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Woody and arboreal habitats of the Green Salamander (Aneides aeneus) in the Blue Ridge Mountains

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ABSTRACT -- The green salamander (Aneides aeneus) is primarily considered a rock crevice dwelling species. However, many early observations from Kentucky, Tennessee, Virginia, and West Virginia report A. aeneus taken from woody and arboreal habitats. There have been only four published records of A. aeneus using such habitats within the Blue Ridge Disjunct population of southwest North Carolina, northeast Georgia, and northwest South Carolina, and no records since 1952. Here I report two personal observations of A. aeneus using arboreal habitats in North Carolina. Additionally, I report nine observations, made by others, of A. aeneus using woody, arboreal, or otherwise non-rock-crevice habitats in North and South Carolina, including the first non-rock-crevice A. aeneus nesting record for the Blue Ridge. I also speculate that woody and arboreal habitats play a much larger role in the life-history of A. aeneus than generally thought, and that the rarity of A. aeneus is linked to the loss of American Chestnut and old-growth forests.

INTRODUCTION AND METHODS

The green salamander (Aneides aeneus) is distributed from central Alabama to southwestern Pennsylvania along the Appalachian Plateau (Petranka, 1998). A separate and smaller cluster of populations, the "Blue Ridge Disjunct", occurs in the mountains of southwest North Carolina, northeast Georgia, and northwest South Carolina (Bruce, 1968; Petranka, 1998). The green salamander is the only representative of the genus Aneides, or "Climbing Salamanders", in the eastern United States and is generally uncommon across its range due to specialized habitat requirements (Petranka, 1998).

Aneides aeneus is almost exclusively observed inhabiting rock crevices of outcrops, which are located within associations of the mixed-mesophytic forest (Gordon, 1952; Corser, 1991; Petranka, 1998). However, early observations from Kentucky, Tennessee, Virginia, and West Virginia report A. aeneus breeding and foraging within woody and arboreal habitats (Gordon, 1952). Pope (1928) and Barbour (1949) report A. aeneus being taken almost exclusively from beneath the exfoliating bark of standing or fallen, yet "solid", dead trees, mostly American Chestnut (Castanea dentata). Fowler (1947) reports A. aeneus being found under the bark of a fallen American Chestnut tree. Barbour (1949) reports one A. aeneus within the cavity of a standing dead American Chestnut and a brooding female beneath the bark of a fallen tree. Pope (1928) reports one individual within a rotted log and a brooding female within the small cavity of a prostrate limb of an Oak (Quercus spp.) tree. Welter and Barbour (1940) and Canterbury (1991) also report observations of A. aeneus beneath the loose bark of dead trees or within rotted stumps.



In contrast with these widespread observations of the use of arboreal habitats and woody debris by A. aeneus in the main range populations, there are only four published records of A. aeneus individuals observed in habitats other than rock crevices in the Blue Ridge Disjunct. Three of these observations were adjacent to, or near, rock outcrops. Bishop (1928) reported an individual A. aeneus observed beneath a piece of bark lying on the surface of a rock several feet above the ground in Tallulah Gorge, Rabun Co., GA. Brimley (1941) reported a single A. aeneus found within a woodpile on August 1,1938 in Highlands, Macon Co., NC. Gordon (1952) reported that this woodpile observation was within 100 feet of a rock outcrop colony of A. aeneus. Gordon (1952) reports an immature A. aeneus individual crawling down a dead oak (Quercus spp.) sapling leaning against a rock outcrop along Clear Creek in Rabun Co., GA. Brimley (1927) and Swartz (1954) report an individual A. aeneus taken by J.O. Pepper on August 3,1926 from the "surface of up-standing tree at about 3 ½ ft up, in damp woods" at Pinnacle Mountain, Pickens Co., South Carolina. While the four non-rock-crevice records are of individuals, A. aeneus nests are known only from rock crevices in the Blue Ridge Disjunct (Snyder, 1971).

Here I report two personal observations of Aneides aeneus using arboreal habitats in North Carolina. Additionally, I report nine observations, made by others, of A. aeneus using woody, arboreal, or otherwise non-rockcrevice habitats in North and South Carolina, including the first non-rock-crevice A. aeneus nesting record for the Blue Ridge Disjunct. Observational descriptions, provided by others, were collected by contacting professional biologists and amateur naturalists familiar with A. aeneus populations in the region. Unless otherwise cited, the following information is summarized from personal communications provided by the observers.

FIELD OBSERVATIONS OF ANEIDES NON-ROCK-CREVICE HABITAT USE IN THE BLUE RIDGE DISJUNCT

The following two observations were made at Biscuit Rock, Highlands, Macon Co, North Carolina, USA, at ca.1,219 m elevation (35°03'N, 82°11'W). On 6 June 2003, at 1900hrs, during a light rain, with the aid of a high power flashlight, I observed an individual A. aeneus in a horizontal position at the bottom of a small, vertical, crevice-like tree cavity (2cm x 37cm), 42cm vertical distance above the ground, and located within a live Rosebay Rhododendron, Rhododendron maximum. The diameter of the trunk was 11 cm at the height of the crevice. On 7 June 2003, at 12:20 hrs, during a heavy rain, with the aid of a high power flashlight, I again observed another individual A. aeneus in a horizontal position at the bottom of a small tree cavity (2cm x 4cm), 72cm vertical distance above the ground, and located within a separate, live Rosebay Rhododendron, R. maximum, approximately 2m from the 6 June 2003 observation. The diameter of the trunk was 8cm at the height of the crevice. Because the trunk of the shrub was slanted, the actual trunk distance the salamander had to travel to reach the crevice from the ground was 97cm. In both observations, the salamanders were small, appeared to be less than one year of age, and retreated further into the cavity upon illumination. Both cavities were apparently created when a horizontal limb detached from the main trunk. Both shrubs were attached to a rock outcrop known to contain a rock-crevice dwelling population of A. aeneus.

The following three observations were located in Cedar Mountain, Transylvania Co., North Carolina, USA, at ca. 900m elevation (35°08'N, 82°41'W). The nearest suitable rock outcrop habitat, referred to as "Sherwood Forest Cave", is >750m from the observations and is know to contain a population of A. aeneus (Wilson, 2001). On September 1974, upon splitting a downed American Chestnut log, Castanea dentata, Herbert Ball discovered an adult female A. aeneus tending a clutch of nine+ eggs (Millie Blaha, pers. com.). The brooding female was photographed by the late George and Millie Blaha (Figure 1) and the following descriptions are approximated, by the author, from their photographs. The log was about 25cm in diameter and contained a hollowed chamber about 6cm in diameter. The clutch contained at least nine eggs suspended from the sides of the chamber. At least four hatchlings were produced within two weeks of the initial discovery (Millie Blaha, pers. com.).

A color photograph was deposited in the N.C. State Museum of Natural Sciences by the author (ALB 10409, Figure 1). On 24 October 1993, Beth and Speed Rogers discovered two A. aeneus individuals under a clay terra cotta dish resting upon a rotting Black Oak (Quercus velutina) stump. The two salamanders were photographed and documented by Mille Blaha (Figure 2). The stump was approximately 40cm in diameter, 75cm high (measured in the field by the author, May 2000), and was cut seven years prior to the observation (Millie Blaha, pers. com.). The two salamanders were about 7.5cm total length (approximated, by author, from photographs). Upon disturbance, the pair crawled down the side of the stump and into a crevice at the base of the stump. A color photograph was deposited in the N.C. State Museum of Natural Sciences by the author (ALB 10410, Figure 2). During the spring of 2000, Speed Rogers, amateur naturalist, found one large A. aeneus climbing on his wooden deck, approximately 4.5m above the ground (Speed Rogers, pers. com.).

The following four observations were made at the Falling Creek Camp, Tuxedo, Henderson Co., North Carolina, USA, at ca 790m elevation (35°11'N, 82°28'W). The nearest suitable rock outcrop habitat, known as "Falling Creek Camp", is >500m from the observations and is known to contain a population of A. aeneus (Wilson, 2001). Beginning in June, 1991, and repeatedly throughout the summer, Joe Duckett, resident camp naturalist, observed an individual A. aeneus living within the entrance of a small tree cavity $(2.5 \text{ cm} \times 5 \text{ cm})$, approximately 1.5m above the ground (approximated, by author, from photographs), and located within a live standing Scarlet Oak (Quercus coccinea). The salamander was feeding on small insects that were attracted to a black sap oozing out of the cavity. The salamander was no longer found after late summer. Identification was confirmed, and the habitat was photographed, by Allen Boynton, non-game wildlife biologist, North Carolina Wildlife Resources Commission, during the summer of 1991. In May, 1997, upon submerging a decorative driftwood log into a fish aquarium, Joe Duckett observed an A. aeneus escape from within an approximately 10 cm wide hollow within the log. The driftwood log had previously been left outside on a porch. During May, 1999, Joe Duckett again repeatedly observed an individual A. aeneus living in a cavity of a standing, yet dead, tree throughout the summer approximately 10m from the 1991 observation. The cavity entrance was 7.5 cm \times 15 cm and located 1.8m above the ground (measured in the field by the author, May 2001). The salamander was no longer found after late summer. During the summer of 1999, Joe Duckett, along with a young camper, observed an individual A. aeneus under a log.

Caesar's Head State Park, Greenville Co., South Carolina, USA, at ca 920m elevation (35°06'N, 82°37'W). On several occasions in the fall of 1989, Mae Lee Hafer, park naturalist and Clemson University graduate student studying A. aeneus, observed A. aeneus individuals climbing on the wooden sides of the Park Naturalist House and on the screened, wooden porch. There are no rock outcrops "relatively close" to the site of observation (Mae Lee Hafer, pers. com.).

Wildcat Wayside, Greenville Co., South Carolina, USA, at ca 340m elevation (35°03'N, 82°30'W). On the nightApparently, the decay that created the chamber was caused by fungal infection initiated by fire damage (Gavin Wilson, professional forester, pers. com.). of 25 April 1981, while searching for the Ringneck Snake (Diadophis punctatus), Rudy Mancke, natural history curator at the South Carolina State Museum, and Ralph Philips observed a large A. aeneus under the exfoliating bark of a fallen oak (Quercus spp.) log, (Rudy Mancke, unpublished field notes)

DISCUSSION

The above observations demonstrate unambiguously that populations of A. aeneus in the Blue Ridge Disjunct 1) utilize non-rock habitats for breeding and foraging, 2) are not restricted to the immediate vicinity of rock outcrops, and 3) will use non-rock habitats throughout the spring and fall dispersal, and summer breeding phases of its annual life cycle. These observations suggest that the microclimates provided by tree cavities or under exfoliating slabs of bark are similar to those of rock crevices which are used for breeding, foraging, and refuge purposes, and that arboreal habitats historically comprised an important component of the ecological niche of A. aeneus.

Woody Habitats

Breeding A. aeneus females require cool, clean, and moist, but not wet, horizontal crevices or narrow chambers in which to suspend their eggs from an overhead substrate (Gordon, 1952). Such habitat provides a specific microclimate necessary for successful embryonic development and is typically observed in shaded rock crevices (Gordon, 1952). Woody breeding habitat apparently occurs within narrow cavities or under slabs of exfoliating bark. These microhabitat features occur during the earlier decay classes of a dead tree (Maser et al., 1988), when the tree is still "solid" as Pope (1928) described. Within the range of A. aeneus, woody and arboreal micro-habitat features such as tree hollows and exfoliating bark are most abundant within temperate hardwood old-growth forests (Hardt and Swank, 1997; Hale and Rusterholz, 1999).

Arboreal Foraging

Aneides aeneus is exceptionally well adapted to forage and dwell in arboreal habitats due to its anatomical and physiological attributes. Although these features are commonly interpreted as adaptations to a life within rock crevices (Gordon, 1952), they strongly suggest an arboreal life-style as well. In behavioral experiments, A. aeneus has an instinctual tendency to climb when confronted with vertical surfaces (Baltar, 1983). Adaptations for climbing include long-legs, expanded toe-pads, a flattened body, and a muscular tail (Gordon, 1952; Wake, 1963). Aneides aeneus is physiologically more tolerant to desiccation than any other salamander in its range, which allows it to withstand the drier conditions encountered when climbing on exposed surfaces such as rock cliffs (Gordon, 1952; Canterbury, 1991) or in trees. The unique lichen colored and patterned dorsum of A. aeneus provides excellent camouflage among the lichens and mosses that are commonly distributed over the surfaces of both rock outcrops, and tree trunks and limbs, within the range of A. aeneus (Karin Heiman, pers. com.). The very presence of such a bright and striking color pattern suggests an adaptation to predation from visual predators such as birds (Brandon and Huheey, 1975), which forage more frequently in trees than on rock. In behavioral experiments, A. aeneus is actually known to prefer bark substrates to rock (Mushinsky, 1976). Finally, other species of Aneides are highly arboreal in habit (Petranka, 1998).

Food is known to be a limiting factor in competition between salamanders (Jaeger, 1972). Plethodon cinereus, an otherwise ground dwelling salamander, was shown to realize higher foraging efficiency by climbing plant stems, where it acquires larger and more abundant invertebrate prey items (Jaeger, 1978). Due to its lack of tolerance to desiccation, P. cinereus is only briefly able to forage on plant stems during periods of high humidity on rainy nights (Jaeger, 1978). A number of other plethodontids in the eastern U.S. have been observed climbing on plant stems on rainy nights, presumably to forage (Hairston, 1949; pers. obs.; R. Wayne Van Devender, pers. com.). Aneides aeneus is known to use its climbing abilities and tolerance to desiccation to avoid competition with other plethodontids by climbing to higher and drier positions on rock outcrops (Baltar, 1983; Cliburn and Porter, 1987). Given the abundance and diversity of potential plethodontid competitor species on the forest floor, the relatively unexploited food resource in arboreal habitats, and the unique adaptations of A. aeneus to take advantage of arboreal habitats, it seems reasonable that arboreal foraging plays a larger role in the life history of A. aeneus than generally reported. Old-growth temperate hardwood forests contain a more complex vertical structure with higher densities of invertebrates (Schowalter, 1995), and cooler and moister microclimates relative to logged forests (Burry and Corn, 1988; deMaynadier and Hunter, 1995).

Such habitats, which historically dominated the range of the Blue Ridge Disjunct populations of A. aeneus (Braun, 1950), likely provide it increased arboreal foraging opportunities and decreased likelihood of desiccation.

Life History Implications

Breeding and foraging in woody and arboreal habitats may explain some apparent inconsistencies in the known life history traits of A. aeneus. For example, the highest seasonal densities of A. aeneus are found in rockcrevices during the spring "posthibernation aggregation and dispersal" and fall "prehibernation dispersal and aggregation" periods, with many fewer individuals observed during the summer "breeding" period (Gordon, 1952; Cupp, 1991; Hafer, 1992). Cupp (1991) suggested that this decrease in density is explained by emigration to outlying outcrops as far as 100m distant, while other herpetologists suggest the missing salamanders simply retreat further into the crevices, out of sight. Aneides aeneus certainly migrates between rock outcrops (Gordon, 1952; Canterbury, 1991), however many Blue Ridge colonies have no other apparently suitable rock outcrops in their vicinity, perhaps as far as 1km (pers. obs.). In addition, retreating deeper into crevices during the non-hibernating phases would seem to reduce foraging efficiency and cause greater intraspecific competition, particularly at colonial sites. Perhaps, instead, the lower densities of visible individuals at rock crevices in the summer are explained by extended foraging forays into arboreal habitats or the utilization of woody breeding habitats.

Another inconsistency that is potentially explained by arboreal foraging forays is the lower frequency of A. aeneus observations at rock crevices during periods of heavy or extended rain. Aneides aeneus is known to become more active during humid periods and is usually only observed outside of rock crevices, on the rock surface, during misting conditions, light rain, or moderate rain (Gordon, 1952; Cupp, 1991; Hafer, 1992). Yet, mysteriously, non-breeding individuals are observed in rock crevices far less often during periods of heavy rain of after long periods of rain, particularly in the summer (Hafer, 1992; pers. obs.). Hafer (1992) concluded that abundant rain makes conditions "too wet" for A. aeneus to come far enough out of the crevices to be observed. However, A. aeneus has been observed crossing roads on rainy nights (Williams and Gordon, 1961). While light or brief rains may create improved conditions for short forays near the rock crevice during the summer, perhaps heavy or extended periods of rain create ideal conditions for arboreal foraging explaining the brief decrease of observations at rock sites. Many plethodontid salamanders exhibit increased activity and foraging outside of their typical microhabitats during rainy periods (Bernardo, pers. com.; Hairston, 1949). In contrast, non-brooding A. aeneus likely seek transitory refuge in the humid conditions offered in rock or woody crevices during dry periods.

Rarity and Population Decline

The scarcity of woody and arboreal A. aeneus observations relative to rock observations is potentially due to a low population density across the landscape, the general inaccessibility of arboreal situations and micro-habitats such as tree cavities, and a general lack of suitable woody habitats (Petranka, 1998). Perhaps the rarity of A. aeneus is linked to the decline of mature American Chestnut trees and the loss of old-growth forests (Braun, 1950).

Many arboreal and woody habitat observations of A. aeneus are associated with American Chestnut, a tree which disappeared from the forest canopy by 1950 after the introduction of Cryphonectria parasitica, an Asiatic blight, around 1904 (Ronderos, 2000). The previous abundance of C. dentata and its rot resistant properties may have maintained the early decay classes necessary for A. aeneus breeding over a longer time frame than other types of woody debris, making habitat less spatially and temporally patchy.

The Clouded Salamander (Aneides ferreus), a close relative of A. aeneus, is found in western coastal forests of the United States and British Columbia and shares similar microhabitat preferences (Petranka, 1998). Aneides ferreus is found under loose bark, in rockface or talus crevices, in lightly decayed logs and stumps, and is arboreal (Petranka, 1998). Although this species is associated with old growth forests, it will thrive following clear-cut logging due to the subsequent abundance of woody debris in the early decay stages (Bury and Corn, 1988). However, A. ferreus populations decline as small diameter woody debris habitats quickly decay and disappear (Bury and Corn, 1988). Similar observations of sudden and temporary local increases in A. aeneus populations were made by Barbour (1949, 1971) following clear-cuts in Kentucky. Over the long-term, A. ferreus may not persist in reforested areas that retain inadequate levels of course woody debris (Butts and McComb, 2000) and may take several hundred years to recover from logging (Corn and Bury, 1991).

A similar scenario may explain the rarity of A. aeneus. Old-growth forests likely provided abundant woody microhabitats and arboreal foraging opportunities for A. aeneus. Populations temporarily increased following a flush of woody habitats, in early decay stages, created by debris leftover from widespread logging and the mortality of American Chestnut during the first half of the last century. As woody habitats associated with old growth and American Chestnut decayed and disappeared across the landscape, A. aeneus populations decreased and became increasingly dependent on rock crevice habitats. The second- and third- growth forests that current-ly dominate the range of A. aeneus typically contain far less woody debris than the primary forest (Hardt and Swank, 1997; Hale and Rusterholz, 1999).

The loss of appropriate woody habitats and optimal arboreal foraging conditions due to the chestnut blight and logging may have restricted A. aeneus primarily to the crevices of rock outcrops (Gordon, 1952; Corser, 1991; Petranka 1998; Corser, 2001). Populations within the Blue Ridge Disjunct comprise two genetically distinctive, and distantly related groups that harbor unique genetic diversity compared with populations throughout the main part of the range (Bernardo et al., manuscript in review). Moreover, Blue Ridge Disjunct populations have experienced severe declines (Corser, 2001) and are at a high risk of extinction according to the IUCN Redbook Criteria (Wilson, 2001), while populations within the Appalachian Plateau appear to be relatively stable (Snyder, 1983; Snyder, 1991). Rock outcrops containing appropriate rock-crevice habitat are small, few, patchily distributed, and isolated throughout the Blue Ridge Disjunct relative to the Appalachian Plateau (pers. obs.; Corser, 2001), perhaps making the Blue Ridge populations more susceptible to stochastic processes and contributing to the reported decline. If A. aeneus did historically utilize a broader spectrum of forest habitats, as the evidence reviewed herein suggests, then the habitat shift to using principally rock outcrops has an anthropogenic origin and the decline of the rock-crevice dwelling populations in the Blue Ridge Disjunct (Corser, 2001) is also attributable to human disturbance, via logging as well as by introduction of the exotic chestnut blight. Thus, conservation of Blue Ridge Disjunct populations is of significant concern.

The observations reported herein have important implications for conserving the remaining populations. While rock crevices currently represent the most critical habitat for A. aeneus, future conservation efforts should recognize the importance of woody and arboreal habitats in surrounding woodlands. Management should allow forests to mature and return to a natural "gap dynamic" (Runkle, 1985) method of regeneration and woody debris production over the next century. Such forests will provide abundant breeding and foraging habitat, as well as provide optimal corridors between existing rock outcrop colonies, facilitating metapopulation persistence (Hanski and Simberloff, 1997). In addition, supplementation of coarse woody debris in areas occupied by A.aeneus might aid recovery by enhancing the availability of both foraging and breeding sites, just as nest boxes are used to augment reproduction in bird populations.

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