Long-term Observations of Salamander Abundance in Twilight Zones of Caves in Georgia, USA

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Abstract.—We used visual-encounter surveys to record species richness and abundance in plethodontid salamanders in the twilight zones of five caves over 19 y beginning in summer of 2000. We found *Plethodon glutinosus* (Northern Slimy Salamander) abundant during summer and *Eurycea lucifuga* (Cave Salamander) relatively abundant in summer, fall, and spring, although this species was most abundant during spring. *Plethodon petraeus* (Pigeon Mountain Salamander), which we observed in only two caves, was less abundant than the other two species, but was most abundant during summer. Although we observed fewer salamanders toward the end of the 19-y period, we found no evidence of a decline when we accounted for cave temperature. The bat populations of these caves virtually disappeared during our study because of white-nose syndrome (WNS) caused by the fungal pathogen *Pseudogymnoascus destructans*; however, we found no evidence of an influence of the decline of bat populations on salamander abundance. Abundance of *P. petraeus* fluctuated from year to year in a manner similar to that of *E. lucifuga,* whereas, the abundance of *P. glutinosus*, whose numbers were dominated by juveniles, varied independently of the other two species.

Key Words.—Cave Salamander; *Eurycea lucifuga*; fungus; guano; Northern Slimy Salamander; Pigeon Mountain Salamander; *Plethodon glutinosus*; *Plethodon petraeus*

Introduction

Although relatively rare, long-term data sets regarding individual species, communities, or ecosystems are needed to fully understand the mechanisms underlying many ecological processes (e.g., Strayer et al. 2017). Moreover, long-term data sets can reveal unexpected patterns and generate testable, novel hypotheses (Coull 1985). Unfortunately, such data sets are uncommon for a variety of logistical reasons including the cost in terms of labor and resources, and the focus on short turn-around times for research projects emphasized by academic and funding institutions (Wolfe et al. 1987). Even so, long-term, ecological studies are needed to document temporal changes in ecosystems, to separate anthropogenic from human causes, and to generate testable hypotheses (Wolfe et al. 1987; Strayer et al. 2017).

Subterranean systems harbor numerous endemic and imperiled taxa, which underlies their importance for biodiversity (Culver et al. 2000), but their ecological dynamics are poorly understood (Graening and Brown 2003; Mammola et al. 2019). Furthermore, cave systems are extremely fragile and vulnerable to human disturbance (Struebig et al. 2009), underscoring the importance of developing an understanding of their ecology to make informed decisions regarding their conservation and management. Plethodontid salamanders are important components of many subterranean habitats (Briggler and Prather 2006; Camp and Jensen 2007; Elliott 2007) with some species being obligate occupants and others using caves facultatively (Petranka 1998). Salamanders that use caves facultatively enter and exit caves, and the pattern of how they use subterranean habitats depends on the species, season, and environmental conditions of individual caves (Briggler and Prather 2006; Camp and Jensen 2007; Lunghi et al. 2014, 2015). Different species that use caves simultaneously create ecological assemblages, however, particularly within twilight zones, the portion near the mouth of the cave that receives some light.

In 2000, we began a series of visual-encounter surveys to investigate the ecology of plethodontid salamanders within the twilight zones of caves located in the Cumberland Plateau of northwestern Georgia, USA. Simple counts of salamanders within caves are not necessarily reliable indicators of the dynamics of larger populations (Dodd et al. 2001; Dodd and Dorazio 2004). Plethodontids that use caves are highly detectable using this method (Miller and Niemiller 2008; Ficetola et al. 2012), however, and long-term datasets may at least be suggestive of overall trends in salamander use of this fragile habitat.

During our study, the pathogenic fungus *Pseudogymnoascus destructans*, which causes white-nose syndrome (WNS) in bats, invaded the caves we

were surveying. First recorded in New York, USA, in 2006, this disease apparently resulted in massive declines in local bat populations of the northeastern U.S. within 4 y of its detection (Brooks 2011). It has since spread throughout much of the U.S. with similar catastrophic effects in many areas (Ingersoll et al. 2016; O'Keefe et al. 2019). First documented in Georgia caves in the winter of 2013, personnel from the Georgia Department of Natural Resources (DNR) noted a precipitous drop (36%) in the numbers of bats in cave hibernacula within a single year. By 2018, numbers in cave-hibernacula counts declined in Georgia by 95% (Trina Morris and Emily Ferrall, unpubl. report).

At least one species of obligate cave dweller (Grotto Salamander, *Eurycea spelaea*) uses bat guano as a supplemental source of nutrition (Fenolio et al. 2006), raising the possibility that the disappearance of bats may have had a negative impact on the numbers of salamanders that use caves facultatively. Because guano alone is not a sustaining source of nutrition (Soares et al. 2017), the direct importance of guano to salamander nutrition is unknown. On the other hand, because cave-dwelling plethodontids feed heavily on arthropods (Peck 1974; Jensen and Whiles 2000), bat guano may be an indirect source of nutrition because of its importance to cave invertebrates (Ferreira and Martins 1999).

After 19 y of recording data, we sought to answer several questions: (1) Do different species within the same cave exhibit a similar pattern of fluctuation in abundance over time, which would indicate an assemblage-wide response to some environmental factor?; (2) Do salamander numbers of the same species fluctuate similarly across caves, indicating a regional effect?; and (3) Has there been a detectable decline in the numbers of any of the plethodontid species encountered in these caves? Because the loss of one species within an ecosystem can have unexpected consequences for others (e.g., Caut et al. 2009), we asked this last question in the context of the loss of resident bats. After several years, we noticed that many of our salamander counts included both large, presumed adults and small (presumably juvenile) individuals. Therefore, we further sought to determine the demographic structure of the salamander assemblages encountered.

Materials and Methods

In 2000, we began surveying Pettijohn's Cave (PC), Screech Owl Cave (SO), Anderson Spring Cave (AS), and Sitton's Cave (SC). In addition, we began surveying the historic entrance to Ellison's Cave (EC) in 2002. All but SC are located on Pigeon Mountain in the Crockford-Pigeon Mountain Wildlife Management Area of Walker County, Georgia, USA. SC is in Cloudland Canyon State Park on adjacent Lookout Mountain in Dade County, Georgia. We earlier described the specific

location (map coordinates), elevation, surrounding forest, and physical aspects of each cave (Camp and Jensen 2007; Camp et al. 2014). We continued counting salamanders through the spring of 2019.

We used visual-encounter surveys, counting every salamander we observed within the twilight zone. We earlier reported the length of each cave searched (Camp and Jensen 2007). To minimize complicating variability due to season (Dodd 2003), we counted salamanders during each season: summer (July), fall (October), winter (January), and spring (April). Because we saw very few salamanders during winter (Camp and Jensen 2007), we discontinued searching during that season after the first 5 y. We also measured the temperature within each cave at the same location at every visit at a sufficient distance from the opening to avoid the effects of the temperature of the outside air. We could not access EC during the summer of 2013; therefore, we lack data for EC for that year.

In analyzing the number of salamanders observed, we focused on the three most frequently encountered species: the Cave Salamander (*Eurycea lucifuga*), the Northern Slimy Salamander (*Plethodon glutinosus*), and the Pigeon Mountain Salamander (*P. petraeus*). Each of these three species use caves facultatively and together comprised 93% of all salamander encounters over the first 5 y (Camp and Jensen 2007). We tested raw counts for deviation from a normal distribution using a Kolmogorov-Smirnov test and then transformed the count data by taking the natural log of $N + 1$, adding 1 because some of the counts were equal to 0. We then tested for normality of the transformed data with a Kolmogorov-Smirnov test in SPSS ver. 24. Several of the raw counts in our analyses exhibited significant deviations from normality. On the other hand, the smallest *P* value for the tests run on the log-transformed data was 0.063. Therefore, we were confident in the appropriateness of using parametric tests with transformed data.

To test for assemblage-wide or region-wide effects on salamander abundance, we ran correlation analyses on the log-transformed data across all 19 y for the three seasons. We analyzed summer data from PC, SO, AS, and SC for all three species, omitting EC because we were missing 3 y of data from that cave. Because we found neither species of *Plethodon* abundant during spring nor fall surveys, typically observing no more than one or two individuals of either species, we tested only for a regional effect on *E. lucifuga* for fall and spring.

As a result of WNS, the number of bats in caves of the Georgia Cumberland Plateau, including several of our study caves, began showing serious declines in the winter of 2014 (average of 36% decline from previous hibernacula counts: (Trina Morris and Emily Ferrall, unpubl. report). Therefore, we chose to compare the numbers of salamanders encountered during the final
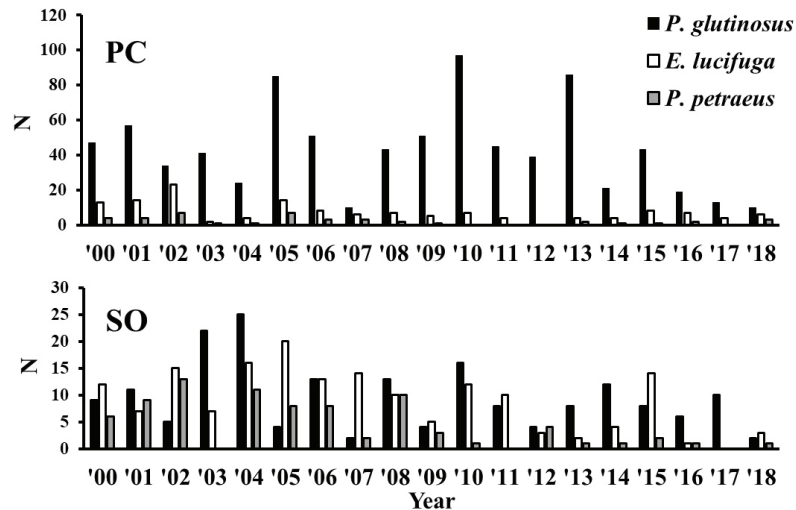
Figure 1. Numbers of the Northern Slimy Salamander (*Plethodon glutinosus*), Cave Salamander (*Eurycea lucifuga*), and Pigeon Mountain Salamander (*Plethodon petraeus*) observed (N) during summer (July) over 19 y in Pettijohn Cave (PC) and Screech Owl Cave (SO) in northwestern Georgia, USA.

5 y of our study (July 2014 to April 2019) to those encountered during the first (July 2000 to April 2005) and second (July 2005 to April 2010) 5-y increments, which preceded the appearance of WNS. Both seasonal and annual variation in cave temperature influence the number of salamanders visible in the twilight zones of caves (Camp et al. 2014). Therefore, we made our comparisons using a series of two-way ANCOVAs, with cave temperature as a covariate while testing the effects of the factors time period and cave, testing each species separately. For *P. glutinosus* and *P. petraeus*, we analyzed summer counts only. For *E. lucifuga*, we tested each season separately because *E. lucifuga* was abundant in spring and fall as well as summer. For all analyses, we tested for significance at an alpha level of 0.05.

For the last 5 y of our study, we recorded the number of presumed juvenile (small: < 50 mm in snout-vent length, SVL) versus presumed adult (large: > 60 mm

SVL) salamanders that we encountered. These values approximate the sizes at which sexual maturity is reached in *P. glutinosus* (Highton 1962; Semlitsch 1980), *E. lucifuga* (Hutchison 1958; Williams 1980), and *P. petraeus* (Jensen et al. 2002). Because almost all individuals were considerably smaller or larger than these respective sizes, actual measurement was not necessary.

Results

From 2000–2019, we recorded 5,583 encounters of nine species of plethodontid salamander and three species of frog (Table 1). Numbers of the most frequently encountered species during summer (*E. lucifuga*, *P. glutinosus*, *P. Petraeus*) fluctuated widely over the 19 y (Fig. 1, 2). Numbers of *E. lucifuga* also exhibited considerable variability during fall and spring (Fig. 3).

Table 1. Total numbers of observations of 11 species of amphibian during summer, fall, and spring visits to twilight zones of five caves over 19 y (2000–2019) in southwestern Georgia, USA, except for EC (2002–2019). Species abbreviations are Dcon = *Desmognathus conanti* (Spotted Dusky Salamander); Ecir = *Eurycea cirrigera* (Southern Two-lined Salamander); Elon = *E. longicauda* (Long-tailed Salamander); Eluc = *E. lucifuga* (Cave Salamander); Gpor = *Gyrinophilus porphyriticus* (Spring Salamander); Pglu = *Plethodon glutinosus* (Northern Slimy Salamander); Ppet = *P. petraeus* (Pigeon Mountain Salamander); Pven = *P. ventralis* (Southern Zigzag Salamander); Prub = *Pseudotriton ruber* (Red Salamander); Lcat = *Lithobates catesbeianus* (American Bullfrog); Lcla = *L. clamitans* (Green Frog); Lpal = *L. palustris* (Pickerel Frog); Lspe unidentified *Lithobates* species; Pcre = *Pseudacris crucifer* (Spring Peeper).

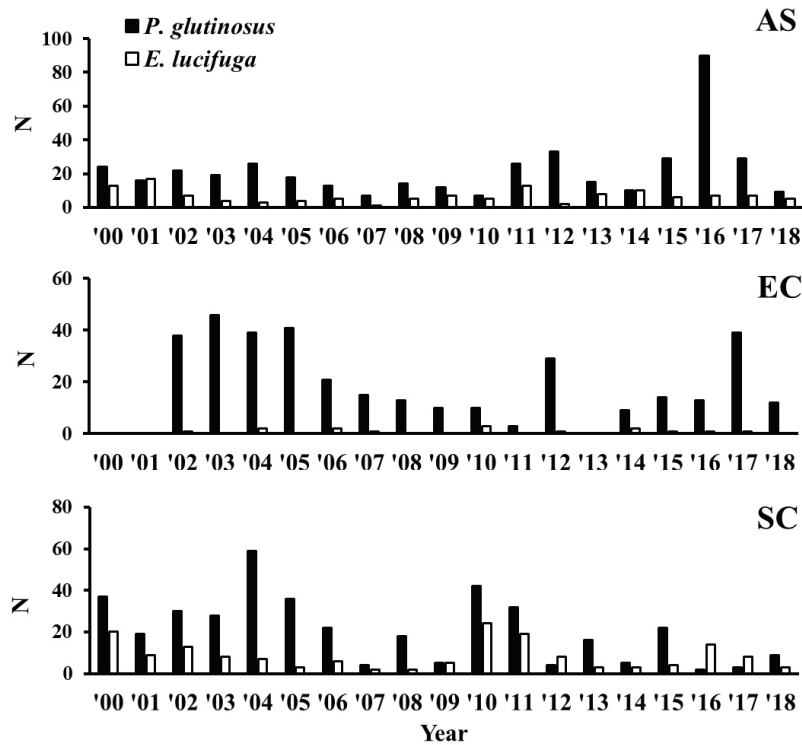| Cave	Dcon	Ecir	Elon	Eluc	Gpor	Pglu	Ppet	Pven	Prub	Lcat	Lcla	Lpal	Lspe	Pcre
PC	0	0	4	691	0	942	95	47	0	1	0	0	1	0
SO	0	0	0	597	0	260	110	0	0	0	1	2	0	2
AS	8	5	131	614	18	457	0	13	4	0	25	119	1	0
SC	0	0	17	483	1	419	0	1	0	0	0	19	0	0
EC	0	0	0	42	18	400	0	0	0	0	0	92	0	0
Totals	8	5	152	2427	37	2478	205	61	4	1	26	232	2	2

Figure 2. Numbers of the Northern Slimy Salamander (*Plethodon glutinosus*) and the Cave Salamander (*Eurycea lucifuga*) observed (N) during summer (July) over 19 y in Anderson Spring Cave (AS), the historic entrance of Ellison's Cave (EC), and Sitton's Cave (SC) in northwestern Georgia, USA.

There was a significant association during summer between *E. lucifuga* and *P. petraeus* abundance in both caves in which the two species occurred together (PC and SO; Table 2). We found no significant correlation between numbers of *P. glutinosus* and either of the two other species where they occur within the same cave. In comparing the same species across caves, we found very few significant correlations during summer (Table 2), the most notable being between *P. petraeus* encountered in PC and SO. The only other significant intraspecific associations during summer was between *P. glutinosus* in SC and those seen in PC and SO. During fall analyses of *E. lucifuga*, we found significant correlations between PC and SO and between SC and AS (Table 3). For *E. lucifuga* during spring, we found significant correlations between PC and each of the other three caves (Table 4).

Table 2. Correlation analyses between salamanders found in four caves during summer in southwestern Georgia, USA. Abbreviations are PC = Pettijohn Cave; SO = Screech Owl Cave; AS = Anderson Spring Cave; SC = Sitton's Cave and subscripts g, l, and p = *Plethon glutinosus* (Northern Slimy Salamander), *Eurycea lucifuga (*Cave Salamander)*, and *Plethodon petraeus* (Pigeon Mountain Salamander), respectively. Correlation coefficients (Pierson's *r*) are below the diagonal, and corresponding *P* values are above. For convenience, an asterisk (*) = significant *r* value at α = 0.05. All analyses were run on log-transformed data.

|	PC_g	PC_l	PC_p	SO_g	SO_l	SO_p	AS_g	AS_l	SC_g	SC_l
PC_g		0.5297	0.8793	0.1628	0.1078	0.2919	0.7806	0.2208	0.0073	0.3066
PC_l	0.156		0.0002	0.7723	0.0662	0.0474	0.6453	0.0897	0.1097	0.7048
PC_p	0.038	0.736*		0.1966	0.1022	0.0044	0.6545	0.7755	0.3865	0.2739
SO_g	0.335	-0.072	-0.312		0.6262	0.9537	0.7146	0.3072	0.0297	0.2093
SO_l	0.382	0.430	0.387	0.121		0.0107	0.1753	0.4812	0.0001	0.9771
SO_p	0.252	0.459*	0.612*	0.015	0.563*		0.9038	0.7612	0.1176	0.6490
AS_g	-0.070	-0.115	-0.011	0.091	-0.326	-0.030		0.4787	0.5402	0.0948
AS_l	0.297	0.400	0.071	0.250	-0.174	-0.076	0.175		0.5007	0.0880
SC_g	0.586*	0.380	0.213	0.496*	0.740*	0.372	-0.152	0.167		0.2427
SC_l	0.250	0.094	-0.267	0.304	0.007	-0.113	0.395	0.402	0.284	
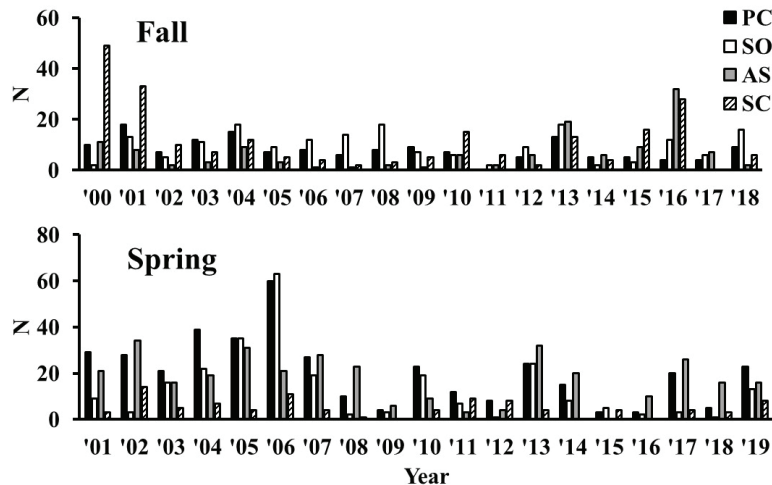
Figure 3. Numbers of the Cave Salamander (*Eurycea lucifuga*) observed (N) during fall (October) and spring (April) over 19 y in Pettijohn Cave (PC), Screech Owl Cave (SO), Anderson Spring Cave (AS), and Sitton's Cave (SC) in northwestern Georgia, USA.

When controlling for the effect of temperature, numbers of salamanders encountered among the three 5-y intervals did not differ significantly, the third of surveys occurring following the disappearance of bats (Tables 5 and 6). There were no significant interactions in any of the analyses (Tables 5 and 6). Over the last 5 y of the study, juveniles predominated in our counts of *P. glutinosus* in all caves (Fig. 4.). We saw small individuals of *E. lucifuga* in significant numbers only during fall and only in AS and SC (Fig. 5). We saw relatively few *P. petraeus* of any size during the last 5 y (Fig. 4).

DISCUSSION

Although we observed considerable fluctuation in salamander abundances within cave twilight zones from year to year, we found no evidence of decline. We found no indication that the loss of the erstwhile bat residents influenced the numbers of salamanders within the caves. Bat guano can be an important source of energy within cave food webs (Ferreira

et al. 2000; Fenolio et al. 2006), and the larvae of at least one obligate, cave-dwelling salamander species (*E. spelaea*) supplements its nutritional needs with bat guano (Fenolio et al. 2006), although guano alone does not represent a sustaining source of nutrition (Soares et al. 2017). Terrestrial species of *Plethodon* and the

TABLE 4. Results of pairwise correlation analyses between the Cave Salamander (*Eurycea lucifuga*) found in each of four caves during spring in southwestern Georgia, USA. Abbreviations are PC = Pettijohn Cave; SO = Screech Owl Cave; AS = Anderson Spring Cave; SC = Sitton's Cave. Correlation coefficients (Pierson's *r*) are below the diagonal, and corresponding p values are above. For convenience, an asterisk (*) = significant *r* value at α = 0.05. All analyses were run on log-transformed data.

	PC	SO	AS	SC
PC		< 0.001	0.001	0.011
SO	0.770*		0.187	0.158
AS	0.662*	0.318		0.877
SC	0.562*	0.339	0.039	

TABLE 5. Results of Two-way ANCOVAs comparing numbers of summer (July) encounters of the Northern Slimy Salamander (*Plethodon glutinosus*) and the Pigeon Mountain Salamander (*Plethodon petraeus*) from southwestern Georgia, USA, among time periods (2000–2005, 2005–2009, 2014–2019). Abbreviations are Factors = Time Period and Cave and covariate = Temperature inside cave.

Factors	*P. glutinosus*			*P. petraeus*		
	F	df	P	F	df	P
Time Period	0.249	2, 36	0.781	0.377	2, 18	0.691
Cave	0.170	3, 36	0.916	0.098	1, 18	0.757
Time Period × Cave	0.697	6, 36	0.653	0.833	2, 18	0.451
Time Period × Temperature	0.279	2, 36	0.758	0.264	2, 18	0.771
Cave ×Temperature	0.059	3, 36	0.981	0.177	1, 18	0.679
Time Period × Cave × Temperature	0.564	6, 36	0.756	0.936	2, 18	0.411

TABLE 3. Results of pairwise correlation analyses between the Cave Salamanders (*Eurycea lucifuga*) found in each of four caves and the Cave Salamanders in each of the other three caves during fall in southwestern Georgia, USA. Abbreviations are PC = Pettijohn Cave; SO = Screech Owl Cave; AS = Anderson Spring Cave; SC = Sitton's Cave. Correlation coefficients (Pierson's *r*) are below the diagonal, and corresponding p values are above. For convenience, an asterisk (*) = significant *r* value at α = 0.05. All analyses were run on log-transformed data.

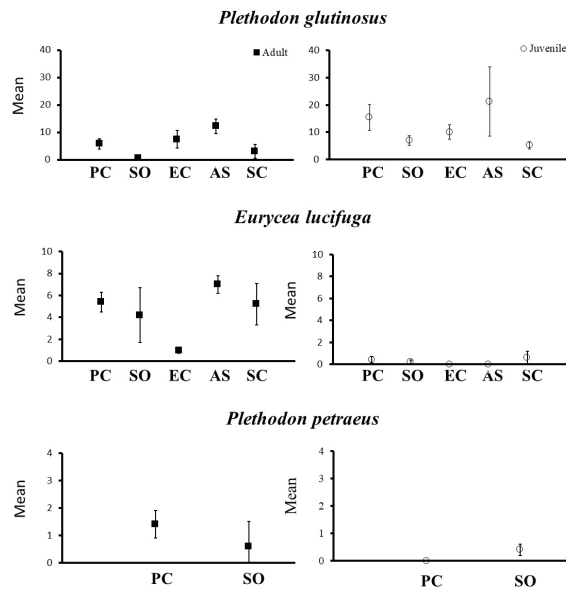|	PC	SO	AS	SC
PC		0.012	0.596	0.207
SO	0.556*		0.908	0.656
AS	0.132	-0.029		0.019
SC	0.305	-0.111	0.526*	

Figure 4. Mean numbers of juveniles and adults of Northern Slimy Salamanders (*Plethodon glutinosus*), Cave Salamanders (*Eurycea lucifuga*), and Pigeon Mountain Salamanders (*P. petraeus*) observed (N) in Pettijohn Cave (PC), Screech Owl Cave (SO), the historic entrance of Ellison's Cave (EC), Anderson Spring Cave (AS), and Sitton's Cave (SC), Georgia, USA, during summer from 2014–2019. Whiskers represent ± 1 SE. The Pigeon Mountain Salamander occurs only in PC and SO.

Figure 5. Mean numbers of juveniles and adults of the Cave Salamander (*Eurycea lucifuga*) observed (N) in Pettijohn Cave (PC), Screech Owl Cave (SO), the historic entrance of Ellison's Cave (EC), Anderson Spring Cave (AS), and Sitton's Cave (SC), Georgia, USA, during fall and spring from 2014–2019. Whiskers represent ± 1 SE.

terrestrial metamorphosed form of *E. lucifuga* feed on invertebrates and likely do not feed directly on guano. We cannot rule out the possibility that the aquatic larvae of *E. lucifuga* are copraphagous, however, even though there are no reports of this phenomenon in the literature. A more likely effect of guano on salamanders may be its influence on the abundance of invertebrates. On the other hand, all three of our focal species use surface habitats for foraging when the forest is sufficiently moist (Jensen et al. 2002; Camp and Jensen 2007), which means these salamanders are not as dependent on the food web within caves as obligate cave dwellers.

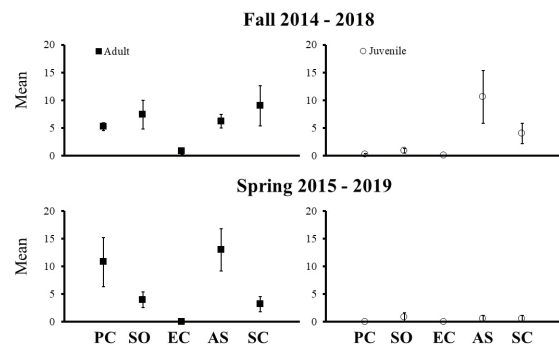A notable result of our analyses was the strong association in the fluctuation of year-to-year abundance between *P. petraeus* and *E. lucifuga*. Although not closely related phylogenetically, these two species appear to respond similarly in abundance to the environmental cues (e.g., temperature and possibly precipitation) that trigger numerical responses within twilight zones. These two species are similar ecologically in that, unlike *P. glutinosus*, they are restricted to geographic ranges that correspond closely to karst regions (Petranka 1998); however, our conclusions are tentative because of the relatively low numbers of *P. petraeus* and our inability to run comparable correlation analyses during fall and spring.

An obvious difference between *P. glutinosus* and the other two focal species was the predominance of juveniles during our surveys during 2014–2019. In karst regions, *P. glutinosus* regularly use caves (Dodd et al. 2001; Niemiller and Miller 2009; Niemiller et al. 2016; Zigler et al. 2020) as do other members of the *P. glutinosus* species complex, including *P. albagula* (Briggler and Prather 2006; Taylor et al. 2015) and *P. mississippi* (Himes et al. 2004) among others (Humphries 1956; Peck 1974). Although Taylor et al. (2015) reported greater numbers of adult *P. albagula* in caves than juveniles, the predominance of *P. glutinosus*

Table 6. Results of Two-way ANCOVAs comparing numbers of seasonal encounters of the Cave Salamander (*Eurycea lucifuga*) from northwestern Georgia, USA, among time periods (2000–2005, 2005–2009, 2014–2019). Abbreviations are Factors = Time Period and Cave and covariate = Temperature inside cave.

Factors	Summer (July)			Fall (October)			Spring (April)		
	F	df	P	F	df	P	F	df	P
Time Period	0.384	2, 36	0.684	0.027	2, 36	0.973	1.961	2, 36	0.156
Cave	0.440	3, 36	0.726	0.332	3, 36	0.802	0.796	3, 36	0.796
Time Period × Cave	0.545	6, 36	0.771	0.291	6, 36	0.937	0.299	6, 36	0.933
Time Period × Temperature	0.454	2, 36	0.639	0.060	2, 36	0.942	1.373	2, 36	0.266
Cave × Temperature	0.428	3, 36	0.734	0.422	3, 36	0.738	0.364	3, 36	0.779
Time Period × Cave × Temperature	0.559	6, 36	0.759	0.226	6, 36	0.966	0.296	6, 36	0.935

juveniles in our counts may underscore the importance of these caves as brooding sites. While we saw only a single nest of *P. glutinosus* during this study (Camp and Jensen 2004), members of this complex are known to use subterranean sites including caves (Noble and Marshall 1929; Wells and Gordon 1958) and abandoned mines (Trauth et al. 2006) as nesting sites.

Although we found some concordance among caves in year-to-year, intraspecific variation in abundance, correlation was far from exact. This cave-to-cave variation is likely the result of variance in both surface and subterranean habitats associated with the various caves. As stated earlier, our study species use both habitats, and local differences in both environments probably influence how individual salamanders respond.

Perhaps the most salient finding is the dynamic nature of the salamander assemblages that occupy cave twilight zones at any given time. Not only do the numbers of individual species fluctuate from season to season and year to year, abundances of individual species fluctuate in different ways. For example, abundance of *E. lucifuga* was highest in the fall during some years for some caves but highest during spring for others, whereas abundance of *P. glutinosus* was always highest during summer. Fluctuations in assemblage composition can be consequential to assessments of biodiversity and conservation management (Gómez-Rodríguez et al. 2010). Moreover, the ever-changing composition of these salamander assemblages undoubtedly has consequences for the nature of ecological interactions within salamander species, between salamander species, and between salamander species and the broader cave environment. The dynamic nature of this system offers rich opportunities for answering ecological questions regarding how different species react to fluctuating environmental cues, both biotic and abiotic, and the influence that such fluctuations have on their interactions.

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