deposit spermatophores in polyandrous aggregations (some species of Ambystoma), the site of deposition is highly variable within populations. In such species, competition among males apparently places a premium on rapid deposition and this precludes stereotyped deposition in front of the female's snout (Arnold 1976).

Other aspects of sperm transfer are strikingly similar in plethodontids, ambystomatids, salamandrids and Proteus, suggesting that the basic mechanism of sperm transfer is ancient. The following characteristics, in addition to site of spermatophore deposition, are common to these four families: (1) The spermatophore consists of a gelatinous base, attached to the substrate, and an apical sperm mass; (2) The male faces away from the female during spermatophore deposition; (3) The female orients to glands in the male's cloaca (ambystomatids, Fig. 4; salamandrids and Proteus) or

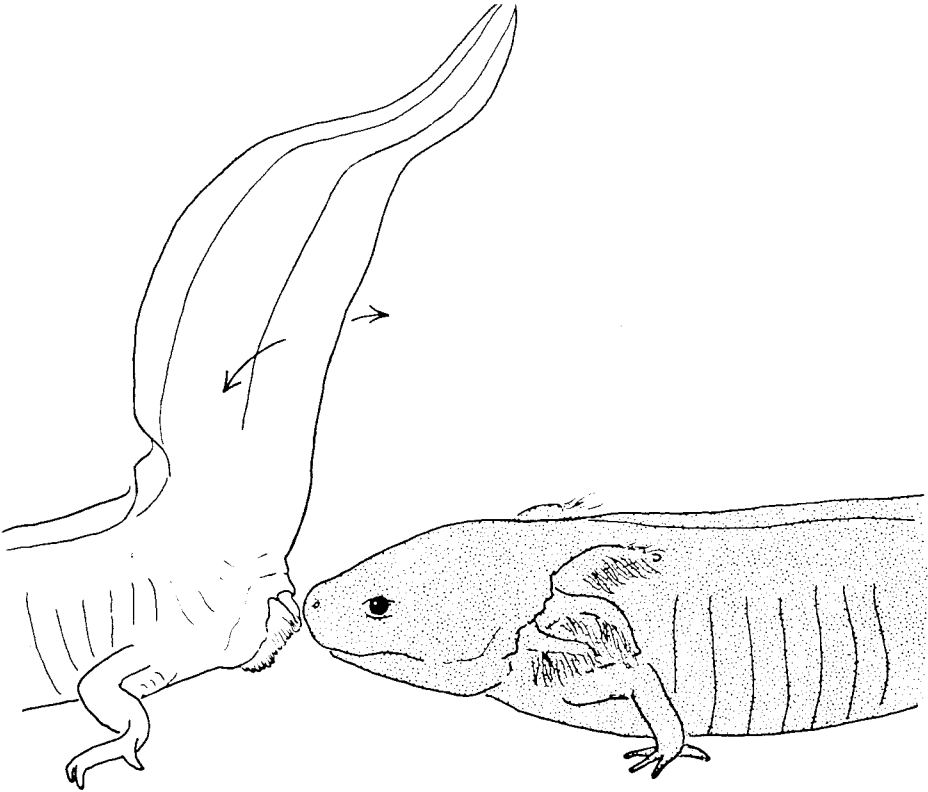


Fig. 4. The tail-nudging walk of *Ambystoma mexicanum*. The male exposes his cloacal papillae by elevating his tail. The female (stippled) nudges these papillae as she follows him during sperm transfer. From a 16 mm movie.

to the dorsum of the male's tail base (plethodontids) just before spermatophore deposition and as the male departs from the spermatophore; (4) The male responds to contact with his cloaca or tail just before and during sperm transfer. Thus the shared syndrome of traits involved with sperm transfer includes the morphology of the spermatophore, the site of deposition, the position assumed by the sexes and the cues used during sperm transfer. Whether one adopts the view that these shared traits are homologous or that two or more families have independently evolved the same syndrome of attributes, one must conclude that behaviors directly concerned with sperm transfer evolve very slowly compared with the preliminary behaviors of courtship.

THE USE OF COURTSHIP GLANDS AND EPIDERMAL SECRETIONS

Exocrine secretions appear to serve three functions during courtship: identification of species and sex, orientation during the locomotory phases of courtship, and persuasion (Tinbergen 1953) of the female prior to spermatophore deposition. None of these supposed functions has been established with conclusive experimentation. Instead the appeal of each function rests on simple observational data and preliminary experimentation. The observational record is, however, extensive enough to reveal promising avenues for critical experimentation.

Identification of Species and Sex

Epidermal secretions may play a role in species and sex identification in ambystomatids and plethodontids, but specialized male courtship glands do not appear to serve these functions. Capacity for sex and species identification has been established for several species by the simple technique of housing males with only conspecific males or with only heterospecific females. Under these conditions, males usually fail to court and deposit spermatophores (Arnold 1976; Noble and Brady 1930). Since in all salamanders the male contacts the female's epidermis with his snout before spermatophore deposition, chemoreception has been proposed as a mechanism for sex and species identification (Arnold 1976; Noble and Brady 1930; Organ and Organ 1968). The case for chemoreception as a major sensory modality for species and sex identification in ambystomatids and plethodontids remains circumstantial, however. Visual cues may also be important for species and sex identification in plethodontids (Organ 1960b; Organ and Organ 1968).

The only direct evidence for chemoreception as a mechanism for sex and species identification in North American salamanders comes from Twitty's (1955, 1961a) work with the salamandered genus Taricha. Twitty (1955) found that male T. rivularis were attracted to sponges soaked with skin secretions from conspecific females, but they ignored control sponges that lacked secretions. In another field experiment, females from four populations (T. rivularis, T. granulosa, T. torosa torosa and T. t. sierrae) were anchored side by side in a stream naturally inhabited by T. rivularis and T. granulosa (Twitty 1961a:454). Native male T. rivularis showed a strong response to conspecific females and female T. t. sierrae and a weak response to T. granulosa and T. t. torosa females. Twitty rarely found T. rivularis males clasping sympatric T. granulosa females in nature (Twitty 1955, 1961a). Twitty and Davis (1964) found that T. rivularis males would occasionally clasp sympatric T. granulosa females if skin secretions from conspecific females were introduced into the aquarium. Such heterospecific clasping was ephemeral and never resulted in complete courtship. Blinded T. rivularis

males were also able to discriminate between conspecific and hetero-specific females. Although chemoreception is strongly implicated in preventing hybridization between T. rivularis and T. granulosa, the precise role of this sensory modality has not been elucidated. Experiments with anosmic males might provide additional clarification. It is not known whether females play any role in species recognition. The problem is particularly interesting since artificially produced hybrids between T. rivularis and T. granulosa are viable and fertile, yet hybridization is very rare in nature (Twitty 1961b).

Cedrini and Fasolo (1971) monitored the olfactory bulb in spinal female Triturus cristatus and reported discrimination between skin secretions from males and females.

Orientation during Courtship

Salamandrids (Cynops, Notophthalmus, Taricha and Triturus), ambystomatids (some Ambystoma spp.) and, apparently, Proteus (Briegleb 1962) engage in a tail-nudging walk before spermatophore deposition. During such walks chemoreception appears to be a major channel of communication to the female. During the walk the male's elevated tail exposes cloacal papillae to the female behind him (Fig. 4). In Triturus these papillae are the exit points of the male's abdominal glands (Zeller 1905), but the identity of comparable papillae in Ambystoma has not been established (Arnold 1976). Delivery of secretions might be accomplished by physical contact, since the female repeatedly nudges the papillae with her snout, or via water currents produced by the male's tail undulations (Noble 1927b). The function of the various cloacal glands has not been tested by behavioral experimentation. Recent electrophysiological studies, however, indicate that extracts of the male's abdominal gland elicit strong responses in the olfactory bulb of female Triturus (Cedrini and Fasolo 1971).

Plethodontid females may orient by chemoreception during the tail-straddling walk that precedes spermatophore deposition. Male Eurycea bislineata possess a glandular bump on the dorsum of the tail base, and the female's snout rests on this bump during the tail-straddling walk (Noble 1929). In most plethodontids there is no visible structure in this region, but histological work might be focused here with profit.

Persuasion

Male salamanders possess a diverse array of epidermal glands that are repeatedly applied to the female during preliminary courtship. Noble (1927a) called these "hedonic" glands, but the name

has long since served its purpose. Whatever function these glands have, we will never know if they are hedonic (pleasure-giving). Since the function of male glands is still unresolved, they should be called "courtship" glands and particular glands should be named in reference to their anatomical position (e.g., mental gland, sub-mandibular gland, genial gland).

The behavioral contexts in which courtship glands are employed provide some clues as to their function. Recent behavioral observations leave the problem of function largely unresolved but they do suggest a priming rather than triggering function for courtship glands. In particular, the contexts in which Notophthalmus use genial glands and plethodontids use mental glands have not been generally recognized so emphasis will be placed on these salamanders.

The use of cephalic glands in salamandrid courtship. Male Notophthalmus possess 3-4 glandular pits on each side of the head posterior to the eye (Cope 1889; Hilton 1902). These glands may be called "genial" glands in reference to their position on the cheek. They are applied to the female's nares as the male clasps her dorsum (Fig. 5). This clasping posture is commonly maintained for 45 minutes or more and during this time the genial glands are repeatedly applied to the female's nares. The complex temporal structure of the clasping display has been recognized since the earliest descriptions of Notophthalmus courtship (Zeller 1890; Jordan 1891; Humphries 1955); additional details were given by Arnold (1972).

The courtship of Notophthalmus presents an enigma that may eventually lead to an elucidation of genial gland function. In some courtships the male never uses his genial glands. Instead, the male deletes the entire clasping display and goes directly to spermatophore deposition and sperm transfer. Such abbreviated courtship occurs if the female actively approaches the male; he will then delete capture and clasping and immediately begin spermatophore deposition (Arnold 1972; Humphries 1955). The male captures the female and subjects her to the lengthy clasping display only if she attempts to escape from him when he first encounters her.

The short-circuit of courtship can be explained, in part, by the results of Rogoff's (1927) experiments to determine the effect of genial gland secretions on the female. In the first experiment, delivery of genial gland secretions to the female was enhanced. Secretion of the glands was increased by injecting males with pilocarpine hydrochloride, and the nares of the female were held against the gland apertures. Such females subsequently followed the male, but control females did not. Delivery of secretions was blocked in two separate experiments by occluding the genial gland apertures of the male and by occluding the female's nares. Both manipulations

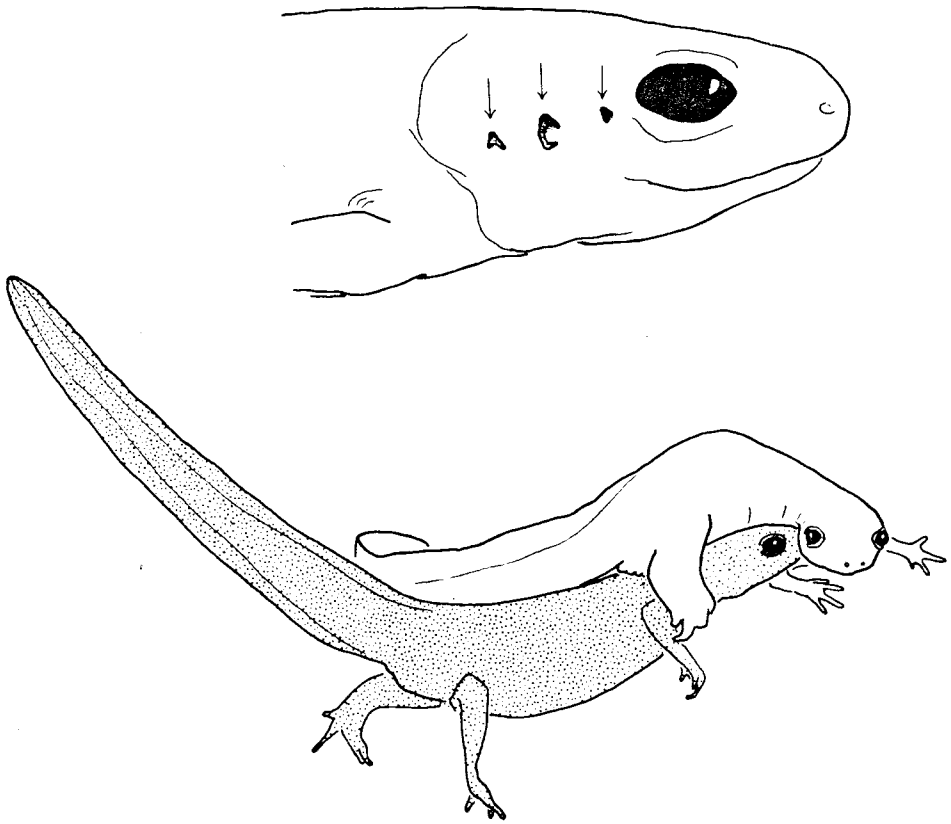


Fig. 5. Application of the male's genial glands during the clasping display of *Notophthalmus viridescens*. The three apertures of the male's genial glands are located on his cheek (above). During the clasping display (below), the male positions the female's head with his forelimb and presses his genial glands against her nares. From FMNH 85546 and a 16 mm movie.

had the same result: the females failed to follow the male. Rogoff's results were reported in a brief note, and the experiments could profitably be repeated. The experiments suggest that genial gland secretions enhance female responsiveness during the tail-nudging walk that precedes spermatophore deposition.

Why is glandular application deleted in some courtships? Perhaps the male adjusts his courtship to the sexual responsiveness of his partner, deleting glandular application if the female already is responsive at the onset of courtship and attempting to make the female responsive by repeated application of his genial glands if she is not. This working hypothesis is complex and a complete test will require several experiments. In particular we suppose that

females differ in sexual responsiveness, and that males can assay and change female sexual responsiveness.

A comparison of Notophthalmus with Taricha presents a new problem. In Notophthalmus, the clasping by the males is facultative, but in Taricha clasping is an obligatory precursor to spermatophore deposition. The basis of this difference is not understood. Male Taricha clasp the female's dorsum with both the forelimbs and hindlimbs. From this position the male repeatedly shifts forward and rubs a submandibular gland over the female's nares (Fig. 6). The duration of the clasping display is even longer than in Notophthalmus and may continue for several hours (Arnold 1972; Davis and Twitty 1964; Smith 1941). During this period the submandibular gland is applied a few times each minute.

The use of mental glands and premaxillary teeth in plethodontid courtship. Male plethodontids develop a disc-shaped protuberance on the chin. This protuberance is called the mental gland (Noble 1929) and is absent in females. The mental gland is composed of a dense cluster of exocrine glands, which release their secretory product on the surface of the chin or mentum. Sever (1976) recently reviewed the histology of these glands. The secretory product appears to be a glyco- or mucoprotein (Lanza 1959; Sever 1975). The relative development of the gland corresponds to courtship season. In seasonal breeders, the gland hypertrophies during the courtship season, but in aseasonal breeders the gland remains in a constant state of development (Houck, this volume). Development and maintenance of the gland is apparently mediated by gonadal hormones. Testosterone injection can induce mental gland development in female Eurycea quadridigitata in just a few weeks (Sever 1976).

A Dunn (1926) pointed out, some plethodontids have extraordinary premaxillary teeth, which protrude forward in males and actually pierce the lip (Fig. 7). The morphology and development of

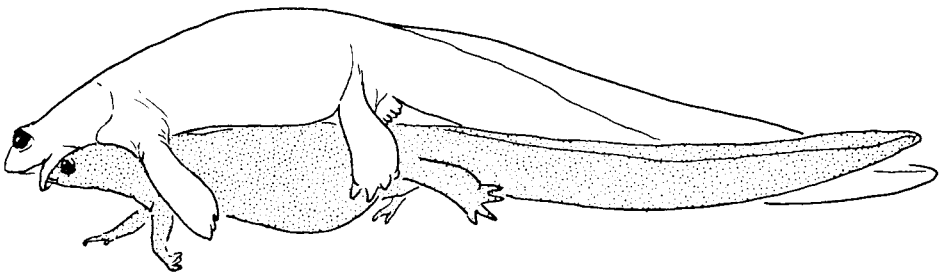


Fig. 6. A male Taricha granulosa (above) rubbing his submandibular gland on the female's snout. From a 16 mm movie.

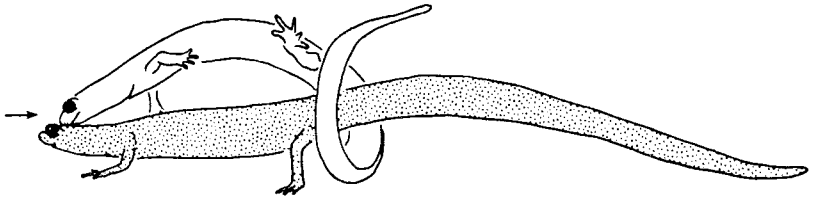
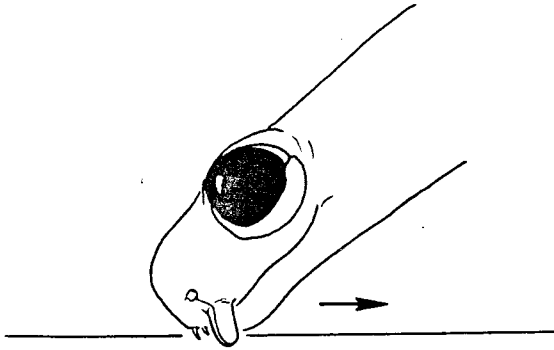
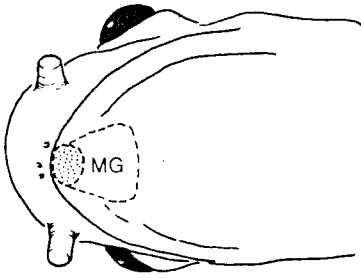


Fig. 7. Delivery of mental gland secretions in Eurycea bislineata. The male's premaxillary teeth pierce his lip (upper figure). The approximate extent of the mental gland (MG) is indicated with a dotted line. The region of secretory release is indicated with stippling. During courtship (middle and lower figures) the male appears to introduce mental gland secretions into the female's circulation by abrading her skin with his premaxillary teeth. In the lower figures, the male has just pulled his premaxillary teeth and mental gland over the female's head in the direction indicated by the arrow. From FMNH 90632 and a 16 mm movie of a pair courting underwater.

premaxillary teeth has been studied in two sexually dimorphic genera (Desmognathus and Eurycea). Adult males differ from females in kind and number of premaxillary teeth (Noble 1929; Noble and Pope 1928; Stewart 1958). The male's teeth are monocuspid rather than bicuspid as in females. They are longer in males and protrude anteriorly to the symphysis of the lower jaw, sometimes piercing the lip. Eurycea bislineata males show a seasonal replacement of premaxillary teeth; the specialized monocuspid teeth are maintained only during the winter courtship season (Stewart 1958). Adult male E. bislineata have fewer premaxillary teeth than females or immature males (Stewart 1958). Sexual dimorphism in premaxillary teeth is apparently mediated by gonadal hormones. The specialized teeth of Desmognathus are replaced by bicuspid teeth in castrated males, and ovariectomized females grow male teeth when impanted with testes (Noble and Pope 1929). When female Eurycea quadridigitata are injected with testosterone ethanate, they develop protruding premaxillary teeth as well as mental glands and nasolabial cirri (Sever 1976 and pers. comm.).

In some plethodontids, males appear to deliver mental gland secretions by "vaccinating" the female with the premaxillary teeth (Fig. 7). This function for premaxillary teeth was first proposed by Organ (1961a). During courtship Desmognathus males press the mental gland against the female's dorsum and then fling themselves away from the female in a snapping motion. Organ (1961a) proposed that the premaxillary teeth abrade the female's skin during this snapping action, and that mental gland secretions are introduced directly into her superficial circulation. The morphology of the male's snout certainly suggests this interpretation. The Desmognathus mental gland is situated on a platform anterior to the mandibular symphysis (Organ 1961; Sever 1976). Since the male moves posteriorly during the snapping action his mental gland will rub the female's dorsum and the protruding premaxillary teeth might immediately abrade the same site. The male arches his head downward at the onset of snapping, sometimes lifting his forefeet off the substrate, so that only his mentum and premaxilla touch the female. The positioning probably would enhance the proposed effect. The snapping action that Organ (1961a) observed in Desmognathus apparently is widespread in plethodontids. I have observed a similar action in Eurycea bislineata, Plethodon cinereus, P. richmondi, Bolitoglossa flavimembris, B. occidentalis, and B. subpalmata as well as in Desmognathus fuscus and D. monticola. Salthe and Salthe (1964:574) observed this action in Pseudoeurycea belli. In Bolitoglossa occidentalis females, scratches could be observed on the dorsum of the trunk after courtship, but in other species scratches were not visible to the unaided eye. A second action, similar to snapping, may also have the effect of "vaccinating" females with mental gland secretions. In this action, which may be called "pulling," the male applies his mentum to the female's dorsum in a

succession of quick strokes without lifting his head from her body. A male Eurycea bislineata in the act of pulling is illustrated in Fig. 7. Pulling has been observed in the same species that employ snapping, as well as in Aneides lugubris and Hydromantes platycephalus; in male Hydromantes the maxillary as well as premaxillary teeth protrude. All of these species have protruding premaxillary teeth and mental glands; snapping and pulling were not observed in species that lack mental glands and protruding premaxillary teeth (Pseudotriton ruber and Ensatina eschscholtzi). Both actions are usually performed with the male perpendicular to the female, but occasionally they are executed with the male parallel to and on top of the female (Fig. 7). Both actions may be executed anywhere on the female's dorsum but most commonly on the female's trunk. Snapping may occur during preliminary courtship as well as during the tail-straddling walk, but pulling was observed only in the former context. The male performs snapping during the tail-straddling walk by turning back towards the female and applying his mentum to her dorsum. Females sometimes react to snapping or pulling by arching the back or by bolting forward slightly, but snapping is often executed without disrupting the tail-straddling walk.

Some species deliver mental gland secretions by slapping the mental gland on the female's snout (Fig. 8). This mode of application has been observed only in large species of the genus Plethodon (P. jordani, P. glutinosus, and P. yonahlossee; Arnold 1976; Organ 1960a). Arnold (1976) gave a complete account of the action in Plethodon jordani. Presumably the mental gland secretions are taken in through the nares, perhaps via the nasolabial grooves. Species of Plethodon exploit one or the other of the two different modes for delivery of mental gland secretions. Variations in mental glands and premaxillary teeth in this genus coincide with the two delivery modes. Species that employ the snapping and pulling modes (P. cinereus and P. richmondi) have relatively small mental glands situated forward on the mentum just behind the mandibular symphysis and the protruding premaxillary teeth. The premaxillary teeth of these species are specialized; the anterior cusp is recurved (Highton 1962; Noble 1927a) and ideally suited for a rasping function. Species that slap the mental gland on the female's snout have relatively large mental glands situated near the center of the chin (Fig. 8). The premaxillary teeth are simple (Highton 1962) and do not protrude.

In light of the fact that premaxillary teeth are used in conjunction with the mental gland during courtship, it is not surprising that the premaxillary teeth act as a unit separate from the maxillary teeth during ontogeny (Noble 1927a). Many curious features of premaxillary tooth morphology will probably be understood as our knowledge of plethodontid courtship increases. The most extreme condition is seen in the genus Oedipina (Wake 1966). In species

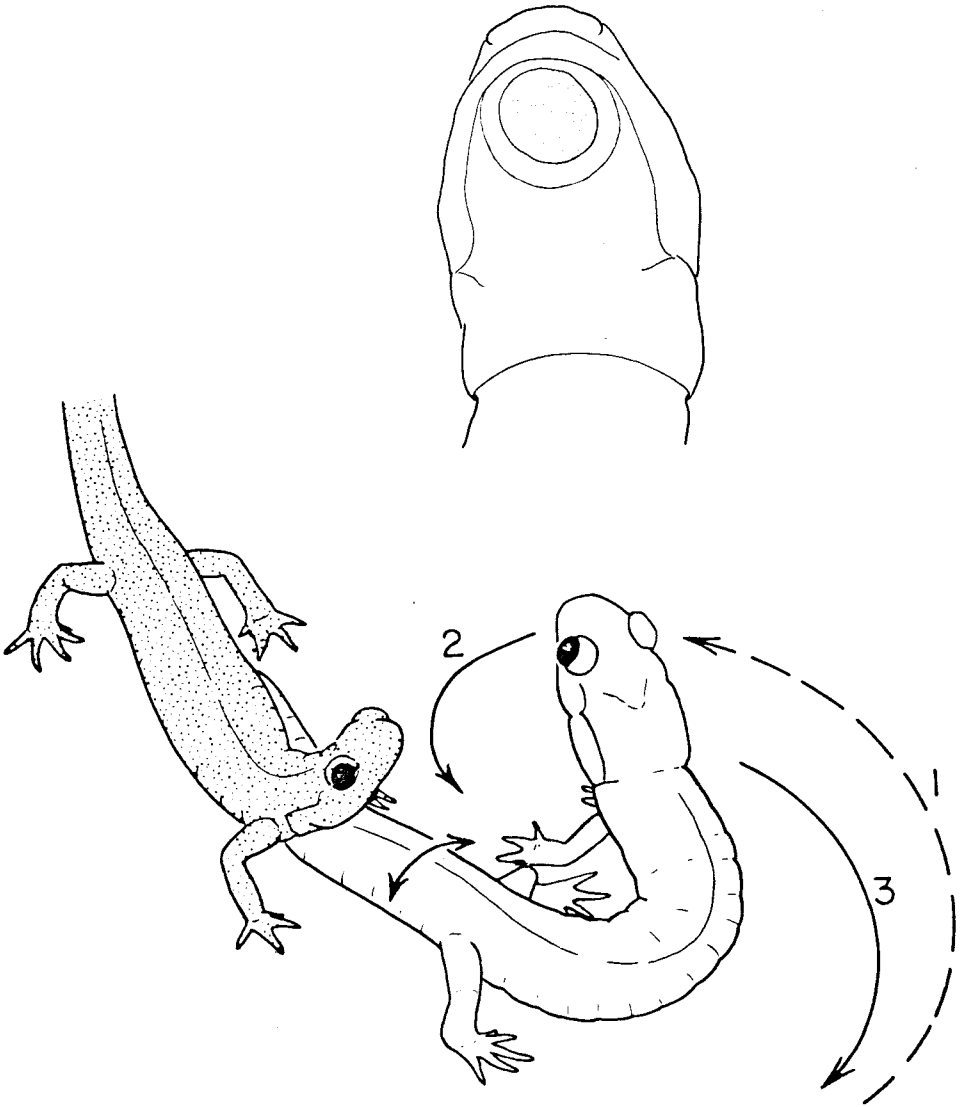


Fig. 8. Delivery of mental gland secretions in Plethodon jordani. The male has a large disc-shaped mental gland on his chin (above). The region of secretory release is indicated with stippling. During the tail-straddling walk (below), the male slaps his mental gland on the female's nares. From FMNH 47748 and a photograph of a courting pair.

such as O. carablanca and O. elongatus, maxillary teeth are completely lacking, but males retain two premaxillary teeth that

protrude and pierce the lip (Brame 1968). In other species (*O. parvipes*) the pars dentalis of the premaxilla is so reduced that it houses only a single tooth (Wake 1966), while a few maxillary teeth are retained (Brame 1968). Is the retention of a single premaxillary tooth in *O. parvipes* related to its utility in courtship?

While it is clear that mental gland secretions are delivered to the female during courtship, the function of these secretions remains an open question. The context in which the mental gland is used suggests that its secretions have a priming effect on the female. Extensive courtship observations are available for only one plethodontid species, *Plethodon jordani*. During some courtships the male repeatedly slaps his mental gland on the female's head during a prolonged tail-straddling walk. In other courtships the tail-straddling walk is brief and slapping never occurs (Arnold 1976). Such courtship variability may reflect male response to differences in female receptivity. The pattern of repeated delivery of secretions to the female suggests that the secretion primes rather than triggers sexual responsiveness. Salthe and Salthe (1958) offer an alternate hypothesis. They suggest that mental gland application in *Pseudoeurycea belli* simply tests the receptivity of the female. Many other interpretations are possible. Mental gland secretions may be needed to induce ovulation in some females, for example. There is an obvious need for physiological studies of the effects of mental gland secretions. We need to know whether mental gland secretions increase the probability that the female will respond to the male's spermatophore.

THE SEXUAL RESOURCES OF THE MALE

One of the most important points to emerge from recent quantitative studies of salamander courtship is that male sexual resources are limited (Arnold 1976; Halliday 1976). This observation sets the stage for a new round of inquiry into the phenomenon of courtship evolution. If the male's sexual resources limit his genic representation in the next generation, then alternative patterns for the distribution of sexual resources could have profound effects on male reproductive success. For example, should the male expend his entire spermatophore supply early in the courtship season with a few females, or should he conserve spermatophores and court for a longer time? The problem is one of distribution.

Our goal is a testable theory for the distribution of sexual resources. There is not enough information, at present, to formalize a general theory, but we can characterize the task of the theory. The theory should make predictions about measurable variables that show dramatic variability across taxa. Furthermore, the variables should have a direct relation to fitness. Some aspects of courtship are easily measured, have a direct relation to particular components

of male fitness, and differ among salamander taxa. From these standpoints, the most promising variables for a theory to work on are: (1) the male's temporal investment per spermatophore, (2) the number of spermatophores deposited per courtship, and (3) the temporal distribution of spermatophores among courtships. The following sections simply point out the need for a theory by surveying taxonomic differences in these variables. I will also sketch the outline of a theory by offering some preliminary interpretations of courtship differences.

Number of Spermatophores per Courtship

This aspect of courtship is rather uniform within families but strikingly different among families. For example, one spermatophore per courtship is an almost invariant rule in plethodontids. In Plethodon jordani one spermatophore was deposited in each of 49 courtships, and two were deposited in two courtships (Arnold 1976). A few courtships with spermatophore deposition have been observed in 17 other species of plethodontids and these provide no exceptions to the P. jordani pattern (Organ 1960a, 1960b, 1961a, 1961b; Stebbins 1949). In my own observations of Pseudotriton, Eurycea, Desmognathus, Plethodon, Aneides, Ensatina, Chiropterotriton, Pseudoeurycea, and Bolitoglossa, one spermatophore was the rule, two spermatophores were rare, and three spermatophores were never deposited in a single night. The deposition of a second spermatophore does not seem to depend on the success of the first spermatophore as Organ and Organ (1968) suggest. In many instances Plethodon jordani males terminated courtship after a single spermatophore deposition even though the spermatophore failed to inseminate the female (Arnold 1976).

In contrast to plethodontids, ambystomatid males are very fecund. A male Ambystoma maculatum can deposit 81 spermatophores in a single evening with one female. Determinations of spermatophore production by a single male courting a single female for one night are available for five species of Ambystoma (Table 1). Species means range from 12 to 40 spermatophores per night. Dicamptodon males also deposit numerous spermatophores per night of courtship (R. Nussbaum, pers. comm.). In contrast, Rhyacotriton males deposit only 1-3 spermatophores per night of courtship (Arnold 1972).

Salamandrids deposit relatively few spermatophores in a courtship, but more than plethodontids. Quantitative studies of Triturus yield a range of 1-4 spermatophores per courtship (Halliday 1974). Halliday's thorough studies of factors affecting spermatophore number per courtship in Triturus are discussed elsewhere in this volume. Literature reports for Euproctus, Notophthalmus, Cynops, and

Table 1. Number of Spermatophores Deposited by Ambystoma Males during a Single Evening of Courtship with One Female.

Species	Mean	Standard Deviation	Range	Sample Size	Reference
<u>A. maculatum</u>	40.4	18.8	10-81	29	Arnold (1976)
<u>A. tigrinum</u>	20.6	6.4	8-37	32	Arnold (1976)
<u>A. dumerili</u>	13.0	2.9	9-16	4	Brandon (1970)
<u>A. laterale</u> ¹	19.3		1-32	4	Uzzell (1969)
	23.6	9.2	13-34	9	pers. observ.
<u>A. jeffersonianum</u>	12.4		6-21	8	Uzzell (1969)

¹The two estimates for this species are both based on animals from Livingston Co., Michigan.

Salamandra, as well as my own meager records for Salamandra and Pleurodeles, all fall in the range of 1-4 spermatophores per courtship (Bedriaga 1882a; Dähne 1926; Despax 1923; Häfeli 1971; Jordan 1891; Kawamura and Sawada 1959; Sawada 1963; Tsutsui 1931; and Zeller 1890). Gallien (1953), however, reported a maximum of 6-7 spermatophores for Pleurodeles waltli, and I have one record of five successive spermatophore depositions for Cynops pyrrhogaster. I intercepted Notophthalmus viridescens adults as they migrated to a breeding pond in early spring; consequently none of the males had courted. The mean number of spermatophores per courtship was 3.8 (standard deviation = 1.8, mode = 3, range = 1-8, n = 18 males). Thus, maximum daily spermatophore production by salamandrids is less than the mean production by Ambystoma.

Courtship Investment per Spermatophore

Males invest courtship time, metabolic energy and materials in each spermatophore. Courtship time is the easiest aspect of investment to measure and, given our current knowledge, the most suitable for taxonomic comparison. Courtship time per spermatophore, not the actual time for deposition, can be estimated by dividing the total time elapsed for a series of courtships by the total number of spermatophore depositions. The energetic investment in the spermatophore itself could be estimated by dry weight or, better yet, by bomb calorimetry. No such determinations are available for any salamander. Although courtship time is only part of the male's spermatophore investment, this variable shows considerable variation among salamander taxa.

Plethodontids invest a surprising amount of courtship time in each spermatophore. A sample of 60 courtships by Plethodon jordani yields an estimate of 56 minutes of courtship per spermatophore (Arnold 1976). Less extensive observations on other plethodontids suggest that this is not an exceptional estimate. Indeed, some plethodontids appear to make much larger temporal investments: in Ensatina the tail-straddling walk alone may last for 5-6 hours (Arnold 1972; Stebbins 1949).

Ambystomatid males invest a small amount of time in each spermatophore. Ambystoma maculatum invest 1.4 minutes and A. tigrinum 4.5 minutes per spermatophore (Arnold 1976). Ambystoma dumerili (Brandon 1970), A. opacum, A. laterale, A. texanum, A. mexicanum and A. gracile appear to deposit spermatophores at comparable rates. None of the Ambystoma species so far observed spend as much courtship time per spermatophore as plethodontids, but species that insert a tail-nudging walk between spermatophore depositions (A. tigrinum, A. dumerili, A. mexicanum, A. laterale) spend more time per spermatophore than species that lack a tail-nudging walk (A. maculatum, A. opacum and A. texanum).

The diversity of temporal structure in salamandrid courtship thwarts any simple comparison with plethodontids and ambystomatids. Salamandrid species differ in the kinds of courtship actions that are intercalated between spermatophore depositions. Species that intercalate more actions between successive spermatophores take a longer time but the actual durations of these actions have been timed only in the genus Triturus (Halliday 1974, 1976). The following discussion will simply focus on the sequence diversity in the family.

Most salamandrid males execute a display as a preliminary courtship activity before any spermatophores are deposited. During such displays glandular secretions from the male's cloaca or head are delivered in a variety of ways. The male may execute his display while clasping the female or while stationed in front of her. Some species intercalate this same display, or parts of it, between successive spermatophore depositions, but other species simply deposit successive spermatophores without repeating the preliminary courtship display. The preliminary displays of Cynops, Notophthalmus, and Triturus share many behavioral components and are probably homologous (Arnold 1972). The diversity of actions performed between successive spermatophore depositions increases in the series Cynops, Notophthalmus, and Triturus. Cynops males deposit spermatophores in rapid succession while marching forward in a straight line. Notophthalmus males execute a lateral displacement of the sacrum between spermatophore depositions and consequently the interval between spermatophore depositions is longer than in Cynops. In Triturus this same action is executed (called "creep on"; Halliday 1974),

but, in addition, various components of the preliminary display (retreat and static displays) may be inserted between spermatophore depositions (Halliday, this volume). Taricha and Salamandra perform the preliminary display while clasping the female (Davis and Twitty 1964; Häfeli 1971; Joly 1966). Both genera repeat the clasping display between spermatophore depositions. Salamandra salamandra males actually release and recapture the female between successive spermatophore depositions despite the fact that the male does not release the female during sperm transfer (Arnold 1972). The simplest temporal structure in the family, that of Cynops, is comparable to the most elaborate structure in the ambystomatid genus Ambystoma, as in A. tigrinum.

A relationship between courtship investment and spermatophore success is important because it would help explain the otherwise perplexing elaborateness of salamander courtship. Elaborate, time-consuming courtship may be adaptive because it promotes the success of the male's spermatophores. Spermatophores can fail to inseminate the female for a variety of reasons: the female may have no interest in the spermatophore, the female may be interested but simply fails to find it, or she may find it but then fumble her attempt to retrieve sperm. An elaborate courtship can guard against these kinds of failure by diagnosing the female's interest before spermatophore deposition (and hence eliminating spermatophore deposition with nonresponsive females), by enhancing the female's responsiveness with courtship glands, and by coordinating locomotion during the sperm transfer process. The best test would relate particular kinds of failure to particular deficiencies in male courtship, and it should be conducted with a single population of salamanders. Although the ideal test has not been made, we can relate differences in spermatophore failure to courtship differences in two congeneric salamanders. Ambystoma species with simple, rapid courtship seem to have low success with each spermatophore because spermatophore placement is haphazard (Arnold 1976). Ambystoma maculatum males hardly pause between spermatophore depositions and place their spermatophores in a great diversity of sites. The male does not orient the female during spermatophore discovery, and the probability of the female finding a particular spermatophore is correspondingly low. In species with a tail-nudging walk such as A. tigrinum, there is much less variability in deposition site, and the female is more likely to find the spermatophore (Fig. 9).

Courtship investment per spermatophore may affect the probability of sperm transfer during a courtship. Species with greater investments per spermatophore seem to have a higher success rate per spermatophore. The available data are presented in Fig. 9. There is a suggestion of a trend in these data; it will be interesting to see if the relationship persists in the face of additional information.

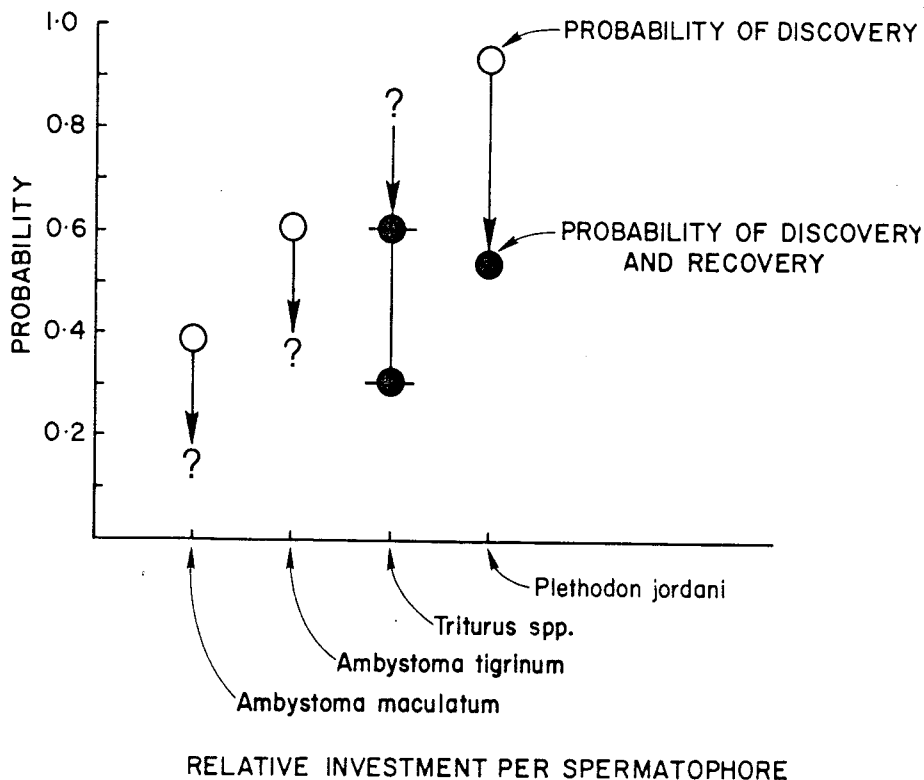


Fig. 9. The success of individual spermatoophores as a function of the male's relative investment per spermatoophore. Data on the probability of discovery by the female and the probability of sperm mass recovery were taken from Arnold (1976) and Halliday (1972). The range indicated for *Triturus* is for three species studied by Halliday.

For the moment we can consider only six species in three genera. The relative spermatoophore investments of these species were ordered by the following considerations. *Ambystoma tigrinum* males spend more time per spermatoophore than *A. maculatum* because they insert a tail-nudging walk between spermatoophores. *Triturus* males intercalate parts of their preliminary display, as well as a tail-nudging walk, between spermatoophore depositions. *Plethodon jordani* males engage the female in a very lengthy tail-straddling walk before spermatoophore deposition. The same kind of relationship emerges from detailed studies of particular *Triturus* species (Halliday 1974). Spermatoophores deposited in the later sequences of courtship, and hence after more courtship has been expended, are more successful.

The Total Spermatophore Supply and Its Distribution

The male's total spermatophore supply and his potential for daily production can be determined by the simple expedient of exposing him to a succession of females (Arnold 1976) or by inducing spermatophore depositions on successive days with artificial females (Halliday 1976). Three such determinations are graphed together in Fig. 10. The total spermatophore supply can be estimated for two species, but the sample sizes are very small in each case. The average total supply for five *Ambystoma maculatum* males was 77.0 spermatophores (standard deviation = 39.3, range = 28-137; Arnold 1976), and the average for five *Triturus vulgaris* males was 47.8 (standard deviation = 16.6, range = 27-73; Halliday 1976). Both of these are probably underestimates since the *Ambystoma* males were

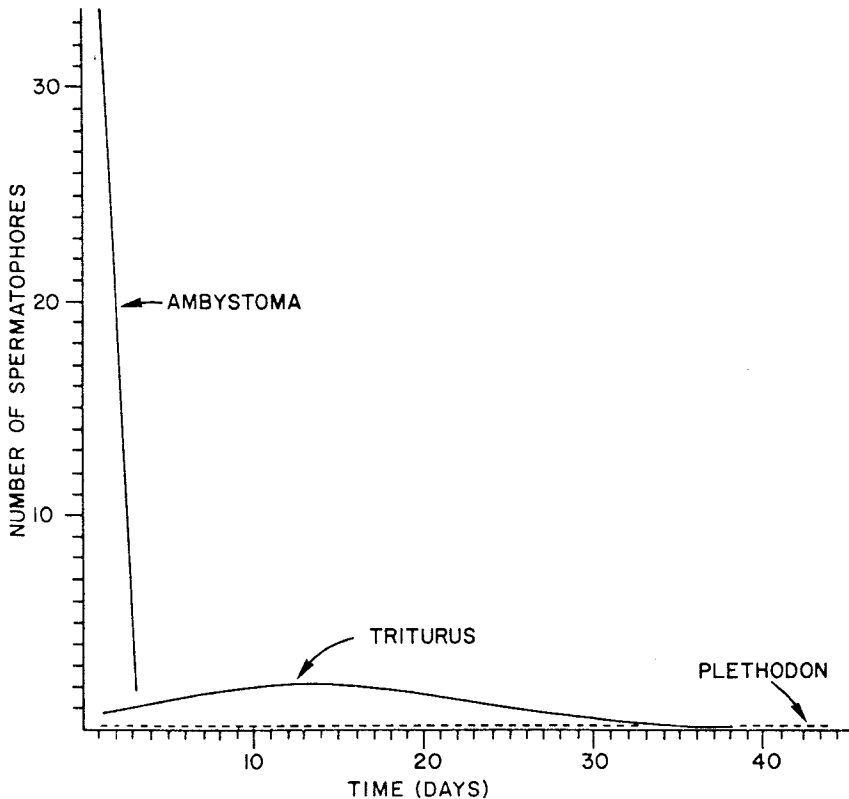


Fig. 10. Spermatophore production on successive days in three salamander genera. Data on *A. maculatum* and *P. jordani* are from Arnold (1976), and data on *T. vulgaris* are from Halliday (1976).

allowed to court virgin females for only three successive nights, and the Triturus males may have expended some of their supply in nature. The total supply of Plethodon jordani males could not be estimated for the latter reason. We will need many more determinations in order to detect individual, population, specific and generic differences in total spermatophore supply.

The finite spermatophore supply is distributed in very different ways by different genera (Fig. 10). The supply can be expended by depositing numerous spermatophores in a few nights of courtship as in Ambystoma, by depositing a few spermatophores each day for a few weeks as in Triturus, or by depositing one spermatophore each week for several weeks as in Plethodon. The particular pattern of distribution is probably related to the length of the courtship season. In Ambystoma there is a premium on early insemination of females during a short courtship season but, in Plethodon, females do not oviposit until well after the courtship season begins, and the period of active courtship lasts for several weeks (Arnold 1976). Thus the timing of oviposition in relation to courtship, and climatic constraints on the length of the courtship season, may have profound effects on the evolution of spermatophore distribution. If the courtship season is long, selection may favor males that conserve spermatophores and are thereby capable of inseminating females encountered late in the season. If the courtship season is short, selection may favor males that expend all of their spermatophores on the first few females they encounter; conservation is pointless.

INTERACTIONS BETWEEN RIVAL MALES

Competition between male salamanders for mating success is a neglected topic. Competition between males in nature has long been known (Blanchard 1930; Breder 1927; Ritter 1897; Tsutsui 1931), but the tactics employed during such competition can usually be appreciated only in the laboratory where close observation is possible. Only a few taxa have been observed closely, but even these present a surprising array of tactics. Interactions between rival males are fascinating in their own right, but they could also have a great impact on the evolution of courtship. The full extent of this impact, however, is unknown.

Contests between rivals are not trivial if sexual success is limited by the other sex. The relative sexual success of a contestant depends both on the success of rivals and on the individual's success. A particular behavior may evolve because it depresses the success of rivals or because it directly promotes sexual success. Contests between rivals for mating success have two components: an offensive component, "sexual interference," and a defensive component, "sexual defense" (Arnold 1976). In the ideal case, sexual

interference depresses the sexual fitness of rivals by active usurpation of mating success. Sexual defense depresses the rival's success by defense of a limiting sexual resources such as a female.

Sexual interference and sexual defense take a variety of forms in salamanders (Arnold 1976). Sexual interference can be accomplished by stealing a female, disrupting the spermatophore depositions of rivals, by covering the spermatophores of rivals, or by duping rivals into unprofitable spermatophore depositions. Sexual defense can be accomplished by transporting females away from rivals or by chasing rivals away from females. Competition has been observed among ambystomatid and plethodontid males (Arnold 1976; Organ 1958, 1960a, 1960b, 1961a; Storez 1969) and in the salamandrid genera Taricha and Pleurodeles (also see Joly 1966, for remarks on Salamandra).

Interactions between Ambystomatid Males

Ambystoma maculatum males actively cover the spermatophores of rivals (Fig. 11). This behavior has an important consequence: the rival's sperm are rendered inaccessible to the female (Fig. 12). A male courting a female in the absence of rivals will also cover his own spermatophores. Is this behavior nonadaptive? Probably not, if we consider the typical social context for courtship in this species. A. maculatum usually court in polyandrous aggregations: as many as 10-50 males may simultaneously vie for representation in the female's spermatheca. A male will cover any spermatophore he encounters in such aggregations, and, because of the abundance of rivals, he is more likely to encounter a rival's spermatophore than his own. One might suppose that spermatophore covering is advantageous only if the rival's spermatophores outnumber the male's spermatophores, but Arnold (1976) showed that spermatophore covering is advantageous regardless of relative abundance so long as at least one rival spermatophore is present. Thus spermatophore covering is an evolutionarily stable strategy in the sense of Maynard Smith (1974). The trait is advantageous when covering males are in low frequency, and a population of covering males cannot be invaded by males that do not cover. The universality of spermatophore covering in the genus Ambystoma coincides with this theoretical prediction. Multiple spermatophores have been reported in almost every Ambystoma species studied so far: A. annulatum (Spotila and Beumer 1970), A. jeffersonianum (Uzzell 1969), my observations on A. opacum, A. maculatum, A. tigrinum, A. laterale, A. macrodactylum, A. gracile, A. texanum, A. mexicanum; as well as literature reports for these species (Gascó 1881; Noble and Brady 1933; Smith 1911; Uzzell 1969).

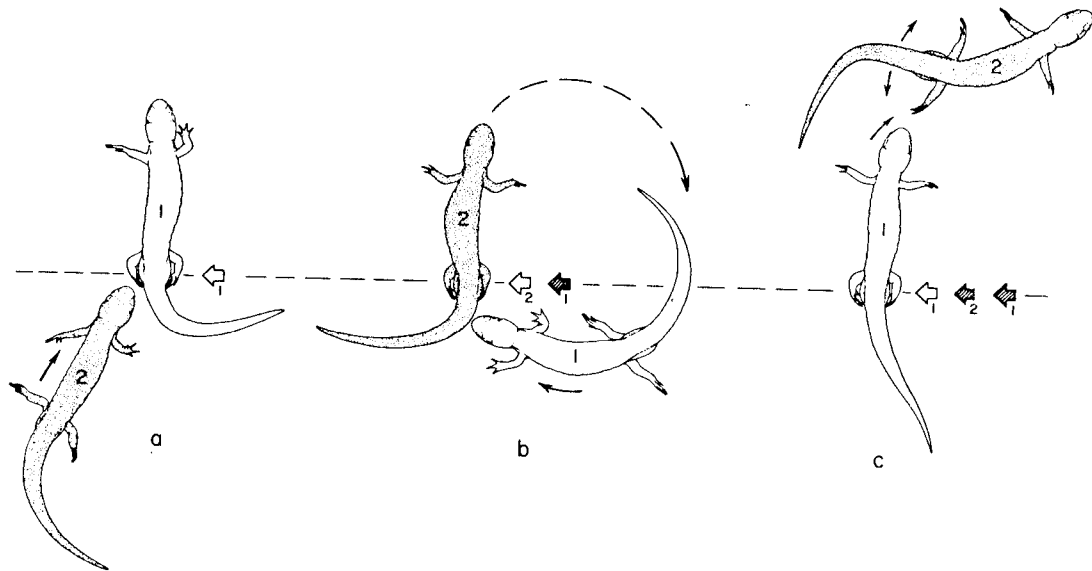


Fig. 11. Active spermatophore covering in *Ambystoma maculatum*. (a) Male 2 approaches as male 1 deposits a spermatophore (indicated with an open arrow 1). (b) Male 1 has circled around as male 2 now covers the spermatophore of male 1 with one of his own. (c) Male 1 has moved behind male 2 and now covers the spermatophore of male 2 with his spermatophore. The spermatophore is now a triple structure as in Fig. 12. (From Arnold 1976). Reproduced with permission of Verlag Paul Parey, Berlin and Hamburg, copyright 1976.

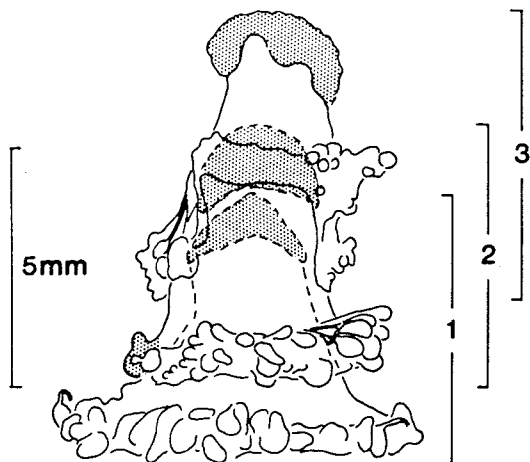


Fig. 12. A triple spermatophore of *Ambystoma maculatum*. Notice that the sperm masses (stippled) of the two lower spermatophores are completely enclosed by the spermatophore bases on top of them. (From Arnold 1976). Reproduced with permission of Verlag Paul Parey, Berlin and Hamburg, copyright 1976.

Spermatophore covering occurs in a slightly more elaborate context in some species. *Ambystoma tigrinum* males will actively intrude into the courtship of another male and dupe the rival into unprofitable spermatophore deposition (Fig. 13). Males guard against such sexual interference by transporting the female away from rivals before beginning the vulnerable process of sperm transfer (Arnold 1976). The male transports the female by shoving her for a distance of several body lengths. This shoving behavior almost invariably precedes epochs of spermatophore deposition even if the male is alone with the female. The same kind of shoving behavior has been observed in the closely related species *A. mexicanum* and *A. dumerili* (Arnold 1972; Brandon 1976; Gasco 1881), but interactions between males have not been studied.

Sexual monopoly of the female may be one of the main functions of clasping in *Ambystoma*. Storez (1969) found that *A. laterale* males could transport the female away from rivals while clasping her. This species clasps the female's dorsum in much the same posture as *Taricha* (Fig. 6), and the female is transported by vigorous swimming movements of the male's tail (Kumpf and Yeaton 1932). Storez (1969) suggested that swimming transportation is elicited only in the presence of rivals, but it can also be observed in solitary pairs (pers. observ.). *A. gracile* and *A. macrodactylum* males also are able to transport females during clasping (Knudsen 1960, pers. observ.). The nature and impact of male-male interactions is by no means clear for these three *Ambystoma* species since only a few observations are available for each of them. Storez (1969) noted that an intruding male *A. laterale* will sometimes try to clasp

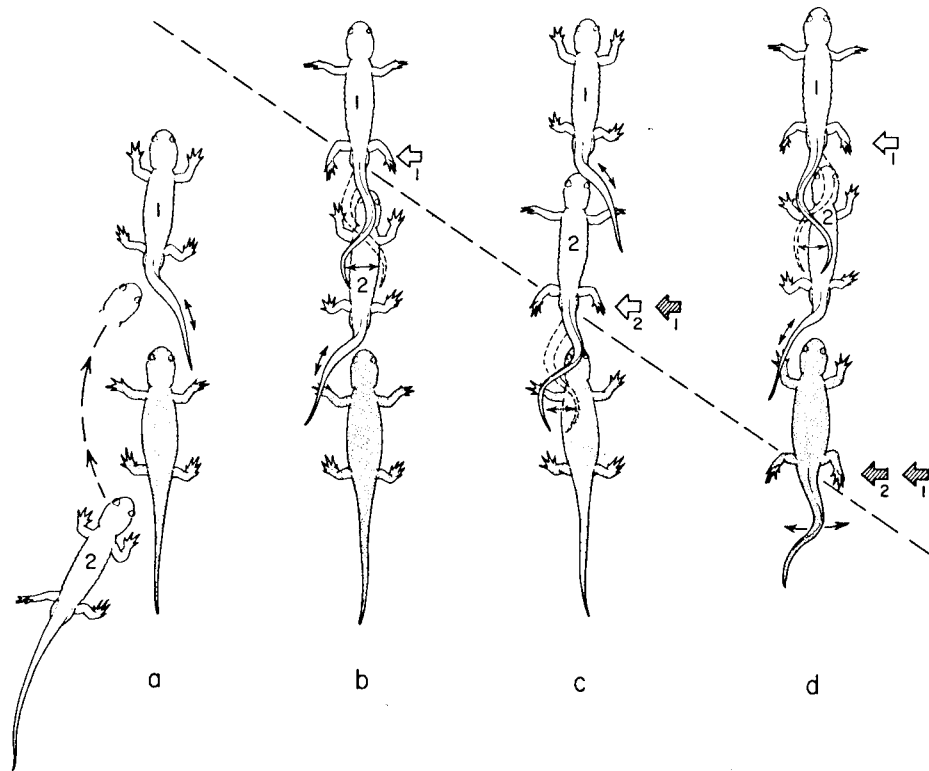


Fig. 13. Sexual interference in Ambystoma tigrinum. (a) Male 2 intrudes as male 1 leads the female (stippled) in a tail-nudging walk. (b) Male 2 has now moved between male 1 and the female and monitors the female's position by tapping with his tail. Male 1 deposits a spermatophore. (c) Male 2 covers male 1's spermatophore with one of his own. (d) The female attempts to retrieve sperm from the double spermatophore. Only the sperm of male 2 is accessible, however. Male 1 deposits another spermatophore. (From Arnold 1976). Reproduced with permission of Verlag Paul Parey, Berlin and Hamburg, copyright 1976.

a clasping pair, and Kumpf and Yeaton (1932) observed males clasping each other. I observed the latter behavior in A. gracile. A. gracile males also follow other males during spermatophore deposition, but I did not see spermatophore covering in this context. Detailed observations of male-male interactions in these species may help elucidate the significance of clasping.

A. jeffersonianum, A. laterale, A. macrodactylum and A. gracile males rub their chins on the female's snout during clasping (Anderson 1961; Kumpf and Yeaton 1932; Licht 1969; Mohr 1930; Storez 1969; Uzzell 1969). It is not known whether males possess a special gland on their chins. The behavior may simply stop females from moving forward so that the male can dismount and begin sperm transfer.

Aggressive interactions between sexually active males have been observed in the ambystomatid genus Rhyacotriton (Arnold 1972). When several males were housed 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. Preliminary courtship was observed on several occasions (Fig. 1) and spermatophores were discovered in the cages but spermatophore deposition was never observed.

Interactions between Salamandrid Males and the Significance of Clasping

In two clasping genera, Pleurodeles and Taricha, males grapple for the possession of females, but a clasping male sometimes can transport the female away from rivals. In Taricha the male clasps the dorsum of the female (Fig. 6) and transports her with vigorous swimming motions of his tail. In the field I have watched a male spirit the female away from rivals in this way. Female monopoly is not foolproof, however. Two males may attempt to clasp the same female in the laboratory, and the ensuing grappling contest may last for many minutes. "Balls" of newts, each composed of one female and several males, are sometimes found in the field.

Only laboratory observations are available for Pleurodeles. Males capture the female by rushing beneath her and clasping her forelimbs (Fig. 14). A clasping male can transport the female by swimming with his tail and walking with his hindlimbs. An intruding male sometimes succeeds in clasping the original male's hindlimbs or the distal portions of the female's forelimbs. If the intruder seizes the female's forelimbs, both males may grapple for possession of the female for several minutes, sometimes wrapping their tails around the female or the more dorsal contestant. Casual observations suggest that the original male has the competitive advantage in both Pleurodeles and Taricha.



Fig. 14. The clasping posture of *Pleurodeles waltl*. (a) The male, under the female, clasps her forelimbs with his forelimbs. (b) The male's forelimb posture in lateral view. This male is using his tail as an adjunct to forelimb clasping by wrapping it around the female's body.

Sexual interference during sperm transfer has not been observed in Taricha, although it may occur. In Pleurodeles the male releases one of the female's forelimbs during sperm transfer (Bedriaga 1882b; Arnold 1972). On one occasion an intruding male succeeded in clasping the female's free forelimb and sperm transfer was disrupted by the resulting struggle. Intrusion during sperm transfer may place the two rivals in unbiased competition since their positions are symmetrical and the original male no longer has the advantage of a more stable posture. Males appear to be sensitive to the vulnerabilities of sperm transfer. A male will quickly reclasp the female's free limb and transport her away if any other animal contacts him during sperm transfer.

Clasping undoubtedly serves several functions in Pleurodeles and Taricha in addition to sexual monopoly. In both genera males are able to transport the female to the water surface for breathing. The necessity of breathing places a severe constraint on courtship in Triturus males which must abandon the female to breathe (Halliday 1976, 1977; Halliday and Sweatman 1976). Taricha and Pleurodeles can retain the female during breathing and are less likely to curtail or hasten courtship because of oxygen debt. Relative freedom from the constraints of oxygen debt is not a universal advantage of clasping; male Notophthalmus are unable to transport the female to the surface.

Clasping also enables males of some taxa to apply courtship glands to a restrained female. Male Notophthalmus apply genital glands and Taricha apply submandibular glands. Pleurodeles males do not rub special epidermal glands on the female but the male's everted cloaca is sometimes applied to her snout during clasping.

Clasping probably increases the coordination of partners during sperm transfer. In taxa which clasp the female's dorsum (Notophthalmus, Taricha) the male dismounts directly over the female's head and places his spermatophore in front of her snout. Clasping may facilitate this alignment. In Euproctus and Salamandra clasping facilitates the placement of spermatophores near the female's vent. Pleurodeles males constrain the female's movement during sperm transfer by clasping one of her forelimbs.

In modern salamandrids clasping is maintained because it serves several functions: sexual defense, sexual interference, freedom from breathing constraints, facilitation of gland application and coordination during sperm transfer. Clasping takes many forms and may be polyphyletic. In order to elucidate the selective pressures responsible for the origin and diversification of clasping modes particular attention should be directed to conflicts between the various postulated functions of clasping. For example, the peculiar clasping mode of Notophthalmus seems to facilitate application of cephalic glands while precluding breathing at the water surface.

Interactions between Plethodontid Males

Two kinds of male-male interactions have been observed in plethodontid salamanders: homosexual courtships in which one male behaves as a pseudofemale, and aggressive encounters in which sexual rivals bite and pursue each other. In homosexual courtships, one male elicits a tail-straddling walk and dupes the other male into an unprofitable spermatophore deposition. Such interaction has been observed in Pseudotriton ruber (Organ and Organ 1968), Desmognathus ochrophaeus (pers. observ.), Ensatina eschscholtzi (pers. observ.), Plethodon glutinosus (Arnold 1972), P. jordani (Arnold 1976; Organ 1958), P. ouachitae (Arnold 1972), and P. yonahlossee (Organ, pers. comm.). Aggressive interactions between courting males have been observed in Eurycea bislineata (Arnold 1972), Pseudotriton ruber (Organ and Arnold pers. observ.), Desmognathus (Organ 1961a; pers. observ.), Plethodon glutinosus (Organ 1960a), P. caddoensis (Arnold 1972), P. ouachitae (Arnold 1972), P. jordani (Arnold 1976; Organ 1958), and P. welleri (Organ 1960b).

James Organ was the first to observe these two kinds of interactions in plethodontids. He proposed that aggressive interactions between males serve the function of sex recognition, but attached no adaptive significance to the phenomenon of homosexual courtship (Organ 1961a; Organ and Organ 1968). Arnold (1976) suggested that homosexual courtship is an adaptive mode of sexual interference in plethodontids rather than an incidental malfunction indicating poor ability for sex recognition. Aggressive interactions between males certainly indicate a capacity for sex identification (since aggression between the sexes is much rarer), but the main function may be to disperse rivals and so guard against homosexual courtship and other kinds of sexual interference (Arnold 1976).

Thurrow (1976) reports aggressive interactions between the sexes of various Plethodon species as well as between males and between females. Thurrow suggests that aggressive interactions in Plethodon may be important in the allocation of space as well as in the allocation of sexual resources. In contrast to Thurrow, I never observed aggressive interactions between females; however, my observations were made only during the courtship season. We need well designed laboratory studies, as well as field experiments, to determine whether aggressive interactions represent contests for retreats and food as well as for mates. It is clear, however, that aggressive behavior is a real part of the biology of many plethodontids.

The Evolution of Courtship Variables and the Impact of Male-Male Interactions

The male's courtship investment per spermatophore varies among salamander taxa. This courtship variable is probably molded by two

conflicting selective pressures: sexual success with particular females and sexual competition among males. Each taxon has responded to these two pressures with a characteristic compromise. Lengthy courtship before spermatophore deposition promotes the success of each spermatophore. Selection may favor rapid courtship, however, if sexual rivals are likely to intrude, and if the male has no means of monopolizing the female. This seems to be the most plausible explanation for the very rapid courtship of various Ambystoma species such as A. annulatum, A. maculatum, and A. opacum, which characteristically court in polyandrous aggregations and have no means of monopolizing females. Plethodontids and some Ambystoma species (A. laterale and A. tigrinum) may be able to exploit the advantages of lengthy, elaborate courtship because males are able to defend the female against intruding rivals.

In addition to courtship investment per spermatophore, the number of spermatophores per courtship seems to evolve in response to at least two conflicting selective pressures. No salamander species has a fool-proof system for sperm transfer, and the more spermatophores the male deposits, the greater the likelihood of sperm transfer. The male's spermatophore production is limited, however. If sexually receptive females are available for a long time, selection may favor males that deposit relatively few spermatophores per courtship and can thereby inseminate females encountered later in the season. This principle may explain the salamandrid and plethodontid patterns of low, sustained spermatophore production and the explosive productivity of Ambystoma. The courtship season of Plethodon is much longer than that of Ambystoma (10 weeks vs. 1-2 weeks; Arnold 1976). Unfortunately there are no published data on the length of salamandrid courtship seasons. Thus the length of time during which receptive females are available may determine the male's pattern for spermatophore allocation.

CONCLUSIONS

Salamander courtship is notable for complexity at two levels. Many species have elaborate courtship with complex temporal structure, and there is considerable courtship diversity in the order Urodela. The elaborateness of salamander courtship is largely a response to the difficulties of indirect sperm transfer. Many arthropods, which, like salamanders, attach spermatophores to the substrate, have intricate sexual behavior (Schaller 1971). In contrast, salamanders that practice external fertilization (cryptobranchids and hynobiids) have relatively simple sexual behavior, and the male's activities are directed towards eggs rather than females (Smith 1907; Kerbert 1904; Sasaki 1924; Thorn 1962, 1963, 1966; Rehberg 1962). Taxonomic diversity in sperm transfer behavior can be attributed to the long phylogenetic history of salamanders.

Salamanders have organized their sexual behavior around spermatophores for millions of years. The behavioral radiation we see today is the reflection of an ancient commitment to an intrinsically difficult mode of insemination.

Many archaic courtship activities probably represent important solutions to adaptive hurdles. The plethodontid tail-straddling walk and the 90° turn of salamandrids are major innovations in the process of sperm transfer. Both behaviors lessen the chance that receptive females will fail to find the spermatophore. The plethodontid trait of injecting mental gland secretions with the premaxillary teeth is probably an ancient solution to the problem of female non-receptivity.

Diversification in techniques for female persuasion is one of the striking features in the behavioral evolution of salamanders. This radiation can be understood in a general way as a consequence of rapid coevolution between male ability for persuasion and female responsiveness. Studies of behavioral isolation between populations of *Cynops* suggest that these two behavioral traits can co-evolve rapidly (Kawamura and Sawada 1959; Sawada 1963). The precise dynamics of the evolutionary process are not clear, however. We do not know how female responsiveness affects selection for male behavior within populations. The selective advantage of coyness in females, a second major problem, has only recently been approached with experimentation (Halliday, this volume). Thus, while we can appreciate an extensive radiation in techniques for persuasion, we are still speculating about its causes.

The main thesis of this review is that the sexual dynamics of extant populations will illuminate the macroevolution of salamander courtship. Courtship activities seem to serve several functions: identification of mating partners, female persuasion, coordination during sperm transfer, sexual defense of the female and sexual interference. Thus courtship behavior has probably been molded by separate, and sometimes conflicting, selective pressures exerted by sexual partners and sexual rivals.

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