

# **BROODING POSTURES AND NEST SITE FIDELITY IN THE WESTERN SLIMY SALAMANDER, *PLETHODON ALBAGULA* (CAUDATA: PLETHODONTIDAE), FROM AN ABANDONED MINE SHAFT IN ARKANSAS**

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**Abstract.** We examined brooding postures and nest site fidelity in a nesting aggregation of western slimy salamanders (*Plethodon albagula*) from an abandoned mine shaft located in the Ouachita National Forest of southwestern Arkansas. From November 1999–December 2001, we collected a photographic record of brooding and nesting behavior. Females oviposit a free-hanging, grape-like egg cluster within relatively dry nest perches along the walls of the mine shaft. We recorded six female brooding postures from 101 observations involving 101 egg clutches. The most common brooding posture (34.6% of the time) was one in which the female positioned her shoulder region next to or in contact with her egg clutch. Body coiling around the egg clutch occurred 20.8% of the time and at about the same frequency as brooding postures involving eggs touching the head (17.8%) or trunk (22.8%). Six females (6.3%) exhibited nest site fidelity; one female returned to the same nesting site in each of three nesting seasons, but successfully brooded a clutch during the first season only. Egg predation by a ringneck snake was observed during the 2001 nesting season. Our results suggest that brooding postures may function as a predator defense mechanism and may also serve as an anti-microbial defense. The autumn/winter nesting season appears to serve as an anti-predator strategy in this species.

**Key Words.** Western slimy salamander; *Plethodon albagula*; Brooding behavior; Brooding postures; Nest site fidelity; Arkansas.

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Parental investment theory predicts that parental care can be costly for an individual (Trivers 1972). Maternal care, which refers to any form of parental behavior that can increase the inclusive fitness of the parent, involves caring for eggs or young once outside the mother's body (Clutton-Brock 1991). In some species of vertebrates, egg brooding is a costly form of parental care (Ng and Wilbur 1995). A brooding parent may spend an extended period of time and energy with the eggs, thereby becoming more susceptible to predation, or may become stressed because of a trade-off between foraging and brooding (Townsend 1986). Caring for young may even contribute to a reduced reproductive potential for the following season (Hairston 1983).

Brooding is an evolved behavior associated with parental care in most species of lungless salamanders of the family Plethodontidae; brooding behavior is exhibited primarily by females that lay terrestrial eggs (Forester 1979; Ryan 1977; Salthe and Mechem 1974). The possible survival advantages bestowed upon eggs and/or hatchlings by the presence of an attending female are reviewed elsewhere (Bachmann 1984; Forester 1984) and include such benefits as protection from predators, prevention of desiccation, and inhibition of fungal growth or bacterial infection.

Despite a wealth of ethological data on the biology of plethodontid salamanders (e.g., see summary articles in Bruce et al. 2000), there still remain major gaps in our understanding of brooding behavior in most terrestrial plethodontids. This is true for large eastern *Plethodon* (Highton and Larson 1979) in the *P. glutinosus* complex (Highton 1995; Highton et al. 1989). Much of what is known about brooding in *Plethodon* is for the red-backed salamander, *P. cinereus*, a small eastern species. Behavioral studies examining this species have focused on brooding females that either laid and brooded eggs in the laboratory, or were removed along with their egg clutches from natural nesting cavities and then were sequestered in a laboratory setting (Bachmann 1984; Heatwole 1961; Highton and Savage 1961; Ng and Wilbur 1995; Peterson 2000; Vial and Priebe 1967). Many nesting and associated behavioral phenomena, therefore, have been derived from observations made during experimental manipulation of brooding females, their egg clutches, and/or their nesting environments (e.g., Peterson 2000). Naturally-occurring egg clutches

with attending females in most large, terrestrial species of *Plethodon* are unobservable, as clutches normally are deposited in secluded microhabitats beneath the surface of the forest floor or in areas largely inaccessible to researchers (e.g., in burrows). Therefore, critical data are lacking on nesting phenology, nest site selection, nesting frequency and fidelity, microhabitat characteristics of nests, nest preparation, and general brooding behavior. By studying attending females and their nests in situ, researchers could conceivably discover potentially novel information and bridge gaps in our overall understanding of the complex life cycles in these terrestrial salamanders.

The western slimy salamander, *Plethodon albagula*, is a large, upland forest species distributed throughout the Interior Highlands Ecoregion (IHE) of Arkansas, Missouri, and Oklahoma (Conant and Collins 1998). This species is known to utilize caves in which eggs are brooded (Barnett 1970; Noble and Marshall 1929; Wells and Gordon 1958); it also nests in abandoned mine shafts scattered throughout the Ouachita Mountains of the IHE (Saughey et al. 1985, 1988; Heath et al. 1986). Other than the anecdotal accounts mentioned above, no detailed study of the nesting ecology and brooding behavior of females at natural nesting sites exists for *P. albagula*.

We initiated a long-term investigation on the nesting ecology of *P. albagula* in the Ouachita Mountains during the 1999 nesting season. The study site, a mine shaft located in the Ouachita National Forest near Hot Springs, Arkansas, was created in the late 1880s. A substantial number of females were known historically to nest annually within this particular mine (Heath et al. 1986; Saughey et al. 1988); initially, we sought to answer some of the more basic questions about female nesting that were readily observable and recordable without disturbing females and/or their egg clutches. Our primary objectives were to document brooding postures and nest site fidelity by female *P. albagula*.

## MATERIALS AND METHODS

The study site, Spillway Mine, is an abandoned mine shaft located in the vicinity of Blakely Mountain Dam (Garland County, Arkansas). The mine, a linear shaft measuring approximately 2 m in height and 1.5 m in width, extends horizontally approximately 149 m into an east-facing, moderate-

ly-sloping, rocky hillside. Entrance to the mine is gated; a narrow, sloping crawlspace leads onto the mine floor. The first 30–35 m of the shaft floor contain a pool of water nearly year-round. For the present study, we periodically (mostly monthly) made 11 visits to the mine, starting on 5 November 1999 and ending 30 November 2001. These visits cover portions of three nesting seasons. The typical nesting season spanned from late August–late January. Nesting females and their egg clutches were rarely touched or physically disturbed during the first two nesting seasons, although we did measure nesting microhabitats during the 2000–01 nesting season.

We employed a photographic, mark-recapture method to identify females (Forester 1977) from early November 1999 through early October 2001; thereafter, we permanently marked females using visible implant fluorescent elastomer (VIE) dyes (Donnelly et al. 1994). Also during October 2001, we assigned each individual nesting site a numerical location marker to facilitate monitoring of nesting chronology. At this time, females were taken from their egg clutches. We measured snout-vent length (SVL, from the tip of the snout to the anterior margin of the vent to the nearest mm), tail length (TL, to the nearest mm), and mass (to the nearest 0.1 g) before returning females to their nests. Egg clutches with attending females were routinely photographed in situ at nesting sites that were conspicuous: i.e., those found in minor crevices, perches, and depressions along the exposed surface of each wall face. Black and white photographs for Figs. 1 and 2 were reproduced from scanned color slides using Adobe Photoshop 5.0. Some brooding females were excluded from the study due to our inability to obtain precise photographs of their brooding postures. The linear distance within the shaft had been measured previously by U.S. Forest Service personnel into 3.06-m (10-ft) increments using numerically-labeled metal stakes; therefore, we adopted out of convenience the use of English linear distance (in feet) from the mouth of the mine to an individual female, a brooding female, and/or an egg clutch. This numbering system helped designate individual females and/or nesting sites and hastened data gathering. For example, the female in Fig. 2 is L361.5, representing a brooding female whose nest is located on the left wall of the mine shaft at a distance of 361.5 ft (110.5 m) from the entrance.

As is the case for most plethodontid salamanders, brooding individuals of *P. albagula* position

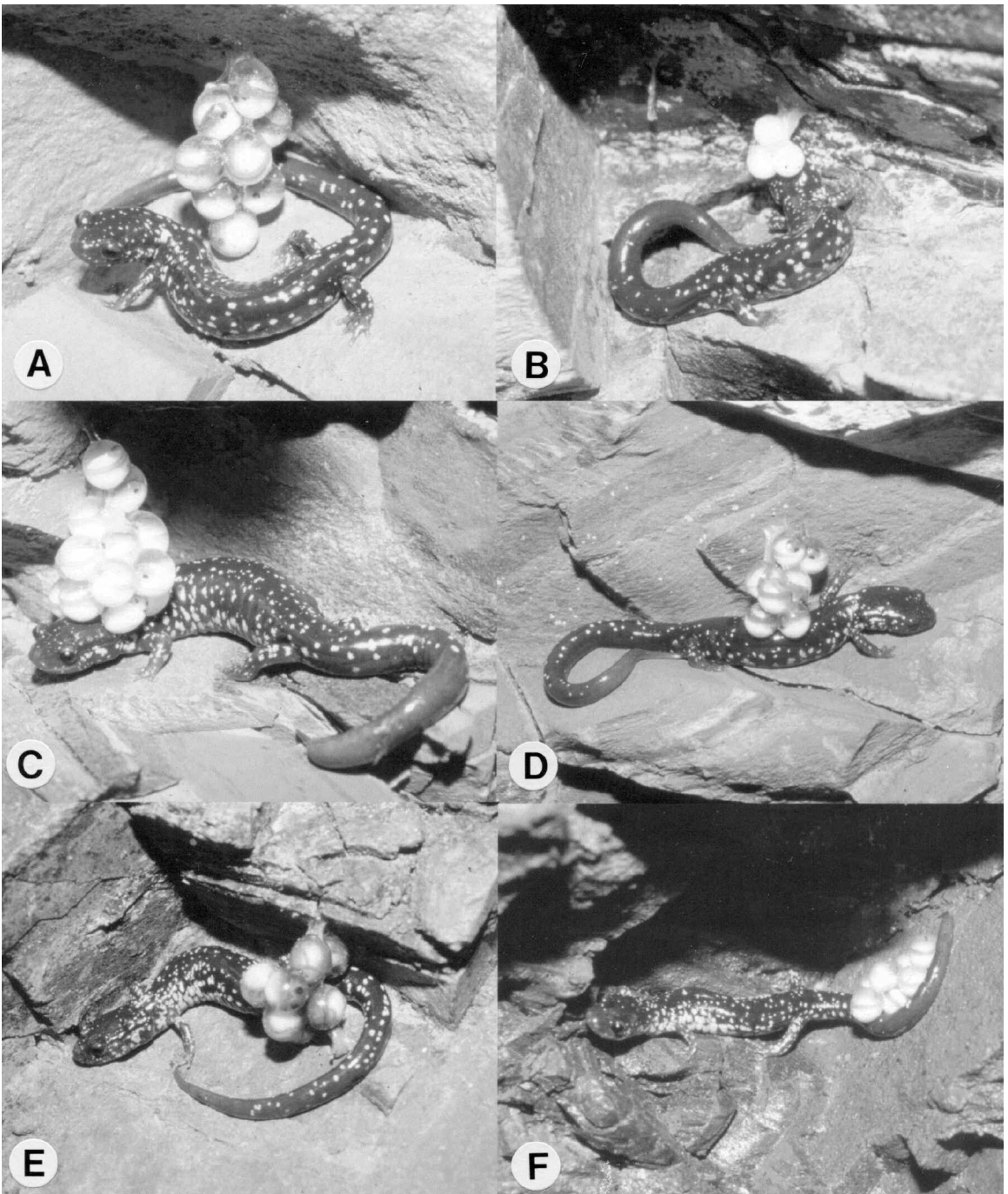
their bodies in contact with or in close proximity to their developing egg clutches. In most instances, only a small number of eggs within a clutch were observed to be actually touching a female's body. To assist in our analysis of brooding posture, we grouped the most common variations in female body position, tallying (from photographs) only those where maternal contact (or near contact) was evident; nearly all of these belonged to one of six of the following categories: (1) egg clutch encircled by body (EEBD); (2) eggs near or touching head and snout (ETHD); (3) eggs near or touching shoulder region (ETSH); (4) eggs near or touching body trunk (ETTR); (5) eggs near or touching pelvic region (ETHP); and (6) eggs near, touching, or encircled by tail (ETTL).

Postural data for egg contact (or near contact) with body regions were analyzed using Chi Square tests. To avoid pseudo-replication (using multiple observations of the same female), only the initial body posture of each female was utilized in the above analysis.

## RESULTS

Nest site microhabitats along the walls of the mine shaft normally allowed a female to oviposit and brood a single, grape-like, egg cluster in a cavity such that the eggs hung freely, and the female could rest on a horizontal surface below the egg clutch (see nesting perches in Figs. 1 and 2). Occasionally, we observed oviposition as females glued individual eggs directly to the gelatinous, primary stalk or to previously-oviposited eggs already attached to that stalk. For example, one female posed with her front feet on the substrate below the nesting site. She then twisted her body to invert the pelvic girdle so that the cloaca was adjacent to the ceiling of the nesting site. Oviposition appeared to be a lengthy process as one female spent more than an hour laying a single egg.

The point of stalk attachment for the egg cluster was on the ceiling/slanted wall of a crevice or on an exposed surface within a shallow depression; each egg clutch was apparently positioned to allow the clutch initially to hang freely. As embryonic development progressed, the egg clusters often changed configuration dramatically during growth of individual embryos. Of the 51 egg clutches recorded for 2001, seven (14.3%) were known to fall from their attachment site or to disappear. Two

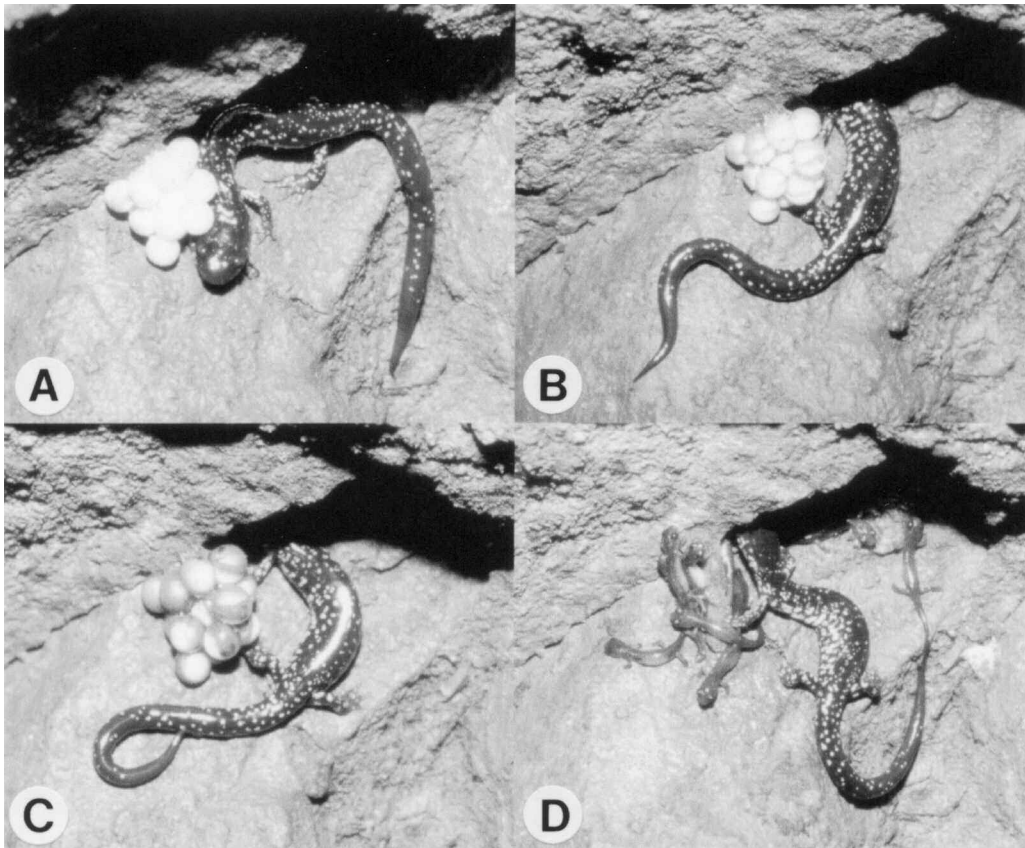


**Figure 1.** The most common brooding postures in female *Plethodon albagula* from Spillway Mine. A–F are representative positions EEBD, ETHD, ETSB, ETTR, ETHP, and ETTL, respectively (see text for explanations). The gelatinous, egg stalk from a previous nesting season can be seen hanging to the left of egg clutch in B.

of the fallen egg clutches hatched on the ground with the female attending the eggs.

A total of 101 brooding females provided 101 postural observations during the three nesting sea-

sons. Average SVL, TL, and mass of 36 brooding females measured during the 2001 nesting season were 61.2 mm (range, 55–72 mm), 65.1 mm (range, 58–84 mm), and 4.7 g (range, 3.9–8.1 g), respec-



**Figure 2.** Brooding postures of a female *Plethodon albagula* (L361.5 = 110.52 m) during the 2001 nesting season. A–D correspond to examination dates 14 September, 28 September, 26 October, and 30 November, respectively.

tively. The most common brooding position was category 3 (ETSH), occurring 34.6% (35/101) of the time; this was followed by postures 4 (ETTR, 22.8%, 23/101), 1 (EEBD, 20.8%, 21/101), 2 (ETHD, 17.8%, 18/101), 5 (ETHP, 3.0%, 3/101), and 6 (ETTL, < 1.0%, 1/101). The six postural categories were not equally observed. Position 3 was most frequently displayed, and positions 5 and 6 were performed least frequently ( $\chi^2 = 48.1$ ,  $df = 5$ ,  $P < 0.001$ ). Positions 1, 2, and 4 had nearly identical expression frequencies ( $\chi^2 = 0.45$ ,  $df = 2$ ,  $P < 0.975$ ).

Less than 3% (3 of 101) of the brooding females was observed venturing more than 0.5 m from their egg clutches. As embryonic development progressed, female movement sharply decreased. A female's brooding posture often changed between visits. Among five females that were observed in at least two nesting seasons, considerable variation in body posture was evident (Table 1). Among these females, the most common brooding posture recorded was category 3 (ETSH) followed by cate-

gories 1 (EEBD), 2 (ETHD), and 4 (ETTR). We also observed that several females maintained a specific posture for a prolonged period of time. A striking example of this behavior is shown in Fig. 2, in which a female maintained a presumed stationary position between mine visits (a span of 29 d). Even following the hatching of her offspring, this female remained in the ETTR brooding position.

We verified that at least six females (six of 95, 6.31%) exhibited nest site fidelity. Three brooding females were observed at a specific nesting site (L276 = 84.4 m, L308 = 94.2 m, and L341 = 104.3 m) in the 1999 and 2001 seasons. Interestingly, different females utilized each of these same nesting sites during the 2000 nesting season. Two other brooding females were found at nesting sites (L280.5 = 85.8 m and R198 = 60.5 m) during the 2000 and 2001 nesting seasons. These data suggest that at least some female *P. albagula* oviposit during consecutive reproductive seasons, whereas others may exhibit the more typical biennial reproduc-

**TABLE 1.** Most common body postures in five brooding female *Plethodon albagula* observed during at least two nesting seasons. See text for explanation of abbreviations for categories 1–4. The plus sign (+) represents an observed posture.

Female	EEBD 1	ETHD 2	ETSH 3	ETTR 4
L276				
5 November 1999	–	–	+	–
30 December 1999	–	+	–	–
28 September 2001	–	–	+	–
26 October 2001	–	+	–	–
30 November 2001	+	–	–	–
L308				
5 November 1999	+	–	–	–
14 September 2001	–	–	–	+
28 Sept.ember 2001	+	–	–	–
26 October 2001	–	–	+	–
30 November 2001	+	–	–	–
L341				
5 November 1999	–	–	+	–
14 September 2001	–	–	–	+
26 October 2001	–	+	–	–
L280.5				
2 September 2000	–	–	–	+
6 October 2000	–	–	+	–
3 November 2000	–	–	+	–
14 Sept.ember 2001	–	+	–	–
28 September 2001	+	–	–	–
26 October 2001	+	–	–	–
30 November 2001	–	+	–	–
R198				
6 October 2000	–	–	+	–
3 November 2000	–	–	+	–
20 December 2000	–	–	–	+
14 September 2001	–	–	+	–
28 September 2001	+	–	–	–
26 October 2001	+	–	–	–
30 November 2001	–	–	+	–
Totals	8 (29.6%)	5 (18.5%)	10 (37.0%)	4 (14.8%)

tive cycle of other members of the *P. glutinosus* complex (Highton 1962; Semlitsch 1980; Trauth 1984). In one case, a brooding female was observed at the same nesting location (R335) during all three nesting seasons. In 1999, she successfully brooded a clutch of 14 eggs at R335 (104.2 m). In 2000 and 2001, she returned to the same nesting site without producing a clutch. In 2001, a clutch was found on the ground within 1 m from her nesting site; this

might have been her clutch. This female, however, remained close to her 1999 nesting site and was observed on several occasions defending this site from a neighboring brooding female (R334 = 102.1 m). Three attacks were observed within a 24-h period; the neighboring female was driven away by bites to her body and tail. Lastly, one other brooding female was found occupying nest site L269 (82.2 m) in 1999, but occupied site L265 (81.05 m)

during the 2000 nesting season. She did not appear to produce a clutch in 2000. Predation of a nest by a ringneck snake (*Diadophis punctatus*) was observed on one occasion (R8 = 2.4 m). Two egg clutches (R10 = 30.6 m and L20 = 6.1 m) disappeared within 2 wk after oviposition. At least two unattended egg clutches were observed to harbor fungal growth, and neither hatched successfully.

## DISCUSSION

Semiaquatic plethodontids, such as *Desmognathus brimleyorum* (Trauth 1988), *D. fuscus* (Hom 1987; Juterbock 1987), and *D. ocoee* (Forester 1984), attend their eggs by way of body surface contact in nesting conditions typically described as being moisture-laden with a saturated substrate within an enclosed nesting cavity (Forester 1984). Variation, however, exists in the selection of nesting sites among *Desmognathus* species and presumably reflects some degree of adaptability in desmognathine salamanders to local environmental conditions (Martof and Rose 1963). One might, therefore, expect similar variation in terrestrial plethodontids as females choose suitable nesting conditions for brooding chambers. Our results indicate that female *P. albagula* oviposit egg clutches in relatively open, exposed nesting perches in the mine shaft; this type of nesting microhabitat is most similar to the cave microenvironment as previously described for this species (Barnett 1970; Noble and Marshall 1929). The assumption that brooding plethodontids possibly reduce the desiccation of their egg clutches during incubation by preventing water loss through body contact with their eggs, as reported for *D. ocoee* (Forester 1984), appears less plausible for *P. albagula*. Potential full body contact or near contact through body coiling (our EEBD) around the egg clutch in *P. albagula* occurred only about 21% of the time. Wareing (1997) found that brooding female red-backed salamanders (*P. cinereus*) spent 50–80% of their time in direct contact with their egg clutches, but only 21.4% of the time in the body coil position. She found that brooding females exhibited head contacts in 57.1% (16/28) of the observations in a laboratory setting, whereas Hom (1987) found that eggs were usually lying on the dorsal surface of the head, neck, and shoulders of females of *D. fuscus* in natural nests. In *P. albagula*, a female's selection of an attachment site for her egg clutch may have some

influence on whether she could achieve and maintain a particular brooding posture; however, we suggest that additional factors other than the prevention of egg desiccation might better explain a female's body position and response to her egg clutch.

Suspension of the egg clutch from an overhanging rock face undoubtedly allows full air circulation around the entire egg cluster, thus potentially ensuring adequate respiration of embryos in a terrestrially-laid egg. This egg attachment method also may make it easier for the female to exude antimicrobial secretions on the eggs. Antimicrobial properties of amphibian secretions are well known (see review by McCallum 1994). If the egg cluster were lying on the ground, the surface with the most contact with the substrate would be the most difficult for the female to apply secretions. In this way, suspending the mass from the rock face may function as a protective method from pathogenic attack. With respect to the two egg clusters that we observed with obvious fungal growth in them, both had fallen. Whether they had fallen and then became infected (or were, perhaps, infertile and had been abandoned) could not be determined. Collembolids were observed congregating on old egg stalks and on the remains of egg clutches, but they were not seen on protected egg clutches. This observation suggests that collembolids may avoid the brooding female's secretions or that she may feed upon them when they are found on the egg cluster.

Suspending the egg cluster from an overhang has an additional advantage in that a female can detect if something is attempting to eat her eggs, provided she is near or in contact with them. While individuals of *P. albagula* may be able to see their surroundings in the mine shaft, it is unlikely that they can do so in total subterranean darkness present deep within the talus where they are typically thought to brood eggs. Of the observations in this study, 78.9% of female observations were near or in contact with their eggs. Because another 21% of female observations were in EEBD, it is highly unlikely that most predators could reach the eggs without touching a female or moving the egg cluster against her body. A freely-hanging egg cluster is capable of swaying when bumped (or tapped with a finger). If a neighboring female or other predator were to attack the egg clutch, the egg cluster should swing into the brooder, thus allowing time to flee or defend the nest. It is possible that this mechanism functions primarily against neighboring or maraud-

ing females. We also observed oophagy in a female which was found near a fallen egg clutch; she contained four eggs in her digestive tract (three in the stomach and one in the large intestine). A ringneck snake was observed feeding upon an egg clutch with the resident female posing in a threat display but not attacking the snake or fending it off. Salamander eggs have been retrieved from ringneck snakes' stomach samples (Barbour 1950) suggesting that this behavior may be commonplace. Ringneck snakes are also known to be predators on small species of salamanders and on small individuals of larger species (up to 80% of their diet: Uhler et al. 1939; see also Forester 1979). Our observations suggest that posturing is probably not an effective deterrent against this snake species.

Females typically begin entering the mine shaft and depositing eggs in late August or early September; most females have completed brooding by late December. Because of this time frame, primary predators such as snakes are hibernating, leaving only conspecifics to attack eggs. A temporal displacement of the brooding season in *P. albagula* precludes most snake predation, except in the very early part of the season. Snake predation may provide a significant evolutionary force, selecting against early brooding females and also those females that brood their egg clutches relatively close to the mouth of the mine shaft. Females that oviposit farther away from the mouth of the mine presumably have a greater chance for survivorship, making them less accessible to snakes compared to those females ovipositing near the mouth of the mine.

In conclusion, female *P. albagula* devote an extended period of time brooding their egg clutches during an autumn/winter nesting season. Nest site fidelity and annual oviposition were observed in this species for the first time. During brooding, attending females make contact with eggs using several postures. The adaptive significance of this egg guarding behavior remains unclear, although anti-predator and anti-microbial mechanisms seem most plausible.

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