Comments on the Female Reproductive Cycle and Philopatry
By Desmognathus ochrophaeus (Amphibia, Urodela, Plethodontidae)

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ABSTRACT—A photographic, mark-recapture study of the Blue Ridge dusky salamander, Desmognathus ochrophaeus, revealed that at least some females oviposit during the spring and summer on an annual basis. Females exhibited a propensity for the same segment of the reproductive habitat during successive years. The adaptive value of this behavior is discussed.

INTRODUCTION

The timing of oviposition in Desmognathus ochrophaeus has become controversial. Dunn (1926:105-119), Fitzpatrick (1973:44), Huheey and Brandon (1973:66-67) and Martof and Rose (1963:415-416) have suggested females oviposit annually beginning in early spring and continuing into late summer. Bishop and Chrip (1933:197) supported an annual cycle, but felt periods of oviposition might vary over the species' range. Organ (1961:208) presented data supporting a biennial cycle; while Tilley and Tinkle (1968:302) contended that females may oviposit on a biannual basis. More recently, Tilley (1973:396-397) has suggested that reproduction in D. ochrophaeus is annual, but that females may oviposit three times in two years.

This paper reports the results of a mark-recapture study of brooding (parental care of the eggs) D. ochrophaeus females. Its purpose is three fold: (1) to document the ability of individual females to oviposit during consecutive reproductive seasons; (2) to suggest that brooding females are philopatric; (3) to comment on the potential adaptiveness of philopatry.

STUDY AREA

This investigation was conducted near Highlands, Macon County, North Carolina, during the summers of 1972 and 1973. The study was confined to the margin of a slow-moving, mountain stream (on N.C. 1538, 5.15 km from its junction with U.S. 64N) in a mixed mesophytic forest at a maximum elevation of 1265 m. At this locality, females and their eggs were abundant beneath decaying logs, rocks, leaf litter and mats of moss (Thuidium delicatulum, Atrichum undulatum and Minium ciliare).

MATERIALS AND METHODS

Initially, the stream was divided into 28 five-m segments using surveyor's stakes. During August 1972 and June through August 1973, a weekly search was made of each segment to locate brooding females. Upon discovery, the location (stream segment) of the brooding female was recorded; she and her eggs were placed in a 9-cm petri dish, and they were transported to the laboratory facilities of the Highlands Biological Station. To reduce oophagy (egg eating) by females during transport, eggs were first wrapped in moist paper toweling.

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In the laboratory, females were anesthetized in a saturated solution of tricaine methanesulfonate. Each female was weighed to the nearest .00 g, measured (snout-vent, mm) and photographed. All photographs were taken on 2 X 2 color transparency film using a 35 mm Pentax Spotmatic camera equipped with a macro-lens and an electronic flash. This technique was developed by S. G. Tilley of Smith College (pers. comm.).

After being revived in a dish of tap water, most females were returned within 24 hours to the stream segment from which they had been removed. Some females were maintained in the laboratory for behavioral studies; but none were confined longer than five weeks and all were subsequently released within their original stream segment.

In the southern portion of its range, *D. ochrophaeus* individually exhibits distinctive dorsal patterns (Tilley, 1969). In Macon Co., N.C., males tend toward uniform melanism, while females are boldly patterned with dorsal spots, stripes, or combinations of these patterns. Furthermore, patterns are often brightly colored with red and yellow pigments, and 9% of the females possess red cheek-patches. Such pattern distinctness permits individual recognition within a series and matching of color transparencies of the same female from different years.

Color transparencies taken during 1972 were arranged into six categories, five of which were based on the females' dorsal pattern: (1) single spots, (2) paired spots, (3) solid stripe, (4) ziz-zag stripe, (5) no pattern (melanistic dorsum). Females which exhibited characteristics of more than one category were assigned to the group which seemed to best describe them, while females possessing red cheek-patches were placed in the sixth category regardless of dorsal patterns. Those females brooding in successive summers were identified by comparing projected transparencies from 1972 and 1973. Individuals were first grouped by pattern type, and this pattern similarity reduced comparisons to a workable number. For example, a female with paired spots collected during 1973, need only be compared with 36 females, the number of females from 1972 possessing paired spots. Minute, individual variations then permitted positive identification and matching (Fig. 1). If a female was not matched during the first series of comparisons, a second series was made to reduce the potential of error. All matchups were examined by the author, his wife and at least one other person for verification.

RESULTS AND DISCUSSION

One-hundred and nineteen brooding females were collected and photographed during the last two weeks of August 1972. During mid-June to late-August 1973; 316 brooding females were collected and photographed in the same 140-m stream segment. The disparity in yearly sample sizes is not only a function of the time spent searching, but the manner of search. In 1972, only
those females brooding in relatively accessible areas (i.e., under moss, stones and logs) were recorded. During 1973, the search included selectively digging 2-4 cm into muddy stream banks and sorting through rotten logs which had been ignored the previous summer.

Because of the inaccessibility of their nesting sites, it seems inevitable that many of the females photographed during 1972, may have again oviposited, but were not recaptured in 1973. It seems probable that many gravid females follow root channels and other subterranean passageways deep into the stream bank prior to oviposition. Huheey (1975) reported observing the emergence of a *D. ochrophaeus* and her brood from a stream bank. This suggests that the use of a photo-technique (or for that matter any mark-recapture technique) may result in misleading data related to population density, reproductive frequency and survivorship.

Although the photo-technique described above has apparent drawbacks when applied to population dynamics of woodland-stream salamanders, the following may be implied from its use in the present study: (1) some (probably most) females oviposited in successive summers; (2) females remain in, or return to the same segment of a stream for reproductive purpose during successive years.

My recapture data support an annual reproductive effort for some females (Table 1), although a biannual cycle as well as a cycle in which females oviposited three times in two years remain possibilities. I have observed gravid females, apparently capable of oviposition, as late as mid-October; but the number of such females was limited and a careful check of the surface habitat revealed no brooders. Nevertheless, it is possible that some females oviposit in hibernacula during the winter months (Tilley, 1973:397) and thereby escape detection. The developmental period for *D. ochrophaeus* ranged from 57 to 74 days, and it seems improbable that individuals which had oviposited in the late spring or early summer could have developed a fully yolked set of follicles by mid-October. This contention is supported by metabolic studies of the species (Fitzpatrick, 1971, 1973). Fitzpatrick (1971:685) noted that females, once they had terminated brooding, foraged until temperatures consistently dropped below 10°C (mid-October in Ohio, the site of his study). During this foraging period, females replaced lipids and lean body tissues depleted as a result of brood maintenance; and, at the same time, produced intermediate sized follicles. When environmental temperatures dropped below 10°C for an extended period, *D. ochrophaeus* exhibited a metabolic "shut down" as an apparent means of energy conservation (Fitzpatrick, 1971:688). Vitellogenesis was not completed until early spring (Fitzpatrick, 1973:49) when the average daily low rose above 10°C. Perhaps females observed by me in mid-October were gravid for the first time, but had matured too late in the previous reproductive season to successfully mate and oviposit.

The photo-technique utilized in this study not only confirms that *D. ochrophaeus* females oviposited in successive summers, but that reproductive effort by a given female tends to occur in the same segment of the stream during successive years (Table 1). This may be a consequence of females remaining within a small home area throughout the year; but more likely it indicates that gravid females migrate (home) from nearby terrestrial habitats to a "preferred" or "previously known" stream segment during the reproductive season. The tendency of an individual to remain in or return to its home area or birth place is defined as philopatry (Mayr, 1965:670). Although

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some females may remain within the stream channel throughout the year, the species, as a whole, is terrestrial and during the spring and early fall, adults may often be observed beneath rocks and logs far from the nearest stream. Furthermore, the ability of non-brooding plethodontid salamanders to return to a home area following displacement is well documented (Barthalmus and Bellis, 1969; Barthalmus and Savidge, 1974; Huheey and Brandon, 1973:71-73; Madison, 1969; Madison and Shoop, 1970); as is homing to the nest by brooding females (Forester, 1974:49; Gordon, 1961:201; Rose, 1966; Snyder, 1971:75-77; Wood, 1968).

If females return to a specific stream area in successive years, it seems logical to ask what selective advantage is conveyed by such behavior? Twitty (1961:420-429) observed reproductive migrations of newts (Taricha) and determined that a high proportion of both sexes returned yearly to the same stream segment. Twitty (pp. 420-421) noted that philopatry served to partition the resources contained within the reproductive habitat and wondered to what extent this behavior might obstruct gene flow within a population.

In the present study of *D. ochrophaeus*, only the behavior of brooding females was considered, and therefore the effect of inbreeding on gene flow is beyond the scope of this paper. If females exhibit a tendency to remain in, or return to, a given locality for reproductive purposes, two potential adaptive advantages must be considered: spatial and trophic resource partitionment.

There can be little doubt that *D. ochrophaeus* females occur with greater frequency in certain stream segments. However, this disproportionate distribution can hardly be considered density dependent, spatial partitionment, since nesting sites are strongly correlated with the quality of the habitat. The stream described in this paper represents a habitat fluctuating between marginal and optimal. In segments of the latter type, females occurred in the greatest densities, occasionally as close as four cm; while in segments of the former type, the number of females was minimal. Disproportionately large numbers of females were collected in the following segments: 0-1, 9-16, 24-25 (Fig. 2). In each instance the stream spread out, forming an extensive, moss-laden seepage. Likewise, disproportionately small numbers of females were collected in segments 1-2, 6-7, 20-24 and 25-27. In these segments either one or a combination of both of the following conditions existed: (1) the stream became subterranean, or (2) the banks were high (45-60 cm) above the water, rocky and relatively dry. In either case, the segment was unsuitable, or at best marginal, as a nesting site.

In a related study (Forester, 1974:26-28), foraging activity by females ceased with oviposition and the onset of brooding behavior. Furthermore, a comparison of the stomach contents removed from adult males, gravid females and brooding females conclusively supports the contention that the latter remain in the nesting cavity from oviposition until the dispersal of hatchlings; and that what feeding occurs is opportunistic. Therefore, spatial partitionment of the habitat is unnecessary to insure the effective distribution of food resources among attending females.

From the preceding discussion, it is apparent that philopatry by *D. ochrophaeus* females did not evolve in response to selective pressures for spatial or trophic partitionment of the reproductive habitat. What then, is the adaptiveness conveyed to the species by this behavior?

I suggest that perhaps philopatry has arisen in *D. ochrophaeus* females as a means of maximizing fitness. During the non-reproductive season females are often found considerable
distances from the water (Bishop, 1943:203; Forester, pers. obs.) In a given geographic area, the
number of aquatic habitats suitable for nesting may be limited (Forester, pers. obs.), therefore,
any behavior which results in a female (or male) returning to (i.e., relocating) a suitable and
possibly isolated stream is adaptive. Furthermore, since most stream margins consist of optimal
habitats interspersed with suboptimal habitats, any behavior which results in a female returning to
a specific segment of a stream in which she has previously experienced reproductive success may
be considered highly adaptive, and therefore, a means of maximizing fitness.

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LITERATURE CITED

Barthalmus, G. T. and E. D. Bellis. 1969. Homing in the northern dusky salamander, Desmognathus fuscus

——— and ——— 1972. Home range, homing and the homing mechanism of the salamander,

8(3):251-254.


——— and H. C. Chrisp. 1933. The nests and young of the Allegheny salamander, Desmognathus

Dunn, E. R. 1926. The salamanders of the family Plethodontidae, pp. 105-119. Smith College, Northampton,
Mass.

Fitzpatrick, L. C. 1971. Thermal acclimation and metabolism in the Allegheny Mountain Salamander,


Forester, D. C. 1974. Parental care in Desmognathus ochrophaeus Cope (Urodela: Plethodontidae): A
Michigan.


Huheey, J. E. 1975. Another function of maternal brooding behavior in salamanders of the genus
Desmognathus. J. Herp. 9(2):257.

——— and R. A. Brandon. 1973. Rock-face populations of the mountain salamander, Desmognathus


——— and R. C. Shoop. 1970. Homing behavior, orientation, and home range of salamanders tagged


Organ, J. A. 1961. Studies on the local distribution, life history, and population dynamics of the salamander


Snyder, D. H. 1969. The function of brooding behavior in the plethodontid salamander, Aneides aeneus: A
Michigan.


