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COURTSHIP BEHAVIOR IN THE PLETHODONTID SALAMANDER *GYRINOPHILUS PORPHYRITICUS*

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ABSTRACT: Courtship behavior in the spring salamander *Gyrinophilus porphyriticus* is described for the first time. This species is a member of the family Plethodontidae, and is generally acknowledged as exhibiting the largest number of primitive characters in the family. Like all plethodontids, it exhibits a tail-straddle walk that usually leads to spermatophore deposition. The early stages of courtship are characterized by extensive head-sliding (rubbing the snout over the nares, head, and body of the female) by the male. Later, during the tail-straddle walk, the female often rubs her snout laterally over the base of the male's tail. During the period immediately preceeding spermatophore deposition, the male undulates his tail beneath the female's chin. That males lack a mental gland (that secretes courtship pheromones) and yet perform extensive head-sliding suggests that this behavior serves a tactile function in *G. porphyriticus*, rather than to administer courtship pheromones. Given the large number of primitive characters exhibited by *G. porphyriticus*, head-sliding is viewed as a precursor to the behaviors used in pheromone-delivery seen in other plethodontids. The mental gland of other species may be secondarily derived and may have evolved subsequent to tactile stimulation.

Key words: Courtship behavior; *Gyrinophilus porphyriticus*; Phylogeny; Plethodontide; Salamanders

BECAUSE there is a new appreciation for the utility of mapping characters onto an independently derived phylogeny (Brooks and Mclennan, 1991), an understanding of the evolution of courtship behavior in salamanders is rapidly changing. Houck and Sever (1994) were the first to apply these methods to courtship behavior in the family Plethodontidae. By inferring that the ancestral male plethodontid possessed a mental gland and premaxillary teeth, they offered a hypothesis of character evolution in the family that features (a) changes in the ancestral mental gland and delivery modes and (b) secondary losses of the gland and associated delivery mode. In species with fan-shaped mental glands (Houck and Sever, 1994), the seasonally enlarged premaxillary teeth of the male are used to administer mental gland secretions that promote female receptivity (Ar-

nold and Houck, 1982; Houck and Reagan, 1990).

As with any hypothesis of character evolution in a clade, an unfortunate circumstance regarding Houck and Sever's (1994) hypothesis is that detailed descriptions of courtship exist for only a small proportion of plethodontids. For example, there are few data on courtship for the basal members of each plethodontid subfamily. In addition, there is little resolution on familial relationships among salamanders, and so it is difficult to determine likely ancestral character states (e.g., Duellman and Trueb, 1986; Larson, 1991; Larson and Dimmick, 1993; Sever, 1991, 1994).

In this paper, I describe the courtship behavior of *Gyrinophilus porphyriticus*, a plethodontid that lacks a mental gland and seasonally enlarged premaxillary teeth in males (Sever, 1976). This species occupies

a basal position in the phylogeny of the tribe Hemidactyliini, subfamily Plethodontinae (Larson, 1984; Wake, 1966) and is generally thought to exhibit the greatest number of ancestral characteristics of all the plethodontids (Collazo and Marks, 1994; Dunn, 1926; Wake, 1966). Following the description, I comment on how the behavior of *Gyrinophilus* bears on Houck and Sever's hypothesis. I suggest a different ancestral condition than Houck and Sever did, and I propose that this alternate hypothesis offers a more parsimonious view of plethodontid courtship evolution.

MATERIALS AND METHODS

I collected individuals of *G. porphyriticus* from the Cowee Mountains and Nantahala Mountains of Jackson and Macon counties, North Carolina from July–October 1992. They were brought to the Highlands Biological Station where they were housed in clear plastic shoe boxes (9 × 17 × 31 cm) filled with sphagnum moss and were kept moist with stream water. They were fed ad libitum salamanders [*Desmognathus ochrophaeus* and *Eurycea wilderae*: their preferred food; this species is a salamander specialist (Bruce, 1979)]. Prey salamanders were not offered unless all previous prey had been consumed. Animals were kept in an environmental chamber at 11 C and 95% relative humidity.

I anesthetized each *G. porphyriticus* in a 1% solution of MS-222, sexed it, and then measured it for snout–vent length to the nearest 0.1 mm. Identification of sex was based on one or both of two characters: I identified females by the presence of large, yolky ova and/or folds in the cloaca, and I identiﬁed males by the presence of coiled, black vasa deferentia and/or pappillae in the cloaca. I observed the vasa deferentia by shining a high intensity, fiber optic beam of light through the animal's body.

I staged male-female encounters from December 1992–February 1993. For each male-female encounter, a single male and a single female were placed in an individual chamber [either a clear plastic shoebox or an aquarium (24 × 46 × 30 cm)] lined with damp paper towels. Each male was

TABLE 1.—Summary of courtship data for six pairings of *Gyrinophilus porphyriticus*. Time spent in each phase of courtship is in minutes. Initiation is time from start of pairing to first attempt by male to persuade the female; male-female contact is time from first persuasion attempt to beginning of tail straddle walk; tail straddle walk is time from its initiation to the deposition of the spermatophore; spermatophore deposition is the time required for the male to perform this action; and sperm retrieval is the time from spermatophore deposition to pickup of the sperm cap by the female. Dashes indicate that time was not recorded.

Trial	Initiation	Male-female contact	Tail-straddle walk	Spermato-phore deposi-tion	Sperm retrieval
1	58	15	75	—	—
2	4	5	28	—	—
3	27	33	18	4	2
4	43	90	15	1	1
5	17	47	24	12	2
6	71	73	19	4	3

exposed to each female only once (and vice versa). An encounter began by placing the male and female together at 2030 h and was terminated the following morning, when I noted the presence or absence of a spermatophore(s) and when I examined the female for insemination (Arnold et al., 1993). From 2030–2400 h, the encounters were conducted under red light (directed away from the chambers) to accomodate visual inspection of courtship progress every 15 min. I observed the male-female encounter continuously if the male-female contact phase was reached. After 2400 h, the red light was turned off.

RESULTS

I staged 112 male-female encounters among 10 females and 12 males. Of these, 34 proceeded to the male-female contact phase. Fifteen of these encounters engaged in the tail-straddle walk, and nine of these 15 resulted in insemination of the female. I collected quantitative data for six of the 15 encounters that proceeded to the tail-straddle walk (Table 1).

This species followed the stereotypical courtship of other plethodontid species: a preliminary courtship phase (characterized by contact between the male and female) followed by a tail-straddle walk that resulted in the deposition of a spermato-

phore, and that terminated when the female picked up the sperm mass in her cloaca. The overall pattern for *Gyrinophilus* is similar to that reported by Organ and Organ (1968) for the closely related *Pseudotriton ruber.* I follow Arnold (1976) and Promislow (1987) in cataloguing the courtship of *Gyrinophilus.*

Several behaviors are noteworthy. The male never turned back toward the female during the tail-straddle walk, a behavior seen in most other plethodontids for which courtship has been described. Because males of *Gyrinophilus* do not have mental glands (Sever, 1976), this observation is consistent with the hypothesis that males turn back toward the females to apply courtship pheromones [via snapping, pulling, and slapping (Arnold, 1972)] that are produced by the mental gland. Snapping, pulling, and slapping were never observed for *Gyrinophilus.*

However, the male extensively rubbed his chin over the female's head (including the nasolabial grooves and cheeks) during the male-female contact phase of courtship. Arnold (1976) used the term "head-sliding" in reference to this behavior.

Male Actions

Contact.—The male approached and contacted the female with his snout.

Head-sliding.—The male rubbed his snout and chin laterally over the female's body and (especially) the head, snout, and nares.

Tail-straddle walk.—The male moved forward while the female straddled his tail.

Spermatophore deposition.—The male lowered his cloacal vent to contact the substrate, and deposited a spermatophore.

Moving forward with tail flexed.—After spermatophore deposition, the male always flexed his tail at a 90° angle relative to the axis of his body.

Hind quarters arched and tail undulating.—During the tail straddle walk, spermatophore deposition and sperm transfer, the male often (11 out of 15) raised the base of his tail while performing undulations of the entire tail. This action forced the female's chin and snout to contact and rub against the base of the male's tail.

Female Actions

Moving away.—A non-receptive female (97 out of 112) avoided the male. Avoidance was carried out by walking away. Moving away was not rapid as in other plethodontids (e.g., Promislow, 1987).

Head swinging.—When in the tail-straddle walk, during spermatophore deposition and sperm transfer, the female swung her head laterally over the base of the male's tail. Contact with the tail was usual during this action.

Tail-straddle walk.—While astride the male's tail, the female moved forward with the male.

Sperm transfer.—The female lowered her cloaca over the apical sperm mass of the spermatophore. The female sometimes pressed her cloaca firmly over the spermatophore, while moving the cloacal region of her body laterally. When this occurred, the gelatinous base of the spermatophore was flattened on the substrate. Sperm transfer was always successful if this occurred.

Temporal Relations

Courtship began with contact of the female by the male. As soon as male-female contact began, the male performed head-sliding. The head-sliding was performed constantly during this phase. The female (a) remained still (12 out of 34), (b) walked slowly while the male remained in contact (four out of 34), or (c) moved away (18 out of 34). Females that eventually engaged in the tail-straddle walk remained still or walked slowly while the male remained in contact.

During the tail-straddle walk, the male occasionally (eight out of 15) undulated his tail while in contact with the female's chin. The female always performed head-swinging while in contact with the base of the male's tail. The behavior may be related to the possible presence of sexually dimorphic caudal courtship glands in *Gyrinophilus* (Houck and Sever, 1994).

During the tail-straddle walk, the pair continued to move forward until spermatophore deposition. Spermatophore deposition occurred while the pair was sta-
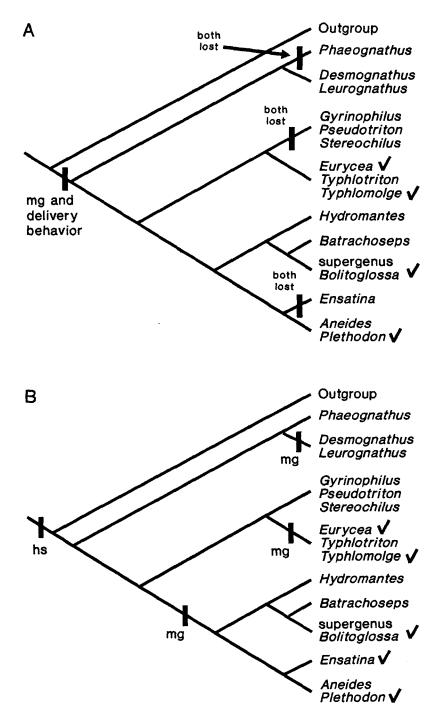
FIG. 1.—Changes in courtship behavioral characters partitioned on the topology specified by molecular and morphological comparisons for the main subdivisions of the family Plethodontidae. The main groupings are the subfamily Desmognathinae and the subfamily Plethodontinae, which contains the tribes Hemidactyliini, Plethodontini, and Bolitoglossini. Checks indicate at least one episode of loss of mental gland and delivery behavior (in A) or at least one episode of loss of mental gland (in B); m.g. = mental gland; h.s. = head-sliding. The outgroup can be considered to be any other family of internally-fertilizing salamanders. (A) In Houck and Sever's (1994) hypothesis, the ancestral plethodontid possessed a mental gland and sexually di-

tionary, although the male often (seven out of 15) undulated his tail and the female would head-swing (12 out of 15) during deposition. Following deposition, the male moved his tail to the side (preventing his tail from interfering with the spermatophore during forward movement), arched his hindquarters, and moved forward a short distance. This distance may be related to the length of his body (Arnold et al., 1993; Beachy, 1996). The female also moved forward, keeping in contact with the male. She lowered her cloaca over the apical sperm mass, during which she occasionally (five out of 15) pressed her cloaca firmly on the spermatophore.

After sperm transfer was complete, the female disengaged and moved away from the male. The male initiated the male-female contact a second time after the initial sperm transfer phase in at least 20% (three of 15) of these encounters.

Time spent in each phase of courtship varied greatly (Table 1). In several cases, I examined and measured the spermatophore (mean length of spermatophore base = 5.5 mm; mean width = 3.9 mm; mean height = 3.63 mm) and spermatozoa (mean length = 440 μm). My descriptions and measurements closely matched the observations of Wortham et al. (1977).

DISCUSSION

Most of the descriptions of plethodontid courtship have concerned the derived genera *Plethodon* and *Desmognathus*. In order to test hypotheses of courtship evolution, it is critical to obtain descriptions of the putative basal genera (e.g., *Phaeognathus, Ensatina, Hydromantes*). *Gyrinophilus* is generally interpreted to possess the largest number of ancestral characters of all plethodontid genera, so description of its courtship is especially informative.

This is the first report of courtship in *Gyrinophilus*. Bishop (1941) observed two adults each grasping the other's tail in its jaws, apparently not courtship behavior but perhaps predation or agonistic behavior. *Gyrinophilus*, like its sister taxon *Pseudotriton* (Organ and Organ, 1968), exhibits a simple courtship pattern characterized by lack of behaviors for pheromone delivery (associated with the lack of a mental gland) seen in other genera of plethodontids (e.g., *Eurycea, Desmognathus, Plethodon*).

Previous failures to observe courtship (cf. Arnold et al., 1993) may be due to several factors: encounters staged during the non-breeding season, not using sexually mature individuals, using non-gravid females, using animals that were taken several months or years previous to pairing, and feeding animals a non-salamander diet. In addition, using containers that are too small (i.e., not long enough) may prevent the completion of the tail-straddle walk. During my trials, the length of the courtship chamber affected the continuation of the tail-straddle walk: i.e., a short chamber forced the pair to experience constant turning. Often, the female terminated the tail-straddle walk after several abrupt turns by the male.

Houck and Sever (1994) hypothesized that a mental gland was absent in the outgroup to plethodontids but was present in the ancestral plethodontid (Fig. 1A). This ancestral plethodontid also possessed sexually dimorphic premaxillary teeth like those seen in males of species of *Desmognathus* (Organ, 1961). From this ancestral plethodontid, *Gyrinophilus* (and several other taxa) would be presumed to have undergone secondary loss of the mental gland and dimorphic teeth, and the be-

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morphic premaxillary teeth used by the male to administer secretions from the mental gland into the female. If mental gland and delivery behavior can evolve concurrently, then there are at least eight events (seven are reversals) in (A). If evolution (or loss) of mental gland and delivery behavior is considered as two separate events, there are at least 16 events (14 are reversals). (B) In the alternate hypothesis, the ancestral plethodontid lacked a mental gland but exhibited head-sliding, the hypothesized precursor to pheromone delivery behaviors. There are nine events (six are reversals) in this hypothesis. In (A), head-sliding and delivery behaviors are not considered to be homologous. Head-sliding and delivery behaviors are considered homologous in (B).

haviors used to administer the pheromones (Fig. 1A).

While the phylogeny of the salamander families is currently not resolved, there is a consensus that the nearest outgroup to the family Plethodontidae is one whose members have internal fertilization (Larson and Dimmick, 1994; Sever, 1991). In all of these possible outgroups for which descriptions of courtship are available (e.g., Ambystomatidae, Amphiumidae), the male uses his snout and chin in head-sliding over the female's body and nares (Arnold, 1977; Bishop, 1941; Briegleb, 1962; Pfingsten and Downs, 1989; Verrell, 1982). None of these families possesses a mental gland. Thus, in contrast to Houck and Sever's hypothesis, I suggest that the ancestral state of courtship behavior in plethodontids is characterized by the presence of head-sliding and the absence of a mental gland (Fig. 1B). In this alternate hypothesis, head-sliding in *Gyrinophilus* and *Pseudotriton* is seen as homologous to head-sliding of the outgroup. Thus, head-sliding may represent the precursor to the pheromone delivery behaviors seen in plethodontids that possess mental glands. In this hypothesis, head-sliding in the ancestral plethodontid can be (a) retained in the descendant and/or (b) modified in the form of slapping, snapping, and pulling.

Given that it is critical to use a rigorous, independently derived phylogeny to evaluate the competing hypotheses, it is instructional to review the well supported aspects of plethodontid phylogeny: (1) the two subfamilies, Desmognathinae and Plethodontinae (Larson, 1984; Wake, 1966); (2) the three plethodontine tribes, Hemidactyliini (exclusive of *Hemidactylium* whose status is uncertain), Plethodontini, and Bolitoglossini (Larson, 1984; Wake, 1966, 1993); (3) the monophyly of the clade consisting of *Gyrinophilus, Pseudotriton,* and *Stereochilus,* and the basal position of this clade in the Hemidactyliini (Lombard and Wake, 1986; Wake, 1966); (4) the basal position of the Hemidactyliini within the Plethodontinae (Lombard and Wake, 1986; Wake et al., 1987); (5) the basal position of *Phaeognathus* within the

Desmognathinae (Titus, 1992); (6) the basal position of *Ensatina* within the Plethodontini (Larson et al., 1981); and (7) the basal position of *Hydromantes* relative to *Batrachoseps* and the supergenus *Bolitoglossa* (Lombard and Wake, 1986; Wake, 1966, 1993).

Except for *Hydromantes,* these basal groups lack mental glands. *Gyrinophilus* (this study), *Pseudotriton* (Organ and Organ, 1968), and *Ensatina* (Stebbins, 1949) each exhibit head-sliding (and I hypothesize that *Phaeognathus* does as well). Houck and Sever's (1994) hypothesis includes a high frequency of these basal groups involved in secondary loss of the mental gland. They also implicitly consider that head-sliding is not homologous to pheromone delivery behaviors. In this view, the evolution of the mental gland and pheromone delivery behavior are concurrent (Arnold and Houck, 1982; Arnold et al., 1993; Houck and Sever, 1994). If the hypothesis of concurrent evolution of the mental gland and pheromone delivery behavior is true, then at least eight events (seven are reversals) are required to explain the taxonomic distribution of mental gland and pheromone delivery behavior (Fig. 1A). If this hypothesis is false, then more frequent events (16 with 14 being reversals) must be invoked. In any case, Houck and Sever's hypothesis requires only one event of mental gland evolution (Fig. 1A).

Houck and Sever's hypothesis does not preclude or address the presence of head-sliding in the ancestral plethodontid. At least one plethodontid, *Plethodon jordani,* utilizes head-sliding in addition to other delivery behaviors (Arnold, 1976). Many others (e.g., species of *Desmognathus*) do not exhibit head-sliding. If head-sliding is an ancestral plethodontid character and is not homologous to the pheromone delivery behaviors, then many instances of loss of head-sliding would need to be invoked.

In the alternate hypothesis, secondary losses of the mental gland are less frequent and never seen in the basal groups mentioned above. Furthermore, head-sliding is hypothesized to be homologous to the de-

livery behaviors in the derived genera for which courtship has been described. If head-sliding is seen as the precursor to pheromone delivery behaviors, then concurrent evolution of the mental gland and pheromone delivery behavior is not necessary. In this hypothesis, at least nine events (six are reversals) must be invoked. Three of these events are independent evolution of the mental gland (Fig. 1B). The possession of head-sliding behavior in an ancestral plethodontid would be beneficial to a descendant that possessed the derived mental gland, and makes the evolution of the mental gland easier to explain because it becomes a stepwise process: i.e., the behavior necessary to deliver any courtship pheromones is present when the mental gland evolves.

If head-sliding preceded the evolution of the mental gland, then it may be interpreted as serving a tactile role. Such behavior can be seen in other families of salamanders (e.g., Arnold, 1977; Verrell, 1982) and may be presumed present in the outgroup to the plethodontids. If the head-sliding behavior of the male is interpreted as tactile stimulation, then the secondary acquisition of the mental gland for pheromonal production was favored by the already present tactile behavior.

It is unfortunate that the clade that has the highest diversity of mental gland types and pheromone delivery modes for the fewest number of species [i.e., the "non-gyrinophiline" hemidactyliines (i.e., *Eurycea, Typhlotriton,* and *Typhlomolge*)] is also the group whose phylogeny is least understood. Further resolution of phylogeny of these hemidactyliines and other plethodontid groups, coupled with courtship descriptions for additional species, should do much to assist an understanding of courtship evolution in the plethodontids.

Homoplasy appears to be a general theme in morphological evolution in salamanders, and it applies especially to the Plethodontidae (Sever, 1994; Wake, 1991). Because both of the hypotheses considered here also invoke homoplasy in order to provide a view of parsimonious character evolution (Fig. 1), it appears that be-

havioral homoplasy may also be an important and confounding consideration in attempts to understand plethodontid evolution.

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