**SHORT COMMUNICATION**

# A new maximum body size record for the Berry Cave Salamander (*Gyrinophilus gulolineatus*) and genus *Gyrinophilus* (Caudata, Plethodontidae) with a comment on body size in plethodontid salamanders

Nicholas S. Gladstone[1], Evin T. Carter[2], K. Denise Kendall Niemiller[3],
Lindsey E. Hayter[4], Matthew L. Niemiller[3]

**1** *Department of Earth and Planetary Sciences, University of Tennessee, Knoxville, Tennessee 37916, USA*
**2** *Department of Ecology and Evolutionary Biology, University of Tennessee, Knoxville, Tennessee 37916, USA*
**3** *Department of Biological Sciences, The University of Alabama in Huntsville, Huntsville, Alabama 35899,
USA* **4** *Admiral Veterinary Hospital, 204 North Watt Road, Knoxville, Tennessee 37934, USA*

Corresponding author: *Matthew L. Niemiller* (matthew.niemiller@uah.edu)

*http://zoobank.org/2BCA9CF1-52C7-47B6-BDFB-25DCF9EA487A*

## Abstract

Lungless salamanders in the family Plethodontidae exhibit an impressive array of life history strategies and occur in a diversity of habitats, including caves. However, relationships between life history, habitat, and body size remain largely unresolved. During an ongoing study on the demography and life history of the paedomorphic, cave-obligate Berry Cave Salamander (*Gyrinophilus gulolineatus*, Brandon 1965), we discovered an exceptionally large individual from the type locality, Berry Cave, Roane County, Tennessee, USA. This salamander measured 145 mm in body length and represents not only the largest *G. gulolineatus* and *Gyrinophilus* ever reported, but also the largest plethodontid salamander in the United States. We discuss large body size in *G. gulolineatus* and compare body size in other large plethodontid salamanders in relation to life history and habitat.

## Keywords

amphibian, habitat, life history, paedomorphosis, subterranean

## Introduction

Body size in amphibians is driven by strong selective pressures, because it interacts with many aspects of life history (Whitford and Hutchison 1967, Blueweiss et al. 1978, Hairston and Hairston 1987, Stearns 1992). Although several ecological and evolutionary mechanisms can be responsible for body size variation in amphibians, overarching patterns are elusive (*e.g.*, Bernardo and Reagan-Wallin 2002, Adams and Church 2008, Slavenko and Meiri 2015). In response to Tilley and Bernardo (1993), Beachy (1995) argues that a primary influence on body size in amphibians is a delay in larval and juvenile period. In general, *K*-selected characteristics are correlated with increased longevity and a shift toward larger propagule size in stable environments. Prolonged developmental periods may promote neoteny (or prolonged maturation) and can be associated with reduced energy demand (McNamara and McNamara 1997). This suggests a possible correlation between increased body size and both paedomorphic and *K*-selected life history strategies. However, the relationship between amphibian body size and these life history strategies is largely unresolved (Yeh 2002, Wiens and Hoverman 2008).

While the reduction of body can be associated with paedomorphic traits (e.g., Alberch and Alberch 1981, Yeh 2002), Wiens and Hoverman (2008) concluded that obligately paedomorphic salamanders (Amphiumidae, Cryptobranchidae, Proteidae, Sirenidae) exhibit larger body sizes compared to those within clades that undergo metamorphosis. This pattern does not seem to translate to paedomorphic species within clades that possess metamorphic or direct-developing species (Wiens and Hoverman 2008). In fact, paedomorphic *Eurycea* (Plethodontidae) associated with springs and caves of the Edward's Plateau in Texas are characterized by reduced body size relative to their obligately metamorphic congeners, while both metamorphic and paedomorphic *Ambystoma* (Ambystomatidae) share similar body size (Ryan and Bruce 2000, AmphibiaWeb 2018).

Caves and other subterranean habitats are often viewed as extreme and inhospitable environments characterized by an absence of primary production and limited resources (Culver and Pipan 2009). Salamanders are one of only two vertebrate groups to have successfully colonized and obligately live in subterranean habitats. Fourteen species from two families (Plethodontidae and Proteidae) occur exclusively in caves, and most have evolved paedomorphosis (Goricki et al. 2012, in press, Niemiller et al. unpubl. data), which may be a response to limited food resources within terrestrial cave habitats (Brandon 1971, Wilbur and Collins 1973, Ryan and Bruce 2000). Few studies have examined the relationship between cave inhabitation and body size, and changes in body size may not necessarily be associated with shifts from surface to subterranean habitats (Romero 2009, Pipan and Culver 2017). However, many cave-obligate species (i.e., troglobites) exhibit *K*-selected life history traits such as reduced growth rate, delayed sexual maturity, and increased longevity (Brandon 1971, Culver and Pipan 2009, Hüppop 2012), and some troglobites and stygobites are larger than their surface congeners, such as in amblyopsid cavefishes (Poulson 1963, 1985, Niemiller and Poulson 2010).

The plethodontid genus *Gyrinophilus* Cope, 1869 includes four semi-aquatic to paedomorphic species endemic to the highlands of eastern North America. Three species are paedomorphic stygobionts found in caves of the Interior Low Plateau and Appalachians karst regions of Alabama, Tennessee, Georgia, and West Virginia in the United States (Niemiller et al. 2009, Goricki et al. 2012). Here, we report on a Berry Cave Salamander, *G. gulolineatus* Brandon, 1965, from the type locality in Roane Co., Tennessee that exceeds the current maximum body size record for the species and represents the largest *Gyrinophilus* and plethodontid salamander reported in the United States. *Gyrinophilus gulolineatus* is known from just ten localities in the Clinch and Tennessee River watersheds in the Appalachians karst region of eastern Tennessee (Figure 1). The largest *G. gulolineatus* previously reported measured 136 mm snout-vent length (SVL; tip of the snout to the posterior margin of the vent) from the type locality (Brandon 1965, 1966).

## Methods

As part of an ongoing study on the demography and life history of *Gyrinophilus gulolineatus*, we captured a large *G. gulolineatus* at the type locality, Berry Cave (Tennessee Cave Survey no. TRN3), on 12 August 2018. Berry Cave is located 0.37 km west of the Tennessee River near Wright Bend in Roane County, Tennessee. The main entrance is in a large sink, with the passage from the entrance steeply sloping down to the main stream passage. The passage can be followed downstream to the northeast for ~160m along the stream until large debris and sediment buildup block further exploration. The stream is characterized by a series of riffles and shallow (<0.5 m) pools with primarily chert, cobble, and coarse gravel substrate and significant amounts of coarse woody debris, detritus, and fine mud and sediment in some areas. The salamander was observed and captured in the margin of a shallow (<0.5 m deep) pool located in a small passage upstream from the main entrance chamber. When first encountered, all but the salamander's head was out of the water, as it appeared to be moving partially over land to continue upstream.

The salamander was captured with a handheld dip net and immediately transferred to a clear plastic bag for processing. We massed to the nearest 0.5 g using a Pesola® spring scale and measured to the nearest 0.5 mm snout-vent length (SVL; tip of the snout to the posterior margin of the vent) and total length (TL; tip of the snout to the end of the tail) using a metric caliper. The salamander was measured four times by MLN, confirmed by NSG and ETC, and then photographed using an Olympus Tough TG-5 Camera. We also noted any physical abnormalities and the overall health of the salamander. Finally, we marked the salamander by injecting a 1.2 × 2.7 mm visible implant (VI) alpha tag (Northwest Marine Technology Inc., Shaw Island, WA) into the dermis of the tail. The salamander was released at its point of capture following processing.
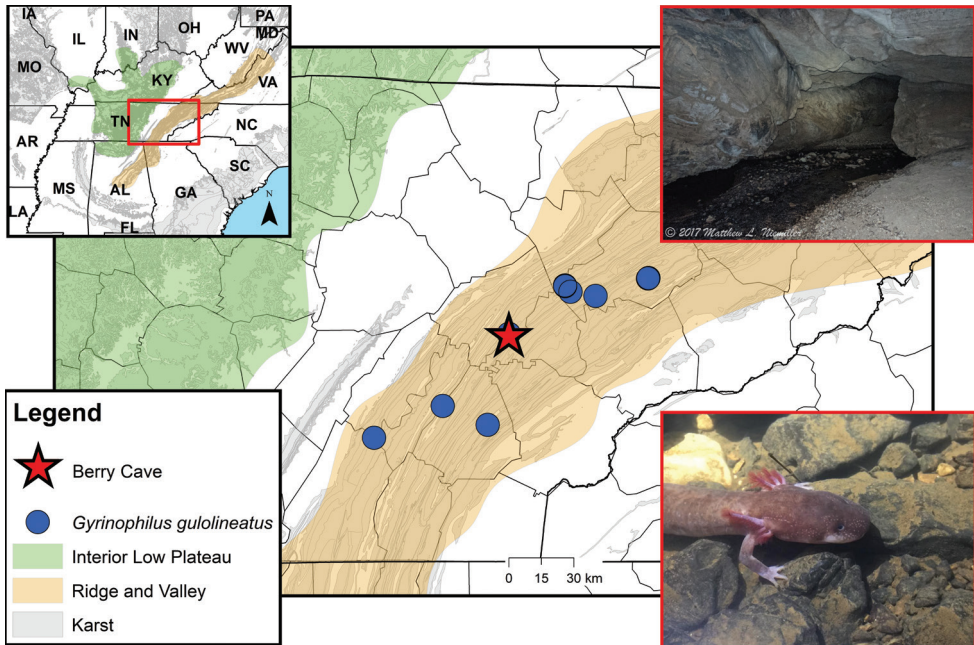
**Figure 1.** Geographic distribution of the Berry Cave Salamander (*Gyrinophilus gulolineatus*) in relation to karst adapted from Weary and Doctor (2014). Blue circles represent cave localities from which the species has been reported, and the red star represents the location of Berry Cave. The top right image shows the main stream passage near the entrance of Berry Cave that continues throughout the entirety of our sampling area. The bottom right image shows the large individual captured on 12 August 2018. Photo credits: Matthew L. Niemiller.

To provide a comparison of body size relations across other large-bodied plethodontids, we later compiled a list of maximum body sizes, modes of development, and habitat for several plethodontid salamanders by conducting a search of the primary literature and relevant field guides (see Table 1 and references therein).

## Results

The *Gyrinophilus gulolineatus* observed and captured at Berry Cave on 12 August 2018 measured 145 mm SVL and 238 mm TL, with a mass of 35 g (Figure 2). Head width measured 22 mm. There was notable damage to the posterior end of the tail, and it is likely that this individual was >250 mm TL before tail tissue loss. Additionally, the two distal-most gill rachises on the right side of the head were notably smaller than those on the left side, while the most proximal right gill rachis was enlarged relative to that on the left side of the head.

A list of maximum body size and total length for several large plethodontid salamanders is reported in Table 1. Based on our literature review, *G. gulolineatus* is the largest plethodontid based on body size (SVL) in the United States, while

**Table 1.** Mode of development (DD = direct development, m = metamorphic; OP = obligately paedomorphic, FP = facultatively paedomorphic), habitat (AQC = aquatic cave, SAC = semi-aquatic cave, SAT = semiaquatic terrestrial, SUT = surface terrestrial), maximum body size (SVL) and total length (TL) of select plethodontid salamanders based on literature sources and the current study.

| Size and life history characteristics of select plethodontid salamanders | | | | | |
|---|---|---|---|---|---|
| Species | Mode of development | Habitat | SVL (mm) | TL (mm) | References |
| *Bolitoglossa dofleini* | DD | SUT | 130 | 205 | Feder et al. (1982) |
| *Desmognathus quadramaculatus* | M | SAT | 103 | 189 | Bakkegard and Rhea (2012) |
| *Gyrinophilus gulolineatus* | OP | AQC | 145 | 238 | Brandon (1965, 1966), this study |
| *Gyrinophilus palleucus* | OP | AQC | 113 | 186 | Lazell and Brandon (1962), Dent and Kirby-Smith (1963), Niemiller et al. (unpubl. data) |
| *Gyrinophilus porphyriticus* | M | SAT/ SAC | 134 | 221 | Brandon (1966), Niemiller et al. (2010), Niemiller et al. (unpublished data) |
| *Gyrinophilus subterraneus* | FP | SAC | 117 | 199 | Niemiller et al. (2010) |
| *Isthmura bellii* | DD | SUT | 146 | 327 | Smith (1949), Feder et al. (1982), Raffaelli (2014) |
| *Isthmura gigantea* | DD | SUT | 161 | 276 | Taylor and Smith (1945) |
| *Isthmura maxima* | DD | SUT | 128 | 244 | Parra-Olea et al. (2005) |
| *Phaeognathus hubrichti* | DD | SUT | 138 | 268 | Schwaner and Mount (1970), Bakkegard and Guyer (2004), Graham et al. (2009) |
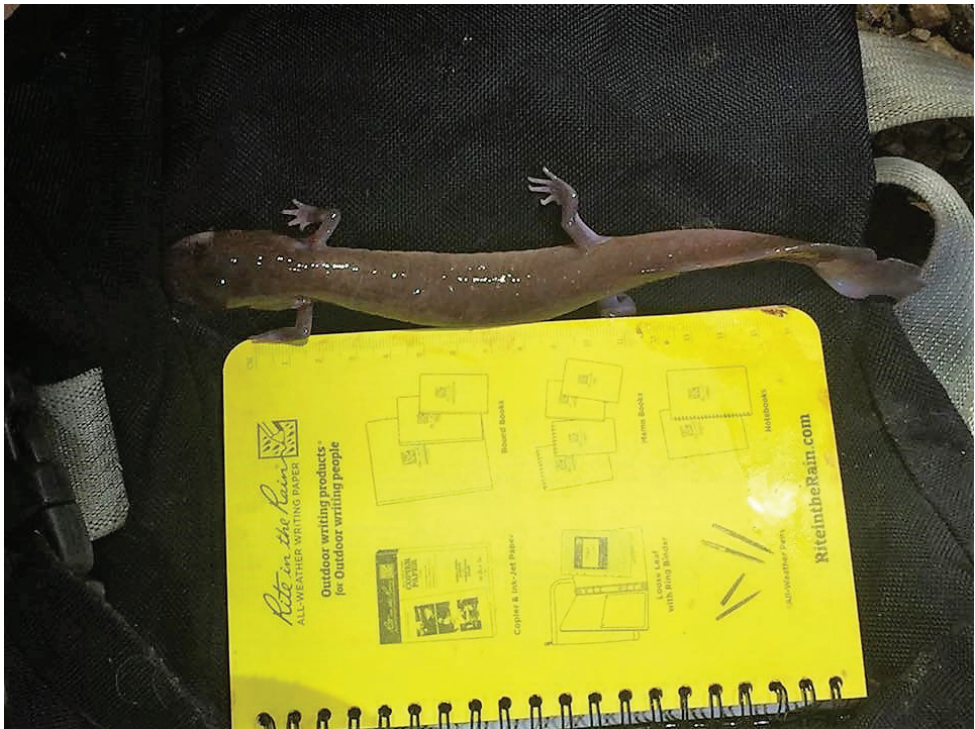


**Figure 2.** Dorsal view of the *Gyrinophilus gulolineatus* captured at Berry Cave. Photo credit: Matthew L. Niemiller.

only *Phaeognathus hubrichti* attains a greater total length. Body size in *G. gulolineatus* rivals that observed in the direct-developing *Isthmura bellii* species complex endemic to Mexico.

## Discussion

Plethodontid salamanders exhibit considerable variation in life history strategies and habitat that has resulted in an extraordinary range of growth rates and age at maturity (Tilley and Bernardo 1993, Beachy 1995, Beachy et al. 2017). Representative species with notable larger body sizes included in Table 1 represent four primary modes of development in salamanders, with paedomorphic and direct-developing species exhibiting larger body sizes relative to metamorphosing species. Larger species also are correlated with aquatic habitats, apart from the *Isthmura bellii* species complex, which inhabits Neotropical montane forests in southern North America.

Larger plethodontids are likely to occur in well-oxygenated, moist to fully aquatic habitats, which largely relax allometric constraints on gas exchange. This is particularly relevant to those species that exhibit paedomorphic life history strategies. Paedomorphic individuals may be able to grow unimpeded in their permanently aquatic state owing to indeterminate growth. Obligate paedomorphosis has evolved multiple times within Plethodontidae, with the subfamily Spelerpinae having the greatest richness of paedomorphic species (Chippendale 1995; Ryan and Bruce 2000; Bonnet et al. 2014). Additionally, neoteny has been predicted to be the primary causal mechanism of paedomorphosis in salamanders (Duellman and Trueb 1986, Ryan and Bruce 2000). Larger amphibian body sizes are further associated with longer juvenile periods, which significantly covary with age at maturation (e.g., *Desmognathus quadramaculatus* and *Gyrinophilus porphyriticus*, Bruce 1988, Beachy 1995, Beachy et al. 2017).

Many of the largest plethodontid salamanders are direct-developing (e.g., *Phaeognathus hubrichti* in the United States; *Isthmura bellii* in Mexico). Direct-developing species are generally characterized by having larger eggs and longer embryonic development relative to metamorphic or paedomorphic species, and this may related to attaining larger body sizes (Wake and Hanken 2004). There are, however, tradeoffs related to larger body size in these terrestrial plethodontids. The habitat must support gas exchange through adequate temperature and moisture gradients, and these taxa have evolved physiological mechanisms, such as waxy secretions, to reduce water loss. Second, terrestrial environments typically have lower food availability, and, accordingly, terrestrial salamanders often experience more extended periods of inactivity (Jaeger 1979, 1981, Scott et al. 2007). *Phaeognathus*, for instance, has rarely (if ever) been observed outside of burrows in densely forested ravines. Larger body size in such species is in accordance with the 'starvation hypothesis' that predicts that greater mass is positively correlated to seasonality and periods of low resource availability (Lundberg 1986), because larger individuals can persist through low-resource events by having

greater energy stores and typically more efficient metabolism owing to positive allometry. The starvation hypothesis has received recent support in multiple amphibian taxa, where body size is positively related to extended inactivity (Valenzuela-Sánchez et al. 2015) and increased precipitation seasonality (Goldberg et al. 2018).

Cave environments are often characterized by low food resources and few natural predators, which likely shaped much of the evolution of many subterranean taxa (Gibert and Deharveng 2002). However, this archetype may not be representative of all subterranean systems, as many caves possess a high surface-environment connection with significant allochthonous organic input (i.e., higher influx of organic matter) driving both terrestrial and aquatic food webs. Cave obligate salamanders often exhibit reduced growth rates and low metabolic demand (e.g., Hervant et al. 2000), and they may also exhibit greater longevity owing to the slow pace of life and low predation pressure associated with subterranean environments (Brandon 1971, Culver and Pipan 2009, Voituron et al. 2011, Hüppop 2012). High resource environments may thus permit more rapid growth and sustain a larger overall body size. The exceptionally large *Gyrinophilus gulolineatus* reported here occurred within 10 m of the cave entrance in a high flow zone with an abundance of organic matter accumulated in the cave pool. Berry Cave is a diverse system relative to other caves in the Appalachian Valley and Ridge (Niemiller et al. 2016), likely due to the large influx of organic matter from the surface. There are a variety of invertebrate taxa that serve as prey for *G. gulolineatus* (e.g., isopods, amphipods, crayfish, flatworms, etc.).

While there has been much focus on life history evolution in salamanders, sampling biases may impact interpretations of the relationship between body size and mode of development. Paedomorphic species may be more difficult to capture, and they are often associated with extreme habitats such as underground springs and caves (Ryan and Bruce 2000, Bonnet et al. 2014). More thorough survey efforts and detailed life history observations within harsher or more isolated environments are necessary to better understand how paedomorphosis may relate to body size in amphibians.

Due to its subterranean existence and cryptic nature, many life history characteristics of *G. gulolineatus* have yet to be documented. Active survey efforts are continuing to assess the species' demography in Berry Cave, as well as to better understand the growth of this species. Further biological inventory within the Appalachian Valley and Ridge is underway with the intent to uncover additional localities. Future directions for research include additional life history characterization and study of the species' ecology.

## Acknowledgements

# References

Adams DC, Church JO (2008) Amphibians do not follow Bergmann's rule. Evolution: International Journal of Organic Evolution 62(2): 413–420. https://doi.org/10.1111/j.1558-5646.2007.00297.x

Alberch P, Alberch J (1981) Heterochronic mechanisms of morphological diversification and evolutionary change in the neotropical salamander, *Bolitoglossa occidentalis* (Amphibia: Plethodontidae). Journal of Morphology 167(2): 249–264. https://doi.org/10.1002/jmor.1051670208

Bakkegard KA, Rhea RA (2012) Tail length and sexual size dimorphism (SSD) in desmognathan salamanders. Journal of Herpetology 46: 304–311. https://doi.org/10.1670/10-307

Bakkegard KA, Guyer C (2004) Sexual size dimorphism in the Red Hills salamander, *Phaeognathus hubrichti* (Caudata: Plethodontidae: Desmognathinae). Journal of Herpetology 38: 8–15. https://doi.org/10.1670/145-02A

Beachy CK (1995) Age at maturation, body size, and life-history evolution in the salamander family Plethodontidae. Herpetological Review 26: 179–181.

Beachy CK, Ryan TJ, Bonett RM (2017) How metamorphosis is different in plethodontids: larval life history perspectives on life-cycle evolution. Herpetologica 73(3): 252–258. https://doi.org/10.1655/Herpetologica-D-16-00083.1

Bernardo J, Reagan-Wallin NL (2002) Plethodontid salamanders do not conform to "general rules" for ectotherm life histories: insights from allocation models about why simple models do not make accurate predictions. Oikos 97(3): 398–414. https://doi.org/10.1034/j.1600-0706.2002.970310.x

Blueweiss L, Fox H, Kudzma V, Nakashima D, Peters R, Sams S (1978) Relationships between body size and some life history parameters. Oecologia 37(2): 257–272. https://doi.org/10.1007/BF00344996

Bonett RM, Steffen MA, Lambert SM, Wiens JJ, Chippindale PT (2014) Evolution of paedomorphosis in plethodontid salamanders: ecological correlates and re-evolution of metamorphosis. Evolution 68(2): 466–482. https://doi.org/10.1111/evo.12274

Bruce RC (1979) Evolution of paedomorphosis in salamanders of the genus *Gyrinophilus*. Evolution 33(3): 998–1000. https://doi.org/10.1111/j.1558-5646.1979.tb04753.x

Bruce RC (1980) A model of the larval period of the spring salamander, *Gyrinophilus porphyriticus*, based on size-frequency distributions. Herpetologica: 78–86.

Bruce RC (1988) Life history variation in the salamander *Desmognathus quadramaculatus*. Herpetologica: 218–227.

Culver DC, Pipan T (2009) The biology of caves and other subterranean habitats. Second edition. Oxford University Press, Oxford, U.K.

Duellman WE, Trueb L (1986) Biology of amphibians. McGraw-Hill, New York, USA.

Feder ME, Papenfuss TJ, Wake DB (1982) Body size and elevation in neotropical salamanders. Copeia 1982: 186–188. https://doi.org/10.2307/1444288

Gibert J, Deharveng L (2002) Subterranean ecosystems: A truncated functional biodiversity: this article emphasizes the truncated nature of subterranean biodiversity at both the bottom (no primary producers) and the top (very few strict predators) of food webs and dis-

cusses the implications of this truncation both from functional and evolutionary perspectives. AIBS Bulletin 52(6): 473–481.

Graham SP, Hoss SK, Godwin JC (2009): *Phaeognathus hubrichti* (Red Hills Salamander) record size. Herpetological Review 40: 196.

Goldberg J, Cardozo D, Brusquetti F, Villafañe DB, Gini AC, Bianchi C (2018). Body size variation and sexual size dimorphism across climatic gradients in the widespread treefrog *Scinax fuscovarius* (Anura, Hylidae). Austral Ecology 43(1): 35–45. https://doi.org/10.1111/aec.12532

Goricki S, Niemiller ML, Fenolio DB (2012) Salamanders. In: White WH, Culver DC (Eds) Encyclopedia of caves. Second edition. Elsevier, London, UK, 665–676. https://doi.org/10.1016/B978-0-12-383832-2.00098-0

Hairston NA, Hairston NG (1987) Community ecology and salamander guilds. Cambridge University Press, Cambridge, UK.

Hervant F, Mathieu J, Durand JP (2000) Metabolism and circadian rhythms of the European blind cave salamander *Proteus anguinus* and a facultative cave dweller, the Pyrenean newt (*Euproctus asper*). Canadian Journal of Zoology 78(8): 1427–1432. https://doi.org/10.1139/z00-084

Hüppop K (2012). Adaptation to low food. In: White WH, Culver DC (Eds) Encyclopedia of caves. Second edition. Elsevier, London, UK, 1–9. https://doi.org/10.1016/B978-0-12-383832-2.00001-3

Jaeger RG (1979) Fluctuations in prey availability and food limitation for a terrestrial salamander. Oecologia 44(3): 335–341. https://doi.org/10.1007/BF00545237

Jaeger RG (1981) Dear enemy recognition and the costs of aggression between salamanders. The American Naturalist 117(6): 962–974. https://doi.org/10.1086/283780

Lundberg A (1986) Adaptive advantages of reversed sexual size dimorphism in European owls. Ornis Scandinavica 17(2): 133–140. https://doi.org/10.2307/3676862

McNamara KJ, McNamara K (1997) Shapes of time: the evolution of growth and development. Johns Hopkins University Press, Baltimore, USA.

Niemiller ML, Poulson TL (2010) Subterranean fishes of North America: Amblyopsidae. In: Trajano E, Kapoor BG (Eds) Biology of Subterranean Fishes. Science Publishers, Enfield, 169–282. https://doi.org/10.1201/EBK1578086702-c7

Niemiller ML, Osbourn MS, Fenolio DB, Pauley TK, Miller BT, Holsinger JR (2010) Conservation status and habitat use of the West Virginia spring salamander (*Gyrinophilus subterraneus*) and spring salamander (*G. porphyriticus*) in General Davis Cave, Greenbrier Co., West Virginia. Herpetological Conservation and Biology 5(1): 32–43.

Niemiller ML, Carter ET, Hayter L, Gladstone NS (2018) New surveys and reassessment of the conservation status of the Berry Cave Salamander (*Gyrinophilus Gulolineatus*). Technical Report. U. S. Fish & Wildlife Service, 51 pp.

Niemiller ML, Zigler KS, Stephen CDR, Carter ET, Paterson AT, Taylor SJ, Engel AS (2016) Vertebrate fauna in caves of eastern Tennessee within the Appalachians karst region, USA. Journal of Cave and Karst Studies 78: 1–24. https://doi.org/10.4311/2015LSC0109

Parra-Olea G, Garcia-Paris M, Papenfuss TJ, Wake DB (2005) Systematics of the *Pseudoeurycea bellii* (Caudata: Plethodontidae) species complex. Herpetologica 61: 145–158. https://doi.org/10.1655/03-02

Pipan T, Culver DC (2017) The unity and diversity of the subterranean realm with respect to invertebrate body size. Journal of Cave and Karst Studies 79: 1–9. https://doi.org/10.4311/2016LSC0119

Poulson TL (1963) Cave adaptation in amblyopsid fishes. American Midland Naturalist: 257–290. https://doi.org/10.2307/2423056

Romero A (2009) Cave biology: life in darkness. Cambridge University Press, Cambridge, UK. https://doi.org/10.1017/CBO9780511596841

Ryan TJ, Bruce RC (2000) Life history evolution and adaptive radiation of hemidactyliine salamanders. In: Bruce RC, Jaeger RG, Houck LD (Eds) The biology of plethodontid salamanders. Springer, Boston, MA, 303–326. https://doi.org/10.1007/978-1-4615-4255-1_15

Scott DE, Casey ED, Donovan MF, Lynch TK (2007) Amphibian lipid levels at metamorphosis correlate to post-metamorphic terrestrial survival. Oecologia 153(3): 521–532. https://doi.org/10.1007/s00442-007-0755-6

Sket B (2008) Can we agree on an ecological classification of subterranean animals?. Journal of Natural History 42(21–22): 1549–1563. https://doi.org/10.1080/00222930801995762

Slavenko A, Meiri S (2015) Mean body sizes of amphibian species are poorly predicted by climate. Journal of Biogeography 42(7): 1246–1254. https://doi.org/10.1111/jbi.12516

Smith HM (1949) Size maxima in terrestrial salamanders. Copeia 1949: 71. https://doi.org/10.2307/1437669

Smith HM, Taylor EH (1948) An annotated checklist and key to the Amphibia of Mexico. Bulletin of the United States National Museum 194: 1–118. https://doi.org/10.5479/si.03629236.194

Stearns SC (1992) The evolution of life histories. Oxford University Press. Oxford, UK.

Tilley SG, Bernardo J (1993) Life history evolution in plethodontid salamanders. Herpetologica 49, no. 2: 154–163.

Valenzuela-Sánchez A, Cunningham AA, Soto-Azat C (2015) Geographic body size variation in ectotherms: effects of seasonality on an anuran from the southern temperate forest. Frontiers in Zoology 12, no. 1: 37. https://doi.org/10.1186/s12983-015-0132-y

Voituron Y, de Fraipont M, Issartel J, Guillaume O, Clobert J (2011) Extreme lifespan of the human fish (*Proteus anguinus*): a challenge for ageing mechanisms. Biology Letters 7:105–107. https://doi.org/10.1098/rsbl.2010.0539

Wake DB, Hanken JA (2004) Direct development in the lungless salamanders: what are the consequences for developmental biology, evolution and phylogenesis? International Journal of Developmental Biology 40(4): 859–869.

Weary DJ, Doctor DH (2014) Karst in the United States: A digital map compilation and database. USGS Open File Report 2014–1156; Available: http://pubs.usgs.gov/of/2014/1156/

Whitford WG, Hutchison VH (1967) Body size and metabolic rate in salamanders. Physiological Zoology 40(2): 127–133. https://doi.org/10.1086/physzool.40.2.30152447

Wiens JJ, Hoverman JT (2008) Digit reduction, body size, and paedomorphosis in salamanders. Evolution and Development 10(4): 449–463. https://doi.org/10.1111/j.1525-142X.2008.00256.x

Yeh J (2002). The effect of miniaturized body size on skeletal morphology in frogs. Evolution 56(3): 628–641. https://doi.org/10.1111/j.0014-3820.2002.tb01372.x