

ZAPPALORTI, R. T., AND H. K. REINERT. 1994. Artificial refugia as a habitat-improvement strategy for snake conservation. Pp. 369–375. In J. B. Murphy, K. Adler, and J. T. Collins (Eds.), *Captive Management and Conservation of Amphibians and Reptiles*. Society for

the Study of Reptiles and Amphibians, New York, New York, U.S.A.

Accepted: 24 May 2006

Associate Editor: Brad Moon

*Herpetologica*, 62(3), 2006, 292–301  
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## FECUNDITY, REPRODUCTIVE ECOLOGY, AND INFLUENCE OF PRECIPITATION ON CLUTCH SIZE IN THE WESTERN SLIMY SALAMANDER (*PLETHODON ALBAGULA*)

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**ABSTRACT:** We investigated the reproductive ecology of the western slimy salamander (*Plethodon albagula*) in an abandoned mine shaft in the Ouachita National Forest of south-central Arkansas. The mine habitat provided an opportunity to observe nesting behavior, quantify reproductive output, and evaluate the influence of precipitation on fecundity for a population of *P. albagula* that utilize this particular mine shaft to brood and defend egg clutches. We collected reproductive data on 372 clutches between 1982 and 2004. There was no relationship between the number of eggs per egg clutch versus egg size; snout–vent length, body mass, and tail length were not correlated with clutch size. Thirteen females were found to exhibit nest site fidelity, and 10 females exhibited nest securing. Neither nest site fidelity nor nest securing was found to influence reproductive output by females. The amount of precipitation one year prior to oviposition was correlated with the average number of eggs per clutch. It appears, therefore, that precipitation influences fecundity in this population.

**Key words:** Arkansas; Fecundity; Nest securing; Nest site fidelity; Precipitation; *Plethodon albagula*; Plethodontidae; Reproduction

PLETHODONTID salamanders are excellent organisms for determining ecosystem integrity; for example, Welsh and Droege (2001) proposed that plethodontid salamanders are ideal indicator species for assessing the integrity of forest ecosystems in North America. This argument was based on the sensitivity of plethodontids to environmental variation and on the low temporal variation in counts of plethodontids from repeat surveys within a given site. Yet, because of their secretive nature, there is a lack of information concerning major aspects of plethodontid ecology. Data concerning reproduction by species of large *Plethodon* in a natural setting are especially sparse. Most information pertaining

to the reproductive habits and productivity of some species has been gathered from necropsied specimens, laboratory observations, and anecdotal accounts. Furthermore, smaller eastern species of *Plethodon* (chiefly *P. cinereus*) are the focus of most laboratory studies. Other than seminal studies on the life history of large eastern *Plethodon* (Highton, 1956, 1962, 1995; Highton et al., 1989), little information is known concerning the reproductive ecology of most species within the *Plethodon glutinosus* complex (Highton and Larson, 1979).

Reproductive traits in salamanders are known to be contingent upon a number of factors. Reproductive output has been correlated with mass (Tucker, 1999), body size (Tilley, 1968), snout–vent length (Bruce, 1969; Fraser, 1980; Hairston, 1983; Lotter, 1978; Nagel, 1977; Semlitsch, 1980; Semlitsch and West, 1983), lipids (Scott and Fore, 1995),

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and food abundance (Yurewicz and Wilbur, 2004). Moreover, the number of eggs per clutch and size of the eggs have been linked to a tradeoff between fecundity and the positive relationship between body size and hatchling survivorship (Hairston, 1983). Therefore, examining fecundity of natural populations is vital to provide information related to the life history and ecology of these abundant and widespread organisms. This information, in turn, can be used for management decisions dealing with woodland salamanders.

Trauth et al. (2006) documented nest site fidelity (NSF) in *P. albagula* for several females that returned to and secured specific nesting sites. This phenomenon has not been documented, to our knowledge, in other caudates; however, Mathis et al. (1995) reviewed site tenacity in *P. taylori* (formerly *P. glutinosus*, see Nishikawa, 1990) and *P. cinereus* (Gergits and Jaeger, 1990), and more recently site fidelity has been documented in *P. angusticlavius* (Briggler and Puckette, 2003), *P. cinereus* (Maerz and Madison, 2000), *P. ouachitae* (Anthony et al., 2002), and *P. kentucki* (Marvin, 2001). Marvin (2001) hypothesized that habitat site fidelity may increase reproductive success and, thus, ensure optimal foraging and ovipositional sites. Another phenomenon, nest securing, in which a female positions herself at a specific nest site for an extended period prior to oviposition, has also never been documented in *Plethodon*. Forester (1981), however, observed this behavior in *Desmognathus ochrophaeus*.

Climate, primarily in terms of humidity and temperature, is known to spur breeding migration and influence reproduction in aquatic-breeding ambystomatid salamanders (Baldauf, 1952; Briggler et al., 2004; Palis, 1997; Semlitsch et al., 1996; Semlitsch, 1985; Sexton et al., 1990) and provide suitable breeding conditions for some members of the family Plethodontidae (Semlitsch and McMillan, 1980; Corser and Dodd, 2004). Environmental conditions have been found to influence activity in *Plethodon* (Grover, 1998; Heatwole, 1962; Feder, 1983; Semlitsch and West, 1983). However, the influence of climate on the reproductive ecology of salamanders belonging to the genus *Plethodon* is not well documented.

Our study focused on *Plethodon albagula* (western slimy salamander), a large woodland salamander that typically inhabits rocky wooded hillsides and seepages of the Interior Highlands ecoregion from southern Missouri throughout northern and western Arkansas and into eastern Oklahoma (Conant and Collins, 1998; Trauth et al., 2004). *Plethodon albagula* is one species that was named following the creation of the *Plethodon glutinosus* species complex (Highton et al., 1989). The life history of this species is characteristic of the genus *Plethodon* in that mating and oviposition occur terrestrially, and females brood their egg clutches from oviposition until hatching (Pough et al., 1998). Egg deposition typically occurs in rotting logs, under large rocks or in underground rock crevices, and occasionally in the twilight zones of caves or mine shafts (Noble and Marshall, 1929; Trauth et al., 2004; Trauth et al., 2006; Wells and Gordon, 1958). In Arkansas, females of *P. albagula* oviposit and brood egg clutches from late August to late January (Trauth et al., 2004), and to our knowledge, no study has focused on the natural reproductive ecology of this species.

An abandoned mine shaft constructed in the Ouachita National Forest near Hot Springs, Arkansas, offered a unique opportunity to gain insight into the ecology of this widespread species. Historically, *P. albagula* has been found to utilize the mild conditions (elevated humidity and reduced temperatures) that the mine offers for both refuge and reproductive purposes (Heath et al., 1986; Saugey et al., 1988; Trauth et al., 2006), and females of *P. albagula* have been documented ovipositing and brooding egg clutches along the mine shaft walls since 1982 (D. Saugey, unpublished data). Our objectives were to document the reproductive ecology of the *P. albagula* within this abandoned mine shaft. As stated above, the relationship between body parameters and fecundity in *Plethodon* is controversial; therefore, we tested for relationships between body parameters and clutch size. Also, given the opportunity to examine females both returning to and securing specific nest sites over a period of years, we tested the differences of clutch sizes of females exhibiting nest site fidelity and nest

securing to determine if these phenomenon hinder reproductive output. Furthermore, in attempt to determine the influence of precipitation on reproduction, we examined whether a relationship existed between precipitation and fecundity in *P. albagula*.

#### MATERIALS AND METHODS

This study was conducted at Spillway Mine located in the vicinity of Blakely Mountain Dam (Garland County, Arkansas). The linear mine shaft, measuring approximately 2.0 m in height and 1.5 m in width, extends horizontally 149 m into an east-facing, moderately-sloping, rocky hillside. The mine's entrance is gated and leads onto a sloping crawlspace where 30–35 m of the initial shaft floor contains a shallow pool of water nearly year round. Air temperature remains around 16 C.

For the present study, we made 160 visits to Spillway Mine from August 1982 to March 2005. Throughout the late summer to mid-winter months (August–January), when females of *P. albagula* brood egg clutches, the mine was visited at least once per month during the years 1982–1988, 1995, and 2000–2004. During these visits, the number of clutches and eggs per clutch were counted. During the 1983–1984 and 2000–2004 visits, egg diameters were measured to the nearest 0.1 mm using calipers (measurements were taken within two weeks of oviposition). During 2001 and 2004, the snout–vent length (SVL, from the tip of the snout to the anterior margin of the vent, to the nearest 1 mm), tail length (TL, to the nearest 1 mm), and body mass (to the nearest 0.1 g) of 48 brooding females (31 in 2001; 17 in 2004) were also measured. SVL and TL were measured using a ruler, and body parameter measurements were made during late fall to minimize clutch abandonment. The number of eggs per clutch was counted at the first observation of each new clutch, and a mean clutch size per year was generated for statistical analysis.

To identify individual females, we utilized the combination of photographic mark-recapture technique, visual implant elastomer dye (VIE) markings (Bailey, 2004), and documentation of the animal's location in the mine. From December 1999 to January 2004,

each brooding female was photographed each time that her clutch was encountered and, during October 2002 and June–November 2004, each adult salamander was photographed and marked using VIE. The linear distance of the mine had been previously measured and labeled with metal stakes in 3.06-m increments by U.S. Forest Service personnel, and beginning in October 2001, each nesting site was given a number to help designate individual females and clutches.

#### Statistical Analyses

*Fecundity.*—Stepwise linear regression analysis was used to test for relationships between body parameter measurements and fecundity. Independently, the mean number of eggs in a clutch ( $n = 48$  in 2001 and 2004) and initial egg diameters ( $n = 17$  in 2004) were used as responses, whereas SVL, TL, and body mass were used as predictors. Linear regression was used to test for a correlation between number and initial egg diameter of eggs in each clutch for 1983–1984 and 2002–2004 ( $n = 91$ ).

*Nest site fidelity and nest securing.*—A Mann-Whitney *U*-test ( $\alpha = 0.05$ ) was used to test for the following: (1) a difference between the SVL of 11 females who were found to exhibit nest site fidelity and 40 females who did not in 2001 and 2004 and (2) differences between the number of eggs in a clutch for 10 females who exhibiting nest securing and 24 females who did not secure nests in 2004. A Wilcoxon signed rank test was used to determine if there was a significant between-year difference in clutch sizes of females who exhibiting nest site fidelity.

*Influence of precipitation.*—Climatic conditions were recorded at the Blakely Mountain Dam's weather station, located approximately 2.0 km from Spillway Mine. Stepwise linear regression analysis was used to test whether precipitation influenced reproductive output (= clutch size), during both the period of 1 August–31 July each year and, because *P. albagula* typically reproduces biennially (Highton, 1956; Trauth, 1984), 1 March–31 February each year, prior to oviposition. Variables from the stepwise linear regression were added or removed only if the variance ratio for the regression was significant at  $P <$

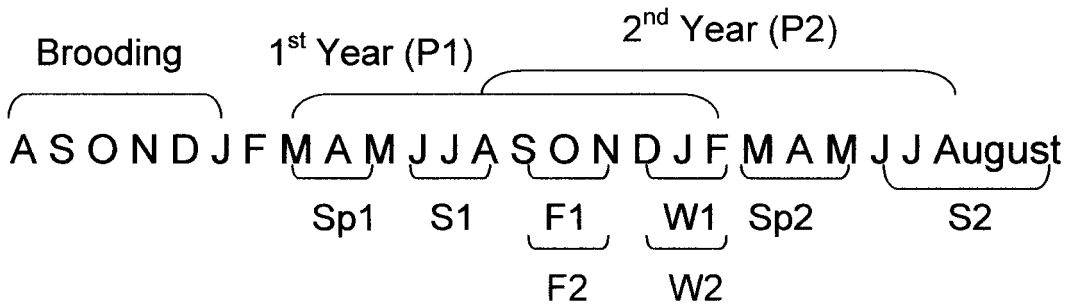


FIG. 1.—Outline of the seasonal and yearly precipitation variables tested with in a biennial reproductive cycle of *P. albagula* in Arkansas. The variables tested were chosen to incorporate the time period from the spring months following oviposition to the late summer months where oviposition would occur in a typical biennial cycle. Precipitation variables were grouped by year (P), and season (Summer [S], Fall [F], Spring [Sp] and Winter [W]) with 1 and 2 dictating the first and second year of the biennial cycle following the brooding season. Amount of precipitation during the second year (P2) of the biennial cycle influenced fecundity in *P. albagula*.

0.05. Stepwise linear regression test were performed using (1) the total number of clutches in the mine (1982–1988, 1995, 1999, and 2000–2004) and (2) the average number of eggs per clutch (1983–1986, 1995, and 2000–2004) as responses, and as predictors, we tested 10 environmental variables (i.e., seasonal precipitation: winter [December, January, February], spring [March, April, May], summer [June, July August], and fall [September, October, November], yearly precipitation, and total number of days the amount of precipitation was zero, less than or over 1.27 cm, and over 2.54 or 3.81 cm [Fig. 1; Table 1]). Monthly climatic data from 1987, 1988, and 1995 were not reported in the database; therefore, only yearly, not seasonal precipitation values could be extracted for these years. As a result, the stepwise regression was performed excluding seasonal precipitation data from these years; however, because yearly precipitation and mean clutch values were not altered, stepwise and linear (to generate Fig. 3) regression were used to examine the relationship between yearly precipitation and mean clutch size.

The number of clutches was determined by counting every visible clutch with an attending female each year. The number of eggs per clutch was counted at the first encounter of each clutch (during August and within two weeks of oviposition), and a mean value was obtained for each year before being used in our analysis. Initial egg diameters were measured the first time that a clutch was

encountered. Statistical analyses were performed using MINITAB® Release 13.32 software.

## RESULTS

A total of 372 clutches, containing 4128 eggs (mean = 10.16) was examined from 1983–2004 (Fig. 2). Tail length, body mass and SVL were not found to be correlated with number of eggs per clutch or initial egg diameters. However, a significant correlation existed between SVL and body mass ( $r^2 = 0.52$ ;  $P = 0.02$ ). No correlation was found between initial egg diameter and the number of eggs in a clutch.

Trauth et al. (2006) documented six females exhibiting nest site fidelity (NSF) in this population, and here we document an additional seven females exhibiting NSF. Each of these seven females brooded a clutch during both the 2002 and 2004 nesting season. Since 1999, 13 females exhibited nest site fidelity at Spillway Mine. Females exhibiting NSF were significantly larger (NSF mean SVL = 64.2 mm, range = 58 to 72 mm; Non-NSF mean SVL = 60.2 mm, range = 55 to 68 mm) than other brooding females in the mine (Mann-Whitney  $U$ -test,  $W = 351.0$ ,  $P = 0.019$ ); however, the clutch sizes of females using a nest site for the second time were not significantly greater than their previous clutch sizes (Wilcoxon signed rank test,  $W = 35.0$ ,  $P = 0.238$ ; Table 2).

We recorded 10 females securing nest sites during June 2004, or remaining at specific

TABLE 1.—Values for each predictor tested in the stepwise regression analysis for years 1 and 2 of the biennial reproductive cycle of *P. albagula* in Arkansas, with the mean number of eggs per clutch for each year. Refer to Fig. 1 for explanation of seasonal precipitation value abbreviations.

|        | $\bar{x}$ clutch size | Seasonal precipitation (cm) |       |       |       |        | Number of days of precipitation (cm) |       |       |       |       |
|--------|-----------------------|-----------------------------|-------|-------|-------|--------|--------------------------------------|-------|-------|-------|-------|
|        |                       | W                           | Sp    | S     | F     | Total  | 0                                    | <1.27 | >1.27 | >2.81 | >3.24 |
| Year 1 |                       |                             |       |       |       |        |                                      |       |       |       |       |
| 1983   | 10.59                 | 52.45                       | 35.71 | 44.66 | 43.66 | 176.48 | 249                                  | 319   | 37    | 23    | 11    |
| 1984   | 9.61                  | 16.33                       | 43.13 | 26.94 | 43.66 | 130.06 | 239                                  | 306   | 24    | 16    | 12    |
| 1985   | 12.56                 | 30.07                       | 36.09 | 31.52 | 28.04 | 125.72 | 223                                  | 320   | 39    | 20    | 9     |
| 1986   | 11.86                 | 24.54                       | 38.96 | 23.37 | 75.54 | 162.41 | 261                                  | 333   | 27    | 11    | 6     |
| 1995   | 10.64                 | 29.18                       | 36.16 | 38.76 | 38.68 | 142.78 | 269                                  | 322   | 40    | 20    | 11    |
| 2000   | 9.41                  | 31.14                       | 52.29 | 23.44 | 26.72 | 133.59 | 275                                  | 323   | 38    | 18    | 7     |
| 2001   | 9.31                  | 28.37                       | 38.81 | 38.81 | 26.72 | 132.71 | 264                                  | 310   | 45    | 23    | 16    |
| 2002   | 9.28                  | 33.09                       | 34.18 | 19.4  | 42.34 | 129.01 | 275                                  | 328   | 35    | 14    | 5     |
| 2003   | 10.48                 | 42.09                       | 44.27 | 21.66 | 33.62 | 141.64 | 259                                  | 321   | 39    | 20    | 10    |
| 2004   | 9.78                  | 19.05                       | 20.44 | 35.86 | 21.38 | 96.73  | 264                                  | 334   | 30    | 17    | 12    |
| Year 2 |                       |                             |       |       |       |        |                                      |       |       |       |       |
| 1983   | 10.59                 | 52.45                       | 43.15 | 26.94 | 43.66 | 166.2  | 246                                  | 329   | 31    | 21    | 13    |
| 1984   | 9.61                  | 16.33                       | 36.09 | 31.52 | 28.04 | 111.9  | 235                                  | 305   | 27    | 16    | 7     |
| 1985   | 12.56                 | 30.07                       | 38.96 | 23.37 | 72.59 | 164.9  | 236                                  | 323   | 37    | 17    | 10    |
| 1986   | 11.86                 | 25.53                       | 46.73 | 48.2  | 34.44 | 154.9  | 252                                  | 319   | 37    | 18    | 12    |
| 1995   | 10.64                 | 29.18                       | 43.71 | 21.51 | 38.68 | 133.1  | 270                                  | 332   | 32    | 19    | 14    |
| 2000   | 9.41                  | 31.14                       | 38.81 | 38.81 | 26.72 | 134.7  | 285                                  | 318   | 34    | 16    | 8     |
| 2001   | 9.31                  | 28.37                       | 34.18 | 19.4  | 42.34 | 124.3  | 264                                  | 313   | 44    | 22    | 13    |
| 2002   | 9.28                  | 33.09                       | 44.27 | 21.66 | 33.62 | 132.6  | 263                                  | 321   | 39    | 16    | 10    |
| 2003   | 10.48                 | 42.06                       | 20.44 | 35.86 | 21.38 | 119.7  | 292                                  | 357   | 37    | 23    | 12    |
| 2004   | 9.78                  | 19.05                       | 29.97 | 43.66 | 35.15 | 127.8  | 255                                  | 325   | 37    | 12    | 7     |

nest sites in the mine until the fall of 2004, at which time each female oviposited. Therefore, we hypothesized that these females were securing and defending specific nest sites, as brooding defense behavior has been observed at Spillway Mine (Milanovich et al., In press). However, no significant difference was found between the clutch sizes of females that secured nests and the clutch sizes of females that did not (Mann Whitney *U*-test,  $W = 146.5$ ,  $P = 0.214$ ; Table 2). Seven of these 10 females brooded a successful clutch, which was similar to that of the remaining egg clutches from 2004 (67%). The seven females with successful clutches who secured nest sites were found at that specific site for over six consecutive months from taking refuge during the summer months to oviposition to the hatching of their clutch. Three of these females exhibited both nest securing and nest site fidelity in 2004. Finally, stepwise linear regression of 10 climatic variables (Table 1) on the clutch sizes of *P. albagula* in Spillway Mine revealed that total precipitation during the year prior to oviposition was the only significant predictor of clutch size (Fig. 3).

#### DISCUSSION

Fecundity in some plethodontid salamander species has been shown to be correlated with SVL (Bruce, 1969; Tilley, 1968; Trauth et al., 1990). However, in terrestrial *Plethodon* the relationship between SVL and fecundity is not universal. For example, a positive relationship between SVL and fecundity has been reported for *P. cinereus* in some studies (Fraser, 1980; Nagel, 1977), whereas other studies have not found evidence for such a relationship (Blanchard, 1928; Lotter, 1978). However, a positive relationship between SVL and fecundity has been reported for *P. glutinosus* (Semlitsch, 1980), *P. jordani* (Hairston, 1983), *P. larselli* (Herrington and Larsen, 1987), *P. serratus* (Herbeck and Semlitsch, 2000), and *P. websteri* (Semlitsch and West, 1983). All of the above data were obtained by counting the dissected number of mature ova prior to oviposition and correlating the number of ova with SVL of females. We did not find a significant correlation between fecundity and any body parameter that we measured. Because we did not obtain number of mature ova by

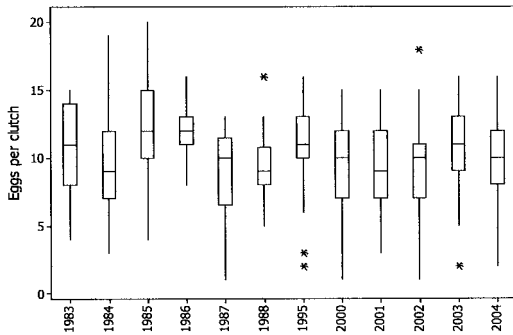


FIG. 2.—Box plot of the clutch sizes of *P. albagula* at Spillway Mine for 12 years from 1983–2004.

dissection, but by actual number of eggs deposited, we propose that terrestrial *Plethodon* may not oviposit the maximum number of eggs allowable. For individual females, the maximum number of mature ova may not be the maximum number of healthy ova at the time of oviposition. Highton and Savage (1961) found that the number of eggs in natural nests were less than the number of ovarian eggs found by Blanchard (1928) in *P. cinereus*, and, in our case, oophagy has been observed at Spillway Mine (Milanovich et al., In press) which may reduce the number of eggs observed. Our findings agree with those of Yurewicz and Wilbur (2004) who reported that larger female *P. cinereus* did not brood larger clutches. Contrary to Hairston (1983) and Salthe (1969), we did not observe a significant relationship between egg diameter and number of eggs; consequently, females that produced larger clutches did not produce smaller eggs, whereas females with smaller clutches did not brood larger eggs.

We found that females exhibiting nest site fidelity (NSF) were larger (SVL) than other females nesting in the mine. Typically, larger females can be viewed as being older females; thus, this phenomenon (larger females exhibiting NSF) may be related to a female's ability to defend the nest site of choice. Another possibility is that a nesting hierarchy exists among females in the population. We found that there were nest sites in the mine that were sought after more often than others. A larger portion (33%) of the nest sites where NSF or nest securing occurred were located within a 100 m stretch of the mine where

TABLE 2.—Summary data of clutch characteristics for the two years *P. albagula* females exhibited nest site fidelity between 2001 and 2004, and for females who secured or did not secure nest sites in 2004.

|                              | Nest site fidelity |        | Nest securing |           |
|------------------------------|--------------------|--------|---------------|-----------|
|                              | Year 1             | Year 2 | Secure        | No secure |
| <i>n</i>                     | 11                 | 11     | 10            | 24        |
| $\bar{x}$ clutch size        | 11.36              | 9.91   | 9.11          | 10.04     |
| median                       | 11                 | 10     | 10            | 11        |
| Quartile ranges<br>(25%,75%) | 8.5,16             | 9,13   | 9,13          | 8,16      |
| SD                           | 3.01               | 2.74   | 2.66          | 3.14      |

a consistent number of clutches were brooded each year. This suggests nest selection is a highly selective process, and we speculate that this is influenced by microhabitat preferences, kinship recognition, or natal site fidelity. Bachmann (1984) found a number of *P. cinereus* nests under a single log; therefore, female *Plethodon* collectively nesting may be a common life history trait used to avoid predators or increase nest success. Briggler and Puckette (2003) found nest site selection was important in hatching success in *P. angusticlavius* nesting in a crevice cave in northwest Arkansas. Furthermore, Trauth et al. (2006) documented a female returning to and defending the same nest site for three consecutive years. We found that this same female returned to the exact site two additional years; thus, she returned to and defended the same nest site for five consecutive years. While Ng and Wilbur (1995) and Yurewicz and Wilbur (2004) found that

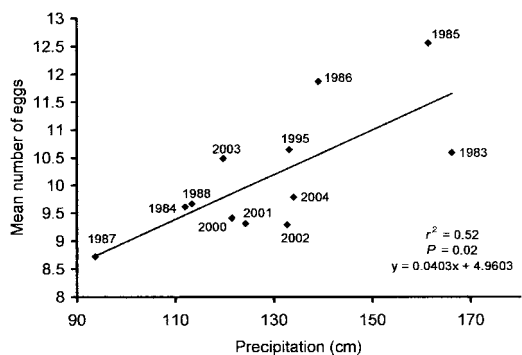


FIG. 3.—The relationship between the average number of eggs per clutch and amount of precipitation during the second year of the biennial cycle ( $n = 12$ ).

brooding status negatively affected future reproduction in *P. cinereus*, Hom et al. (1990) hypothesized, after implementing a dynamic optimization model, that nest defense may not have an energetic cost. Our data imply that the fecundity of females exhibiting NSF or nest securing did not differ from those females who did not return to or secure a specific nest site. These phenomena may actually provide some advantage to the brooding female or her clutch, as three females secured a particular nest site where they previously brooded and clutches with an attending female who secured a nest site were more successful.

Precipitation has been found to influence reproductive output in reptiles (Goldberg 1975; Stamps, 1976; Smith et al., 1995; Taylor, 2003; Wallis et al., 1999) and timing of oviposition in anurans (Telford and Dyson, 1990). While daily activity in salamanders has been associated with moisture (Feder, 1983; Heatwole, 1962), our study indicates that an increase in annual precipitation 12 months prior to *P. albagula* oviposition led to an increase in fecundity the following reproductive season (see Fig. 3). The difference in the response to precipitation during different time periods may be contingent upon the biennial reproductive cycle of *P. albagula*. Under a biennial cycle regime, such as has been observed for *P. glutinosus* in Florida (Highton, 1962) and Alabama (Trauth, 1984), females would not develop ovarian follicles the spring following oviposition, but ova would enlarge beginning the second spring and after mating occurred (Trauth, 1984). Fraser (1980) found that, in female *P. cinereus*, condition during the second year of the biennial cycle did not influence the number of oocytes that matured, but did alter the rate of oocyte maturation. In contrast to Fraser's (1980) findings, our results indicate that the condition of each female during the second year of the biennial cycle determines the number of oocytes that can be oviposited. This effect may explain the lack of correlation between female size and fecundity found in terrestrial *Plethodon* both in our study and others (Blanchard, 1928; Fraser, 1980; Lotter, 1978). Fecundity appears to be directly related to foraging opportunities and, conceiv-

ably, the lipid reserves obtained from foraging and not the size (SVL) of the animal.

Activity in terrestrial plethodontid salamanders is known to be humidity dependent (Feder, 1983), and foraging opportunities have been found to be largely restricted to rainfall events or periods of high humidity and optimal temperatures (Fraser, 1976; Jaeger, 1972, 1978, 1980; Jaeger et al., 1995; Maiorana, 1976). For example, Jaeger et al. (1995) found a significant correlation between the mean number of prey per stomach and amount of rainfall. Jaeger (1980) also found foraging success was directly related to rainfall. Although moisture levels were found to increase activity in small-bodied *Plethodon* (Bailey et al., 2004; Petranka and Murray, 2001), Grover (1998) suggested that increased precipitation regulated abundance of arthropods, which could provide more optimal foraging opportunities for larger *Plethodon*, even though activity levels may not increase. Increased food availability has been correlated with fecundity in fish (Calow and Woollhead, 1977; Reznick and Yang, 1993) and reptiles (Jones et al., 1987; Pianka, 1970; Smith et al., 1995; Turner et al., 1969; Vitt and Ohmart, 1977; Wallis et al., 1999), and higher food levels have been found to increase the amount of lipids and alter reproduction in salamanders (Bernardo, 1994; Scott and Fore, 1995). The tail can be important for lipid storage in salamanders (Fitzpatrick, 1976; Maiorana, 1977); Fraser (1980) and Yurewicz and Wilbur (2004) found that females of *P. cinereus* with removed tails produced fewer new ova. Although Yurewicz and Wilbur (2004) found that increased growth (due to increased food rations) did not affect future reproduction, Grover and Wilbur (2002) found female *P. cinereus* in plots with experimentally elevated moisture developed a larger number of ova, which were deposited the following spring, and Maiorana (1977) found female *Batrachoseps attenuatus* oviposited significantly fewer eggs during periods of dry weather. Our data coincide with Grover and Wilbur (2002) and suggest there is an important relationship between fecundity and foraging opportunities in *P. albagula*. The lack of a significant difference between the numbers of eggs in consecutive brooders further supports our

data by showing the influence of precipitation during the year prior to oviposition; i.e., because annual brooders only have one year to obtain lipid reserves to produce new ova. Because we did not find a relationship between the number of days with or without various levels of rainfall, the number of foraging opportunities may be less important than their quality. Rainfall events spanning across a number of days, even though producing less combined rainfall than some one day events, could create more and longer opportunities to forage (Jaeger, 1980).

In summary, we found that the long-term nature of our study allowed us to gain a broad perspective of the trends in reproductive output, reproductive ecology, and the influence of precipitation on fecundity in a large terrestrial *Plethodon*. Fecundity in *P. albagula* was not correlated with SVL, clutch and egg sizes were not interdependent, and long-term fecundity of this population was stable. Reproductive traits (nest site fidelity and nest securing) that we hypothesized would hinder reproductive output did not alter overall egg production. Moreover, the significance of precipitation on the reproductive output of *Plethodon* was clear which gives rise to implications concerning population dynamics and the evolution of life history traits for any number of terrestrial salamanders.

*Acknowledgments.*—We thank R. Grippo and B. A. Wheeler for statistical assistance and M. C. Crump for aid with weather data. Critical review of drafts of the manuscript by R. G. Jaeger, C. Phillips, R. D. Semlitsch, and two anonymous reviewers greatly improved its content. This research was funded by the Department of Agriculture, U. S. Forest Service Challenge Cost-Share Agreement No. 03-CS-11080901-090. SET thanks the Arkansas Game and Fish Commission and the U. S. Army Corps of Engineers for permission to conduct observations of salamanders.

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Accepted: 19 April 2006  
Associate Editor: Mike Sears