

DISTRIBUTION AND ENCOUNTER RATES OF GREEN SALAMANDERS (*ANEIDES AENEUS*) AT THE PERIPHERY OF THEIR RANGE IN NORTHEASTERN MISSISSIPPI, USA

BAILEY WATKINS¹, THOMAS MANN², AND WILL SELMAN^{1,3}

¹Department of Biology, Millsaps College, 1701 North State Street, Jackson, Mississippi 39210, USA

²Mississippi Department of Wildlife, Fisheries, and Parks, Mississippi Museum of Natural Science,
2148 Riverside Drive, Jackson, Mississippi 39202, USA

³Corresponding author, e-mail: will.selman@millsaps.edu

Abstract.—Green Salamanders (*Aneides aeneus*) are considered imperiled throughout most of their range. At the southwestern periphery of their range in northeastern Mississippi, USA, they are associated with Hartselle Sandstone outcrops. Because rock outcrop habitat is rare in the state and historical records for *A. aeneus* are few, we completed 180 visual surveys at 32 different rock outcrops from 2017–2023 in Tishomingo County, Mississippi. We observed *A. aeneus* at 78.1% of sites, including most historical sites and 17 previously undocumented outcrops; they were not observed at several other apparently suitable outcrops. Observed summer encounter rates (mean: 0.53/ person hour searched) were greater than observed in other parts of their range. Encounter rates were greater on public lands compared to private lands, but not different by region we surveyed, night or day surveys, or year. We documented reproduction at 19 outcrops, with female egg brooding initiated between 26 July and 8 August; cyclic reproduction across years was observed. We estimate that at least about 15.7 linear km of known outcrop habitat is available in Mississippi, and the presence of *A. aeneus* is overrepresented in rock overhang microhabitats. Our surveys indicate that *A. aeneus* occurs at most Hartselle Sandstone outcrops in Tishomingo County, but their range is still extremely small in the state. Further, the factors explaining their apparent absence at some outcrops and the historical decline at another location remain unknown. Long-term studies are warranted to better determine the species viability and reproductive patterns in Mississippi.

Key Words.—amphibians; egg brooding; Hartselle Sandstone; imperiled species; Plethodontidae; rock outcrop; Species of Greatest Conservation Need; visual encounter surveys

INTRODUCTION

The southeastern U.S. is a biodiversity hotspot for terrestrial and aquatic salamanders (Milanovich et al. 2010) because of the many ecological niches and long geologic history of the Appalachian Mountains and Cumberland Plateau (Tilley 1980). This region extends southwestward into northern Alabama and extreme northeastern Mississippi (Tishomingo County), providing the latter with habitats unavailable elsewhere in the state. Consequently, those habitats support many salamander species that are typically associated with states to the northeast, such as Cave Salamanders (*Eurycea lucifuga*), Spring Salamanders (*Gyrinophilus porphyriticus*), and Eastern Hellbenders (*Cryptobranchus alleganiensis*). One species whose distribution is restricted to the northeastern corner of Mississippi is the Green Salamander (*Aneides aeneus*), which occurs patchily throughout much of the Appalachian Plateau and the Ridge and Valley provinces (Petranka 1998). The species is most

frequently observed in deep crevices of rock outcrops that are surrounded by mature forest (Smith et al. 2017). They are highly adapted and specialized to live and breed in and around rock outcrops (Walker and Goodpaster 1941), and recent studies have shown their seasonal dependence upon arboreal habitats in the spring (Waldron and Humphries 2005). In all 13 of the states where *A. aeneus* occurs, it is ranked as Vulnerable (S3), Imperiled (S2), or Critically Imperiled (S1; <https://explorer.natureserve.org/>). *Aneides aeneus* is also currently under review for listing under the Endangered Species Act (U.S. Fish and Wildlife Service 2015) and are listed as Near Threatened in the Red List of Threatened Species of the International Union for the Conservation of Nature (Soto 2021).

Within Mississippi, *A. aeneus* has been reported from nine distinct sites, and all but two of these are located within Tishomingo State Park (TSP; Woods 1968; William Cliburn, unpubl. report). Furthermore, all records are associated with Hartselle Sandstone



Figure 1. Representative photograph of a Hartselle Sandstone rock outcrop in Tishomingo State Park, Mississippi, USA. This location is a previously unsearched rock outcrop, Z2, where we documented five new locations for Green Salamanders (*Aneides aeneus*). For perspective, the photograph is taken facing northwest, with the primary rock wall on the right (east), a secondary wall is on the left (west), and a third wall is out of the photograph on the other side of the boulder to the left. (Photographed by Will Selman)

rock formations, a geologic layer that exhibits large rock wall formations (maximum height: about 12 m; Merrill et al. 1988; Fig. 1). These rock formations were deposited during the Carboniferous Period, approximately 360–299 mya (Thompson 2011), and they are more similar to the geology of the southern Appalachians of Alabama, Tennessee, and Georgia than to the geology elsewhere in Mississippi. Even though Mississippi is on the periphery of their range, the species has been consistently observed in TSP since the 1960s with varying encounter rates reported (Rauch et al. 2016). In Mississippi, however, they are considered a Species of Greatest Conservation Need (S1 species - Critically Imperiled; Mississippi Museum of Natural Science 2015), are known from a very small region in the state (about 5.3 km²), and are very susceptible to extirpation (Mississippi Museum of Natural Science 2015). Furthermore, there is no recent information published about their population status therein. Therefore, the primary objectives of our study were to determine the distribution and encounter rates (i.e., catch per unit effort, CPUE) of *A. aeneus* in northeastern Mississippi. Secondary objectives of our study were to describe *A. aeneus* habitats in Mississippi, determine if *A. aeneus* is extant at historical sites, report on reproductive activity, and compare encounter rates across different regions, property ownership types, and survey times.

MATERIALS AND METHODS

In 2017 (March–November), 2018 (April–October), and 2019 (April–December), we completed 93 surveys at 25 rock outcrop sites located on both private and public lands to document the presence of *A. aeneus* (Fig. 2; Appendix Table). During July and August 2021–2023, we conducted 87 surveys at 32 rock outcrop sites also on private and public lands (Fig. 2; Appendix Table). The distinction between these two property types was made due to the different land management activities on these properties that may impact *A. aeneus* populations. For example, timber harvesting occurs regularly on private lands, and the loss of trees may impact arboreal habitat and/or change rock outcrop microclimate for *A. aeneus* (Pauley and Watson 2005; Newman et al. 2022; Smith 2024).

Rock outcrop habitat varied, ranging from continuous or semi-continuous rock walls (up to 15–20 m) at or near the point of original erosional exposure (i.e., typically near the top of steep slopes) to scattered boulders downslope from the original erosional surface; the latter are often tilted differently from the original bedding plane. Most of the rock outcrop locations were heavily forested with moderate to steep topographic relief. We selected sites based on the knowledge that *A. aeneus* has only been found in Mississippi at Hartselle Sandstone outcrops, and we consulted a detailed local geological map (Merrill et al. 1988) that highlights the small area in Tishomingo County that has this unique geological formation. Along with the geological map, these outcrop sites were also known from previous surveys (e.g., Woods 1968; Rauch et al. 2016), identified via Google Earth (i.e., where exposed rock was visible during winter aerial images), or located while walking/searching in wooded areas. Because this is a relatively small region in the state (< 30 km²), we believe that most of the major Hartselle Sandstone outcrops in Mississippi were identified using these methods. Indeed, Aldridge et al. (2024) completed LIDAR surveys for sheer rock faces in Tishomingo State Park independent of this study, and all the locations we surveyed were nearly identical to the rock outcrop habitats that were remotely sensed. Nonetheless, we acknowledge that future surveys could find additional small outcrops in Mississippi that might be suitable habitat for *A. aeneus*.

For all surveys from 2017–2023, we used area-constrained survey techniques to survey at each rock outcrop. At each outcrop, we used hand-held

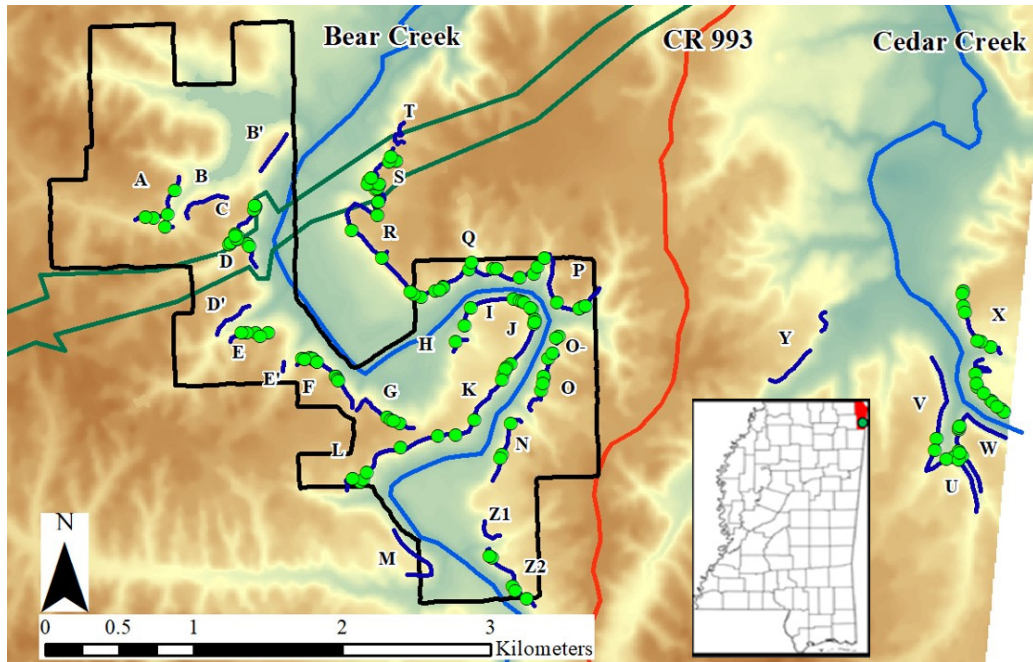


Figure 2. Locations of Hartselle Sandstone rock outcrops and Green Salamander (*Aneides aeneus*) locations from 2017–2023 in northeastern Mississippi, USA. Dark blue lines indicate the approximate location of the surveyed rock outcrops (letters match those in the Appendix Table), while green points indicate locations where individual *A. aeneus* were documented. Also depicted on the map include Tishomingo State Park (black boundary), the Natchez Trace Parkway (green boundary), Bear and Cedar creeks (light blue), and Tishomingo County Road 993 (red line). The green dot on the inset map of Mississippi represents the location of the larger map.

flashlights and headlamps to search crevices and openings in the rock formations during daytime and/or nighttime hours. We searched all rock formations completely between 0 and about 2.0 m height above the ground, and this includes all rock surfaces and crevices. Most rock outcrops could be surveyed in their entirety during a single visit, although some more extensive outcrops (e.g., Site Q) required multiple visits to be surveyed completely. For every individual salamander we found, we identified it to species, and we counted all salamanders and other lithophilic reptiles and anurans. For each *A. aeneus*, we also recorded the age-class (juvenile/adult) and the location with a handheld GPS; specific GPS locations are withheld from this manuscript, but they were deposited with the Mississippi Natural Heritage Program at the Mississippi Museum of Natural Science. For the 2021–2023 surveys, we recorded the salamander height above ground, type of crevice (e.g., horizontal, vertical, honeycomb, hole; Fig. 3), whether the salamander was tending eggs (hereafter, brooding females), and the person search hours expended at each rock outcrop as a measure of effort. We collected the latter information to calculate the encounter rate (CPUE): the number of salamanders observed at a rock outcrop divided by the total

person search hours expended during that rock outcrop survey. We included the time to collect data and tissue samples for a related study in the person search hours. Waldron and Humphries (2005) found significant use of trees by *Aneides*, but we conducted no formal surveys of trees in the proximity of outcrops for *Aneides*. Thus, we acknowledge that our CPUE calculation does not reflect possible differences in local *Aneides* populations based on differences in use of trees among sites or the differences in forest composition (i.e., different tree species, stand condition, and proximity to outcrops). Also, there were many differences across rock outcrops (e.g., rock crevice frequency, width, depth, and height above the ground among sites), and these differences may have affected the detectability of salamanders.

To determine if encounter rates of *A. aeneus* varied across the limited distribution of the species in Mississippi, we divided the rock outcrops into three regions, with sites west of Bear Creek in what we called the West Region, sites east of Bear Creek and west of Tishomingo County Road 993 in the Central Region, and sites east of County Road 993 in the East Region (Fig. 2). We designated these regions because Bear Creek, a significant geographical barrier, separates the western and central sites, and a long

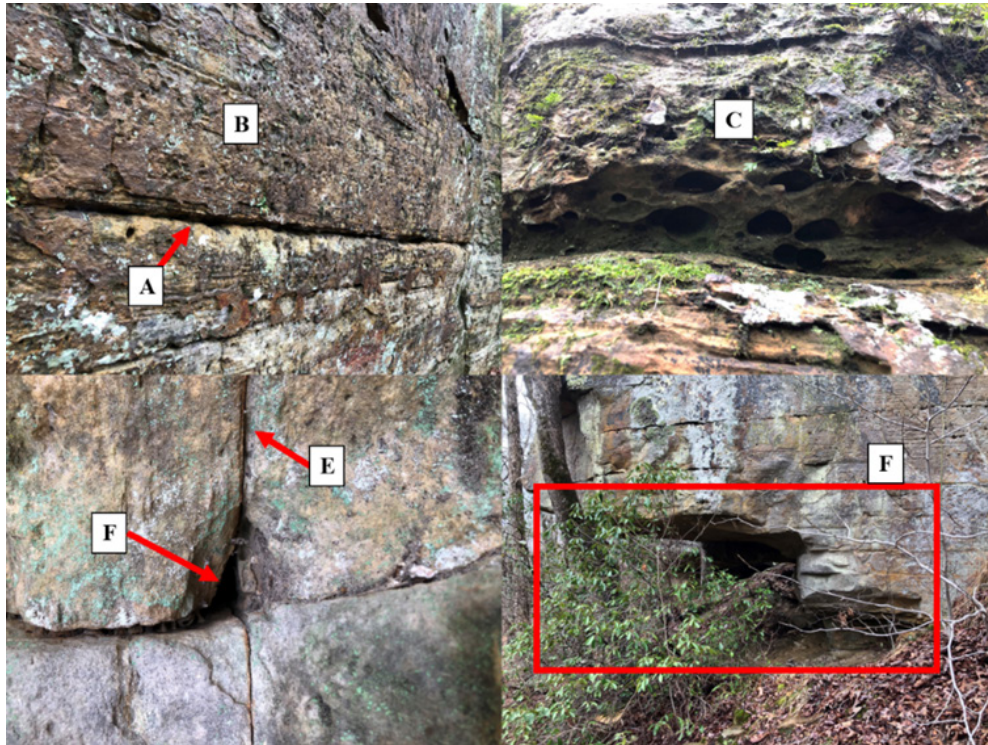


Figure 3. A comparison of Hartselle Sandstone microhabitat types where Green Salamanders (*Aneides aeneus*) were detected in Tishomingo County, Mississippi, USA. A rock outcrop with (A) a long horizontal crevice and (B) with exposed rock face above. (C) Honeycomb habitat in Hartselle Sandstone exhibited a series of scooped-out sections in the rock, and these sections were sometimes extensive. (D) Holes were classified as singular, deep and narrow recesses that extended perpendicular into the rock face and (E) a vertical crevice extends above the hole. (F) Overhang habitat was underrepresented along Hartselle Sandstone outcrops, but *A. aeneus* were overrepresented in these habitats. (Photographed by Will Selman).

geographical distance of unsuitable habitat separates the central and eastern sites. We then performed two Kruskal-Wallis tests to determine if CPUE was the same by region using all site CPUE data and rock outcrop sites with only non-zero data. Similarly, we used Wilcoxon Ranked Sums (two groups) or Kruskal-Wallis (three groups) tests for independently *a priori* hypotheses to determine if CPUE was the same in day versus night surveys on private and public lands, and by year (2021/2022/2023). For all statistical analyses, we used the software JMP 12.2.0 (SAS Institute, Cary, North Carolina, USA), with significance of tests at $\alpha = 0.05$.

RESULTS

Distribution.—We completed 182 surveys at 32 rock outcrop sites, and we observed *A. aeneus* at 25 of 32 sites (78.1%; Fig. 2). We confirmed their presence at eight of the nine historical sites, and we also documented *A. aeneus* from 17 new rock outcrop sites from which the species had not been previously documented. At most outcrop sites where the species

was observed, multiple discrete sightings were often made along the length of the rock outcrop site. Of the seven rock outcrop sites where we did not detect *A. aeneus*, five were on public land (B, B', D', E', T), and two were on private land (M, Y). Only one of these sites had a historic record (M), and we surveyed this site four times without detecting *A. aeneus*. Previous records encompass a minimum convex polygon area of approximately 5.3 km², while the additional records from this study increase the occupied area to about 7.9 km² (50.0% area increase; Fig. 4).

Encounter rates.—During July/August 2021–2023 (excluding 2017–2020 surveys), we completed 87 surveys of all 32 rock outcrop sites, and we searched for 492.1 person hours. We documented 1,102 salamanders associated with rock faces and crevices including 586 Slimy Salamanders (*Plethodon glutinosus*) complex (53.0% relative abundance [RA], 1.19/h), 254 *A. aeneus* (23.0%, 0.52/h), 205 Long-tailed Salamanders (*Eurycea longicauda*; 18.7%, 0.42/h), 42 Southern Two-lined Salamanders (*Eurycea cirrigera*; 3.8%, 0.09/h), eight unknown

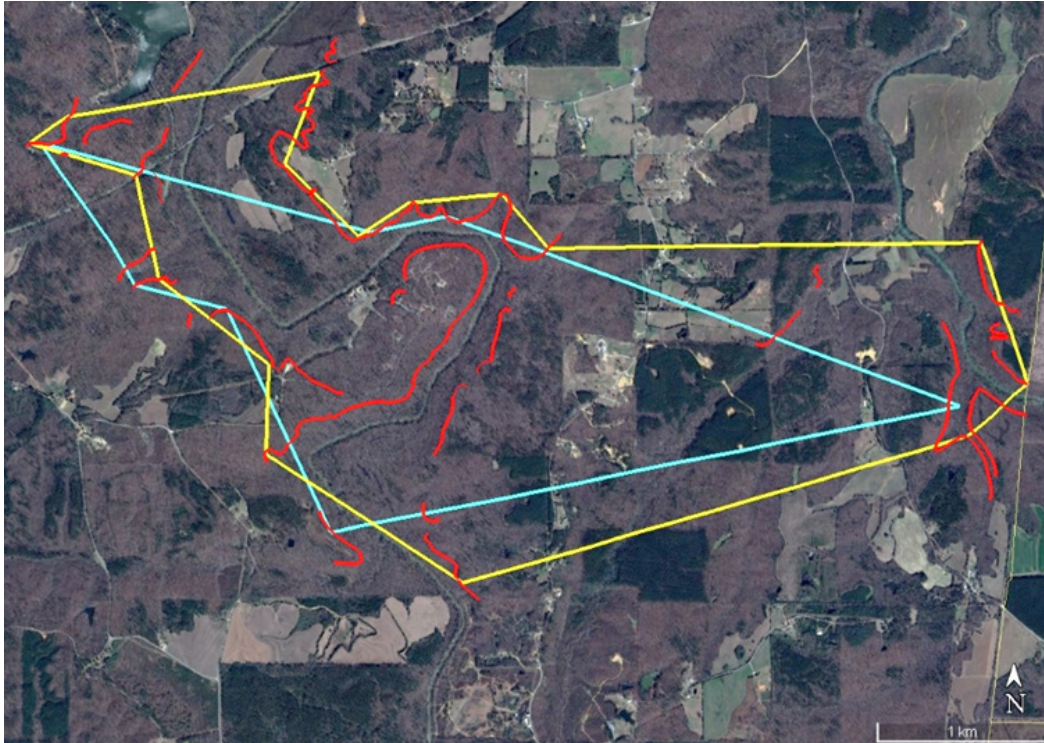


Figure 4. A comparison of the known range of Green Salamanders (*Aneides aeneus*) prior to this study (blue polygon) and known range after this study (yellow polygon) in Tishomingo County, Mississippi, USA. The red lines are approximations of rock outcrops.

salamanders (< 1%), and seven Cave Salamanders (*Eurycea lucifuga*; < 1%, 0.01/h; Appendix Table). Mean *A. aeneus* CPUE of all surveys was 0.52/h \pm (standard deviation) 0.69 (range of values 0–4.0). There was some variation by region (Central: mean = 0.65/h \pm 0.90, range of values 0–4.0; West: mean = 0.42/h \pm 0.61, range of values 0–2.4; East: mean = 0.28/h \pm 0.49, range of values 0–1.6), but there was no significant difference by region ($H = 2.91$, $df = 2$, $P = 0.234$; Fig. 5). A similar analysis with all non-zero CPUE sites also indicated no regional differences in CPUE ($H = 1.14$, $df = 2$, $P = 0.565$).

Northeastern Mississippi experienced a wet year due to persistent rainfall in 2021 (2021 CPUE Mean = 0.46/h \pm 0.82), while drought existed during the spring and summer of 2022 and 2023 (2022 CPUE mean = 0.49/h \pm 0.63; 2023 CPUE mean = 0.40/h \pm 0.44); however, there was no significant differences in CPUE by year ($H = 0.99$, $df = 2$, $P = 0.610$; Fig. 5). Similarly, there was no significant differences in the CPUE in surveys conducted during the day (Mean CPUE = 0.51/h \pm [0.65] compared to night (Mean CPUE = 0.43/h \pm 0.73; $Z = 0.21$, $df = 1$, $P = 0.649$; Fig. 5). CPUE on public land rock outcrops, however, was significantly higher (Mean CPUE = 0.54/h \pm 0.74) than CPUE on private land rock

outcrops (Mean CPUE = 0.22/h \pm 0.43; $Z = -2.03$, $df = 1$, $P = 0.042$; Fig. 5).

Reproduction.—We found gravid females in 2021 from 19 July until 28 July and in 2022 from 14 July until 9 August. Females initiated egg brooding on 26 July 2021 and 3 August 2022. In 2023, we began our surveys later, and we observed a brooding female on the first day of surveys on 24 July 2023. Observations of brooding females extended until the end of the study period in all years.

Of the 254 *A. aeneus* individuals we found from 2021–2023, 39 (15.4%) were brooding females. We observed brooding females at 13 sites (B, C, F, I, J, K, O-, P, Q, S, W, X, and Z2), and the highest percentage of brooding females was observed at site O- (four of 11 individuals). Along with brooding location variability, we noticed a difference in the number of brooding females observed by year. The percentage of brooding females were fourfold higher in 2021 (21%; 16 of 77) and sixfold higher in 2023 (32%; 17 of 53) compared to 2022 (5%; six of 122). Along with gravid and brooding females, we observed evidence of reproduction in the form of small juveniles (< 2 cm SVL) during our surveys. In 2021, we observed four juveniles (5.1% of all individuals observed that year)

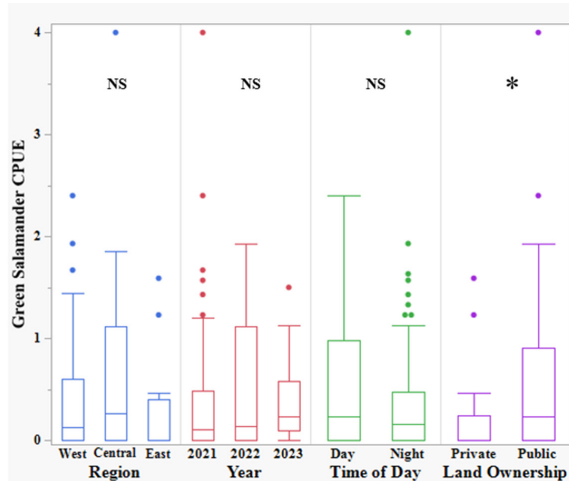


Figure 5. Comparison of Green Salamander (*Aneides aeneus*) catch per unit effort (CPUE) by (from left to right) region, year, time of survey, and land ownership. Horizontal lines are the medians, the boxes are the interquartile range (IQR; 25th -75th percentile), the vertical lines represent the last point that is within 1.5×IQR, and the dots are outlier points. The abbreviation NS = non-significant difference and the asterisk (*) = significant difference.

at two sites (K-1, L-3) and zero juveniles in 2023 (0%), but in 2022, we observed 40 juveniles (33%) at eight sites (F-13, C-6, S-3, V-1, Q-7, N-1, X-8, W-1).

Habitat.—Based on GPS points collected from rock outcrop sites, we estimate that we searched about 15.7 linear km of rock outcrops and rock faces that are potential habitat for *A. aeneus*. Of the 15.7 km, about 9.9 km (63.1%) of rock outcrop habitat occurs within protected lands of TSP and the Natchez Trace Parkway (NTP). The remaining 36.9% is privately owned, and parcels of three private landowners contain the majority of rock outcrop habitat (88.1% of private property rock outcrops).

Of the 254 *A. aeneus* individuals we observed, 142 (55.9%) were in horizontal crevices, 50 (19.7%) were in holes, 39 (15.4%) were on exposed rock faces/ledges, 14 (5.5%) were in vertical crevices, and 9 (3.5%) were in honeycomb formations (i.e., large series of scooped-out areas of the rock). The mean height above ground level for individuals was 1.3 m (standard deviation = 0.49, range of values 0.22–2.74), but few observations could be completed above 2 m due to inability to access higher crevices. Another interesting observation was the strong tendency of *A. aeneus* individuals to be found under large rock overhangs (Fig. 3), with 10% of observations in these locations even though their habitat availability was

about 5%.

DISCUSSION

Distribution.—We found *A. aeneus* at most rock outcrop sites surveyed in northeastern Mississippi and in every historical site except for one. We found individuals at 17 previously unsurveyed rock outcrops, and many of the rock outcrop sites had multiple discrete locations that we documented within each site. Our survey results increase the potential area of occupation in the state by > 50%. To the best of our knowledge, many of the new sites we found were due to the extensive searching of previously unsearched or unknown rock outcrops within and outside TSP. Some of the areas were remote and/or on private lands, and previous surveys mostly focused on easily accessible locations on TSP. The percentage of sites where we found *A. aeneus* in Mississippi (78.1%) was higher than what has recently been reported in other states. In comparison, the highest percentage of occupied sites previously reported was in North Carolina (77.2%, 44 of 57 sites; Williams et al. 2020). In Tennessee, Niemiller et al. (2022) found *A. aeneus* at 47 of the 84 survey sites (55.9%), while Newman et al. (2018) found 49.2% of sites occupied in northwestern South Carolina. John (2017) found only 15.5% of sites occupied at Redstone Arsenal in northern Alabama. Because most species typically exhibit rarity or scattered populations on the edge of their range compared to the core of their range (Channell 2004; Steen and Barrett 2015), one would not expect higher rates of sites occupied at peripheral sites (i.e., Mississippi) compared to core areas of the range (i.e., Tennessee, North Carolina, Alabama). Thus, comparative studies in neighboring regions of northwestern Alabama may provide additional insights to determine if this is a local pattern we observed or if it extends more broadly into neighboring areas.

We were unsuccessful in locating any individuals at site M, a private property site previously reported by Rauch et al. (2016). We are unsure why no individuals were detected during our four surveys, but it could possibly be due to historical events at the site including rock mining that occurred at the site until approximately 2015. Mining also occurred at a site on TSP (Site A) prior to its establishment as a state park in 1935, however, so mining may not entirely explain their absence at site M. Indeed, Hinkle et al. (2018) found that *A. aeneus* was observed in 70% of sites with evidence of extensive mining. So, while mining may have had an adverse effect on the

population, it is not likely to be the only contributing factor to our non-detection. Future efforts should continue to survey sites like site M where we did not find *A. aeneus*. Further, it is possible that additional rock outcrop habitat may occur in Mississippi, yet it will likely be smaller and disjunct from the primary areas we surveyed.

Encounter rates.—Our overall CPUE estimate (0.52/search hour) was similar to densities found in Tennessee (0.52/h; Niemiller et al. 2022). Unlike Tennessee, however, our surveys were completed entirely during the summer, and previous studies have found that *A. aeneus* fall encounter rates in Tennessee and North Carolina (Tennessee: 1.5–3.0/h; North Carolina: 0.84–1.06/h) were greater than summer encounter rates (Tennessee: 0.2–0.4/h; North Carolina: 0.29–0.43/h; Niemiller et al. 2022, Williams et al. 2020). Thus, using a similar seasonal comparison, the summer encounter rates we observed in Mississippi were higher than reported in either North Carolina or Tennessee studies, both states considered to be within the core range of *A. aeneus*. Previous studies have found that detection and encounter rates of *A. aeneus* can vary widely depending on numerous environmental, seasonal, observer experience, and physiological factors (Waldron and Humphries 2005; John 2017; Newman et al. 2018, Niemiller et al. 2022), and summer, when our surveys were completed, has not typically been considered a season where high encounter rates would be expected (Williams et al. 2020, Niemiller et al. 2022). Because we did not survey in other seasons, it is not possible to know how different seasons or environmental conditions might have factored into our encounter rates. Previous summer rock outcrop surveys at these sites, however, yielded 10-fold differences in CPUE across years; for example, surveys in July 2017 at site F had a CPUE of 13.3/h, while two years later in July 2019 the CPUE was 1.3/h (unpubl. data). The latter CPUE is similar to the CPUE found in this study for the same site. Therefore, we suspect some of these CPUE differences may also be associated with dynamic yearly shifts in recruitment and survival (i.e., Boom and Bust).

While the overall encounter rate of *A. aeneus* in Mississippi is higher than other states, some Mississippi sites appear to have experienced long-term declines. For example, it seems that a marked decline has occurred at site I (Cabin Cliffs) since the 1970s, especially considering that Woods (1968) reported *A. aeneus* was extremely abundant at this

site. Further, Rauch et al. (2016) documented 13 individuals in five surveys in 2008 and 2009, while only two and one individuals were observed there in 2017 and 2019, respectively (unpubl. data). In 2021–2023 CPUE surveys, we only detected three individuals at this location, so it is unknown why *A. aeneus* at this location have declined long-term. First, other studies also found that similar declines occurred for *A. aeneus* populations between the 1970s and 1980s, and climate change, habitat loss, and epidemic disease were considered the most likely scenarios to explain the declines (Snyder 1991; Corser 2001). These explanations do not seem plausible for our study, however, as declines have only been observed at a single site and not the entirety of the Mississippi distribution. Second, it could be due in part to scientific collection pressures in the past (Corser 2001). Based on specimen records from the Mississippi Museum of Natural Science (Emily Field, pers. comm.) and in other museums (VertNet.org), at least 63 specimens were collected at Tishomingo State Park over a 12-y period (between 1956–1967). It is unknown from what rock outcrop(s) these individuals were collected, but a portion were likely collected from Cabin Cliffs given its prominence as a study site by Woods (1968). If they were collected from one or a handful of sites, that could lead to difficulty in recovery/recolonization of the site. Third, declines could be due to impacts from nearby cabins and recreational practices. Rauch et al. (2016) indicated that cabin renters dumped fire ashes and refuse over the cliffs, potentially impacting this population. Lastly, we noticed that many crevices were completely covered at this site with mosses in 2021–2023, obscuring some of the crevice habitat. The advance of moss could be due to succession via a lack of disturbances that have not happened at this rock outcrop in a long time (i.e., 20+ y without growing season fires occurring on a longer rotation; canopy openings from occasional blowdowns, and desiccation of rock faces). Gordon (1952) indicated that moss invasion into brooding crevices resulted in *A. aeneus* females abandoning it over time, so this may be an explanation into local declines at this site. It is possible that two or more of these factors could also be interacting at a local scale at this rock outcrop. Future surveys to assess moss coverage and other habitat changes through time would be valuable at multiple sites.

With our extensive search of the areas within and bordering TSP, we did not detect any *A. aeneus* CPUE differences between regions and surprisingly,

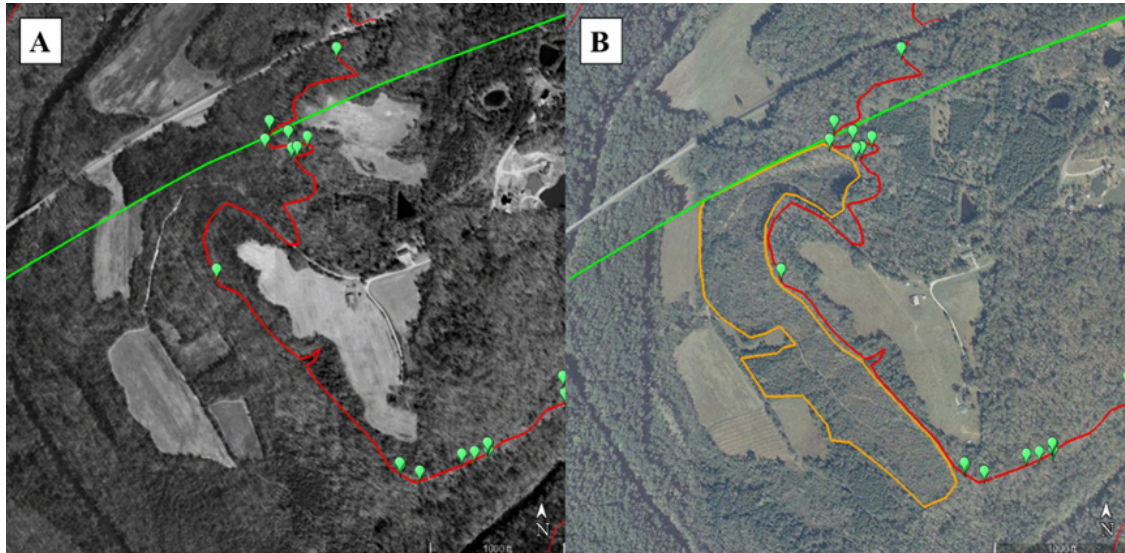


Figure 6. A comparison of forest harvesting on private and public land surrounding rock outcrops (red line) and observed Green Salamander (*Aneides aeneus*) locations (green pins) in Tishomingo County, Mississippi, USA. (A) 1996 aerial photograph of private property (below green line) and Natchez Trace Parkway Property (above green line). (B) 2004 aerial photograph of same location depicting timber harvest (orange polygon) that occurred between 1996 and 2004. Tishomingo State Park is in the bottom right corner of both images. (Images from Google Earth Pro).

we found no difference in CPUE across years despite dramatically different environmental conditions between years. The only difference found in CPUE was the $2.7\times$ higher encounter rates observed on public compared to private land. While some locations on private land held large tracts of extensive rock faces and mature forests, others had adjacent forests that had been disturbed by logging activities within the last 10–20 y. For example, based on time lapse imagery on Google Earth, the adjacent forest downslope of site R (CPUE: 0.16/h) was harvested in the late 1990s/early 2000s, while adjacent forest along the Natchez Trace Parkway (Site S; CPUE: 1.68/h) remained intact (Fig. 6). Further, other sites had timber operations that left a large buffer around the rock face (> 100 m; e.g., site X), and high CPUE was found at this location. Because *A. aeneus* can be seasonally highly arboreal, prefer larger trees near rock outcrops, and are associated with a greater density of trees near rock outcrops (Waldron and Humphries 2005; Smith et al. 2017), timber harvesting activities near rock outcrops could have detrimental impacts on populations. Alternatively, timber harvesting activities farther away may have less to no impact on the population.

Reproduction.—We observed about a two-week difference in the initiation of egg brooding in 2021 (19 July) and 2022 (8 August). In an earlier study in TSP, Woods (1968) reported a similar initiation of

egg laying at TSP on 15 July, and that egg laying was short lived and occurred simultaneously throughout TSP. Because 2021 was a wet year, it seems possible that this could have influenced the early egg-brooding initiation, whereas the drier conditions of 2022 may have delayed egg-brooding initiation. In West Virginia, Canterbury and Pauley (1994) observed that females initiated egg brooding in the second week of June and tended eggs through mid-August, so our initiation dates occurred later in the season than more northerly latitude sites.

We also found that about 11% of all *A. aeneus* observations were egg brooding females compared to about 1.5% observed in Tennessee (five of 329; Niemiller et al. 2022). Because we completed all our surveys in July/August and most of the surveys by Niemiller et al. (2022) were performed between April and June (outside of egg deposition season), our higher percentage of egg brooding female observations is expected. Future studies should consider the timing of their surveys and how they coincide with the egg brooding season to determine the reproductive activity at each site.

One interesting finding of this study was the alternation among a high number of brooding females in one year (2021) immediately followed by a high number of juveniles the following year (2022), while there were dramatically fewer brooding females during a dry year (2022) and zero juveniles the following year (2023). It seems possible that wet years stimulate

more females to reproduce, and subsequently, a high number of juveniles the following year. This pattern seems to suggest that there could be boom and bust years for *A. aeneus* reproduction similar to other salamanders (Whiteman and Wissinger 2005). Alternatively, there could be other interacting factors, such as female biennial reproduction (Snyder 1991; Canterbury and Pauly 1994) or juvenile survival, that may also be influencing the patterns observed. Thus, additional investigations into the potential for cyclic reproductive patterns in *A. aeneus* should be a topic of future long-term studies.

Habitat.—Our study is the first to estimate the approximate linear distance of habitat to *A. aeneus* in Mississippi and the first to measure the approximate extent of occupied area in the state. Compared to other states within the range of *A. aeneus*, the extent of habitat in Mississippi is miniscule. While it is small in scale, we have found that the approximate area of occupied habitat is > 50% more than previously documented in the state. Further, most of the rock outcrop habitat in Mississippi occurs on public lands, but some extensive rock outcrops that hosted *A. aeneus* populations also occurred on private land (e.g., R, U-X). Similarly, Hardman (2014) also found that private lands can harbor *A. aeneus* populations and in some states, private land holdings with rock outcrops could be massive (e.g., Tennessee, Alabama). Private lands, however, are more difficult to access for surveys and are underrepresented in most *A. aeneus* studies. Nonetheless, while private properties may hold populations that are currently unknown to biologists and managers, our study is the first to document lower encounter rates of *A. aeneus* on private lands possibly due to differences in land management in comparison to public lands. To identify private landowners that have high potential for rock outcrop habitat suitable for *A. aeneus*, using LIDAR data and slope analyses could be a worthwhile venture in other states (Aldridge et al. 2024).

From a microhabitat perspective, Woods (1968) indicated that rock overhangs shade potential crevices, and thus, it seems likely that overhangs may promote a more stable crevice environment. Our data seem to corroborate this, as *A. aeneus* were overrepresented in overhang areas compared to their availability. Furthermore, the climate/rainfall could have had an interacting effect on the rock microhabitat chosen by these salamanders, because the weather was very different in 2021 (wet) versus 2022 and 2023 (drought). Indeed, *A. aeneus* are more

commonly observed in crevice openings when there has been less rain in the 24 h preceding the survey (Smith et al. 2017).

We found that *A. aeneus* occupied crevice heights similar to the observations by Cliburn and Porter (1987; mean height = 1.25 ± 0.59 m, range of values 0.3–3.96); however, many of the rock walls extended well above our maximum survey height (about 2 m), and rock walls sometimes reached 15–20 m. Therefore, it seems very likely that numerous individuals went unobserved in higher crevices. Future surveys should focus on surveying heights that are typically out-of-reach by most surveys (i.e., above 2 m).

One interesting aspect for further exploration would be to quantify how Hartselle sandstone habitat in Mississippi and northern Alabama compares to other rock habitat types throughout the range of *A. aeneus*. Qualitatively, Hartselle Sandstone appears to have fewer crevices and is not as tall/extensive in comparison to other rock habitat used by *A. aeneus* in their range. Further, it may be that the Hartselle Sandstone outcrops have different microclimates or microhabitats compared to other rock geologies used by *A. aeneus* in other parts of their range. If there are rock morphology or structural differences, those differences may explain why Hartselle rock outcrop sites in Mississippi were occupied at a high rate and had higher summer encounter rates/CPUEs compared to other parts of the range. Furthermore, extensive surveys for *A. aeneus* in the Hartselle Sandstone in northern Alabama are lacking yet warranted. If completed, an Alabama study would provide a suitable and interesting comparison to this study.

Management and conservation.—Because the majority of our survey sites are within public ownership (TSP and NTP), they are protected from some of the documented threats to *A. aeneus* (e.g., mining, clear-cut logging, etc.). Sites on private property, however, are still vulnerable to management changes that could negatively affect this species. For example, some sites were bordered by large agricultural areas, and others (sites R, T, and the north end of X) had recently been logged up to the rock faces. To ensure high quality forest habitat around rock outcrops, landowners should be contacted by and work with state biologists regarding with property registration conservation programs for these special habitats; depending on the details of the agreement, forest buffers should be considered (Soto 2021). For sites that are degraded and logged, it would also be beneficial to

plant trees in the areas that have favorable rock habitat (Soto et al. 2021).

In summary, *A. aeneus* still occurs in a small area of Mississippi, but it is found in many more locations than previously documented. Further, encounter rate data indicate Mississippi is similar to or above other states within the range of the species. Our data could be helpful for state managers when evaluating the conservation status of the species and serve as a baseline for future surveys. We also recommend that a subset of these rock outcrops be regularly assessed as part of a long-term monitoring program for the species in the state.

Acknowledgments.—This project was funded by a Competitive State Wildlife Grant through the Southeastern Association of Fish and Wildlife Agencies (SE-U2-F16AP00113) and a State Wildlife Grant via the Mississippi Department of Wildlife, Fisheries, and Parks and the U.S Fish and Wildlife Service Division of Federal Aid (#F21AF03948). Along with State Wildlife Grant funding, Millsaps College Science Fellowship Awards also supported this project, and we are grateful to Tim Ward and Leah Babb for administering these funds. Field activities for BW and WS were approved by Mississippi Department of Wildlife, Fisheries, and Parks through scientific research and collecting permit numbers 0513211, 0510221, and 0510231. The Animal Care and Use Committee of Millsaps College also approved the project (WS041717). We would like to thank Kaitlin Cross, Sheena Feist, and Debora Mann for assisting with surveys, as well as the many Millsaps College undergraduate research students who helped (Jack Welsh, Thomas Weber, Bryce King, Tyler Hamby, Peyton Parker, Braden Robinson, Connor Ladner, Greyson Hewitt, Katie Williams, and Lucas Rutherford). We are also grateful to AirBNB homeowners Lisa and Arthur in Belmont, Brooke in Iuka, and Wesley and Brittany in Iuka for being such great and hospitable hosts. We also appreciate the willingness of several private landowners for allowing us to survey for salamanders on their properties, and for Ruth Elsey for reviewing an earlier version of the manuscript.

LITERATURE CITED

Aldridge, C.A., A. Moczulski, K.T. Wilson, and E.C. Boone. 2024. Detecting sheer rock outcrops using digital elevation models for ecological

- conservation. *IEEE Journal of Selected Topics in Applied Earth Observations and Remote Sensing* 17:6712–6720.
- Canterbury, R.A., and T.K. Pauley. 1994. Time of mating and egg deposition of West Virginia populations of the salamander *Aneides aeneus*. *Journal of Herpetology* 28:431–434.
- Channell, R. 2004. The conservation value of peripheral populations: the supporting science. Pp. 1–17 *In* Proceedings of the Species at Risk 2004 Pathways to Recovery Conference. Hooper, T.D. (Ed.). Species at Risk 2004 Pathways to Recovery Conference Organizing Committee, Victoria, British Columbia, Canada.
- Cliburn, J.W., and A.B. Porter. 1987. Vertical stratification of the salamanders *Aneides aeneus* and *Plethodon glutinosus* (Caudata: Plethodontidae). *Journal of the Alabama Academy of Science* 58:18–22.
- Corser, J.D. 2001. Decline of disjunct Green Salamander (*Aneides aeneus*) populations in the southern Appalachians. *Biological Conservation* 97:119–126.
- Gordon, R.E. 1952. A contribution to the life history and ecology of the plethodontid salamander *Aneides aeneus* (Cope and Packard). *American Midland Naturalist* 47:666–701.
- Hardman, R.H. 2014. Modeling occurrence of the Green Salamander, *Aneides aeneus*, in the Blue Ridge Escarpment. M.Sc. Thesis, Western Carolina University, Cullowhee, North Carolina, USA. 42 p.
- Hinkle, M.P., L.A. Gardner, White, E., W.H. Smith, and R.D. VanGundy. 2018. Remnant habitat patches support Green Salamanders (*Aneides aeneus*) on active and former Appalachian surface mines. *Herpetological Conservation and Biology* 13:634–641.
- John, R.R. 2017. Movement, occupancy, and detectability of Green Salamanders (*Aneides aeneus*) in northern Alabama. M.Sc. Thesis, Auburn University, Auburn, Alabama, USA. 73 p.
- Merrill, R.K., D.E. Gann, and S.P. Jennings. 1988. Tishomingo County geology and mineral resources. Bulletin 127, Mississippi Department of Natural Resources, Bureau of Geology, Jackson, Mississippi, USA. 178 p. plus color plates.
- Milanovich, J.R., W.E. Peterman, N.P. Nibbelink, and J.C. Maerz. 2010. Project loss of a salamander diversity hotspot as a consequence of projected global climate change. *PLoS ONE* 5: e12189. <https://doi.org/10.1371/journal.pone.0012189>.
- Mississippi Museum of Natural Science. 2015.

- Mississippi State Wildlife Action Plan. Mississippi Department of Wildlife, Fisheries, and Parks, Mississippi Museum of Natural Science, Jackson, Mississippi, USA. 692 p.
- Newman, J.C., K. Barrett, and J.W. Dillman. 2018. Green salamander estimated abundance and environmental associations in South Carolina. *Journal of Herpetology* 52:437–443.
- Newman, J.C., E.A. Riddell, L.A. Williams, M.W. Sears, and K. Barrett. 2022. Integrating physiology into correlative models can alter projections of habitat suitability under climate change for a threatened amphibian. *Ecography* 2022: e06082. <https://doi.org/10.1111/ecog.06082>.
- Niemiller, M.L., R. Hardman, D. Thames, D. Istvanko, M.A. Davis, C. Ogle, K.D.K. Niemiller, K.E. Dooley, and T.M. Clark. 2022. The distribution and conservation status of the Green Salamander (*Aneides aeneus*) in Tennessee, USA. *Herpetological Conservation and Biology* 17:249–265.
- Pauley, T.K., and M.B. Watson. 2005. *Aneides aeneus*. Pp. 656–658 In *Amphibian Declines: The Conservation Status of United States Species*. Lannoo, M. (Ed.). University of California Press, Berkeley, California, USA.
- Petranka, J.M. 1998. *Salamanders of the United States and Canada*. Smithsonian Institution Press, Washington, D.C., USA.
- Rauch, T.J., III, J.R. Lee, and A. Lawler. 2016. Green Salamander (*Aneides aeneus*) populations in Mississippi: a preliminary update. *Journal of the Mississippi Academy of Sciences* 61:222–226.
- Smith, W.H. 2024. Woody understory vegetation removal alters the microclimate profiles of rock crevices used by Green Salamanders (*Aneides aeneus*) in the Cumberland Mountains of Virginia, USA. *Herpetological Conservation and Biology* 19:23–32.
- Smith, W.H., S.L. Slemph, C.D. Stanley, M.N. Blackburn, and J. Wayland. 2017. Rock crevice morphology and forest contexts drive microhabitat preferences in the Green Salamander (*Aneides aeneus*). *Canadian Journal of Zoology* 95:353–358.
- Snyder, D.H. 1991. The Green Salamander (*Aneides aeneus*) in Tennessee and Kentucky, with comments on the Carolina's Blue Ridge populations. *Journal of the Tennessee Academy of Science* 66:165–169.
- Soto, K.M., R.K. McKee, and J.C. Newman. 2021. Conservation Action Plan: Green Salamander (*Aneides aeneus*) Species Complex. Southeast Partners in Amphibian and Reptile Conservation, Amphibian and Reptile Conservancy, Inc., Louisville, Kentucky, USA. 15 p.
- Steen, D.A., and K. Barrett. 2015. Should states in the USA value species at the edge of their geographic range? *Journal of Wildlife Management* 79:872–876.
- Thompson, D.E. 2011. *Geologic map of Mississippi*. Mississippi Office of Geology, Jackson, Mississippi, USA.
- Tilley, S.G. 1980. Life histories and comparative demography of two salamander populations. *Copeia* 1980:806–821.
- U.S. Fish and Wildlife Service. 2015. Endangered and threatened wildlife and plants; 90-day findings on 31 petitions. *Federal Register* 80:37568–37579.
- Waldron, J.L., and W.J. Humphries. 2005. Arboreal habitat use by the Green Salamander, *Aneides aeneus*, in South Carolina. *Journal of Herpetology* 39:486–492.
- Walker, K.L., and W. Goodpaster. 1941. The Green Salamander, *Aneides aeneus*, in Ohio. *Copeia* 1941:178.
- Whiteman, H.W., and S.A. Wissinger. 2005. Amphibian population cycles and long-term data sets. Pp. 177–184 In *Amphibian Declines: The Conservation Status of United States Species*. Lannoo, M. (Ed.). University of California Press, Berkeley, California, USA.
- Williams, L., K.A. Parker, Jr., C.R. Lawson, and A.D. Cameron. 2020. Variation in seasonal detection probability and site abundance of populations of *Aneides aeneus* and *A. caryaensis* in North Carolina, USA. *Herpetological Conservation and Biology* 15:238–252.
- Woods, J.E. 1968. The ecology and natural history of Mississippi populations of *Aneides aeneus* and associated salamanders. Ph.D. dissertation, University of Southern Mississippi, Hattiesburg, Mississippi, USA. 89 p.



BAILEY WATKINS completed research on Green Salamanders as an Honor's Student in Biology at Millsaps College in Jackson, Mississippi, USA. He graduated with a B.S. in Biology in May 2023, and he is currently serving as a Scientist 3 at Allen Engineering and Science in Mobile, Alabama, USA. (Photographed by Will Selman).



THOMAS M. MANN has been a Zoologist with the Mississippi Natural Heritage Program at the Mississippi Museum of Natural Science, Mississippi Department of Wildlife, Fisheries, and Parks, in Jackson, Mississippi, USA, since 1990. Tom received his B.S. degree at the University of Miami (Florida, USA) in 1972, and his M.S. degree at Florida Atlantic University, Boca Raton, Florida, USA, in 1977, where he studied the impact of developed shoreline in southeast Florida on nesting and hatchling sea turtles. As Natural Heritage Program Zoologist, Tom has been involved in more general surveys throughout the State of Mississippi but has also undertaken focused surveys on the distribution and abundance of Gopher Tortoises (*Gopherus polyphemus*), Diamond-backed Terrapins (*Malaclemys terrapene pileata*), Gulf Saltmarsh Watersnakes (*Nerodia clarkii*), the Alabama Red-bellied Cooter (*Pseudemys alabamensis*), and Florida Harvester Ants (*Pogonomyrmex badius*). More recently, in collaboration with Dr. Debora Mann, Tom has studied previously unknown migratory behavior in Webster's Salamander (*Plethodon websteri*), and morphological variation in this species throughout its range. (Photographed by Katelin Cross).



Will Selman is an Associate Professor of Biology at Millsaps College in Jackson, Mississippi, USA. He received his B.S. from Millsaps College and his Ph.D. from the University of Southern Mississippi. Recent research includes the distribution and call phenology of Crawfish Frogs (*Rana areolata*) in central Mississippi, the distribution and abundance of *Graptemys* turtles in the Tombigbee River system of northeastern Mississippi, and surveys for rare salamanders in northeastern Mississippi; many of these studies emphasize the involvement of undergraduate students. He is also currently working on a book, *The Amphibians and Reptiles of Mississippi*. (Photographed by Will Selman).

Appendix Table. Surveys for Green Salamander (*Aneides aeneus*) at rock outcrop sites in Tishomingo County, Mississippi, USA, 2017–2023. The column labeled Rock is the rock outcrop location as depicted in Figure 2, and Effort refers to the number of person hours of survey effort at each site. Abbreviations are Total #S = number of observation surveys from 2017–2023, * = presence of reproducing *A. aeneus*, CPUE #S = number of encounter rate surveys from 2021–2023, Aa = *Aneides aeneus* (Green Salamander), Aa CPUE = *Aneides aeneus* Catch Per Unit Effort, Ec = *Eurycea cirrigera* (Two-lined Salamander), Elo = *Eurycea longicauda* (Long-tailed Salamander), Elu = *Eurycea lucifuga* (Cave Salamander), and Pg = *Plethodon glutinosus* complex (Slimy Salamander).

Site	Rock	Region	Total #S	Public/ Private	Aa Present?	CPUE # S	Effort	Aa	Aa CPUE	Ec	Elo	Elu	Pg
Rock Quarry Branch	A	West	4	Public	X	3	24.45	4	0.12	8	9		6
Gatehouse Rock	B	West	12	Public	X	7	8.82	1*	0.08	1	12		19
Disgo Rock	B	West	4	Public	-	3	8.28		0.00		11		3
Saddleback Ridge	B'	West	1	Public	-	1	4.92		0.00				2
Classic Rock	C	West	6	Public	X	4	20.28	21*	1.18	1	3		2
Caution Rock	D	West	4	Public	X	1	4.25	2	0.47				1
Long Tail Rock	D'	West	1	Public	-	1	3.33		0.00		8		
Castle Rock A	E	West	5	Public	X	2	3.34	1	0.30		1		6
Kenobi Rock	E'	West	1	Public	-	1	1.58		0.00				1
Spring Hill	F	West	39	Public	X	5	38.68	42*	1.19	3	15		98
Drip Rock	G	West	8	Public	X*	3	6.15		0.00		6		10
Dining Hall Rock	H	West	4	Public	X	3	2.92	3	1.03				1
Cabin Cliff	I	West	5	Public	X	3	21.92	3*	0.08		2		34
Pavilion to Cabin	J	West	3	Public	X	2	11.65	4*	0.47				13
Pavilion	K	West	8	Public	X	4	33.02	8*	0.19	1	5		32
CC Camp	L	West	3	Public	X	2	7.07	5*	0.71	1			4
Old Quarry	M	West	4	Private	-	2	9.1		0.00		2		6
Rock N	N	Central	4	Public	X	3	5.32	4*	0.75		3		3
O Trail	O	Central	5	Public	X	3	10.03	4*	0.40		3		5
O negative Rock	O-	Central	1	Public	X	1	2.75	11*	4.00		2		3
Swinging Bridge Far East	P	Central	3	Public	X	2	18.0	13*	0.83		4		21
Swinging Bridge East	Q	Central	8	Public	X	5	52.54	39*	0.75	1	31		52

Appendix Table, continued

Site	Rock	Region	Total #S	Public/ Private	Aa Present?	CPUE # S	Effort	Aa	Aa CPUE	Ec	Elo	Elu	Pg
Swinging Bridge West	R	Central	6	Private	X	3	25.43	4*	0.16	4	31		27
Rock S	S	Central	5	Public	X	2	25.55	42*	1.68	1	7		45
TNT Rock	T	Central	5	Public	-	3	9.72		0.00		15		2
Bloody Springs South	U	East	7	Private	X	2	14.65	1*	0.07	10	2		38
Bloody Springs West	V	East	10	Private	X	5	35.23	2	0.09	5	9	2	70
Bloody Springs East	W	East	5	Private	X	4	26.30	12*	0.68	4			37
Rock X north	X	East	4	Private	X	2	25.08	20*	0.80	1	7	5	30
Rock Y	Y	East	4	Private	-	1	8.00		0.00	1	1		10
Rock Z1	Z1	Central	2	Public	X	2	5.52		0.00		4		4
Rock Z2	Z2	Central	2	Public	X	2	18.18	8*	0.43		12		2
Total			182		25 of 32	87	482.9	254		42	205	7	586
							CPUE		0.53	0.09	0.43	0.01	1.21
							%RA	0.22		0.04	0.18	0.01	0.55