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# REPRODUCTIVE BIOLOGY OF THE NORTHERN SLIMY SALAMANDER (*PLETHODON GLUTINOSUS*) FROM A CAVE IN NORTHERN ALABAMA, USA

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**Abstract.**—The Northern Slimy Salamander (*Plethodon glutinosus*) is a common inhabitant of caves throughout its range in the eastern U.S. Despite its abundance and broad distribution, little is known regarding its reproductive biology, particularly from caves and other subterranean habitats. We investigated the reproductive ecology of a population of Northern Slimy Salamanders inhabiting a cave in Marshall County, Alabama, USA, over two nesting seasons: September 2019 to January 2020 and August 2020 to December 2020. We conducted 37 surveys (20 in Season 1 and 17 in Season 2) to monitor the development and success of 26 nests (six in Season 1 and 20 in Season 2) in 90.6-m of cave passageways nearest the main entrance of the cave. We also obtained information on post-hatching parental care and dispersal, and we observed defense and diet behaviors. Oviposition likely occurred from July through August each season. Eggs hatched during an 85-d period that extended from 3 October through 27 December, and we estimated that the incubation period lasted 100–115 d. Clutch size averaged  $7.5 \pm 3.2$  eggs in Season 1 and  $11.7 \pm 2.9$  eggs in Season 2. Nest mortality was high, with complete failure of 54% of nests. Most hatchlings remained in and near nests for 43–66 d before dispersal. During this time, attending females continued to guard and defend their offspring, a behavior not previously reported for this species. We also observed nesting females opportunistically feeding on several cave-adapted invertebrates, including species not previously known from the diet.

**Key Words.**—Cumberland Plateau; diet; life history; nesting; oviposition; parental care; Plethodontidae

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## INTRODUCTION

The Northern Slimy Salamander (*Plethodon glutinosus*) is a large terrestrial lungless salamander (family Plethodontidae) widely distributed throughout much of the eastern U.S., ranging from northern and central Alabama northward into Illinois, Indiana, and Ohio, and northeastward into New York and New Hampshire (Highton et al. 1989; Beamer and Lannoo 2005). Northern Slimy Salamanders are most abundant in mature, mesic forests with large amounts of cover available, such as fallen logs and rocks (Bishop 1941; Grover 1998; Petranka 1998). Moisture is critical for cutaneous respiration in this species, as it is for other members of the family. During periods of prolonged drought and inhospitable temperatures on the surface, Northern Slimy Salamanders are known to move into subterranean habitats to avoid desiccation (Bishop 1941; Beamer and Lannoo 2005).

In karst regions, Northern Slimy Salamanders are known to retreat seasonally into cooler, moister

cave systems in response to inhospitable surface conditions (Taylor and Mays 2006; Camp and Jensen 2007; Niemiller and Miller 2009; Camp et al. 2014; Lamb 2021), and often in great abundance (Niemiller and Miller 2009; Lamb 2021). They are one of the most encountered salamanders in caves in the Interior Low Plateau and Appalachians karst regions in the eastern U.S. (Buhlmann 2001; Camp and Jensen 2007; Niemiller and Miller 2009; Niemiller et al. 2016; Zigler et al. 2020), typically inhabiting the twilight zone of caves during the summer months (Camp and Jensen 2007; Niemiller and Miller 2009; Camp et al. 2014; Lamb 2021). Although generally common throughout its range, the reproductive biology of the Northern Slimy Salamander is poorly known. Timing of oviposition varies geographically in surface habitats, but oviposition likely occurs from July into September (Highton 1962). Few reports of oviposition and egg development exist for surface populations (Rubin 1965), and reports from cave habitats are even rarer (e.g., Camp and Jensen 2004).

Herein, we report the results of a 2-y study on the

reproductive biology of Northern Slimy Salamanders from a cave in northern Alabama, USA, including timing of oviposition, development rates, nest success, and anecdotal observations on feeding and behavior. In this study, we followed the reproductive activities of several female Northern Slimy Salamanders over two nesting seasons through weekly visits from September 2019 to January 2020 and August 2020 to December 2020. In addition to addressing important aspects of the ecology and life history of this species, this study highlights the importance of caves and other karst habitats for reproduction in this species, and other salamanders, as caves provide both mothers and offspring a stable and low risk environment.

### MATERIALS AND METHODS

**Study site and surveys.**—We searched for Northern Slimy Salamanders and, in particular, their nests, at Cherry Hollow Cave (Alabama Cave Survey no. AMS1710) in Marshall County, Alabama. Cherry Hollow Cave is in the Interior Low Plateau karst region within the Tennessee River Basin of northern Alabama. This privately owned cave, developed in Mississippian-aged limestones, occurs in the Whitesburg Mountains, south of the Tennessee River and contains 915 m of human-accessible passages with two entrances: the main spring entrance and an upstream entrance. We limited our study to 90.6 m of cave passages, including the first 56 m of the main cave passage and three shorter offshoots from the spring entrance. These passages averaged  $1.8 \pm 0.4$  m (standard deviation) high and  $2.2 \pm 2.6$  m wide based on measurements taken of the passage every 5 m. Passage width of the study area, however, was variable. For example, the maximum width of the entrance was 11.4 m, but passages in some sections narrowed to 0.2 m. A stream flowed through parts of the study area and exited as a spring at the entrance. The cave walls were scalloped and contained many small cracks and crevices, which were used by female Northern Slimy Salamanders as nesting sites. The floor of the passages included a fast-flowing stream and areas of bedrock-boulder-cobble substrate within which salamanders would hide. Previous surveys by us showed that Northern Slimy Salamanders occurred predominantly in the first 30 m of the cave system, and generally occurred no farther than 56 m into the cave along the main passage.

We conducted surveys every 8 d on average (range of values, 5–16 d) from September 2019 to January 2020 and August 2020 to December 2020.

These dates comprised two nesting seasons, but our visitation depended on weather conditions (Seasons 1 and 2) and COVID-19 concerns (Season 2). We conducted each survey with a team of either two or three researchers, and the surveys consisted of Visual Encounter Surveys (VESs) of human-accessible cave habitats. Our surveys began at the entrance of the cave and continued through the twilight zone into the dark zone within the study area. VESs included searching within debris, gently lifting rocks and other cover on the floor of the cave passage, and searching in crevices along cave walls and ceilings. We returned all cover objects to their original positions to minimize habitat disturbance.

**Imaging and field measurements.**—We used an Extech™ Video Boroscope Inspection Camera (Extech, Boston, Massachusetts, USA) and an Apple iPhone XR (Apple Inc., Cupertino, California, USA) to photograph and video discovered nests from various angles to determine and track nest development, health, and survival. Our goal was to minimize disturbance to prevent attending females from abandoning their nests. The durations of our recordings (videography) of attending females differed, ranging from 1–10 min. We documented the position of each nest and obtained temperature and relative humidity of the nest sites using a handheld Kestrel™ Weather Meter 3500 (Nielson Kellerman, Boothwyn, Pennsylvania, USA) during each visit. Nest position included the horizontal linear distance in meters from the entrance (at the dripline) as well as the height above the floor of the passage. On subsequent surveys, we relocated, photographed, and videographed each nest until either the eggs hatched, or, usually, the young left the nest. We used spotting pattern to identify attending females, and we gave each attending female a unique code name (Appendix Table).

We used the staging table of the congeneric Eastern Red-backed Salamander (*Plethodon cinereus*) to estimate embryonic stages (Kerney 2011). Because we could not track egg development daily and we had difficulties with staging egg development *in situ*, we estimated incubation period as follows. We estimated incubation period for only seven nests (two in Season 1 and five in Season 2). At least one egg hatched in each of these nests, and we were confident in our approximation of when eggs were laid (e.g., we did not overlook a nest during a previous survey). For two nests, we used the midpoint between the dates of the prior survey and the survey during which we

discovered a nest as the estimated date the nest was laid. We took a conservative approach to estimate dates of oviposition for five other nests that we discovered during the first survey of either Season 1 or Season 2. These nests were in early stages of development ( $\leq$  stage 12 *sensu* Kerney 2011). Kerney (2011) does not report specific rates of development for early embryonic stages, but he does mention that the intervals between stages 5 and 6 and between stages 7 and 8 is 24–36 h at 16° C. Marks and Collazo (1998) report that development to midgastrula (stage 7 in *P. cinereus*; Kerney 2011) can take up to 13 d at 13°–14° C in the Seepage Salamander (*Desmognathus aeneus*), another direct-developing plethodontid. During late August and early September in both seasons of our study, temperature of nesting sites ranged from 19.8°–24.4° C, considerably warmer than incubation temperatures of these two studies. Using this information and observations of early

**TABLE 1.** Summary of nests Northern Slimy Salamander (*Plethodon glutinosus*) observed during surveys conducted in Season 1 (September 2019 - January 2020) at Cherry Hollow Cave, Marshall County, Alabama, USA, including number of new nests found during a survey, the number of nests that had completely failed from the previous to the current survey, and the number of nests in which all eggs had hatched and all hatchlings had dispersed from the nest from the previous to the current survey.

Survey date	Nests observed	New nests	Nests failed	All hatchlings dispersed
5 September	4	4		
12 September	4			
19 September	4	1	1	
28 September	5	1		
3 October	5			
9 October	4		1	
17 October	3		1	
24 October	3			
1 November	3			
8 November	3			
15 November	3			
20 November	3			
4 December	3			
12 December	3			
19 December	2			1
27 December	2			
6 January	2			
17 January	1			1
24 January	1			
31 January	1			

development for three other nests for which we were confident of the date of oviposition, we conservatively estimated that oviposition occurred 10 d prior to the date of initial discovery for the remaining five nests. We used the midpoint between the date of the prior survey and the survey for which a hatchling was discovered in a nest as the estimated date of hatching. We considered hatchlings as dispersed from a nest when individuals were no longer observed within 0.5 m of the original site of nest oviposition and typically not observed in the same crevice as the original nest. We observed hatchlings in the vicinity of original nesting sites (within 3 m) but we did not track (i.e., mark) individual hatchlings.

**TABLE 2.** Summary of nests of Northern Slimy Salamanders (*Plethodon glutinosus*) observed during surveys conducted in Season 2 (August - December 2020) at Cherry Hollow Cave, Marshall County, Alabama, USA, including number of new nests found during a survey, the number of nests that had completely failed from the previous to the current survey, and the number of nests in which all eggs had hatched and all hatchlings had dispersed from the nest from the previous to the current survey. Also reported are data that were not available for Season 1, including the number of salamanders, excluding nesting females and their hatchlings observed by life stage (A = adult, J = juvenile, H = hatchling).

Survey date	Nests observed	New nests	Nests failed	All hatchlings dispersed	Salamanders observed
21 Aug	13	13			137 (102A, 35J)
27 Aug	16	3			121 (103A, 18J)
4 Sep	15	2	3		109 (90A, 19J)
11 Sep	13		2		118 (90A, 28J)
18 Sep	11		2		140 (114A, 26J)
27 Sept	11				21 (16A, 5J)
2 Oct	11				12 (9A, 3J)
9 Oct	9	1	3		19 (15A, 4J)
16 Oct	9				7 (7A)
23 Oct	9	1	1		7 (7A)
31 Oct	9				4 (4A)
6 Nov	9				9 (8A, 1J)
13 Nov	9				6 (5A, 1H)
22 Nov	8			1	6 (5A, 1J)
2 Dec	8				12 (8A, 3J, 1H)
18 Dec	6			2	15 (9A, 6H)
28 Dec	5			1	43 (8A, 2J, 33H)

We estimated relative abundance of Northern Slimy Salamanders and other vertebrate species in the study area, particularly in Season 2. We categorized salamanders by size as adults ( $> 55$  mm snout-vent length; SVL), juveniles (20–54 mm SVL), or hatchlings ( $< 20$  mm SVL). To limit disturbance, we coarsely estimated SVL of individuals from photographs and by eye. We used size criteria of these life stages as identified by Highton (1956) for populations of the related Southeastern Slimy Salamander (*P. grobmani*) in Florida.

**Anecdotal observations of nesting behavior and diet.**—In addition to acquiring data on reproductive biology, during the surveys, we obtained information on parental care, defense, and diet. While under illumination, we recorded videos and acquired photographs of attending females interacting with their eggs, their defensive behaviors while we counted eggs, and successful and unsuccessful attempts to consume invertebrate prey by nesting females and hatchlings.

## RESULTS

**Nest abundance.**—We chronicled the development of eggs and behavior of brooding adults for six nests of Northern Slimy Salamanders in Season 1 (2019–2020; Table 1) and 20 nests in Season 2 (2020–2021; Table 2). In Season 1, we discovered four clutches 5 September 2019, one 19 September 2019, and one 28 September 2019. In Season 2, we discovered 13 new clutches 21 August 2020, three 27 August 2020, two 4 September 2020, one 9 October 2020, and one 23 October 2020. We recorded 574 min 35 sec of videos over both seasons, which included 278 min 26 sec of endoscope and 296 min 09 sec of iPhone footage.

**Nest locations.**—We found Northern Slimy Salamanders throughout the length of the study area (from the entrance to the end of the main passage, 56 m deep in the cave), but all nests were  $> 18$  m into the cave (Appendix Table), with a mean distance from the entrance of  $31.8 \pm 13.4$  m ( $23.3 \pm 9.6$  m in Season 1 and  $34.4 \pm 13.1$  m in Season 2). Mean height above passage floor of nests was  $1.2 \pm 0.7$  m in Season 1 and  $1.3 \pm 0.4$  m in Season 2), ranging from 0.0 to 1.7 m. Mean air temperatures recorded at nest sites during Season 1 were  $19.8^\circ \pm 3.9^\circ$  C (range of values  $12.6^\circ$  to  $26.6^\circ$  C) and  $20.8^\circ \pm 2.7^\circ$  C (range of values  $14.3^\circ$  to  $27.5^\circ$  C) during Season 2. Temperatures at nest sites were generally warmer earlier and cooler later

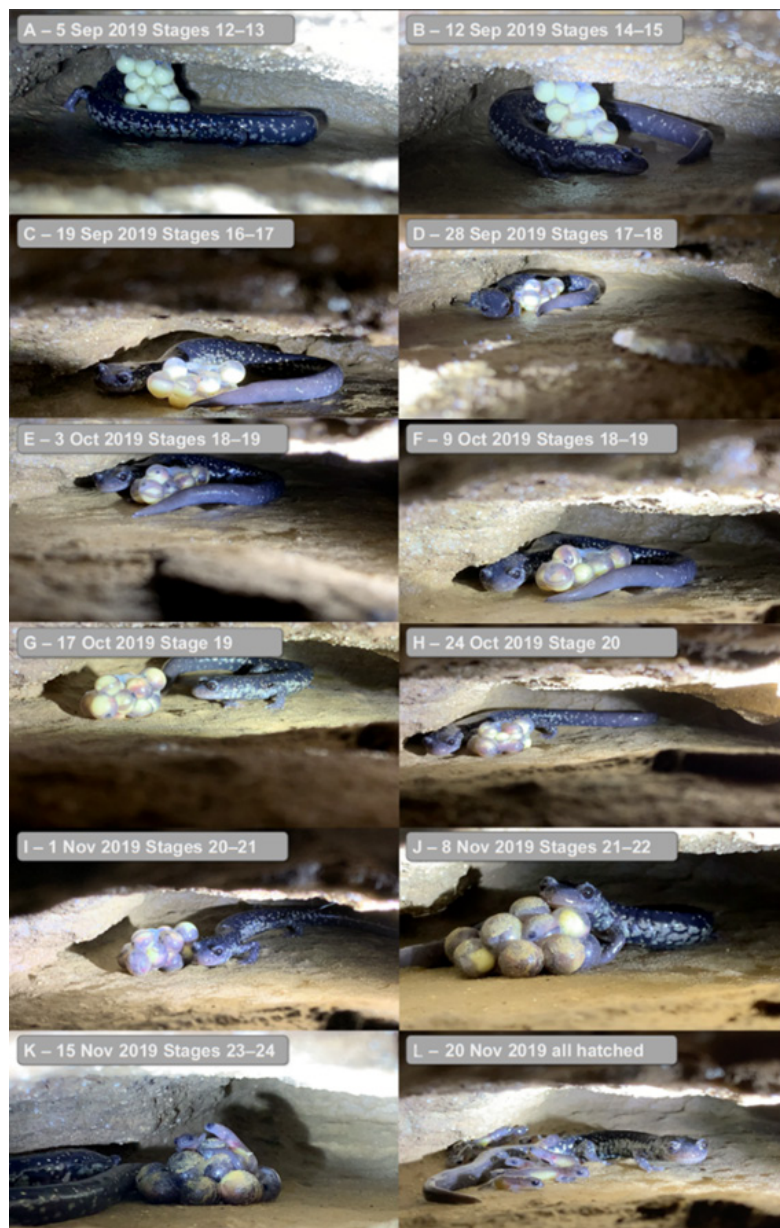
during each nesting season.

Distance separating nests varied. In some cases, nests were located within 10 cm each other, but in other cases, nests were separated by 21.1 m. Most nests were aggregated in two locations: Salamander Condo Room, a small room along the main passage about 18 m from the entrance with a length of 3.5 m, and Tunnel Cluster, a 1.4 m long section of the main cave passage. We found 10 of the 26 nests in the Salamander Condo Room, including five nests in Season 1 and five nests in Season 2. We did not find any nests the Tunnel Cluster in Season 1, but we found five nests there in Season 2. We found nests in the same three crevices in each season, but the females nesting in Season 2 were not those that nested in Season 1. In some cases, the same locations (within 10 cm) were used as nesting sites in both Seasons 1 and 2. We did not find any female nesting in both seasons.

**Clutch size and nest success.**—Mean clutch size of the nests we discovered in Season 1 was  $7.5 \pm 3.2$  eggs ( $n = 6$ , range of values 5 to 14 eggs; Appendix Table). Mean clutch size of the nests we discovered in Season 2 was  $11.7 \pm 2.9$  eggs ( $n = 20$ , range of values 5–16 eggs, Appendix Table).

Half of the nests failed in Season 1; eggs completed development to hatching in only three nests (Table 1). In Season 2, 55% of the nests failed (11/20; Table 2). Mean number of eggs that hatched/successful clutch was  $9.8 \pm 4.4$  hatchlings ( $n = 9$ , range of values 1–15 hatchlings; Appendix Table). Across both seasons, females that oviposited in areas of the cave with relatively fewer conspecifics (breeding and non-breeding) had reared more hatchlings than those that oviposited in areas where conspecific density was greater. The Salamander Condo Room, which featured five nests in both seasons, only had two successful nests, both in Season 1. In Season 2, eggs hatched in only one of five nests within the Tunnel Cluster. Egg mortality was substantial, with just four of 16 eggs hatching.

Several nests (two in Season 1 and 11 in Season 2) experienced a gradual reduction in the number of eggs during a nesting season, but two females apparently lost all eggs in a short period of time (i.e., from one survey to the next survey). For example, the nest of one salamander (Random) had 11 eggs on 27 August 2020 but zero eggs on 4 September 2020. Similarly, the nest of another brooding female (Grape) consisted of 10 eggs on 21 August 2020 but zero eggs on 18 September 2020. In addition, Grape

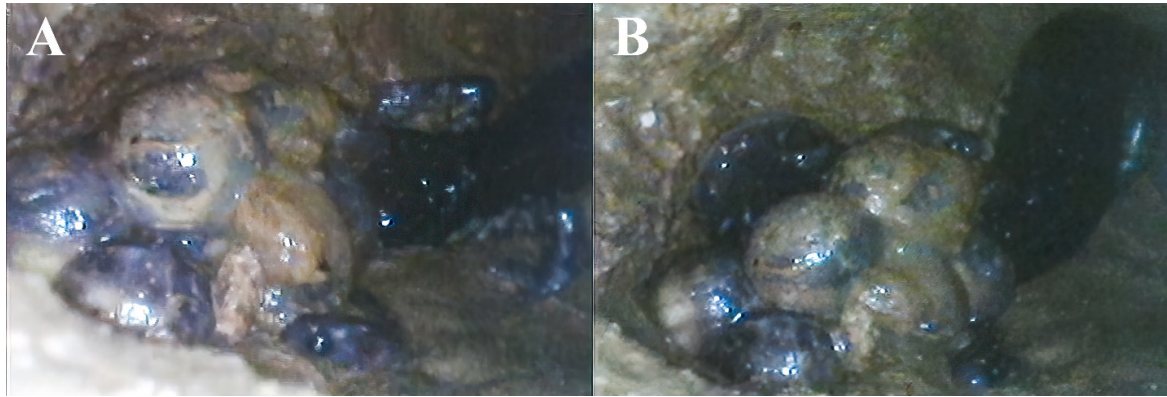


**FIGURE 1.** Stages of egg development from initial nest discovery through hatching for the nest attended by Cleo, a Northern Slimy Salamander (*Plethodon glutinosus*), in Season 1 at Cherry Hollow Cave, Marshall County, Alabama, USA. This was the most successful nest in Season 1, with 14 hatchlings reared from 14 eggs and complete natal dispersal by 17 January 2020. (Photographed by Kayla Wilson).

sported a newly damaged eye on 18 September. We noticed a similar injury on another brooding female (Black Rock), whose clutch suffered considerable mortality. She had no injuries and was brooding six eggs on 4 September 2020 but had just two eggs on 11 September 2020. The eggs were positioned about 2 cm from their original location, and one of them was misshapen. Furthermore, Black Rock was missing part of an eyelid and some skin posterior to her eye.

She had neither of these injuries on 4 September. No eggs, hatchlings, or the female were present on the next survey (18 September 2020).

Of special note were the nests of two other brooding females (Lard and Next to Cleo) in Season 2, which were located 10 cm apart. When discovered on 21 August 2020, Lard was brooding a clutch of 13 eggs, on 27 August, only two eggs, on 4 September, only one egg, and no eggs on 11 September. Lard



**FIGURE 2.** (A) An adult female Northern Slimy Salamander (*Plethodon glutinosus*) burrowing underneath her eggs on 16 October 2020 at 1305 at Cherry Hollow Cave, Marshall County, Alabama, USA. Note the hatchling on the bottom right of the clutch. (B) The nest 93 min later at 1438, with the same hatchling remaining on the bottom right of the clutch. Note the head of the female visible in the front of the photograph, protruding from her eggs, and another hatchling near her head on the top of the clutch. (Photographed by Kayla Wilson).

had a swollen abdomen and was more rotund than other nesting females observed on 27 August 2020. We documented a similar decline in number of eggs with Next to Cleo. Her clutch declined from nine to four eggs during the same time period (37 d). Females more isolated from other nesting females and conspecifics, reared more hatchlings, with a mean of  $11.9 \pm 2.2$  hatchlings (range of values 9–15 hatchlings; Appendix Table).

***Slimy salamander abundance.***—Adult Northern Slimy Salamanders were abundant in the study area, including in the vicinity of nests during the breeding season. For example, we counted 114 adults (not including nesting females) on 18 September 2020. Some crevices with active nests also had up three other adult salamanders; coincidentally all nests failed in these crevices. Five nests in both seasons 1 and 2 were located in a small room along the main cave passage where non-reproductive Northern Slimy Salamanders also were found in high abundance (up to 30 individuals in a 3.5-m long area). Of all 10 nests in this room, only two were successful, yielding five and six hatchlings, respectively. In Season 2, four of the five failed nests in this area were lost before the abundance of non-reproductive salamanders dropped substantially. One of these failed nests featured a female who withstood injuries to her eyelid and scalp shortly before all her eggs were gone.

***Incubation period and hatching.***—In general, the incubation period estimated from seven nests for which we were confident of estimated date of oviposition ranged 78 to 113 d (Fig. 1); however,

incubation periods varied not only between clutches but also among individual offspring within clutches. For example, we estimated that eggs in three nests (e.g., The Pebble, Chanel, and Beetle) in Season 2 developed and hatched in 108–113 d, 95–100 d, and 91–99 d, respectfully. The earliest date we found recent hatchlings was 3 October in Season 1, whereas the latest was 27 December, which represents a period of 85 d in which hatchlings emerged (Table 1). Oviposition likely occurred in late July through August for most nests. Hatchlings were lightly pigmented, and their abdomens, swollen with yolk, dragged along the ground when they walked. We found hatchlings climbing and hanging onto the ceiling of their nest crevices within a day or so after hatching, despite still having an awkward gait because of being encumbered by their yolk reserves. Over the next four to six weeks, the hatchlings gradually become leaner and more darkly pigmented. Hatchlings, even those that dispersed, had not developed any indication of the white, cloud-like blotching pattern on their laterals, characteristic of adults.

***Post-hatching dispersal and parental care.***—Hatchlings often remained near their mother for several days, although time spent with the mother before dispersal or when the mother left the nest was variable. Hatchlings began dispersing as early as 12 December and as late as 31 January 2020 in Season 1. In Season 1, hatchlings of three nests remained in their respective nests up to 43–63 d. In Season 2, hatchlings began dispersing as early as 22 November 2020, but four nests had not begun dispersing by 28



**FIGURE 3.** Defensive behavior (open mouth) of an adult female Northern Slimy Salamander (*Plethodon glutinosus*) to a potential threat to a hatchling (on her right). The salamander is attacking a zip tie we were using to reposition the hatchling for a photograph 12 December 2019 at Cherry Hollow Cave, Marshall County, Alabama, USA. (Photographed by Kayla Wilson)

December 2020. Because of COVID-19 restrictions, we were unable to track most nests through dispersal in Season 2; however, hatchlings of four nests remained in their respective nests up to 19–63 d. Four nests in Season 2 began hatching between 2 December and 18 December 2020. Based on the durations that other hatchlings remained in the vicinity of their nests, hatchlings in the late hatching dates potentially lingered in their nests into February 2021.

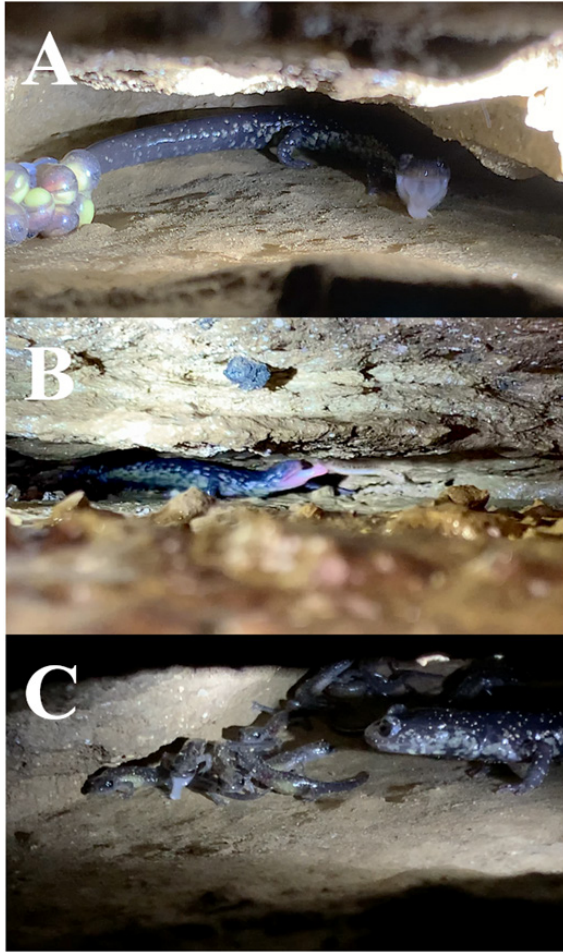
On 16 October 2020, we watched a female crawl beneath her eggs, which appeared to be hatching (Fig. 2). She approached her clutch and gently nudged the eggs with her snout. At the time of the observation, one hatchling was already present, and the mother was tapping the new hatchling with her snout. She began shoveling her head underneath the remaining eggs, moving her head and body forward until she was positioned completely underneath her clutch. About 90 min later, we saw what we assumed was a recent hatchling under the clutch where the female had been crawling, next to her head that was now sticking out from under the eggs (Fig. 2).

**Defensive behavior.**—We observed seven attending females on 12 occasions in total actively defending eggs and hatchlings when videographed with the endoscope. Some females attacked and bit the end of the endoscope, and others did not attack but positioned themselves between their clutch and the endoscope. For example, on 12 December 2019 we were using a zip tie to persuade a hatchling to move into view for photographs when the mother came forward to defend the hatchling (Fig. 3). Initially, she followed the hatchling quickly, and then put her head between the hatchling and the zip tie. She then bit at the zip tie several times, despite not having been touched herself. The mother then followed the hatchling into another part of the crevice when it attempted to flee.

**Feeding and diet.**—Nesting females appeared to take advantage of the light of the camera to locate prey and feed. They were attracted to movement, and often visually tracked any object moving nearby. They would lose interest if the object remained motionless for about 20–30 sec. We observed nine females eat springtails (entomobryid and globular Collembola) on > 20 occasions throughout both seasons (Fig. 4). On 2 October 2020, we watched a nesting female eat two large cave-dwelling crested millipedes (Abacionidae; Jones' Cave Millipede, *Tetracion jonesi*). While eating the millipedes, the female moved her head side to side (Fig. 4), a behavior we assumed was a sign of distress. We watched a different female eat a cave beetle (*Pseudanophthalmus* sp.) on 2 October 2020, and another female ate a harvestman (*Theromaster* sp.) on 31 October 2020.

Attending females were also attracted to the movement of their developing embryos and hatchlings. In most cases, a female would investigate these movements but cease pursuit after tapping her offspring with her snout. We watched two females project their tongues at embryos or hatchlings during Season 2. Furthermore, we watched a female project her tongue onto her eggs 2 and 16 October 2020 and a hatchling 2 December 2020, and another female project her tongue onto a hatchling 2 December 2020. We did not see females directly ingest or harm eggs or hatchlings.

Hatchlings showed little interest in feeding until their yolk reserves were completely diminished. On 12 December 2019, we watched a 22–27-d-old hatchling visually track a springtail (Fig. 4), and another hatchling attempt to eat a small juvenile millipede, likely *T. jonesi*, but it was unsuccessful. We also watched a 13–21-d-old hatchling hunt either a small mite or a springtail 13 November 2020.



**FIGURE 4.** Select observations of feeding attempts by Northern Slimy Salamanders (*Plethodon glutinosus*) at Cherry Hollow Cave, Marshall County, Alabama, USA. (A) A brooding adult female capturing a cave springtail (presumably *Pseudosinella* sp., Entomobryidae) 24 October 2019; (B) An adult female capturing a large adult Jones's Cave Millipede (*Tetracion jonesi*) 2 October 2020; (C) A hatchling (second from left) attempting to eat a globular cave springtail (presumably *Pygmarrhopalites* sp.) 12 December 2019. (Photographed by Kayla Wilson).

## DISCUSSION

Our study documents aspects of reproductive ecology of Northern Slimy Salamanders in a cave in North Alabama, USA. Although other studies have reported nesting of this species in caves (e.g., Highton 1962; Camp and Jensen 2004), none have monitored nesting females, nests, or hatchlings from early development to natal dispersal. In addition, we made several novel observations regarding hatching, parental care, dispersal, feeding, and diet.

**Reproductive biology.**—The number of nests observed differed between seasons; six clutches in Season 1 and 20 in Season 2. Moreover, we did not observe an individual female nesting in both seasons, which suggests that many females in this population reproduce non-annually or perhaps choose different nesting sites inaccessible to direct observation. Northern Slimy Salamanders are thought to exhibit a biennial reproductive cycle in Maryland and Pennsylvania (Highton 1962). In the study area within Cherry Hollow Cave, three crevices were used as oviposition sites in both seasons. Nests were located in the same areas within these crevices between seasons but based on coloration and spotting patterns, the nest were produced by different females. Nest site fidelity and variation in reproductive cycles have been reported previously in another member of the Slimy Salamander species complex. Six of 95 female Western Slimy Salamanders (*Plethodon albagula*) exhibited nest site fidelity (Trauth et al. 2006). In a later study at the same site, seven additional females exhibited nest site fidelity (Milanovich et al. 2006).

Nests of Northern Slimy Salamanders are rarely observed (or at least reported), even in terrestrial habitats, and the few reports indicate variability in clutch size. Clutch size inferred from counts of either ovarian eggs in gravid females or from nests ranges from 13 to 38 eggs in Northern Slimy Salamanders (Bishop 1941; Highton 1962) and other species in the eastern Slimy Salamander complex (Pope and Pope 1949). Camp and Jensen (2004) report a female Northern Slimy Salamander attending a clutch of 17 eggs in a cave in northwestern Georgia. Clutch size in the Western Slimy Salamander typically ranges from nine to 13 eggs in a population inhabiting a mine in Arkansas ( $n = 372$  clutches found between 1982 and 2004; Milanovich et al. 2006). Clutch sizes in our study are comparable to those reported for Western Slimy Salamanders by Milanovich et al. (2006); however, nests may experience unknown levels of egg predation prior to discovery, which confounds determination of clutch size.

Camp and Jensen (2004) estimate an incubation period of 128+ d for a clutch of eggs of a Northern Slimy Salamander in a cave in northwestern Georgia, with hatching extending into early March. The longer incubation period of this clutch compared to those we observed may be associated with differences in air temperatures later in late autumn and winter compared to our study. Highton (1956) estimated the incubation period of the Southeastern



Slimy Salamander (*Plethodon grobmani*) in Florida at 2 mo. Western Slimy Salamanders oviposit from August to October, hatching occurs in December, and adults disperse back to the surface in December and January (Jordan et al. 2018). The incubation period we estimated (78–113 d) is similar to that for Western Slimy Salamanders; however, nests may hatch over a longer period of time in Northern Slimy Salamanders, an 85-d period from October through December in our study and even as late as March in the region (Camp and Jensen 2004).

Estimating the development stages of eggs *in situ* each survey was difficult, as visualizing minute structures within eggs in the field was challenging. In general, eggs in most nests develop quickly through early developmental stages. Eggs in at least one nest, however, remained in stages 13–16 for about 16 d, whereas eggs in other nests progressed through these stages in one week. Eggs in several nests appeared to remain in stages 20–22 up to 36 d, which contrasts with the rate of egg development in Eastern Red-backed Salamanders (Kerney 2011). Differences in developmental times at various stages between Eastern Red-backed Salamanders and Northern Slimy Salamanders in this study likely are related, at least in part, to differences in incubation temperature (12.6°–27.5° C in this study versus 16° C in Kerney 2011) incubation time, which is about 72 d in Eastern Red-backed Salamanders and 100–115 d in Northern Slimy Salamanders, and greater difficulty staging embryos *in situ* in this study.

The hatching process in Northern Slimy Salamanders appears different than that reported for other *Plethodon* salamanders. As eggs approached the date of hatching, they took on an opaque, textured, almost melted look to the outside membrane. From footage of several fresh hatchlings, the egg membranes appear to gradually break down around the embryo, as opposed to forming a tight purse string that the young then squeeze out of, as described in *Plethodon welleri* (Organ 1960). At least one individual had finger-like white gill remnants, which have been reported to exist within 24 h of hatching in related species (Highton 1956; Organ 1960). These structures may have been present in other hatchlings but were very difficult to observe *in situ* due to lighting issues.

**Nest success and predation.**—Nest mortality was significant during both seasons, with more than 50% of nests failing completely. Predators on eggs of Northern Slimy Salamanders have not been documented; however, Ringneck Snakes (*Diadophis*

*punctatus*) and other salamanders, including conspecifics, may prey on eggs of Western Slimy Salamanders (Trauth et al. 2006). In addition, eggs may be lost due to bacterial and fungal infections. Although we did not directly observe predation on eggs during this study, several lines of evidence suggest that the primary cause of egg mortality was oophagy by conspecifics. First, Northern Slimy Salamanders are known to be highly territorial and will be aggressive towards other salamander species and conspecifics (Marvin 1998; Marshall et al. 2004; Camp and Jensen 2007). There is, however, only one confirmed report of cannibalism or oophagy (Powders 1973). An attending female Western Slimy Salamander on a nest in a mine shaft in Arkansas was observed defending her nest from a neighboring female (Trauth et al. 2006). Oophagy was observed in another female located near a fallen clutch of eggs that had four eggs in her digestive tract. The authors hypothesized that neighboring or marauding females may be one of the reasons why female Western Slimy Salamanders suspend their clutches from the ceiling, as a freely swinging cluster is easily bumped, alerting the female to any possible attacks on their eggs. This may be especially important in cave systems, which contain little to no light to see any potential attackers (conspecifics or other predators).

In addition to non-reproductive conspecifics, neighboring nesting female Northern Slimy Salamanders may also prey on eggs of other females. In another section of the cave, five females nested within a meter of each other. One of those females had 10 eggs until 18 September 2020, when all eggs suddenly disappeared, and she had a newly damaged eye. Eggs hatched from only one of the five clutches. Nests that were located in areas with no other nesting females and low abundance on non-reproductive salamanders nearby (i.e., within a meter) tended to have greater nesting success. These observations suggest that one of the keys to low egg mortality is isolation from conspecifics, at least in the Cherry Hollow Cave system. Oophagy (or at least attempted oophagy) by conspecifics has been reported in several other plethodontid salamanders (e.g., Highton and Savage 1961; Polis and Myers 1985; Kuzmin 1991; Camp 1997; Miller 2020), including cave-inhabiting species (Miller et al. 2008).

Another possible explanation for egg mortality is oophagy by attending females, which has been documented to be a significant component of protecting clutches from disease in some *Desmognathus* salamanders (Forester 1979). Attending females may re-

move eggs that have or are succumbing to bacterial or fungal infections. We witnessed decaying eggs with possible fungal growth in five nests shortly before they failed; however, eggs simply went missing between surveys in most cases. In some instances, eggs were found scattered near the nest site, indicative of a predation attempt or possibly removal by the attending female. In most clutches that failed, eggs disappeared a few at a time over the span of a few weeks.

Oophagy by other salamander species co-occurring may also account for egg mortality. The Cave Salamander (*Eurycea lucifuga*) is a common inhabitant of cave systems in northern Alabama (Niemiller et al. 2013) and has been observed attempting to prey on nests of Northern Slimy Salamanders in the region (pers. obs.). Cave Salamanders, however, occur at low densities at Cherry Hollow Cave and we usually found them in areas of the cave where Northern Slimy Salamanders and nests were less abundant. Other potential egg predators observed at Cherry Hollow Cave include Eastern Woodrats (*Neotoma floridana*), Ringneck Snakes, cave crickets, and millipedes.

**Parental care and defense.**—Some of the most interesting and novel behavioral observations made during this study were related to post-hatching care, defense, and dispersal. Parental care after hatching is rarely reported in salamanders (Schulte et al. 2020). A female Northwest Italian Cave Salamander (*Speleomantes strinatii*) was observed in cave-like conditions from oviposition until natal dispersal (Oneto et al. 2010). Two of the hatchlings remained with the female for six weeks after hatching. This is comparable to the length of time hatchlings remained in nests in this study (43–63 d). Hatchlings typically did not disperse *en masse*; hatchlings would steadily disperse from a nest in small numbers between surveys, with 7–16 d between initial and full natal dispersal. Remaining in the nest long after hatching could provide several different benefits to the hatchlings. Attending females always remained until the last hatchling left, sometimes staying even longer, and sometimes simply leaving when no hatchlings remained. We documented one female attacking a zip tie we were using to reposition a hatchling for photography. This event occurred 27 d after hatching began and indicates that females will not only defend their eggs from potential threats, but also their hatchlings. Parental defense may allow hatchlings to continue to safely develop in their nesting site, absorbing their yolk and improving movement. Post-hatching parental care may increase survival rates of

hatchlings, giving them a head start that may decrease juvenile mortality (Semlitsch 1980). Alternatively, the appearance of post-hatching parental care may be an artifact of environmental conditions on the surface or within the cave, which extended the time both attending females and hatchlings remained near nesting sites.

**Feeding and diet.**—The feeding habits of nesting female and hatchling Northern Slimy Salamanders have not been reported previously. Similar to reports for related species (Highton and Savage 1961; Trauth et al. 2006), we never observed females more than 15 cm from their nests. On more than 20 occasions, we watched as females, illuminated by headlamps and the endoscope, attempted to eat invertebrate prey near their nests. The movement of prey, and that of developing embryos and hatchlings, would attract the attention of females, who would often initiate a visual stalking behavior. Although we witnessed several successful feedings, it is unknown whether Northern Slimy Salamanders readily feed in complete darkness of caves.

Invertebrate prey ingested by attending females included springtails, millipedes, *Pseudanophthalmus* cave beetles, and a harvestman. Springtails may be a large component of their diet in surface habitats (Powders and Tietjen 1974). Both globular and entomobryid cave springtails were commonly observed in nesting crevices. *Pseudanophthalmus* cave beetles have been reported in the diet of Northern Slimy Salamanders from a cave (Peck 1974); however, *Theromaster* harvestman have not previously been documented in the diet of Northern Slimy Salamanders. In addition, *Tetracion* millipedes have not been previously reported in the diet. Jones' Cave Millipede is a common troglobiont within the study area of Cherry Hollow Cave. This abacionid relies on chemical secretions containing p-cresol to deter predators (Shear et al. 2010). We witnessed one female eat two adult Jones' Cave Millipedes within 10 min on 2 October 2020. She seemed to struggle after eating them (i.e., repeated opening her mouth and jerking her head from side to side), which may be because of the size of the prey or from chemical secretions. On 12 December 2019, we witnessed a hatchling attempt to eat a young millipede, possibly a *Tetracion* sp. The hatchling did not consume it, but instead contacted the millipede with its tongue and opened its mouth several times after the failed presumed feeding attempt, possibly in response to chemical defense produced by the millipede.

Studies are needed to better understand the diets of subterranean-dwelling Northern Slimy Salamanders, which are among the larger terrestrial predators encountered in caves, a stark contrast to their trophic status in most surface habitats. The feeding observations recorded in this study suggest that the species could potentially function as a top predator in terrestrial cave environments.

**Conclusions and future directions.**—This study provided important information on the reproductive biology, ecology, and behavior of the Northern Slimy Salamander. We documented evidence of females exhibiting non-annual reproductive cycles in the same population, clutch size, incubation time, and nest success, including evidence of oophagy by conspecifics. Our study also provided important insights into hatching, parental care and defense, post-hatching dispersal, and diet; however, several important knowledge gaps in our understanding of the reproductive biology of this species, along with other members of the species complex, remain. Future *in situ* studies of the reproductive biology of the species complex would greatly benefit from a comprehensive study of embryonic development that fully described developmental stages, including drawings and high-quality images of each stage that can be used to track egg development both in the lab and in the field. Aside from Northern Slimy Salamanders, little to no data on reproductive ecology exists for most other members of the species complex, except for Southeastern Slimy Salamanders and Western Slimy Salamanders. It is unknown how often subterranean habitats are used for reproduction and shelter by other members of the Slimy Salamander species complex. Slimy salamanders are among the larger predators found in terrestrial cave habitats, which are ecosystems that are often filled with sensitive and cryptic invertebrate species that have limited distributions. Slimy salamanders, therefore, may play a major role in regulating the population levels of these troglobionts, underscoring the need to understand their predator-prey relationships.

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**APPENDIX TABLE.** Nests of the Northern Slimy Salamander (*Plethodon glutinosus*) at Cherry Hollow Cave, Marshall County, Alabama, USA. Nests are identified by the code name assigned to the brooding female. The \* symbol indicates the nest was found in a minor passage that began 52 m from the entrance. Nests lacking the \* were located in the main passage of the cave. Season 1 refers to the September 2019 - January 2020 breeding season and Season 2 to the August - December 2020 breeding season. For clutch size, the maximum number of eggs is shown and for hatchlings, the number refers to the number of eggs that completed development and hatched.

Nest	Season	Distance from entrance (m)	Height above passage floor (m)	Clutch size	Hatchlings
Ghost	1	18.2	0	6	6
Pool	1	18.2	0.1	5	0
Fungus	1	18.7	0.2	6	1
Pirate	1	20.4	1.2	5	5
Bone	1	21.7	1.5	9	0
Cleo	1	42.8	1.4	14	14
Not ghost	2	18.2	0.0	12	0
Formation	2	19.2	1.6	16	0
Random	2	20.0	0.5	11	0
Dragon	2	20.4	1.2	13	0
Black Rock	2	20.6	1.3	6	0
Toothless	2	25.6	1.7	11	1
Brisby	2	27.5	1.7	16	4
String	2	27.5	1.6	12	0
Orange	2	28	1.7	8	0
Grape	2	28.1	1.3	10	0
Thin Crevice	2	28.8	1.3	5	0
Tag	2	32.5	1.7	11	11
River	2	38.1	1.1	14	9
Lard	2	42.8	1.4	13	0
Next to Cleo	2	42.9	1.4	9	0
Rockfall	2	46.7	1.4	15	15
The Pebble	2	50.1	0.9	14	12+
Chanel	2	56.0	1.3	14	13+
Crypt*	2	54.1	1.7	11	11
Beetle*	2	60.3	1.2	12	7