

BIBLIOGRAPHY (Published)

- Bloomer, Tom J. and Denise Bloomer, 1973. New Jersey's Bog Turtle . . . Destined to Extinction? Bull. N.Y. Herpetol. Soc. 9(3 & 4): 8-12
- Bloomer, Tom J., 1977. *Clemmys muhlenbergi* and Friends: Herptiles that Share the Bog Turtle's Habitat. Journal North. Ohio Assoc. Herpetol. 3(1): 30-34.
- Bloomer, Tom J., 1977. *Hibernacula* Congregation in the *Clemmys* Genus. Journal North. Ohio Herptol. 3(2).
- Fowler, H.W., 1907. Amphibians and Reptiles of N.J. Annual Report N.J. State Mus. 1906:23-250.
- Nemuras, Kenneth T., 1965. The Bog Turtle in Maryland. Bull. Phila. Herpetol. Soc. 13(14-17).

- Nemuras, Kenneth T., 1967. Notes on the Natural History of *Clemmys muhlenbergi*. Bull. Maryland Herpetol. Soc. 3(4): 80-96.
- Nemuras, Kenneth T. and James A. Weaver, 1974. The Bog Turtle: Synonym for Extinction? National Parks Mag. 48(6): 17-20
- Zovickian, William H., 1971. Captive Nesting of Bog Turtles. Int. Nat. Tur. & Tor. Soc. Journal. 5(4): 14-15 & 37.

Unpublished

- Bloomer, Tom. J., 1969-1977. Field notes on *Clemmys muhlenbergi*.
- Holub, Richard J., 1972-1977. Field Notes and Captive Colony Notes on *Clemmys muhlenbergi*.
- Nemuras, Kenneth T., 1972-1975. Correspondence with Tom J. Bloomer and Richard J. Holub.



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PARENTAL CARE IN SALAMANDERS

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The reports of parental care in urodele amphibians are often anecdotal and rarely reviewed in detail (Noble, 1931, 412-414; Porter, 1972, 346; Salthe and Mecham, 1974, 391-395). The purpose of this paper is to review and give a brief description of the types of parental care known to exist in the order Caudata. Parental care can be defined as any behavior towards the offspring by the parent which increases the survival of the offspring (Wilson, 1975). For this report any such behavior, whether active or passive, that might be suspected of being functional in increasing offspring survival will be considered.

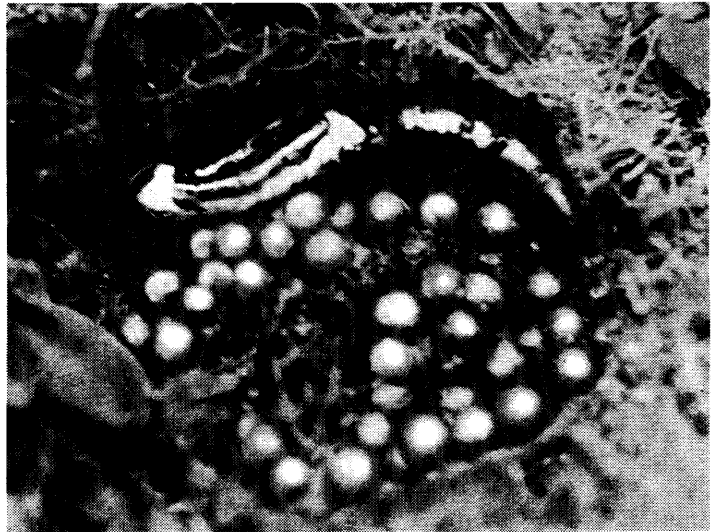
The most primitive salamander in which parental care has been reported is the Asiatic Land Salamander, *Hynobius nebulosus* (family Hynobiidae). Parental care in this species is peculiar for a salamander in that it takes the form of male defense of the nest. Laboratory observations by Thorn (1962) indicate that the male will aggressively attack objects that are brought in the vicinity of the egg mass. Males fed to satiety with earthworms would attack and then deposit a distance from the egg mass any earthworms in the area of the egg mass. Obviously this report of egg mass defence is not solely a feeding response.

Weber (1944) has reported an incidence of parental care in the two-toed amphiuma, *Amphiuma means* (family Amphiumidae). This species typically deposits its eggs in the muddy substratum of ponds. Upon the drying out of a pond Weber noted a female amphiuma coiled about her eggs. He speculated this behavior may reduce the chance of dessication of the eggs.

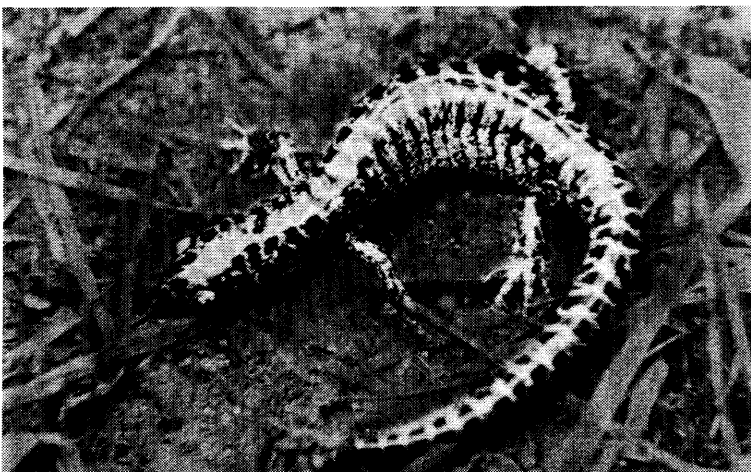
Two species in the family Ambystomatidae are known to exhibit parental behavior. This family is interesting in that several diverse modes of reproduction are exhibited. Most members of the genus *Ambystoma* deposit their eggs in the open water where they are abandoned. These species are the classical example of animals with Mode I reproduction (Salthe, 1969). Species of the genera *Dicamptodon* and *Rhyacotriton* exhibit Mode II reproduction, depositing their eggs under objects in running water. The marbled salamander, *Ambystoma opacum*, and the flatwoods salamander, *A. cingulatum*, utilize a reproductive strategy which does not fit easily into Salthe's (1969) classifications. These species deposit eggs terrestrially, typical of Mode III. However, there is not direct development of the eggs, a necessary concomitant of Mode III reproduction. Upon inundation the eggs hatch and larvae



Adult marbled salamander, *Ambystoma opacum*



Brooding female *A. opacum*



Frosted flatwood salamander, *A. cingulatum*

Photos by Allen Marchisin

emerge. This phenomenon as well as the ovum dimensions are more typical of Mode II reproduction (Anderson and Williamson, 1976).

In a study of the life history of the Giant Salamander, *Dicamptodon ensatus*, Henry and Twitty (1940) make no mention of parental care. However, Nussbaum (1969) noted that the female will spend the entire hatching period, up to 35 days, closely associated with the egg mass. This is especially significant since cannibalism as well as oophagy are well known in this species. Parental behavior apparently does not exist in the olympic salamander, *Rhyacotriton olympicus* (Nussbaum, 1969). This is an exception to the general rule of parental care being a concomitant of Mode II reproduction.

Brooding behavior has long been known in *Ambystoma opacum* (Noble, 1931). This species deposits its eggs terrestrially and remains with the eggs until they are inundated by the rising level of a nearby pond (O'Donnel, 1937). Several advantages of this maternal behavior have been suggested. McAttee (1933) indicated that the presence of the female may ameliorate the harmful effects of dessication of the eggs. Anderson (personal communication) noted aggressive behavior in the female defending the nest and suggested this may serve to ward off potential insect predators. Movements of the female within the nest tend to rotate the eggs and cause the capsules to accumulate a thin layer of soil. This may be of adaptive significance since it has been shown that the clumping of eggs will cause reduced viability (Salthe and Mecham, 1974). Parental care is absent in *A. cingulatum*, but otherwise this species has the same type of reproductive strategy as *A. opacum*. Anderson and Williamson (1976) speculated that the evolution of brooding behavior in *A. opacum* may be partly responsible for this species distributional success contrasted with the restricted range of *A. cingulatum*.

Brooding behavior is most widespread in the lungless salamanders of the family Plethodontidae. The species within this family are so diverse that often the subfamilies, Desmognathinae and Plethodontinae, are given familial status (Porter, 1972).

In the Desmognathinae maternal care has been reported in two species in the genus *Desmognathus*. Wood and Clark (1955) not only found females of the Northern Dusky Salamander, *Desmognathus fuscus*, coiled about their eggs but

also discovered one female that had preyed upon her own eggs. Oophagy had been previously reported in this species (Baldout, 1947). Females of this species (Dennis, 1966) and of *D. auriculatus* (Rose, 1966) are also known to exhibit homing to the nest after being displaced considerable distances. As in most cases of urodele parental care this behavior is functional in the prevention of dessication. Females of *D. fuscus* take a more active role in preventing dessication by crawling over the eggs and expelling water on them during the night (Brode, 1961). As in *Amphiuma means* and *Ambystoma opacum*, brooding behavior in *D. fuscus* includes overt defense of the nest (Dennis, 1966).

There are eight genera in the subfamily Plethodontinae in which some form of parental care has been reported. The first report of parental behavior in the green salamander was that of Ritter (1903). He reported that *Autodax lugubris* (= *Aneides lugubris*) inhabited holes in live oak trees, *Quercus virginianus*, in California. These animals, he speculated, live in kin groups and actually constitute a family. Both the resident adult male and female show aggressive defense of the nest.

The close association of the adults with the eggs may also decrease the chances of dessication (Miller, 1944). In a series of reports on *Aneides aeneus*, Gordon showed that the female coils around the eggs after deposition (Gordon and Smith, 1949), rarely leaves the nest unguarded (Gordon, 1952) and if displaced exhibits homing ability to the nest (Gordon, 1961).

Among all the plethodontids there are only two genera with aquatic larvae, *Hemidactylum* and *Stereochilus*. Behavior which may be interpreted as parental care has been reported in each of these genera. Schwartz and Etheridge (1954) reported a female many-lined salamander, *Stereochilus marginatus*, coiled about her eggs. In the four-toed salamander, *Hemidactylum scutatum*, there appears to be a combination of parental as well as alloparental care. Generally, female four-toed salamanders will stay with the eggs until they hatch. If her eggs are associated with the eggs of another female(s) usually all but one of the females will desert the nest. One female may be found brooding the eggs of several females (Blanchard, 1934; Gilbert, 1941).

There have also been reports of maternal behavior in brook salamanders. Franz (1964) reports a female *Eurycea longicauda* coiled around her eggs.

However there does not seem to be any parental care in *E. lucifuga*, which breeds in identical habitat (Green, 1968). In a study of tropical plethodontid salamanders McDiarmid and Worthington (1970) report that a female of *Pseudoeurycea juregi* remains with the eggs, often coiled about them. This attendance to egg clutches by the female is characteristic of most tropical plethodontids and may be crucial to the development of the embryos (Vial, 1968).

In the first published description of the eggs of *Batrochoseps pacificus* there is no mention of parental care, although the adults seem to remain a few inches away from the egg mass (Davis, 1952). "The question of the extent of maternal care is unanswered," but it does exist in *Hydromantes stastar* (Gorman, 1956). Upon finding egg masses in extremely dry situations Gorman reported emaciated females coiled about their eggs. Once again the importance of protecting the eggs from dessication is brought out.

The genus *Plethodon* is well known for its brooding behavior. It is in this genus that the function of brooding behavior has been most thoroughly considered. Upon removal of a brooding female *Plethodon dunni* from her nest Dumas (1955) noted that the eggs quickly became susceptible to mold. In a study of the brooding behavior of the red back salamander, *Plethodon cinereus*, Highton and Savage (1961) concluded that maternal care will tend to increase the percent survival of the young and that the female will overtly defend her nest. They also speculated on the role of dermal secretions in the prevention of mold. However, Vial and Prieb (1966) showed that the dermal secretions of *Plethodon cinereus*, as well as a number of other salamanders, have no antibiotic components. It is now generally believed that the association of mold with urodele eggs takes place only after the embryos have died of other causes (Salthe and Mecham, 1974).

In summary, parental care is a widespread phenomenon in urodele amphibians. This behavior usually takes the form of an active and aggressive defense of the egg mass (e.g. *Plethodon dunni*, *Ambystoma opacum*, *Aneides lugubris*) and/or the prevention of dessication of the eggs. Dessication can be avoided in several ways: rotating the eggs causing them to accumulate a thin soil layer (e.g. *Ambystoma opacum*), actively expelling water on the eggs (e.g. *Desmognathus fuscus*) or more passively by the adult simply

remaining in bodily contact with the eggs (most cases reviewed here).

Wilson (1975) states that when species adapt to stressful environments parental care is more likely to evolve. This seems to be the selective force which has caused the evolution of parental care in some species of salamanders. Salthe (1969) has classified urodele reproductive strategies into three modes. Very simply, species with Mode I reproduction deposit their eggs in open water where they are abandoned. Mode II reproduction is represented by those species which deposit their eggs under objects in shallow moving water. Mode III animals deposit their eggs terrestrially where direct development of the embryos take place. These modes sequentially represent an increased invasion of the terrestrial (i.e., stressful for an amphibian) environment. Parental care has not been reported in Mode I reproduction, it is usually the rule in Mode II reproduction and is always a concomitant of Mode III reproduction.

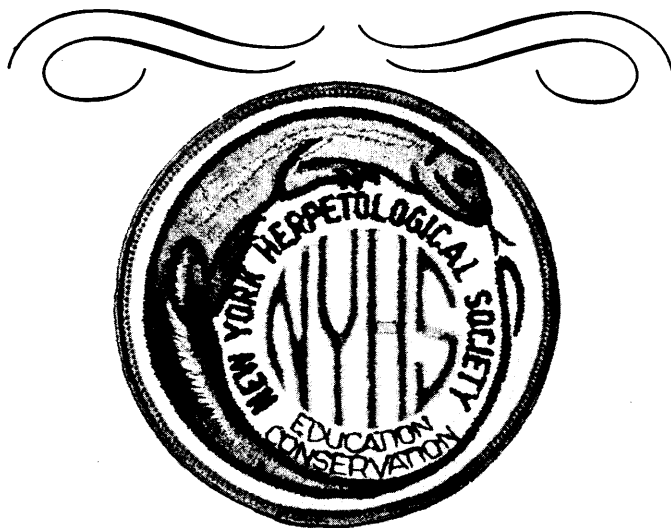
This review should make it apparent that parental care, though widespread in salamanders, is only poorly understood. This behavior should be studied in terms of function and adaptive significance.

LITERATURE CITED

- Anderson, J.D. and Williamson, G.K., 1976. Terrestrial mode of reproduction in *Ambystoma cingulatum*. *Herpetologica* 32 (2): 214-221.
- Baldout, R.J., 1947. *Desmognathus fuscus fuscus* eating eggs of its own species. *Copeia* 1947: 66.
- Blanchard, F.N., 1934. The relation of the female four-toed salamander to her nest. *Copeia* 1934: 137-139.
- Brode, W.E., 1961. Observations on the development in *Desmognathus* eggs under relatively dry conditions. *Herpetologica* 17: 202-203.
- Davis, J., 1952. Observations on the eggs and larvae of the salamander, *Bolitoglossa subpalmata* in Costa Rica. *Rev. Biol. Trop.* 15: 117-121.
- Dennis, D.M., 1966. Nesting habits of *Desmognathus fuscus*. *J. Ohio Herp. Soc.* 5: 163.
- Dumas, P.C., 1955. Eggs of the salamander *Plethodon dunni* in nature. *Copeia* 1955: 65.
- Franz, R., 1964. The eggs of the long tailed salamander from a Maryland cave. *Herpetologica* 20: 216.
- Gilbert, P.W., 1941. Eggs and nest of *Hemidactylum scutatum* in the Ithaca region. *Copeia* 1941: 47.
- Gordon, R.E., 1952. A contribution to the life history and ecology of the plethodontid salamander, *Aneides aeneus*. *Amer. Midl. Nat.* 47: 666-701.
- _____ 1961. The movement of displaced green salamanders. *Ecology* 42: 200-202.
- _____ and Smith, R.L., 1949. Notes on the life history of the salamander *Aneides aeneus*. *Copeia* 1949: 173-174.

- Gorman, J., 1956. Reproduction in the plethodontids of the genus *Hydromantes*. *Herpetologica* 12: 249-259.
- Green, N.B., 1968. Egg laying situations and early larval behavior in *Eurycea lucifuga*. *J. Herp.* 1: 119-120.
- Henry, W.V. and Twitty, V.C., 1940. Contributions to the life histories of *Dicaptodon ensatus* and *Ambystoma gracile*. *Copeia* 1940: 247-249.
- Highton, R. and Savage, T., 1961. Functions of the brooding behavior in the female red backed salamander, *Plethodon cinereus*. *Copeia* 1961: 95-98.
- McAttee, W.L., 1933. Notes on the banded salamander (*Ambystoma opacum*). *Copeia* 1933: 218-220.
- McDiarmid, R.W. and Worthington, R.D., 1970. Concerning the reproductive habits of tropical plethodontid salamanders. *Herpetologica* 26: 57-70.
- Miller, D.H., 1944. Notes on eggs and larvae of *Aneides lugubris*. *Copeia* 1944: 224-230.
- Noble, G.K., 1931. The biology of the Amphibia. McGraw-Hill. New York. 577 p.
- Nussbaum, R.A., 1969. An nest site of the olympic salamander, *Rhyacotriton olympicus*. *Herpetologica* 25: 277-278.
- _____. 1969. Nests and eggs of the Pacific giant salamander *Dicaptodon ensatus* (Eschscholtz). *Herpetologica* 25: 257-261.
- O'Donnel, D.J., 1937. Natural history of the ambystomatid salamanders of Illinois. *Amer. Midl. Nat.* 18: 1063-1071.
- Porter, K.R., 1972. *Herpetology*. W.B. Saunders Co. Philadelphia. 524 p.
- Ritter, W.E., 1903. Further notes on the habits of *Autodax lugubris*. *Amer. Nat.* 37: 883-886.
- Rose, F.L., 1966. Homing to nests by the salamander *Desmognathus auriculatus*. *Copeia* 1966: 251-253.
- Salthe, S.N., 1969. Reproductive modes and the number and sizes of ova in the urodeles. *Amer. Midl. Nat.* 81: 467-490.
- _____. and Mecham, J.S., 1974. Reproductive and courtship patterns in *Physiology of the Amphibia* (B. Lofts ed.). Academic Press Inc. New York.
- Schwartz, A. and Etheridge, R., 1954. New and additional herpetological records from North Carolina coastal plain. *Herpetologica* 10: 167-171.
- Thorn, R., 1962. Protection of the brood by a mole salamander, *Hynobius nebulosus*. *Copeia* 1962: 638-640.
- Vial, J.L., 1968. The ecology of the tropical salamander, *Bolitoglossa subpalmata* in Costa Rica. *Rev. Biol. Trop.* 15: 13-115.
- _____. and Preib, F.B., 1966. Antibiotic assay of dermal secretions from the salamander *Plethodon cinereus*. *Herpetologica* 22: 284-286.
- Weber, J.A., 1944. Observations on the life history of *Amphiuma means*. *Copeia* 1944: 61-62.
- Wilson, E.O., 1975. *Sociobiology*. Belknap Press. Cambridge.
- Wood, J.T. and Clark, R.F., 1955. The dusky salamander: oophagy in nesting sites. *Herpetologica* 11: 150-151.

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