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# Ecology and Sympatric Relations of Crevice Salamanders in Randolph County, West Virginia

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# Ecology and Sympatric Relations of Crevice Salamanders in Randolph County, West Virginia

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# Abstract

## Ecology and Sympatric Relations of Crevice Salamanders in Randolph County, West Virginia

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By implementing a mark-recapture study, I investigated the ecology of three species of sympatric plethodontid salamanders (*Aneides aeneus*, *Desmognathus ochrophaeus*, and *Plethodon glutinosus*) on rock outcrops in the Westvaco Wildlife and Ecosystem Research Forest, Randolph County, West Virginia. By examining activity patterns, vertical stratification, and habitat preference for *A. aeneus*, *D. ochrophaeus*, and *P. glutinosus*, I attempted to offer some insight into how these sympatric species avoid competition on small, isolated rock outcrops. Twenty-one surveys, both nocturnal and diurnal, were performed between 11 May and 17 October, 1999. During this time, 89 salamanders, encompassing five species (*A. aeneus*, *D. ochrophaeus*, *P. glutinosus*, *P. cinereus*, and *Notophthalmus v. viridescens*), were permanently marked using Visual Implant Flourescent Elastomer (VIE) tags. When salamanders were captured from crevices, three measurements were taken: (1) crevice width, (2) crevice height, (3) crevice depth. There was no significant difference between the height and depth of crevices inhabited by *A. aeneus*, *D. ochrophaeus*, and *P. glutinosus*. However, *P. glutinosus* and *A. aeneus* occupied crevices that were significantly wider than those inhabited by *D. ochrophaeus*. Crevice microclimatic conditions (air temperature and relative humidity) did not significantly differ from the ambient. *Aneides aeneus* occupied significantly higher portions of the rock

outcrops than both *D. ochrophaeus* and *P. glutinosus*. *Desmognathus ochrophaeus* occupied higher portions of rock outcrops than *P. glutinosus.* The activity patterns and surface abundance of *A. aeneus* and *D. ochrophaeus* differed seasonally, but the surface abundance of *P. glutinosus* remained constant throughout the study period. Because *A. aeneus*, *D. ochrophaeus*, and *P. glutinosus* vertically stratify and differ in terms of seasonal activity, they avoid interspecific competition.

Aspects of the life history and population demography of the green salamander, *A. aeneus*, were of importance to this project as well. Because little is known about the extent to which *A. aeneus* disperses between isolated rock outcrops, I attempted to monitor movement and dispersal activities of this species by surrounding three rock outcrops with drift fences. Two isolated rock outcrops located at least 300 m from the study area were searched monthly to determine if marked individuals had migrated to other rocks. No marked individuals were ever observed on rocks outcrops outside of the study area. However, one female moved between adjacent rocks within the study area. There was no significant difference between movement patterns of males and females. Adults and sexually immature individuals did not differ significantly in movement patterns.

# **Chapter 1:** Literature Review and Species Description

## Literature Review

Observations of species that share the same habitat suggest that sympatric species can coexist by utilizing different resources (MacArthur and Levins 1967). Three plethodontid salamanders occur in West Virginia, *Aneides aeneus*, *Plethodon glutinosus*, and *Desmognathus ochrophaeus*, that coexist on emergent rocks and boulders on wooded slopes. All three of these species have been observed inhabiting rock crevices, but only *A. aeneus* is found almost exclusively in this habitat. The means by which these three species coexist on emergent rock outcrops was the focus of this project.

Interspecific competition between sympatric salamanders has been extensively studied through field and laboratory tests. These tests were conducted to determine if interspecific competition is occurring and for what resources. It is improbable that two species have identical habitat requirements (Southerland 1986), and as suggested by MacArthur and Levins (1967), two or more species may coexist if they sufficiently differ in resource utilization. Consequently, competition as a determinant of community structure has been questioned (Hairston 1980). There is an abundance of information available on the aggressive and competitive relationships of certain plethodontid salamanders (Fraser 1976; Jaeger 1970, 1971, 1972, 1974).

Canterbury (1991) investigated territoriality and interspecific competition between *A. aeneus* and other rock-dwelling plethodontid salamanders, including *D. ochrophaeus* and *P. glutinosus*, present in West Virginia. Through laboratory tests he observed that *P. glutinosus* exhibited aggressive behavior with *A. aeneus*, which avoids competition by climbing.

Additionally, Canterbury (1991) observed that *D. ochrophaeus* initiated aggressive encounters with *A. aeneus*, but that *A. aeneus* was victorious in such cases. Baltar (1983) suggested that *A. aeneus*, with its flattened shape and smaller body size, is able to occupy smaller crevices than adult *P. glutinosus*. The sympatric salamander species of concern in this project are morphologically dissimilar. One important aspect of this study is to determine if *A. aeneus*, *D. ochrophaeus,* and *P. glutinosus* exhibit any preferences for crevices that have specific dimensions. If each species occupies structurally different crevices, then *A. aeneus*, *D. ochrophaeus*, and *P. glutinosus* may avoid interspecific competition based on habitat preference.

Cliburn and Porter (1987) observed a vertically stratified distribution of *A. aeneus* and *P. glutinosus* in northeastern Mississippi and found that *A. aeneus* occupies higher crevices along cliffs. Vertical stratification among salamanders was first discussed by Brode and Gunter (1958) and Brandon and Huheey (1971). Woods (1968) observed that *P. glutinosus* most often utilized lower crevices than *A. aeneus*. He suggested that vertical stratification was a means by which *A. aeneus* could avoid interspecific competition. Baltar (1983) conducted tests that indicate that a stratification hierarchy exists between three species of crevice salamanders (*P. glutinosus*, *A. aeneus*, and *P. dorsalis*) in Mississippi. Test results indicate that *A. aeneus* occupies the highest crevices along cliffs while *P. glutinosus* occupies lower ones. It is postulated that sympatric *A. aeneus*, *P. glutinosus*, and *D. ochrophaeus* in West Virginia also exhibit a vertical stratification hierarchy. Because *D. ochrophaeus* is a semi-aquatic species, the role it plays in the vertical stratification hierarchy is of special interest to this study.

Differences in the ability to endure extreme temperatures and dry conditions may have a direct affect on species distribution. Dumas (1956) examined the ecological relations of sympatry in *P. dunni* and *P. vehiculum* by comparing observations of temperature, relative humidity, and substratum moisture at collection points of both species. He found that both species differ in their tolerances of temperature and relative humidity, which suggests that coexisting species may not be in direct competition for space. Gordon (1952) demonstrated that *A. aeneus* has a greater ability to tolerate water loss than sympatric species in the southern part of its range. He concluded that *A. aeneus* is able to avoid competition by climbing to higher and drier positions on rock outcrops. Differences in tolerance to environmental conditions may be a significant factor in determining species distribution on rock outcrops.

Crevice salamanders of concern in this project (*A. aeneus*, *P. glutinosus*, and *D. ochrophaeus*) may vertically stratify to avoid interspecific competition. Several physical and environmental factors may determine what crevices they inhabit. The purpose of this study was to determine what physical (body size, crevice size, and activity patterns) and environmental parameters were critical factors in the microdistribution of all three species inhabiting rocks in West Virginia.

## Species Descriptions

*Aneides aeneus*

The green salamander, *Aneides aeneus* (Cope and Packard), ranges from southwestern Pennsylvania to northern Alabama and extreme northeastern Mississippi (Fig. 1). In West Virginia, the green salamander is found in the central counties of the Appalachian plateau, from Monongalia and Preston counties southwest to the Big Sandy River (Green and Pauley 1987) (Fig. 2). The natural history of the species has been studied in several states. Gordon (1952) was the first to do an in depth study of the ecology and natural history of *A. aeneus*. His research, which investigated the distribution, habitat selection, population dynamics, and the ability of *A. aeneus* to withstand water loss, was performed in the southern Appalachians in western North Carolina. Woods (1968) and Snyder (1971, 1991) also investigated the natural history of *A. aeneus* in the southern Appalachians. Canterbury (1991) performed an extensive study on aspects of the ecology and life history of this species in West Virginia. He examined its habitat preference, reproductive behavior, and competitive interactions with sympatric species.

*Aneides aeneus* is a terrestrial salamander and is identifiable by its yellowish-green color that is mottled over its dorsal side (Fig. 3). It has a flattened body, long legs, squared toe tips, and a long and somewhat prehensile tail, all of which are characteristics of the genus *Aneides*. These characteristics allow for suitable living in rock crevices, which is the primary habitat of the species. *Aneides aeneus* prefers rock outcrops that are moist, but not wet, and well shaded from sunlight (Gordon 1952). Females attach eggs to the top or sides of damp rock crevices. In West Virginia, Canterbury and Pauley (1994) found that most egg laying occurs in the first two weeks of June, shortly after mating. Females brood their eggs and hatchlings for several months. In

West Virginia, it is estimated that the duration of the incubation period is 82-90 days (Canterbury and Pauley 1994).

The extent to which *A. aeneus* disperses between isolated rock outcrops is unknown. Individuals have been observed to cross roads during spring months (Williams and Gordon 1961; Cupp 1991). It is speculated that the movement of these individuals may reflect dispersal from winter hibernacula to summer breeding habitat (Petranka 1998). Canterbury (1991) found that several individuals moved between nearby rock outcrops during fall/winter months. *Aneides aeneus* is rarely observed on the forest floor or in areas surrounding the rock outcrops they inhabit (Snyder 1991). Movement and dispersal activity of *A. aeneus* on and between isolated rock outcrops is of special interest to this study.

*Aneides aeneus* is listed as a species of special concern by the WV Division of Natural Resources Nongame Heritage Program. Because of its unusual habitat requirements, it has a patchy distribution throughout much of its range. Populations in the Blue Ridge Escarpment have suffered decline in the 1970's from prolonged drought (Snyder 1991). The patchy distribution of this species, combined with its sensitivity to temperature and moisture changes, puts it at high risk of population decline.

*Desmognathus ochrophaeus*

The Allegheny Mountain dusky salamander, *Desmognathus ochrophaeus* (Cope) (Fig. 4), ranges from the northern edge of the Adirondack Mountains in Quebec, Canada (Sharbel and Bonin 1992), southward to eastern Tennessee and southwestern Virginia (Fig. 5). It is found at various elevations throughout the Appalachian Mountains. In West Virginia, this species reaches its highest elevation at 1,402 m (Pauley 1993). *Desmognathus ochrophaeus* is found throughout the mountainous counties of West Virginia, including Monongalia, Preston, Randolph, Monroe, Mercer, and McDowell (Green and Pauley 1987) (Fig. 6).

*Desmognathus ochrophaeus* is the smallest and most terrestrial of the five *Desmognathus* species found in West Virginia (Green and Pauley 1987). Species of the genus *Desmognathus* are characterized by a lower jaw that is held in position by ligaments joining it to the upper part of the backbone. As a result, *Desmognathus* species have large jaw muscles, a trait commonly used for identification purposes (Goin et al. 1978). There are several subspecies in the *D. ochrophaeus* complex, and the Allegheny Mountain dusky salamander is unique in that it has a relatively straight dorsolateral stripe. Dark, chevron shaped marks align the dorsolateral stripe (Fig. 4) (Green and Pauley 1987). It has 14 costal grooves (Green and Pauley 1987), and its average total length is between 80 and 100 mm with the tail accounting for approximately half of its length (Conant and Collins 1991). Adults and juveniles occupy forested hillsides in or near streams, but they can also be found at high elevations away from water. Mating occurs in spring through autumn and nesting generally takes place underground (Keen and Orr 1980). Females deposit approximately 19 eggs under rocks or woody debris in wet areas (Green and Pauley 1987). During the summer, adults are found away from water, often occurring under leaf litter, woody debris, and rocks (Green and Pauley 1987). At the onset of cold weather conditions, this species is associated with aquatic conditions such as springs, seepages, and bogs (Green and Pauley 1987). Adults are associated with the forest floor, but they have been observed on rock outcrops during summer months. Canterbury (1991) observed *D. ochrophaeus* in rock outcrops where it was sympatric with *A. aeneus*. There is no evidence that nesting occurs near rock outcrops, although adults occupy such sites during the breeding season.

### *Plethodon glutinosus*

The northern slimy salamander, *Plethodon glutinosus* (Green) (Fig. 7), ranges from central New York to central Florida and from central Missouri southward to central Texas (Fig. 8). It is found throughout West Virginia (Fig. 9) in various habitats. It occurs more commonly at low elevations, but it was observed at a record elevation of 1311 m at Green Knob, Randolph County (Pauley 1993).

*Plethodon glutinosus* is a nocturnal woodland salamander that remains terrestrial for its entire life cycle. The name "slimy" salamander for this species is appropriate, because *P. glutinosus*, along with most woodland salamanders, excretes copious amounts of a glue-like substance when threatened (Highton 1995). This species is large, distinguishable by its shiny black dorsum that exhibits various white and/or brassy flecking (Green and Pauley, 1987) (Fig. 7). The ventor of this species us usually gray, but this characteristic may be variable (Green and Pauley 1987). *Plethodon glutinosus* generally reaches a mean length of 20.3 cm (Green and Pauley 1987). Sexual dimorphic characteristics include a circular mental gland on males, and females typically average 0-6 percent larger in SVL than males (Highton 1956, Semlitsch 1980). Values for hatchlings range from 12-31 mm (Highton 1956; Wells and Gordon 1958; Minton 1972). Individuals reach sexual maturity in 4.5 and 5 years, for males and females, respectively. Females deposit their eggs in spring or early summer (Green and Pauley 1987), which likely occurs every two years (Highton 1995).

### *Plethodon cinereus*

The red-backed salamander, *Plethodon cinereus* (Green) (Fig. 10), ranges from southern Quebec and the Maritime Provinces southward to western and southeastern North Carolina and westward to western Minnesota (Fig. 11) (Petranka 1998). In West Virginia, it ranges throughout most the state (Fig. 12), with the exception of the Ohio Valley counties (Green and Pauley 1987). It is found in a variety of forest habitats and reaches its highest elevation at 1463 m.

*Plethodon cinereus* is a small terrestrial salamander that is distinguishable by its orange-red dorsal pattern. There are various morphs of this species, but only one occurred in the study area. The ventral pattern on this species is strongly mottled with black and white flecks. *Plethodon cinereus* may attain a total length of 10.2 cm. Sexually dimorphic characteristics that are unique to males of this species include swollen nasolabial glands, hedonic glands on the tail, a crescent-shaped mental gland near the apex of the lower jaw, and elongated premaxillary teeth (Noble 1927; Smith 1963; Dawley and Crowder 1995). Individuals reach sexual maturity after the third season, and the first eggs are laid in the spring of the fourth year (Green and Pauley

1987). Mating occurs in the fall and spring (Blanchard 1928; Sayler 1966) and females lay their eggs from May to July (Green and Pauley 1987). Approximately 12 eggs are laid in a crevice of a rotting log or stump, under moss, bark, or stones (Green and Pauley 1987).

# **Chapter 2**: Project Overview

Taking into consideration the research that has been conducted on interspecific competition among salamander assemblages, one major goal of this project was to examine the spatial relationships and activity patterns of sympatric salamanders inhabiting small, isolated rock outcrops. Based on a review of the literature, there is evidence that some salamanders vertically stratify to avoid competition (Grode and Gunter 1958; Woods 1968; Brandon and Huheey 1971; Baltar 1983; Cliburn and Porter 1987). However, previous experiments were performed on large rock outcrops/cliffs, in laboratory settings, and did not include the presence of *D. ochrophaeus*. Some of the methods used in prior experiments were repeated in this project to determine if the ecology of sympatric salamanders on small, isolated rock outcrops is consistent with what has been observed on cliffs and large rock outcrops. Additionally, habitat preference was examined for each species in the study area to determine if there was any overlap between the physical and microclimatic characteristics of crevices inhabited by different species. In relation to habitat preference, the relationship between salamander size and crevice dimensions was also investigated.

Further, aspects of the life history and population demography of *A. aeneus* were examined in this project, considering its status as a species of concern. Life history traits of particular interest include population size (as compared to other species in the study area), sex ratio, size, and evidence of reproductive behavior. The extent of dispersal activity of *A. aeneus* was investigated to determine when and if salamanders migrate between adjacent rock outcrops. Movement and seasonal activity patterns of this species were monitored.

## **Chapter 3**: Study Site Description

This study took place in the Westvaco Wildlife and Ecosystem Research Forest (WWERF), located 2.9 miles (4.7 km) southwest (211°) of Adolph, Randolph County, West Virginia (Fig 13). The study site was located below the trailhead to Rocky Run falls, which is approximately 2.4 miles (3.93 km) S from the Birch Fork entrance of the research forest (Figs. 13 and 14), at an elevation of 880 m (038°42'19.47"N, 080°04'30.09"W). The study area consisted of three emergent rocks (Table 1) on a forested, west-facing slope. The forest canopy was closed, leaving the rocks well shaded and allowing only minimal light to penetrate to the forest floor. The dominant tree species in the area include *Liriodendron tulipifera*, *Betula lenta*, *Fagus grandifolia*, *Acer rubrum*, and *Tsuga canadensis*. The sparse understory consists mainly of *Smilax spp.*, *Cimicifuga racemosa*, and saplings of the dominant tree species. The area receives the greatest annual average precipitation (approximately 170.2 cm) in West Virginia. The study site was located on a hillside that is relatively undisturbed. An old skid road that borders one of the rocks in the study area, is used as a trail to Rocky Run Falls. Forest management activities are constantly being implemented in the WWERF, and there are several skid roads winding through the research forest. All of the roads into the WWERF are gated, so virtually no recreational activity takes place in the area. The closest habitat disturbance to the study area is fragmentation caused by the road through the WWERF (located approximately 50 m E). To the west, Rocky Run flows within 26 m of one rock in the field site. The closest rock outcrop that contains a population of *A. aeneus* is located within 302 m at 170°, but it is fragmented from the field site by three logging roads (Fig. 15). Another rock outcrop containing a population of green salamanders, although well hidden by *Rhododendron*, exists 973 m southeast of the field site. This population is separated from the study area by a logging road (Fig. 16).

# **Chapter 4**: Study Site Surveys and Marking Techniques

## Study Site Surveys

The study site was surveyed both day and night, but most effort was focused on night searches. All large boulders within the study site were searched weekly for salamanders from 11 May 1999, to 16 October 1999 when no more salamanders were found due to cold temperatures. There were five large boulders in the study area, but only three consistently contained salamanders. Environmental data, air temperature and relative humidity, were obtained by using an Extech hygro-thermometer (Model 444701) and a Reotemp thermometer. Both ambient and crevice air temperature and relative humidity were taken at the study area. Crevice temperature and relative humidity were recorded by placing the instruments inside crevices within a few centimeters of the salamander(s) inhabiting them. Ambient readings were taken within one meter of the rock and at least two meters above ground. Ambient and crevice environmental data were recorded every time a salamander was captured.

Night surveys were performed as follows: Beginning just before dark, researcher(s) searched along rocks and on the ground surrounding the rocks for salamanders using a flashlight. When a salamander was located, all searching ceased and the salamander was caught. If the salamander was deep within a crevice, a wire, consisting of a clipped and elongated coat hanger with a blunted end, was used to nudge it out. Once the animal was processed (see below) it was returned to its original location on the rock.

Once a salamander was captured, it was given a unique number and the capture location was marked on a scanned picture of the rock (Fig. 17). Time of capture was recorded and it was noted whether the salamander was hidden (within a crevice) or active (moving along rockface). Distance (cm) from the capture location to the ground was also recorded. If the captured salamander was located inside a crevice, measurements were taken on crevice dimensions. First, the position of the crevice, whether it was vertical or horizontal, was noted. Crevice depth was recorded by placing a metric ruler from the entrance to the back of the crevice. If the back of the crevice could not be seen or reached with the ruler, the crevice depth was not determined. Crevice height was recorded, using metric tape, by measuring the vertical height of the entrance, and crevice width was recorded by measuring the horizontal width of the entrance.

Each captured salamander was marked and measured for snout-vent-length (SVL) and total length (TL) to the nearest 0.1 mm with a Spi 2000 dial Vernier caliper. Snout-Vent Length (SVL) measurements were taken from the snout to the posterior end of the vent. Total Length (TL) measurements were taken from the snout to the end of the tail. Each animal was weighed with a 5 or 10 gram Pesola scale.

Night surveys began at dusk and ended when the entire study area had been searched or no new salamanders were observed on the rocks or on the ground. A 50 m section of Rocky Run, located directly below the study site, was surveyed three times for *D. ochrophaeus*. Salamanders captured and marked in the stream were not included in abundance and density estimates, but were included in all other aspects of the study. Rocks located outside of the study area were searched monthly to determine if marked individuals were moving between isolated rock outcrops.

**Drift Fences**

Drift fences are typically used to sample species that move to aquatic breeding sites, but in this project they were used to determine when, and to what extent, salamanders move to adjacent rocks. The fences consisted of aluminum flashing (50.0 cm in height) and were set up to encircle three rocks in the study area. Each rock was given a number (R1, R2, and R3). The fences were placed approximately 2.5 - 3.0 m from the sides of the rocks, however, some exceptions were made in situations where the ground was too rocky to dig pitfalls. In these cases, the fence was placed as close to 3 m from the rock as possible. Pitfalls consisted of plastic buckets 49 cm in diameter and 21 cm in depth. They were paired and placed approximately 6 m apart on opposite sides of, and directly against the drift fence. There were eight pitfalls (on each side of the fence) surrounding R1, 12 surrounding R2, and five surrounding R3. Each pitfall along the drift fence was given an individual number. Three holes were cut into the sides of each bucket, approximately 15 cm from the bottom, to prevent the bucket from overflowing with rainwater. Pitfalls were filled with approximately 10 cm of water, and a saturated paper cloth was left in the water to hold moisture and provide cover.

Pitfalls were opened every week throughout the study period. They were opened during both daytime and nighttime hours, but there was more emphasis on nocturnal surveys. Pitfalls were generally opened at dusk and checked the following morning by 9:00 AM. If the pits were open during the day, they were checked by dusk. Pitfalls were never left open for more than 12 hours without being checked. Salamanders caught in the pitfalls were marked and processed, as described above, and placed on the other side of the fence. The pitfall number from which they were collected was noted.

## Marking Technique

Each salamander was marked using Visible Implant Flourescent Elastomer (VIE) tags during its initial capture. Tags were prepared by mixing a 10:1 ratio of elastomer and curing agent and placed in 0.3 cc syringes. Syringes of elastomer were prepared prior to each night survey and were kept on ice to prevent hardening.

Three colors of elastomer were used (red, orange, and yellow) for marking individuals subcutaneously with syringes in two of four possible locations (Fig. 18). This allowed for 225 unique marks per species. Green elastomer was also available, but was not used due the possibility of having difficulty detecting tag color under the green pigmentation of *A. aeneus*. Syringes were sterilized with swabs containing 70 percent isopropyl alcohol before and after each tag injection. Each salamander was given at least two tags to ensure that, in situations where a tag is lost, the presence of at least one tag would indicate a recapture. Once injected, a UVP mini UV shortwave/longwave lamp was used to observe tags in the field because VIE tags are too difficult to detect under ambient light.

Initially, salamanders were tagged by using methods described by Brinckley et al. (1999). These methods consisted of using a clip board, another board, and a plastic bag to wedge the salamander into a position that would not allow it to move so that it could be tagged. Once the researcher(s) of this project became more experienced with tagging, salamanders were merely held in an elongated position on a flat surface and tagged (Fig. 19).

Visual implant elastomer tags were used in this project rather than toe clipping (Donnelly et al. 1994), the traditional technique of marking salamanders, for two reasons. First, toe clipping may have negative affects on the health of amphibians (Clark 1972). Secondly, in a study conducted by Davis and Ovaska (1999), it was reported that movement patterns of toe-clipped individuals of *Plethodon vehiculum* were drastically reduced when compared to individuals marked with VIE tags. Because movement and dispersal habits of salamanders were of central importance to this project, toe-clipping was not an acceptable means of marking individuals.

# **Chapter 5:** Overview of Findings

Twenty-one mark and recapture surveys were performed between 11 May 1999 and 17 October 1999. The monthly number of person hours spent searching the study area is listed in Table 2. The study site was surveyed 86 person hours and drift fences were opened 439 hours and 37 minutes during the study period.

Ambient air and crevice temperatures showed normal seasonal fluctuations (Figs. 20 and 21). The mean ambient air temperature for the sampling period was 17.2° C, with a maximum temperature of 22.5° C (recorded 4 July), and a minimum of 9.0° C (recorded 23 Sept). The mean crevice air temperature was 17.2° C, and the maximum was 25.0° C (recorded 31 July). The ambient relative humidity also showed seasonal fluctuations (Fig. 22). The mean relative humidity for the sampling period was 90.4 percent.

Eighty-nine salamanders, encompassing five species, were marked during the 1999 field season. Species captured and tagged in the study area included the red eft, *Notophthalmus v. viridescens*, the redbacked salamander, *Plethodon cinereus*, the slimy salamander *P. glutinosus*, the Allegheny Mountain dusky salamander *Desmognathus ochrophaeus*, and the green salamander *Aneides aeneus*. Only *D. ochrophaeus*, *P. cinereus*, and *N. v. viridescens* were captured in both night surveys and pitfalls. Only two red efts and five redbacked salamanders were captured during the study period, and none was recaptured. Tables 3 and 4 list data of all red efts and redbacked salamanders captured in the study area, including their tag code, gender, mass, cranial width, SVL, and total length.

Thirty-eight green salamanders were captured and marked at the study site. Table 5 lists data for all green salamanders captured, including their tag code, gender, mass, cranial width, SVL, and TL. Of 59 captures of green salamanders, 22 (37 %) were recaptures. Of the 38 individuals, 24 were captured once, eight were captured twice, four were captured three times, and one was captured four times. Among all captured sexually mature green salamanders, seven were males, 10 were females, and the sex of 2 adults was unknown. The male to female sex ratio was 1:1.4.

Twenty-two *D. ochrophaeus* were tagged within the study area, and eight were tagged in Rocky Run. Two individuals were measured, but escaped before they could be tagged. Tables 6 and 7 list all *D. ochrophaeus* captured in the study area and Rocky Run, including their tag code, gender, mass, cranial width, SVL, and TL. Of 28 captures of *D. ochrophaeus* in the study site, four (14 %) were recaptures. None of the eight individuals captured and marked in Rocky Run (outside of study area) was recaptured. Of 22 marked individuals, two were captured twice and one was captured three times. Among all sexually mature *D. ochrophaeus* captured at the study site, five were males, nine were females, and the sex of five individuals was unknown.

Fourteen slimy salamanders were tagged within the study area. Table 8 is a list of all slimy salamanders captured, including their tag code, gender, mass, cranial width, SVL, and TL. Of 15 captures, only one was a recapture, and it was recaptured only once. Among all sexually mature slimy salamanders captured in the study area, three were males and two were females.

# **Chapter 6**: Population Demography

## Introduction

Demographic studies involve the analysis of various characteristics of whole populations or subsamples. In this population study, individuals of three species (*A. aeneus*, *D. ochrophaeus*, and *P. glutinosus*) were counted, measured for size, sexed, and tagged. This information, along with the analysis of location and movement patterns, provides baseline natural history data that can be used to calculate the rate of population change and to identify critical stages in the life cycle of all three species. Demographic studies provide the most information of any monitoring method, and suggest ways in which a site can be managed to ensure a healthy population persists (Primack 1998). In this chapter, population estimates are provided for *A. aeneus*, *D. ochrophaeus*, and *P. glutinosus* found on rock outcrops in the study area. Morphometric data is also presented to examine the size structure of the green salamander population. Finally, the movement and dispersal habits of *A. aeneus* on single rocks and between adjacent outcrops is examined. This information is critical to understanding the population demography of green salamanders inhabiting isolated rock outcrops.

## Methods

### Population Estimates

Population estimates of three species captured within the study site were calculated based on 21 mark-recapture surveys performed between 11 May 1999 and 17 October 1999. No populations estimates for *N. v. viridescens* and *P. cinereus* were obtained because no individual of either species was recaptured. Population estimates obtained for this project were based on open, rather than closed, population models because open models allow for immigration and recruitment, as well as death or emigration. Closed models assume no gains or losses of animals within the populations. For *D. ochrophaeus* and *P. glutinosus*, there was abundant suitable habitat for several hundred meters surrounding the study area, increasing the probability that both species disperse along the forest floor. Therefore, it was assumed that their population was open.

Both open and closed models were used to obtain population estimates for *A. aeneus*. Despite the dearth of habitat for *A. aeneus* outside of the study area, their population was considered to be open due to evidence of reproduction within the study site. However, because only one *A. aeneus* nest was observed during the study period, a closed population estimate was obtained using the Schnabel method (1938). Because dispersal was observed between adjacent rocks, open population estimates were also determined for *A. aeneus* on three individual rocks within the study area (R1, R2, and R3). The computer program JOLLEY 3.6 (Center for Conservation Biology, Stanford University; Dunn and Hellman 1997) was used as an abundance estimator, assuming an open population.

## Morphometrics and Size Classes

Morphometric data were analyzed for all salamanders captured within the study area (N=89). The morphometric data collected for each species was averaged for sexually mature individuals. *Desmognathus ochrophaeus* reaches sexual maturity when SVL is 30 mm (Hall 1977). Male and female *P. glutinosus* are sexually mature at 45.0 mm and 58.0 mm SVL, respectively (Highton 1962). Comparisons of morphological data between males and females were performed for *A. aeneus* using 17 green salamanders (seven males and 10 females). Mean measurements taken during all captures of an individual were used in calculations. Comparisons were made based on: (1) SVL in millimeters, (2) total length in millimeters, (3) cranial width in millimeters, and (4) mass in grams. T-tests were performed using Sigma Stat 2.0 for Windows to compare the morphometric data of both sexes.

Green salamanders were divided into 2 millimeter size classes based on SVL measurements. Size classes were partly determined based on methods used by Canterbury (1991), which suggested that all green salamanders greater that 45 mm in SVL are reproductively mature.

## Movement

Upon every capture, the location of the salamander was marked on a scanned image of the rockface (Fig. 17). However, due to low recapture rate for each species in this study, analysis of movement data for home range estimates was not possible. Therefore, linear movements were calculated by measuring the greatest distance between capture locations. The linear distance between capture points was determined for every green salamander that was captured more than once. Comparisons of linear movements between sexes were made using a t-test. An ANOVA was used to compare movements patterns of males, females, and immatures. Movement patterns of adults (both males and females) and sexually immature individuals were also compared (t-test). Rock outcrops containing populations that were not adjacent to the study area (Fig. 16) were surveyed once a month to determine the degree of green salamander migration.

## Results

### Population Estimates

The closed population estimate for *A. aeneus* obtained by using the Schnabel method was 56 individuals within the study area. The population estimates of *A. aeneus*, *D. ochrophaeus*, and *P. glutinosus*, as calculated by JOLLEY, are found in Figures 24, 25, and 26, respectively. The estimated population size of green salamanders (JOLLEY) in the study area was 88.8 individuals. The population estimates (JOLLEY) for *D. ochrophaeus* and *P. glutinosus* were 29.5 and 25.5, respectively. The open population estimates of green salamanders on rocks R1 and R2, are found in Figures 27 and 28, respectively. Too few individuals were captured from rock R3 to obtain an accurate estimate. The estimated population size on R1 and R2 were 8.0 and 26.0 individuals, respectively.

### Morphometrics and Size Classes

The average values for morphometric data collected for *A. aeneus*, *D. ochrophaeus*, and *P. glutinosus* are listed in Table 9. Of 24 *D. ochrophaeus* captured and tagged within the study area, only 5 (21 %) were sexually immature. Of 14 *P. glutinosus* tagged within the study area, nine (64 %) were sexually immature. There was no significant difference between the average measurements of SVL (t-test; P = 0.075; N = 8 M, 11 F), CW (t-test; P = 0.448; N = 7 M, 11 F), TL (t-test; P = 0.582; N = 8 M, 11 F), and mass (t-test; P = 0.806; N = 7 M, 11 F) for male and female green salamanders. Size classes of green salamanders captured in the study area are represented in Figure 29. There was a large proportion of individuals over 48.0 mm SVL. No green salamanders under 18.0 mm or over 55.0 mm SVL were captured in the study area.

## Movement

Linear movements between captures of individual green salamanders on single rock outcrops is listed in Table 10. Only one individual (female) moved between adjacent rock outcrops (Table 11). There was a 3.5 month time interval between captures of this individual. Four females were recaptured, and of these, one individual was captured three times, and three individuals were captured twice. The mean linear distance traveled by females between captures was 1.86 m. Three males were recaptured, and of these, one individual was captured four times and two individuals were captured three times. Movement only occurred between crevices on single rock outcrops, and no marked males were observed to move between rock outcrops. The mean linear distance traveled by males between captures was 3.18 m. Six sexually immature individuals were recaptured, and of these, one individual was captured three times and five individuals were captured two times. The mean linear distance traveled by immatures between captures was 3.34 m. Movement only occurred between crevices on single rock outcrops, and no marked immatures were observed to move between rock outcrops. There was no significant difference between the mean linear distance traveled by males (N = 8) and females (N = 6) (t-test; P = 0.364). There was no significant difference between the linear movements of adults (N = 13) and immatures (N = 8) (t-test; P = 0.617). The results of the ANOVA indicate that there is no significant difference (P = 0.690) between the linear movements of adult male (N = 8), adult female (N = 6), and immature individuals (N = 8). A fall migration or aggregation period was not noticed in this study. Marked individuals were not observed on rock outcrops that were located outside of the study area.

## Discussion

### Population Estimates

Determination of population size for green salamanders may be difficult due to the life history characteristics of the species. Juterbock (1998) suggested that there may not be an accurate way to determine a population estimate for *A. aeneus*. He spent five years conducting a mark-recapture study of this species, and determined that censusing efforts are mostly ineffective due to the inaccessibility of green salamanders for extended periods of time. He observed yearly fluctuations of green salamander populations. He witnessed a dramatic decline in the number of salamanders inhabiting one of his study areas in just one field season. He suggested that populations of terrestrial plethodontid salamanders may naturally have strong fluctuations.

The ideas formulated by Juterbock (1998) offer some insight into the population estimates obtained in this study. The population of green salamanders in the study area was considered to be open based on evidence of reproduction. Sample sizes were low, reflecting the small sampling area, and hence the population estimate was also low. The open population estimate of 88.8 individuals seems accurate when considering the small sampling area. However, changes in activity of *A. aeneus* during the summer and the suggested ability of green salamanders to avoid detection, make estimating their numbers difficult. For example, in early June, the green salamander population dramatically increased when several unmarked individuals were captured. By early July, when green salamanders were at their lowest activity level (Chapter 7), the population crashed and remained under 10 individuals for the rest of the study period. However, the seasonal population fluctuations exhibited by the Jolley population estimate (Figure 24) seem to be exaggerated. If the numbers obtained from the model are accurate, then the green salamander population suffered a dramatic crash in the middle of the field season. The results obtained from Jolley should be interpreted cautiously. By monitoring the population in subsequent years, it may be easier to assess population numbers for *A. aeneus.*

The closed population estimate of 56 individuals seems plausible. However, unmarked individuals were still being captured at the completion of this study. Of 12 captures in August through October, half were unmarked individuals. Further, most of the salamanders captured early in the summer were never recaptured. How marked individuals avoided recapture is unknown. Marked salamanders were not observed in adjacent populations, which suggests that individuals did not avoid detection by migrating to nearby rock outcrops. It is speculated that green salamander migration occurs in late fall or early spring (Canterbury 1991), not during mid-summer, when salamander activity was at its lowest point. Perhaps marked individuals avoided recapture by retreating into deep crevices. Many crevices within the study area were quite extensive, but the depth of many could not be determined due to the meandering nature of the crevices. It is possible that individuals remained in these crevices, far out of site from the crevice entrance. If *A. aeneus* is this difficult to detect in certain times of the year, then both open and closed population estimates may be inaccurate.

Rock R2 contained the most green salamanders in the study area, which was followed by R1 and R3 in order of individuals observed. Open population estimates for R1 and R2 seem low (only 34 individuals). The estimates are useful to compare salamander densities on each rock, but the accuracy of the numbers is questionable. Rock R2 was larger than the other two rocks, and although it was not quantified, it appeared to contain more crevices than the others as well. Perhaps the size and crevice number of R2 allowed more salamanders to inhabit the rock. Rock

R3 was the smallest rock, and too few individuals were observed on it to obtain an adequate population estimate.

The green salamander population within the study area was assumed to be open due to evidence of reproduction. Rock R1 had the only green salamander nest observed in the 1999 field season. The nest was located in a crevice that was 180 cm from the ground. The crevice dimensions were as follows: 1) crevice depth = 10 cm, 2) crevice width = 8.5 cm, 3) crevice height = 1.5 cm. A female with eggs (Fig. 30) was observed in the crevice in the summer of 1998, which indicates that this particular crevice is an optimal nesting habitat. In 1999, a male and female were first observed together in the crevice on 11 May. On 29 May 1999, there were 7-9 eggs in the crevice and the female was present. The female was observed with the eggs throughout the summer, often guarding them when rays from flashlights hit the crevice. The eggs hatched on 20 Aug 1999, at least 83 days after they were laid. This is consistent with what was observed by Canterbury and Pauley (1994) during their study of green salamander reproductive behavior in West Virginia. They found that the incubation period for *A. aeneus* lasted between 82 and 90 days. The hatching date of the eggs observed in this study was earlier than what was observed by Canterbury and Pauley (1994) by 11 days. The earlier hatching date may be attributed to early onset of cold conditions in study area. The elevation of the study area was approximately 300 m higher than the area surveyed by Canterbury and Pauley (1994). The female remained with the juvenile salamanders until late September. She was last seen on 25 Sept 1999, but the study area was not searched again until 16 October 1999. On this later date, two juveniles were observed in the crevice and neither was captured.

## Morphometric Data

The results of this aspect of the study are consistent with previous natural history studies performed with *A. aeneus*. Most of the slimy salamanders found within the study area were sexually immature, suggesting that the individuals found on rock outcrops were not there to secure breeding territories. Most all *D. ochrophaeus* found in the study area were sexually mature, and they were abundant during their breeding season (Chapter 7). However, no sexually mature female on the rock outcrops was gravid. Because Rocky Run is close to the study area, the *D. ochrophaeus* observed on the rocks may have been migrating up the hillside from the stream after females deposited their eggs.

The majority of green salamanders captured in the study area were sexually mature. The high proportion of larger individuals may either reflect the breeding habits of this species, or be an indication of the health of this population. In West Virginia, green salamander eggs hatch in late August or early September (Canterbury and Pauley 1994), and most of the surveys conducted in this project occurred before September. Therefore, few hatchlings were observed in the study area. However, it is also possible that a population shift has occurred, which may have resulted from low recruitment in previous years. No data is available concerning the population demography of this population in previous years for comparison. The population may be cyclic, and size class proportions may shift in future studies.

## Movement

Movement patterns of *A. aeneus* are difficult to observe due to the reclusive habits of the species. The results of this study are not consistent with those from previous studies. Canterbury (1991) found that immatures moved more than adults during the breeding season. Although it was found that sexually immature individuals were more active than adults during the breeding season (Chapter 7), movement during the breeding season was not compared to pre-hibernation movements. All recaptures were made by the end of September and few green salamanders were observed in October.

The extent to which green salamanders migrate is unknown. Individuals have been observed crossing roads in April through June (Williams and Gordon 1961; Cupp 1991), but there has never been any direct evidence of migration between isolated rock outcrops. It was hoped that by using drift fences in this study, dispersing individuals would be caught during seasonal migration. However, not one green salamander was caught in a pitfall trap. The female that moved from rock R1 to R3 had to climb the drift fences surrounding each rock between the time interval of May through August.

Canterbury (1991) observed a fall dispersal and aggregation period in September and October. Such activity and movement patterns were not apparent in this study. Differences in aggregation and movement patterns between the population studied by Canterbury (1991) and the population studied in the WWERF may be related to the differences in elevation between the two study areas. Canterbury (1991) performed his research in Holly River State Park in Webster County, West Virginia (elevation approximately 500-600 m). His study area was approximately 300 m lower in elevation than the area studied in this project. Migration in the WWERF population may take place in early Spring, before the onset of the breeding period. Such activity would reflect the observations of Cupp (1991) and Williams and Gordon (1961) where several individuals were observed crossing roads in the Spring.

To fully understand the extent to which this species migrates to other rock outcrops, a long-term monitoring project needs to be undertaken. By permanently marking individuals with VIE tags and engaging in intensive surveys of adjacent, relatively isolated populations, the degree to which green salamanders migrate could be assessed. In this study, marked individuals were not observed in adjacent green salamander populations. These other populations were surveyed monthly from May to September, 1999. Populations on these other rock outcrops will need to be monitored in the next few years to make certain that individuals marked within the study area of this project do not migrate to adjacent populations.

Although the only marked individual to disperse between adjacent rock outcrops managed to successfully climb two drift fences, this monitoring method could still be used to assess green salamander migration. Rocky soil in the study area made it difficult to place numerous pitfalls along the drift fences surrounding each rock outcrop. I feel that drift fences would still be an adequate means to monitor green salamander migrations, if pitfalls are placed so that a trap is located every meter along the fence.

# **Chapter 7:** Habitat Preference, Vertical Stratification, and Activity

## Introduction

Ecological relationships of sympatric species have long been of interest to ecologists. Gause (1934) and Park (1948) were of the first to investigate resource utilization by similar species. Their research gave way to the competitive exclusion hypothesis (Hardin 1960), which is widely supported in modern ecological research. MacArthur and Levins (1967) later developed a concept of limiting similarity, which stated that species can coexist if they differ sufficiently in resource use. With this in mind, the purpose of this chapter is to investigate the sympatric relations of the plethodontid salamanders that inhabit rock outcrops in West Virginia.

Interspecific competition among plethodontid salamanders has been studied extensively (Dumas 1956; Jaeger 1971, 1974; Fraser 1976; Hairston 1980; Southerland 1986; Hairston et al. 1987). Most of these studies were performed using laboratory tests to determine if competition occurred and for what resources. Several studies have been conducted to determine how competition influences spatial distribution of salamanders. Jaeger (1972) determined that competition was important to determine the altitudinal distribution of sympatric plethodontid salamanders. This behavior may be applicable to salamanders that inhabit rock outcrops if competition is avoided by vertical stratification. Baltar's (1983) test results indicate that a stratification hierarchy exists between three species of cliff-dwelling plethodontid salamanders in Mississippi. In her study, *A. aeneus* occupied the highest crevices along cliffs and *P. dorsalis* and *P. glutinosus* occupied lower crevices.

Canterbury (1991) studied competition behavior of *A. aeneus* with *P. glutinosus*, *P.*

*kentucki*, *D. ochrophaeus*, and *P. wehrlei*. The results of his study (Chapter 1) indicate that when these species are sympatric, they exhibit aggressive behavior. Therefore, the purpose of this chapter is to determine whether the sympatric salamanders inhabiting rock outcrops are avoiding competition by one or a combination of these mechanisms: (A) by distributing themselves spatially along rock outcrops or by climbing (vertical stratification), (B) by having different seasonal activity patterns, or (C) by differing in resource utilization and habitat preference.

## Methods

### Habitat Preference

The percentage of individuals taken from crevices, as compared to captures of active (moving along rockface) salamanders, was obtained for *A. aeneus, D. ochrophaeus*, and *P. glutinosus*. Each time a salamander was captured from, or observed in a crevice, measurements were taken to determine crevice width in cm (at entrance), crevice height in cm (at entrance), and crevice depth in cm. Crevice depth was determined by sliding a ruler to the back of the crevice and measuring the distance to the entrance. When the mouth of the crevice was too small for a ruler to be used to take measurements, a wire was used instead. When crevice depth could not be determined, e.g. the end of the crevice was not visible, the measurement was left unknown. The distance of the crevice to the ground in cm was also measured. A Kruskal-Wallis One Way ANOVA on ranks was used to compare width and height of crevices inhabited by the three species. When there was a significant difference between values for each species, a pairwise multiple comparison procedures (Dunn's Method) was used to indicate which species differed significantly in terms of crevice dimension. A Mann-Whitney rank sum test was used to compare crevice depth values for *A. aeneus* and *P. glutinosus*. *Desmognathus ochrophaeus* was not included in crevice depth analysis due to small sample size. Crevice dimensions were also compared to SVL measurements of *A. aeneus* using a regression analysis.

Microclimatic conditions, air temperature and relative humidity, were measured for each crevice containing a salamander. Both were determined by placing the appropriate instruments, as described in Chapter 4, inside the crevice within a few centimeters of the salamander. When crevices were too small for the relative humidity meter to be placed inside, readings were taken at the crevice entrance (within 5 cm). A t-test was used to determine if there was a significant difference between the two readings. Readings taken at crevice entrances were used in the analysis to represent internal crevice microclimatic conditions when the latter could not be determined. A t-test was used to compare crevice and ambient air temperature. Air temperature and relative humidity values for crevices inhabited by different species were compared using an ANOVA.

## Vertical Stratification

Upon each capture, distance from salamander location to the ground in cm was recorded. Values were obtained on all three rocks within the field site. Because the total height of each rock did not differ by more than one meter, vertical stratification values obtained from each rock were grouped together for analysis. Vertical distance values for *A. aeneus*, *D. ochrophaeus*, and *P. glutinosus* were compared using an ANOVA. A Tukey Test was used as a pairwise multiple comparison procedure when vertical stratification values differed significantly between *A. aeneus*, *D. ochrophaeus*, and *P. glutinosus*. Vertical stratification values obtained for *A. aeneus* were compared to SVL measurements using a regression analysis. Vertical positioning of adult (SVL > 45 mm) and immature green salamanders were compared using a Mann-Whitney rank sum test. These latter tests were run to determine if vertical stratification is a means of intraspecific competitive avoidance.

### Activity

Activity patterns of *A. aeneus*, *D. ochrophaeus*, and *P. glutinosus* during May through October, 1999, were compared by determining the percentage of captures of each species per month. Percent capture values for each species were plotted against monthly surveys. Monthly activity patterns of adult (SVL > 45.0 mm) versus sexually immature individuals were also compared by determining the percentage of captures for both size classes per month.

## Results

### Habitat Preference

Of 59 captures of green salamanders, 29 (49 %) were taken from crevices. Of all captures of *D. ochrophaeus* and *P. glutinosus*, only 24 % (six individuals) and 21% (three individuals), respectively, were taken from crevices. Other salamander species were not found in crevices within the study area.

Kruskal-Wallis One Way ANOVA on ranks showed a significant difference ($P = 0.011$) between the width of crevices inhabited by *A. aeneus* ($N = 33$), *D. ochrophaeus* ($N = 10$), and *P. glutinosus* ($N = 7$). Median values for crevice width for *A. aeneus*, *D. ochrophaeus*, and *P. glutinosus* are 5.5 cm, 2.0 cm, and 14.3 cm, respectively. All pairwise multiple comparison procedures (Dunn's Method) indicate that there is a significant difference between crevice width values for *D. ochrophaeus* and *P. glutinosus* ($P < 0.05$), and for *D. ochrophaeus* and *A. aeneus* ($P < 0.05$). However, there was no significant difference between width values of crevices inhabited by *A. aeneus* and *P. glutinosus* ($P > 0.05$). Crevice height dimensions were also analyzed using a Kruskal-Wallis One Way ANOVA on Ranks. The results indicate that there is no significant difference ($P = 0.160$) between the height of crevices inhabited by *A. aeneus* ($N = 34$), *D. ochrophaeus* ($N = 10$), and *P. glutinosus* ($N = 7$). Crevice depth values could only be analyzed for *A. aeneus* ($N = 24$) and *P. glutinosus* ($N = 7$) due to lack of data for *D. ochrophaeus*. A Mann-Whitney Rank Sum Test indicates that there is no significant difference between the depth of crevices inhabited by *A. aeneus* and *P. glutinosus* ($P = 0.061$). Results of the regression analysis performed on crevice dimensions and SVL measurements of *A. aeneus* are represented in Figs. 31, 32, and 33. There was no relationship between crevice width

($R^2 = 0.0711$), height ($R^2 = 0.0122$), or depth ($R^2 = 0.1321$) and SVL measurements of *A. aeneus.*

There was no significant difference between relative humidity readings taken within crevices and at crevice entrances (t-test; $P = 0.316$, $N = 9$). There was no significant difference between ambient ($N = 25$) and crevice ($N = 25$) air temperature values collected during the study period (t-test, $P = 0.364$). Average monthly ambient and crevice air temperature is displayed in Figure 34. There was no significant difference between ambient ($N = 26$) and crevice ($N = 26$) relative humidity values obtained during the study period (t-test, $P = 0.235$). Therefore, an ANOVA was not used to determine if there was a significant difference between the environmental conditions of crevices inhabited by the sympatric salamander species.

## Vertical Stratification

The mean vertical distance from the ground occupied by *A. aeneus*, *D. ochrophaeus*, and *P. glutinosus*, was 137.7 cm, 70.7 cm, and 38.3 cm, respectively. There was a significant difference between their vertical positions along rockfaces (ANOVA; $P < 0.001$). All pairwise multiple comparison procedures (Tukey Test) indicate that there is a significant difference ($P < 0.001$) between the vertical positions of *A. aeneus* ($N = 64$) and *P. glutinosus* ($N = 17$), and *A. aeneus* and *D. ochrophaeus* ($N = 27$). Based on the results of the ANOVA, there is no significant difference between the vertical positioning of *P. glutinosus* and *D. ochrophaeus* ($P = 0.095$). However, when a t-test was used to compare the vertical positioning of *D. ochrophaeus* ($N = 27$) and *P. glutinosus* ($N = 17$), the results were significant ($P = 0.012$).

There was no relationships between vertical positioning and salamander SVL for *A. aeneus* (regression analysis; $R^2 = 0.0003$; Fig. 35). Average vertical positions of adult and sexually immature green salamanders are 136 cm and 141 cm, respectively. A Mann-Whitney rank sum test indicated that there is no significant difference ($P = 0.393$) between the vertical positions of adult ($N = 35$) and immature ($N = 30$) green salamanders.

### Activity

Monthly activity patterns of *A. aeneus*, *D. ochrophaeus*, *P. glutinosus*, and *P. cinereus* are compared in Fig. 36. The number of captures of *D. ochrophaeus* and *A. aeneus* are compared with reference to search hours in Fig. 37. In May, the occurrence *A. aeneus* peaked when it made up 78 percent of all captures. The occurrence of *A. aeneus* decreased gradually until August, when it made up only 32 percent of total captures, and then peaked once again in September, making up 60 percent of all captures. Finally, in October, green salamander numbers dropped, making up only 33 percent of all captures. *Desmognathus ochrophaeus* did not appear in the field site until June, and their numbers increased gradually until they peaked in August, making up 56 percent of total captures. By October, *D. ochrophaeus* was no longer observed in the study area. *Plethodon cinereus* was observed in low numbers at the beginning of the field season in May, and was not observed again until October, when they made up 44 percent of all captures. The occurrence of *P. glutinosus* was consistent throughout the study period, where it made up between 12 percent and 22 percent of total captures.

Activity patterns of adult (SVL > 45 mm) and sexually immature green salamanders are compared in Fig. 38. In May, capture rates of adults and immatures were 52 percent and 48 percent, respectively. Their capture rates were identical (50 %) in June. Surface abundance of sexually immature individuals gradually increased until it peaked in August, where immatures made up 88 percent of all captured green salamanders. By September and into October, adults made up the majority of captures (68 %).

## Discussion

### Habitat Preference

As indicated by the results, *A. aeneus* inhabits rock crevices more frequently than either *D. ochrophaeus* or *P. glutinosus*. This suggests that, although all three species are sympatric on rock outcrops, they may not be dependent on the same habitat resources. It is not surprising that there was a high percentage of green salamanders captured from crevices when considering their natural history habits, but the low proportion of *D. ochrophaeus* and *P. glutinosus* in crevices questions the role these species play in the distribution of all three species. If *D. ochrophaeus* and *P. glutinosus* are not as dependent on crevices as *A. aeneus*, then these three species may not be in direct competition for habitat. By investigating the differences between dimensions of crevices inhabited by all three species, further insight is offered into how they partition resources.

The tendency for *A. aeneus* and *P. glutinosus* to occupy crevices that were significantly wider than those occupied by *D. ochrophaeus* suggests two things. First, competitive exclusion may force *D. ochrophaeus* into smaller crevices. As noted by Canterbury (1991), *A. aeneus* is a successful aggressor when it encounters *D. ochrophaeus*. This suggests that *D. ochrophaeus* may evade competition by acquiring suboptimal, or, as in this case, smaller crevices. Aggressive interactions between *P. glutinosus* and *D. ochrophaeus* have not been investigated. Therefore, it is uncertain which species would be the successful competitor during interspecific interactions.

The second explanation for *D. ochrophaeus* occupying smaller crevices may be representative of salamander morphology. *Desmognathus ochrophaeus* is smaller than both *A. aeneus* and *P. glutinosus*. Therefore, it may occupy smaller crevices based on body size characteristics, rather than by force from competitive exclusion. There was no significant difference between any dimensions of crevices occupied by *A. aeneus* and *P. glutinosus*, both of which are large terrestrial salamanders. If salamanders occupy crevices that are representative of their size, then *A. aeneus* and *P. glutinosus* would be in more direct competition for space than with *D. ochrophaeus*.

Crevice width was the only measurement that had significantly different results between *A. aeneus*, *D. ochrophaeus*, and *P. glutinosus*. Why crevice width would be a significant factor in resource partitioning is uncertain. *Aneides aeneus* is more dorso-ventrally flattened than both *D. ochrophaeus* and *P. glutinosus*, which may necessitate occupation of wider crevices. However, if the morphological characteristics of *A. aeneus* are important in determining what crevices it occupies, it seems probable that crevice height would also be a significant factor allowing for resource partitioning. If these species avoid competition based on crevice dimensions, it seems more probable that *A. aeneus* would occupy flatter crevices that are too small for *D. ochrophaeus* and *P. glutinosus*. Results of this aspect of the study should be interpreted cautiously and further research is needed to quantify the effects of salamander morphology on resource partitioning among these salamanders.

Because there was no relationship between salamander SVL and the dimensions of the crevices they inhabit, it can be deduced that green salamanders do not avoid intraspecific competition based on crevice characteristics. Canterbury (1991) investigated intraspecific interactions between immature and adult green salamanders, and found that immature individuals do not establish territories, but rather, they move around extensively. Results from this study suggest that immature individuals do not avoid intraspecific competition by occupying crevices that are structurally less desirable to adults. Although the movement of sexually immature individuals during the breeding season was not compared to other seasonal activity, immatures were observed to be more active in midsummer (see Activity section).

Based on the results of this study, microclimatic conditions had no effect on resource partitioning. Because crevice environmental conditions did not vary significantly from ambient values, it is unlikely that the salamanders in this study occupied crevices based on environmental conditions. This aspect of the study is still worth further investigation. To add further insight into the role of microclimatic conditions in crevice-salamander distribution, crevices should be monitored continually throughout the year using Hobo data loggers. These instruments have external probes that can fit into small areas to monitor temperature values. To my knowledge, there are currently no available devices that are small enough to adequately monitor relative humidity values within small crevices. The relative humidity meter used in this study had an external probe that could only fit into larger crevices. Perhaps the results of crevice microclimatic conditions would have been different had more sufficient equipment been used to quantify environmental data.

## Vertical Stratification

The results of this study supplement earlier research efforts, which suggest that *A. aeneus* avoids competition by climbing. Cliburn and Porter (1987) suggested that salamanders vertically stratify based on their climbing ability. *Aneides aeneus* has a greater ability to climb upward than *P. glutinosus* (Cliburn and Porter 1986), which may result in a tendency for *A. aeneus* to climb to higher portions of rockfaces when the two species are sympatric (Baltar 1983). Canterbury (1991) observed the competitive behavior of *A. aeneus* with both *D. ochrophaeus* and *P. glutinosus*. His results indicated that when *A. aeneus* has aggressive encounters with *P. glutinosus*, it avoids competition by climbing. In this study, *A. aeneus* was observed more frequently than both *P. glutinosus* and *D. ochrophaeus* on higher portions of rock outcrops.

In laboratory experiments, Canterbury (1991) found that *D. ochrophaeus* retreated by running, burrowing, and climbing when it encountered *A. aeneus*. In this study, *A. aeneus* was found on significantly higher portions of rockfaces than *D. ochrophaeus*, which occupied the intermediate positions within the study area. If *A. aeneus* is a successful aggressor in situations where it encountered *D. ochrophaeus*, then it would not have to retreat to higher crevices to avoid confrontation. Rather, *D. ochrophaeus* would be expected to be forced to occupy crevices that are not optimal for *A. aeneus.* This suggests green salamanders may occupy higher portions of rockfaces by convention, rather than by force. The results indicate that *A. aeneus* and *D. ochrophaeus* do not usually occur in the same portions of rock, but it is doubtful that their vertical stratification hierarchy represents competitive avoidance due to their seasonal activity patterns (see Activity section).

Results of pairwise comparisons indicate that *D. ochrophaeus* and *P. glutinosus* do not significantly differ in the vertical positions they occupy on rock outcrops. Therefore, crevice dimensions may be the leading factors that allow the two species to avoid competition. As indicated previously, *D. ochrophaeus* and *P. glutinosus* significantly differ in terms of the width of the crevices they inhabit. However, as indicated in the previous section, it seems probable that crevice dimensions other than just width could also be important in determining which crevices these two species inhabit (see Habitat Preference). The significant results of the t-test used to follow up the negative findings of the ANOVA, suggest that *D. ochrophaeus* and *P. glutinosus* do occupy different vertical positions along rockfaces. The results of the t-test, although conflicting with the results of the ANOVA, offer interesting insight into the distribution of these three species when seasonal activity is discussed. The importance of these results is discussed further in the following section of this chapter (see Activity section).

Because *A. aeneus* does not vertically stratify based on SVL, it can be deduced that intraspecific competition is not avoided by this method. As discussed previously, Canterbury (1991) observed that immature individuals do not establish territories, but that they move around more frequently than adults. The movement results of this study (Chapter 6) do not indicate that sexually immature individuals move around more extensively than adults. However, immature individuals were more active than adults during midsummer (see Activity section). Movement and activity patterns are significant factors that play a role in the distribution of immature and adult individuals.

## Activity

Activity patterns observed in this study offer some further insight into how sympatric salamanders avoid competition. From the above discussion, it is suggested that *A. aeneus* avoids interspecific competition with *P. glutinosus* and *D. ochrophaeus* by vertically stratifying. However, when considering the aggressive behavior of *D. ochrophaeus* and *A. aeneus*, vertical stratification as a means to avoid competition becomes questionable. Salamander activity patterns observed in the 1999 study period suggest that *A. aeneus* and *D. ochrophaeus* may avoid competition based on the time of year they are active on rock outcrops, rather than by vertically stratifying.

Because slimy salamanders appeared consistently throughout the study, the fluctuating activity patterns of *A. aeneus*, *P. cinereus* and *D. ochrophaeus* most likely had little or no effect on their occurrence at the field site. *Plethodon glutinosus* is a successful aggressor when sympatric with *D. ochrophaeus* and *A. aeneus* (Canterbury 1991), so it may have forced the latter species to occupy higher positions along the rockfaces. Vertical positions occupied by *A. aeneus* (highest portion) and *D. ochrophaeus* (middle portion) reflect the climbing ability of both species. Although *A. aeneus* occupies significantly higher positions along rockfaces than *D. ochrophaeus*, it most likely is not a result of competitor avoidance due to differences in the activity patterns of both species. Therefore, *P. glutinosus* may force *D. ochrophaeus* to occupy higher portions of rockfaces when *A. aeneus* is at its lowest activity level. In this respect, the result of the t-test used to investigate the vertical stratification of *D. ochrophaeus* and *P. glutinosus* is significant. Because the activity level of *A. aeneus* and *D. ochrophaeus* are not synchronized, the impact of the competitive ability of *P. glutinosus* may only affect one species at a time.

Green and Pauley (1987), suggested that *D. ochrophaeus* seeks aquatic habitats at the onset of colder weather. This describes the activity patterns observed in the study area, where *D. ochrophaeus* did not appear until the onset of warmer conditions in June, and did not leave the study area until September. Dusky salamanders observed within the study area probably moved to Rocky Run at the onset of colder weather. Peak activity of *D. ochrophaeus* occurred when *A. aeneus* was at its lowest activity level (late summer). Therefore, because peak densities of these two species did not overlap, *D. ochrophaeus* and *A. aeneus* most likely do not vertically stratify to avoid competition. Rather, they most likely occupy positions along rockfaces that reflect their climbing ability.

Studies by Cupp (1991) and Gordon (1952) suggest that adult green salamanders reach their highest densities on rockfaces from late October to mid-December. In this study, only 3 individuals were found within the study area in October. The study area was not surveyed after 17 October 1999, so the density of *A. aeneus* may have increased in November and December, but this is unlikely. The onset of colder weather conditions in the study area is most likely earlier than in areas surveyed in previous studies due to geographical and elevational differences. At the onset of freezing weather, adult and juveniles retreat to deep crevices (Gordon 1952; Woods 1968; Cupp 1991). For green salamanders to remain active during these months, they would have had to endure freezing temperatures. To be sure when green salamanders retreat for winter conditions in the WWERF, more populations need to be monitored.

*Plethodon cinereus* was only observed in low numbers within the study area in May and October. Only two individuals of this species were observed on rocks within the study area, and three individuals were taken from pitfalls. Petranka (1998) suggested that adults are most active on the ground surface during spring and autumn, which is consistent with the findings of this study. Pauley (personal communication) suggested that *P. cinereus* becomes diurnal in the fall and travels along hillsides under leaf litter. Perhaps this is why two of the three individuals taken from pitfalls were captured during diurnal hours. Although the number of captured individuals was quite low, the reappearance of *P. cinereus* in October was synchronized with the shedding of leaves. Several individuals outside of the study area were observed under the leaf litter during daytime hours. As suggested by Petranka (1998), temperature and moisture are most likely the primary factors affecting the distribution and movement of *P. cinereus*.

The presence of *P. cinereus* in the study area most likely had little effect on the competitive behavior of the more permanent species. The breeding season of *P. cinereus* only overlaps with *D. ochrophaeus*, but both species breed in different habitats (Chapter 1). This breeding behavior decreases the probability that both species would compete for breeding space. *Plethodon cinereus* becomes less active at the onset of warmer weather (Heatwole 1962), which is consistent with the results of this study. *Plethodon cinereus* and *D. ochrophaeus* did not occur together during the study period, suggesting that there was little or no competition between the two species. Although *P. cinereus* was present in the study area when *A. aeneus* reached its highest numbers, only two individual redbacked salamanders were observed on rocks, and neither was found in a crevice. Therefore, there was probably little competition between these two species.

The activity patterns of adult and sexually immature green salamanders reflect breeding activity and seasonality. Although green salamander surface abundance decreased by late-summer, the proportions of captures of adult and sexually immature individuals fluctuated according to the green salamander breeding period. Green salamander eggs are laid in late May and early June and hatch in late August and early September. The surface abundance of adults fluctuated according to these dates. It was not until the completion of the breeding period that adult captures began to increase. Sexually immature individuals are not territorial during the breeding season (Canterbury 1991), and therefore, were able to move around more freely throughout the breeding period. This would account for the high proportion of sexually immature individuals captured throughout the breeding period.

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# Tables and Figures

**Table 1**. Dimensions of rocks within study area that were surrounded with drift fences, 1999.

| Rock | Diameter (m) | Total Height (cm) |
|---|---|---|
| R1 | 11.96 | 193 |
| R2 | 22.63 | 190 |
| R3 | 9.95 | 179 |

**Table 2**. Monthly person hours spent searching the study area located within the WWERF, 1999.

| Month | Hours Searched |
|---|---|
| May | 18.0 |
| June | 20.0 |
| July | 18.0 |
| August | 18.0 |
| September | 6.0 |
| October | 6.0 |

**Table 3**. Morphological data for all *Notophthalmus v. viridescens* (N = 2) captured and marked on or near rocks at field site in the WWERF, 1999.

| Tag Code | Mass (g) | CW (mm) | SVL (mm) | TL (mm) |
|---|---|---|---|---|
| 1R,2R | 2.5 | 7.6 | 41.2 | 83.2 |
| 2R,3R | 1.9 | 7.4 | 42.3 | 83.6 |

**Table 4**. Morphological data for all redbacked salamanders captured and marked on or near rock outcrops in the study area in the WWERF, 1999. A "U" indicates that the sex of the individual was unknown.

| Tag Code | Sex | Mass (g) | CW (mm) | SVL (mm) | TL (mm) |
|---|---|---|---|---|---|
| 1R,2R | M | 1.4 | 5.6 | 39.7 | 17.8 |
| 2R,3R | U | 0.6 | 4.1 | 34.9 | 64.5 |
| 3R,4R | F | 0.6 | 4.5 | 35.0 | 57.4 |
| 1R,3R | F | 0.5 | 4.3 | 40.0 | 65.2 |
| 2R,4R | F | 0.5 | 3.8 | 29.7 | 51.8 |

**Table 5**. Morphological data for all green salamanders captured and marked on or near rock outcrops within the study area in the WWERF, 1999. A "U" indicates that the sex of the individuals was unknown. An "I" indicates that the individual was not sexually mature.

| Tag Code | Sex | Mass (g) | CW (mm) | SVL (mm) | TL (mm) |
|---|---|---|---|---|---|
| 1R,2R | F | 3.1 | 9.6 | 51.0 | 109.7 |
| 3Y,4Y | F | 2.6 | 8.8 | 54.0 | 68.6 |
| 1R,2O | F | 1.7 | 7.4 | 49.6 | 81.2 |
| 2R,3O | F | 2.6 | 8.2 | 55.0 | 105.7 |
| 1R,30 | F | 3.0 | 8.4 | 54.9 | 112.0 |
| 1R,4O | F | 2.3 | 9.0 | 52.8 | 73.8 |
| 2O,3Y | F | 1.8 | 7.4 | 47.6 | 88.4 |
| 3O,4Y | F | 2.5 | 8.7 | 50.7 | 113.9 |
| 1O,3Y | F | 3.0 | 8.0 | 52.4 | 110.4 |
| 2O,4Y | F | 2.6 | 7.0 | 48.4 | 99.5 |
| 2O,3R | F | 2.2 | 9.4 | 52.2 | 112.2 |
| 1R,4R | M | 1.6 | 8.7 | 46.2 | 62.2 |
| 1O,2O | M | 1.5 | 6.8 | 38.6 | 75.9 |
| 3O,4O | M | 3.0 | 9.3 | 52.6 | 93.8 |
| 1Y,3Y | M | 3.2 | 10.0 | 53.6 | 101.5 |
| 2Y,4Y | M | 3.6 | 10.2 | 54.9 | 119.2 |
| 2R,40 | M | E | 10.9 | 50.8 | 116.6 |
| 1R,2Y* | M | 1.9 | 7.8 | 46.6 | 93.0 |
| 1R,2O | U | 1.4 | 7.1 | 49.4 | 81.3 |
| 2O,3Y | U | 1.6 | 6.6 | 44.7 | 81.1 |
| 1R,2Y* | I | 1.9 | 6.5 | 37.1 | 83.3 |
| 2R,3R | I | 0.7 | 5.5 | 29.1 | 55.2 |
| 3R,4R | I | 1.0 | 6.7 | 37.4 | 79.0 |
| 1R,3R | I | 0.6 | 5.9 | 26.6 | 40.8 |

| Tag Code | Sex | Mass (g) | CW (mm) | SVL (mm) | TL (mm) |
|---|---|---|---|---|---|
| 2R,4R | I | 0.8 | 6.0 | 30.0 | 60.5 |
| 2O,3O | I | 1.1 | E | 35.5 | 83.0 |
| 1O,3O | I | 0.7 | 6.0 | 31.2 | 58.2 |
| 2Y,3Y | I | 1.1 | 7.3 | 41.2 | 79.7 |
| 2O,4O | I | 0.5 | 7.1 | 33.9 | 64.9 |
| 1O,4O | I | 0.5 | 4.5 | 30.1 | 56.4 |
| 1Y,4Y | I | 0.4 | 3.3 | 17.2 | 32.9 |
| 3R,4O | I | 1.5 | 6.9 | 40.2 | 81.7 |
| 3O,4R | I | 0.7 | 4.9 | 25.1 | 53.1 |
| 10,2Y | I | 0.6 | 5.1 | 27.4 | 54.5 |
| 2R,3Y | I | 0.7 | 4.9 | 28.4 | 34.5 |
| 1Y,2O | I | 1.2 | 7.8 | 40.2 | 80.3 |
| 1O,2R | I | 1.2 | 6.0 | 38.4 | 78.8 |
| 1O,3R | I | 0.4 | 4.8 | 30.4 | 59.4 |

* These individuals have the same tag code

**Table 6**. Morphological data for all *D. ochrophaeus* captured and marked on or near rock outcrops in study area in the WWERf, 1999. A "U" indicates that the morphological data is not available for that individual. An "E" indicates that the individual escaped before it could be tagged.

| Tag Code | Sex | Mass (g) | CW (mm) | SVL (mm) | TL (mm) |
|---|---|---|---|---|---|
| 2Y,3O | M | 2.0 | 6.0 | 46.6 | 93.7 |
| 2R,4Y | M | 0.8 | 4.0 | 34.6 | 78.8 |
| 1R,2R | M | 0.9 | 4.0 | 35.2 | 70.1 |
| 2O,4O | M | 1.7 | U | U | U |
| 1O,4O | M | 1.3 | U | U | U |
| 1R,4Y | F | 0.8 | 4.1 | 28.6 | 66.9 |
| 3R,4R | F | 1.0 | 4.7 | 36.0 | 75.9 |
| 2Y,3Y | F | 0.9 | 4.5 | 36.2 | 75.4 |
| 1O,2O | F | 1.0 | 4.1 | 37.3 | 78.5 |
| 3O,4O | F | 2.0 | U | U | U |
| 1O,3O | F | 1.3 | U | U | U |
| 2R,3Y | F | 0.8 | 4.0 | 29.7 | 61.5 |
| 2Y,4Y | F | 1.2 | 5.6 | 40.0 | 75.3 |
| 1R,2O | F | 1.0 | 5.0 | 36.8 | 71.4 |
| 1Y,4Y | F | 1.2 | 5.0 | 36.9 | 75.6 |
| 1Y,2Y | U | 0.7 | 4.4 | 31.5 | 51.3 |
| 1Y,2O | U | 0.7 | 4.3 | 33.9 | 54.8 |
| 1R,2Y | U | 0.3 | 2.8 | 24.0 | 50.9 |
| 3R,4Y | U | 1.0 | 4.4 | 34.6 | 69.5 |
| 1R,3Y | U | 0.7 | 3.2 | 30.2 | 65.0 |
| 2O,3O | U | 0.4 | 3.2 | 25.1 | 55.7 |
| 1Y,2Y,3Y | U | 1.4 | 4.5 | 35.1 | 67.6 |
| E | U | 0.3 | 3.0 | 22.6 | 46.8 |
| E | U | 0.2 | 2.9 | 20.1 | 40.0 |

**Table 7**. Morphological data for all *D. ochrophaeus* captured and marked in Rocky Run, 1999. A "U" indicates the sex of the individual was unknown. A "U" indicates the sex of the individual was unknown.

| Tag Code | Sex | Mass (g) | CW (mm) | SVL (mm) | TL (mm) |
|---|---|---|---|---|---|
| 2R,3R | M | 0.5 | 3.4 | 29.5 | 60.4 |
| 2R,4R | M | 1.4 | 5.0 | 39.3 | 79.8 |
| 1R,3R | F | 1.2 | 4.0 | 38.1 | 79.7 |
| 1R,4R | F | 0.8 | 3.7 | 32.3 | 64.4 |
| 3Y,4Y | F | 1.1 | 4.4 | 37.8 | 84.4 |
| 1Y,4Y | F | 1.2 | 5.0 | 36.9 | 75.6 |
| 1R,2O | F | 1.0 | 5.0 | 36.8 | 71.4 |
| 1Y,3Y | U | 0.4 | 3.2 | 26.0 | 52.2 |

**Table 8.** Morphological data for all *P. glutinosus* captured and marked on or near rock outcrops at study area in the WWERF, 1999. A "U" indicates the sex of the individual was unknown.

| Tag Code | Sex | Mass (g) | CW (mm) | SVL (mm) | TL (mm) |
|---|---|---|---|---|---|
| 1R,2R | F | 6.0 | 9.3 | 59.1 | 117.6 |
| 1Y,2Y | F | 2.3 | 7.2 | 51.5 | 104.5 |
| 3R,4R | F | 6.2 | 11.0 | 58.7 | 113.9 |
| 3Y,4Y | F | 6.5 | 50.9 | 10.9 | 131.8 |
| 2R,3R | F | 2.0 | 6.8 | 47.3 | 93.5 |
| 1R,3R | F | 2.0 | 8.2 | 49.6 | 101.3 |
| 2R,3R | M | 5.0 | 9.5 | 60.3 | 80.0 |
| 1Y,4R | M | 6.5 | 9.5 | 63.8 | 135.1 |
| 2Y | M | 4.9 | 9.3 | 67.3 | 138.0 |
| 1O,2Y | U | 0.5 | 4.9 | 28.4 | 47.0 |
| 2O,3Y | U | 1.5 | 5.7 | 39.3 | 81.6 |
| 1R,2Y | U | 1.4 | 5.5 | 40.7 | 75.6 |
| 1R,2R | U | 0.8 | 4.8 | 29.5 | 51.2 |
| 1O,2O | U | U | 2.0 | 38.0 | 76.2 |

**Table 9**. Average values for morphometric data collected for sexually mature *A. aeneus*, *D. ochrophaeus*, and *P. glutinosus* in the study area in the WWERF, 1999. Standard deviations are listed beside each value in parenthesis.

| Species | Sex | Mass (mm) | CW (mm) | SVL (mm) | TL (mm) |
|---|---|---|---|---|---|
| *A. a.* | M (N=7) | 2.5 (0.8) | 9.1 (1.6) | 49.0 (6.7)* | 94.6 (19.7)* |
| *A. a.* | F (N=11) | 2.5 (0.5) | 8.4 (0.9) | 51.7 (0.8) | 97.8 (16.8) |
| *D. o.* | M (N=3) | 1.3 (0.5)** | 4.7 (1.2) | 38.8 (6.8) | 80.9 (11.9) |
| *D. o.* | F (N=8) | 1.2 (0.4)*** | 4.7 (1.2) | 36.1 (3.9) | 73.2 (5.7) |
| *P. g.* | M (N=3) | 5.5 (0.9) | 9.4 (0.1) | 63.8 (3.5) | 117.7 (32.7) |
| *P. g.* | F (N=6) | 6.1 (2.3) | 10.5 (1.9) | 58.9 (17.9) | 115.8 (13.6) |

* N = 8 males
** N = 5 males
*** N = 10 females

**Table 10**. Distance traveled between captures on single rock outcrops by marked *A. aeneus* in the study area in the WWERF, 1999. An "I" indicates that the individual was sexually immature.

| Rock | Sex | Tag Code | Time Span Movement Took Place | Distance Traveled (m) |
|---|---|---|---|---|
| R2 | F | 3Y,4Y | 12 May - 15 June | 0.90 |
| R2 | F | 3Y,4Y | 15 June - 20 July | 0.47 |
| R2 | F | 1R,4O | 06 June - 31 July | 2.20 |
| R1 | F | 2O,3Y | 12 June - 31 July | 4.06 |
| R3 | F | 1R,2O | 05 June - 20 Aug | 1.65 |
| R2 | M | 3O,4O | 12 May - 05 June | 5.51 |
| R2 | M | 3O,4O | 05 June - 11 June | 8.49 |
| R2 | M | 3O,4O | 11 June - 08 Aug | 1.30 |
| R2 | M | 1O,2O | 12 May - 11 June | 1.52 |
| R2 | M | 1O,2O | 11 June - 20 July | 0.35 |
| R1 | M | 2Y,4Y | 04 June - 05 June | 2.89 |
| R1 | M | 2Y,4Y | 11 June - 15 June | 2.22 |
| R1 | I | 2R,4R | 11 May - 06 June | 1.28 |
| R1 | I | 2R,4R | 06 June - 15 June | 4.06 |
| R1 | I | 1Y,4Y | 04 June - 05 June | 0.68 |
| R2 | I | 1O,2Y | 11 June - 15 June | 4.90 |
| R1 | I | 1O,4O | 29 May - 15 June | 0.00 |
| R1 | I | 3O,4R | 06 June - 15 June | 0.89 |
| R2 | I | 2O,4O | 12 May - 23 Sept | 11.91 |

**Table 11**. Distance traveled between rock outcrops by marked *A. aeneus* in the study area in the WWERF, 1999.

| Rock | | Tag Code | Time Span Movement Took Place | Distance Traveled (m) |
|---|---|---|---|---|
| From | To | | | |
| R1 | R2 | 1R,2R | 11 May - 27 Aug | 26.5 |

**Figure 1**. Range of *Aneides aeneus* in the United States (Petranka 1998). An "X" indicates the occurrence of a disjunct population consisting of a single published record.

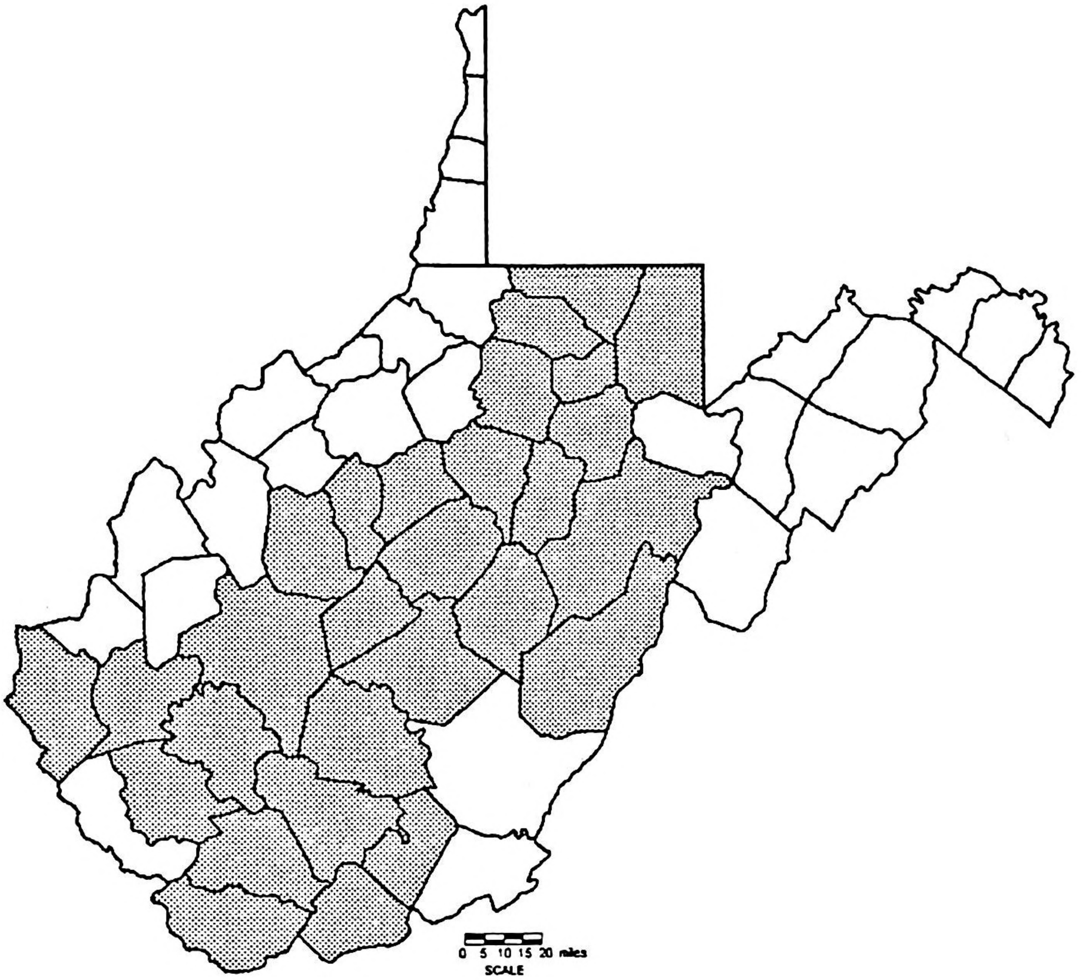

**Figure 2**. Range of *Aneides aeneus* by county in West Virginia (Green and Pauley 1987).

**Figure 3**. Typical adult green salamander, *Aneides aeneus*, in West Virginia. Photo courtesy of Zach Felix.

**Figure 4**. Typical adult Allegheny Mountain dusky salamander, *Desmognathus ochrophaeus*, in West Virginia. Photo courtesy of Zach Felix.

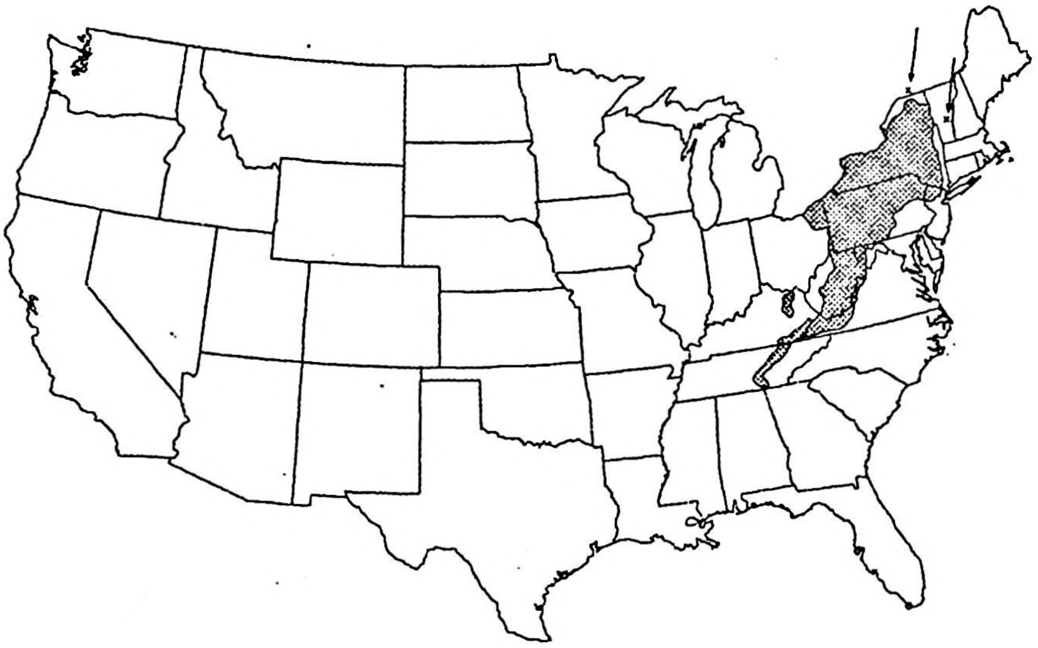

**Figure 5**. Range of *Desmognathus ochrophaeus* in the United States (Petranka 1998). An "X" indicates the occurrence of a disjunct population consisting of a single published record.

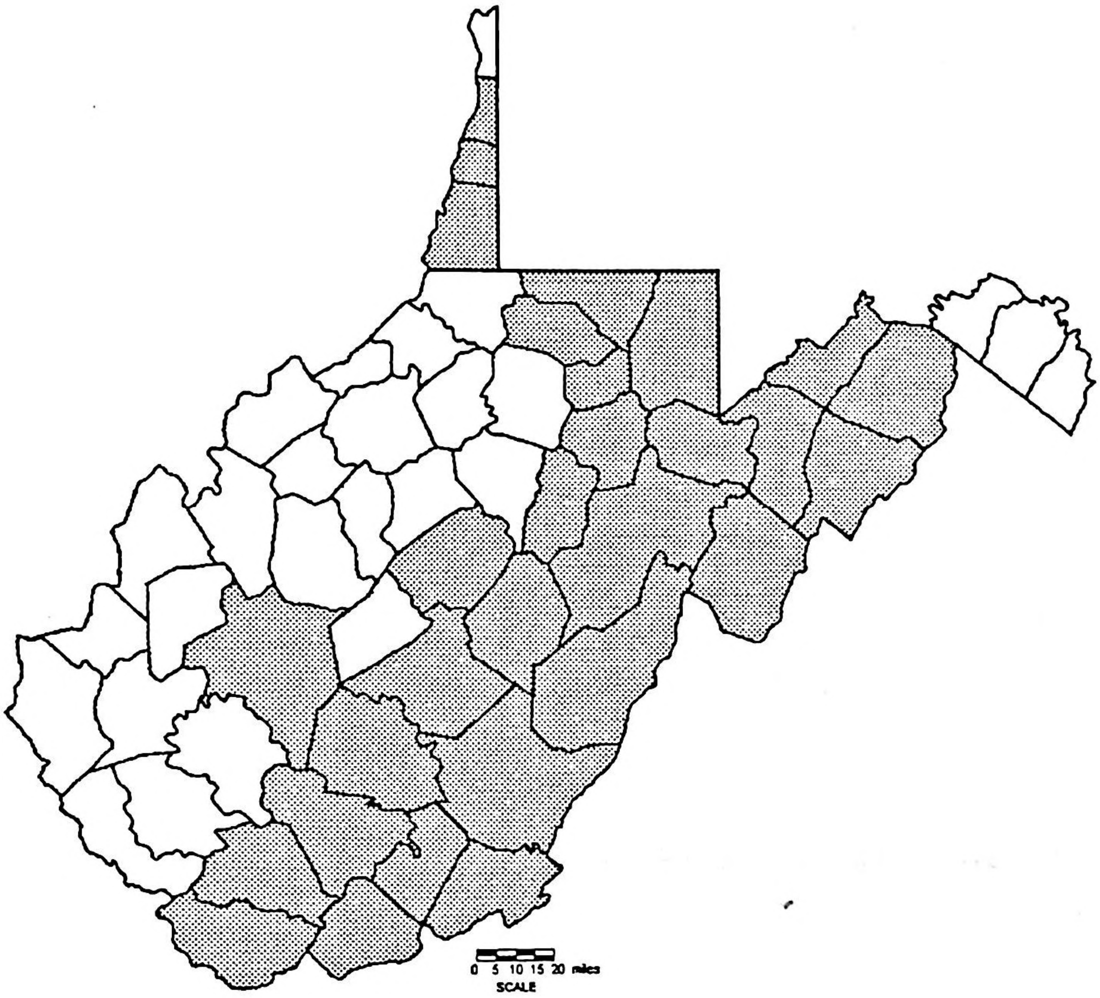

**Figure 6**. Range of *Desmognathus ochrophaeus* by county in West Virginia (Green and Pauley 1987).

**Figure 7**. Typical adult northern slimy salamander, *Plethodon glutinosus*, in West Virginia. Photo by Zach Felix.

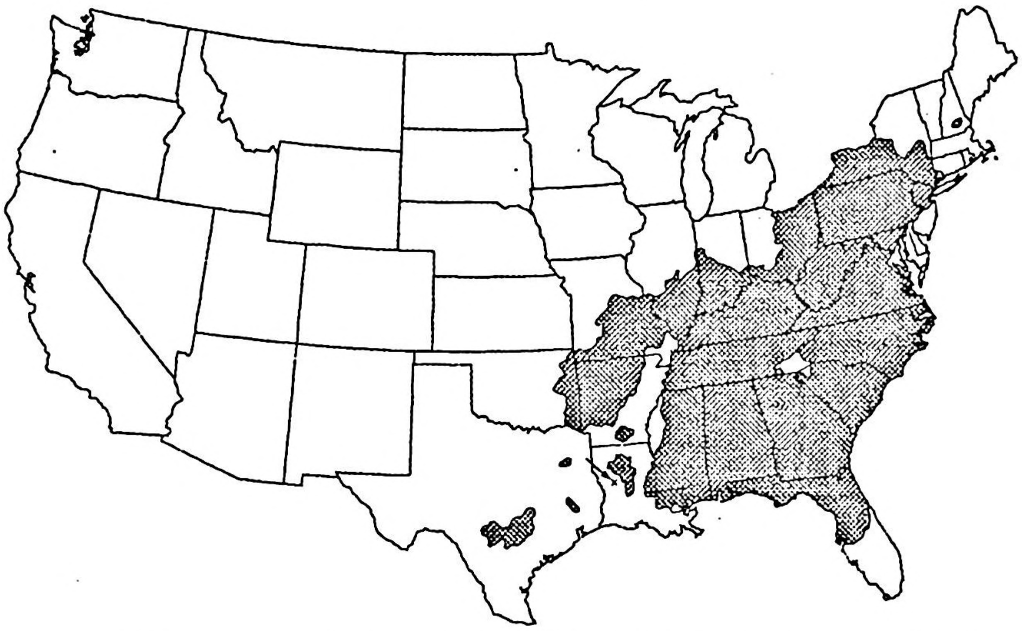

**Figure 8**. Range of *Plethodon glutinosus* in the United States (Petranka 1998).

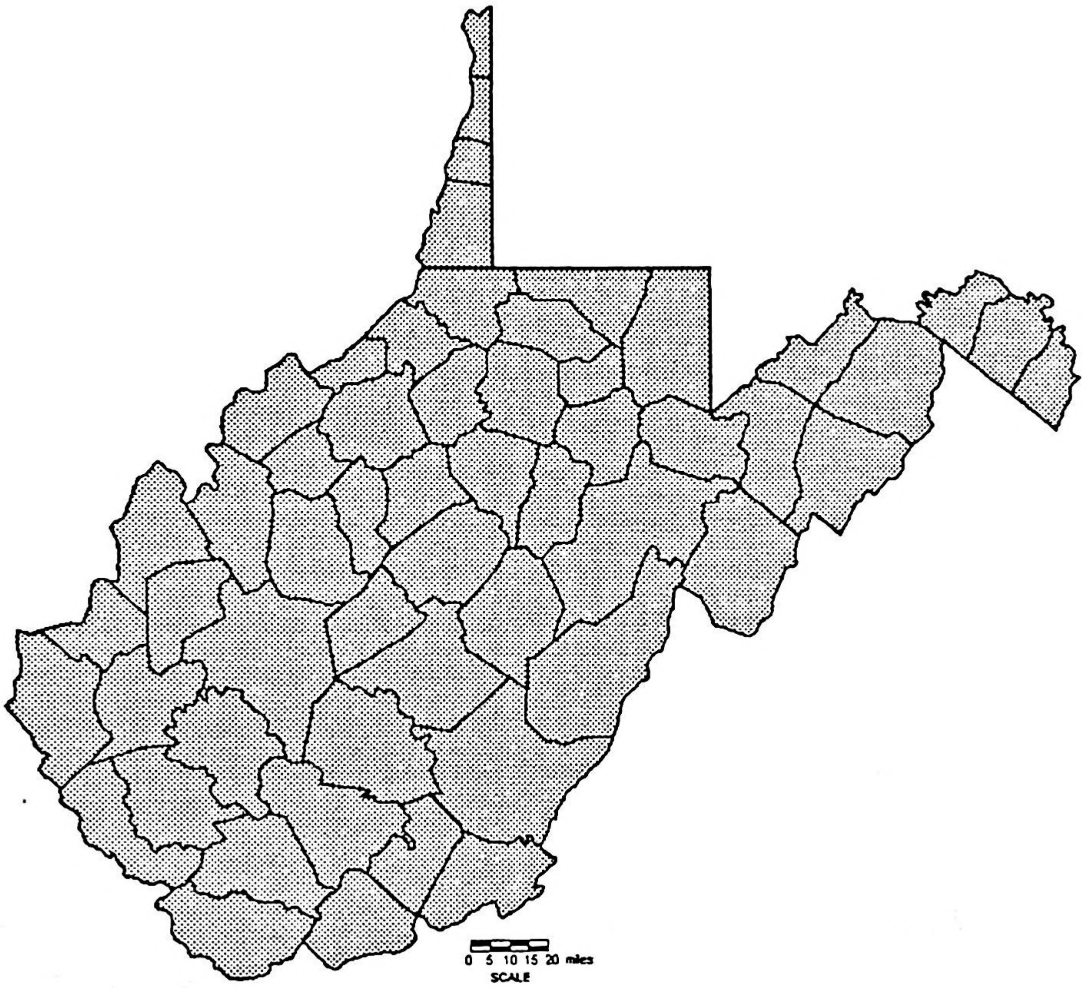

**Figure 9**. Range of *Plethodon glutinosus* by county in West Virginia (Green and Pauley 1987).

**Figure 10**. Typical adult redbacked salamander, *Plethodon cinereus*, in West Virginia. Photo courtesy of Dr. Thomas K. Pauley.

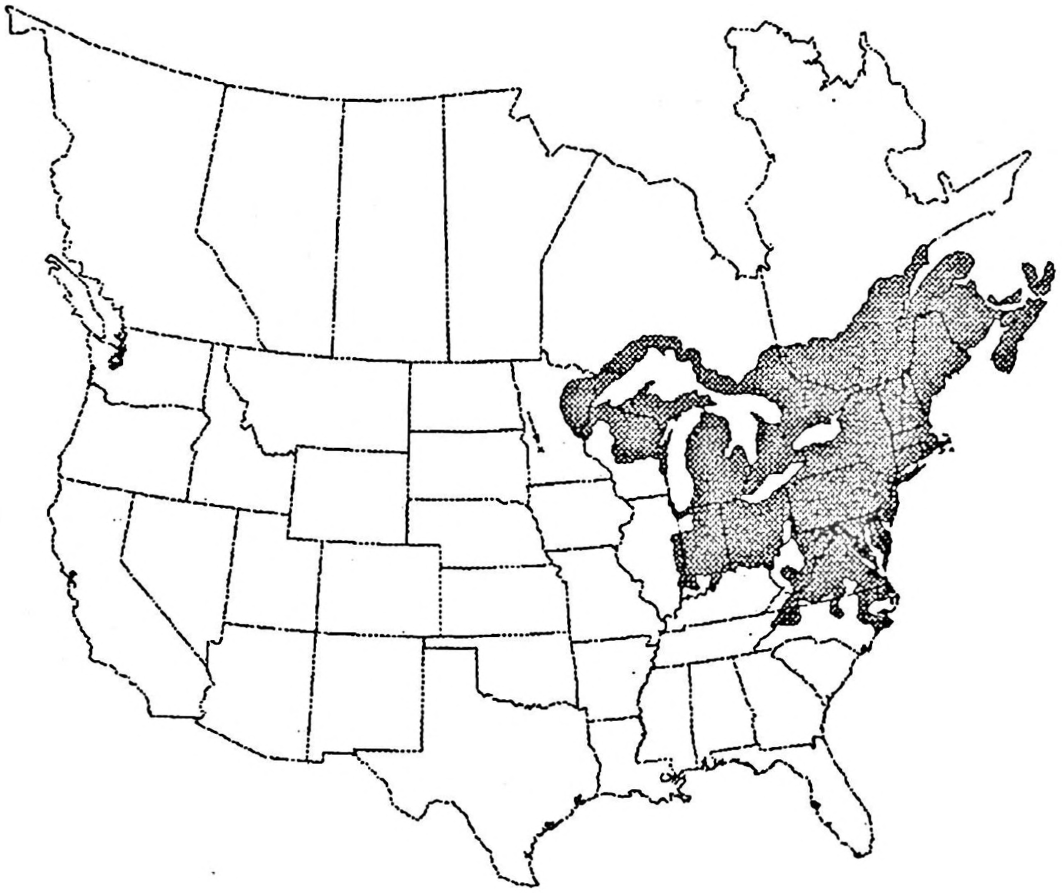

**Figure 11**. Range of *Plethodon cinereus* in the United States and Canada (Petranka 1998). An "X" indicates the occurrence of a disjunct populations consisting of a single published record.

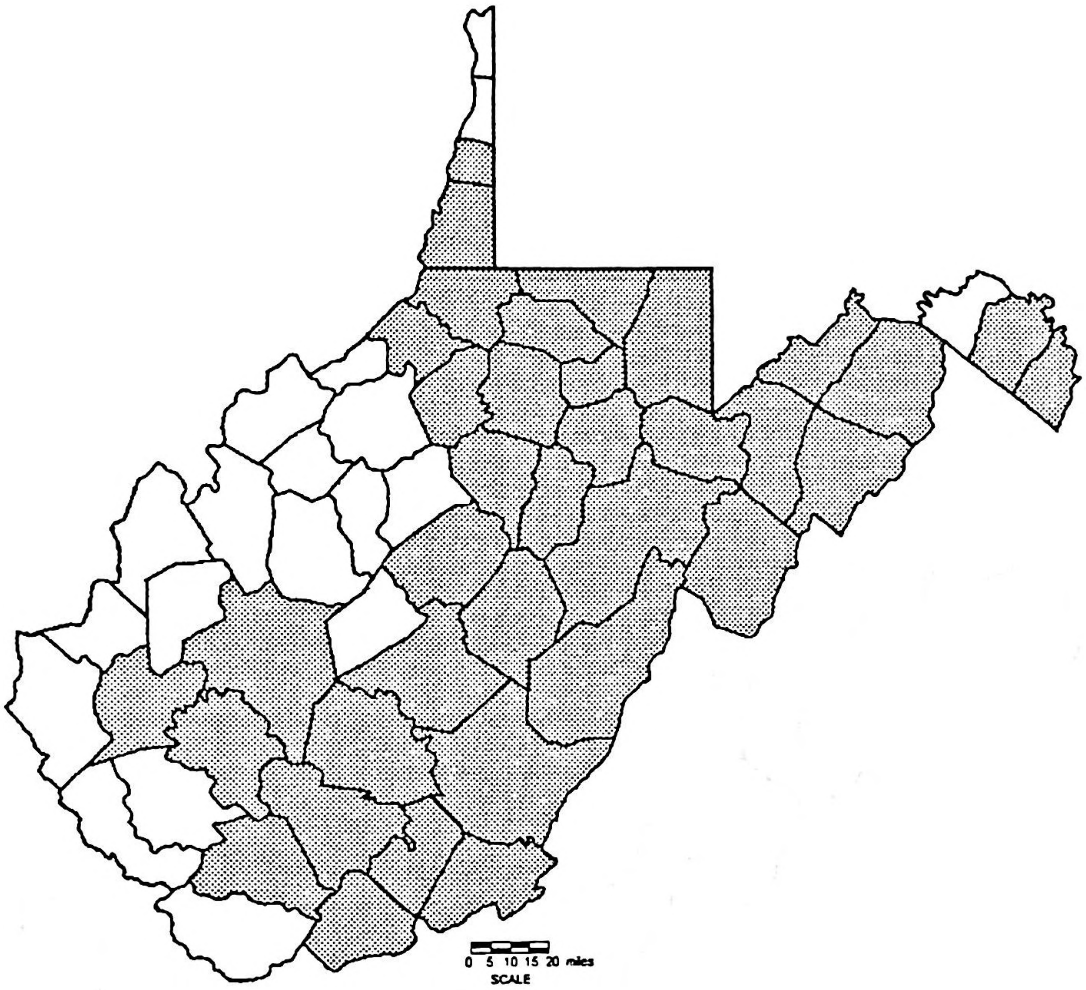

**Figure 12**. Range of *Plethodon cinereus* by county in West Virginia (Green and Pauley 1987).

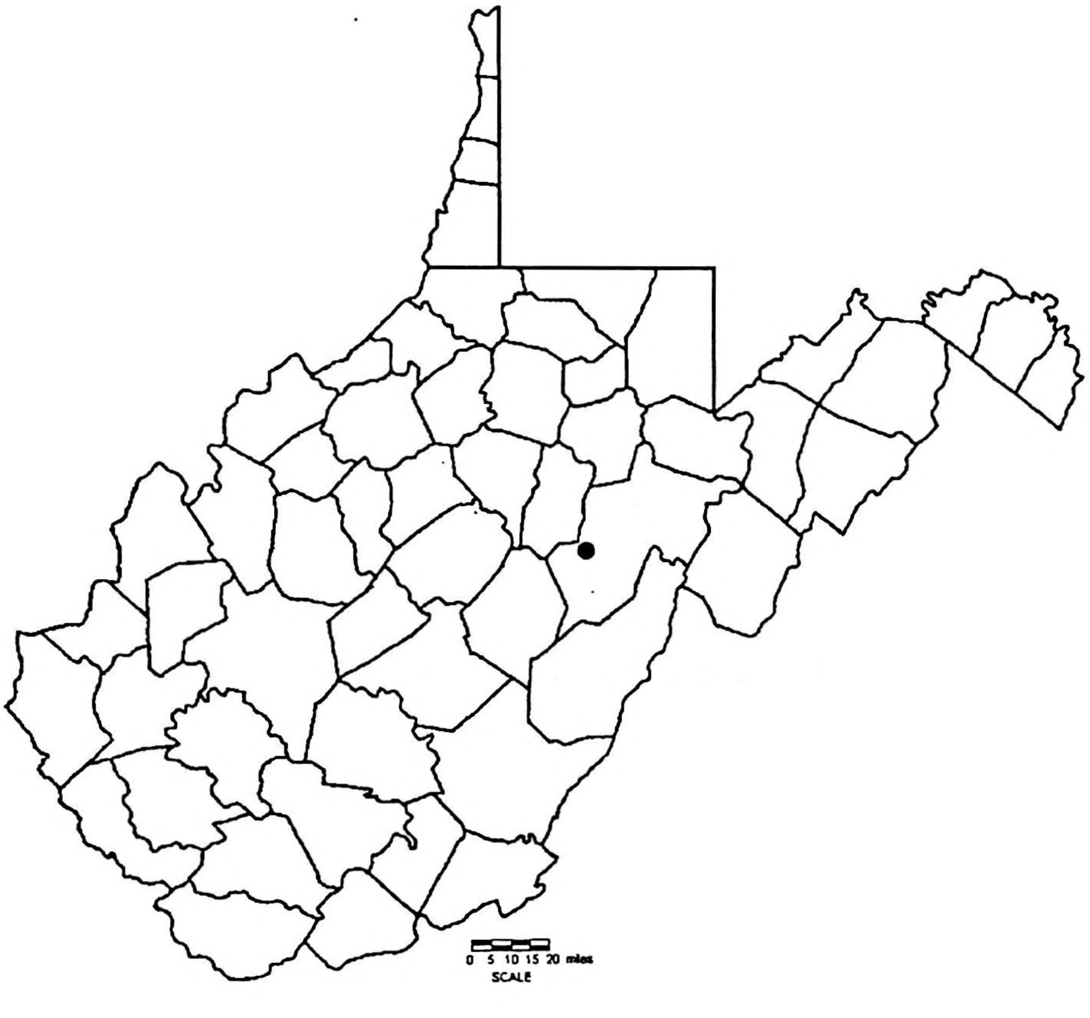

**Figure 13**. Location of study area in.Randolph County, West Virginia.

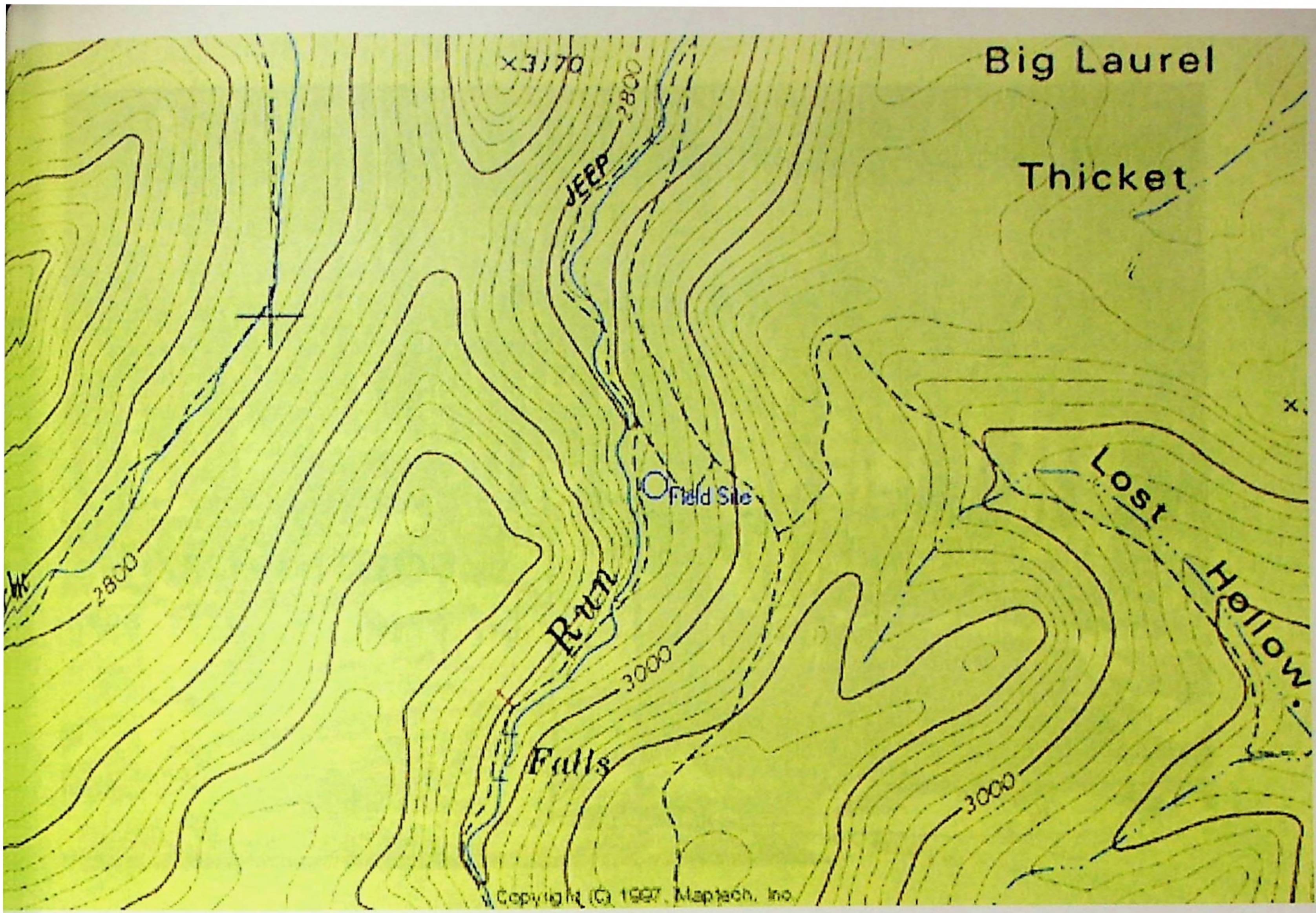

**Figure 14**. Location of study area on USGS topographic map (Adolph quadrangle). Study area is indicated by an open circle.

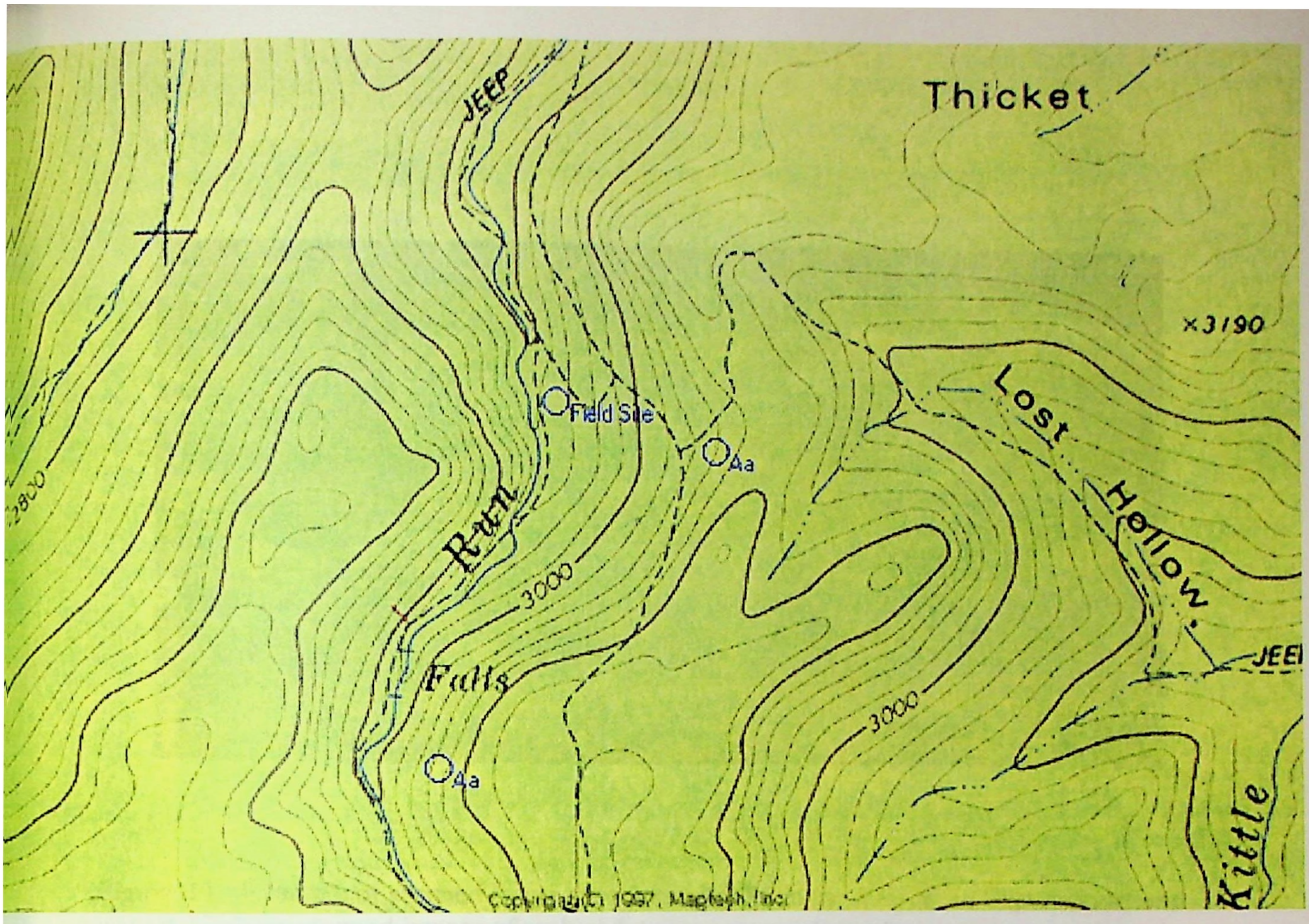

**Figure 16**. Location of other green salamander populations with respect to the study area on the USGS Adolph quadrangle. All populations are marked with open circles.

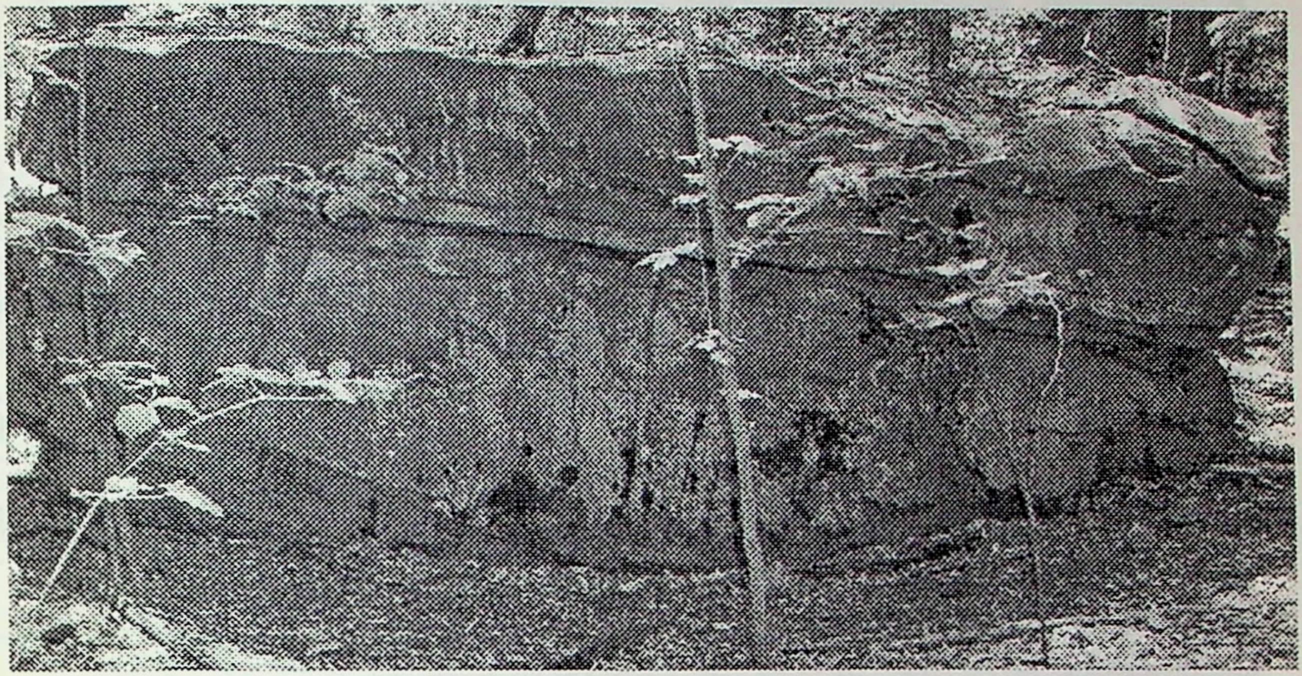

**Figure 17**. Example of scanned image of rock number R2 in the study area. Capture locations were marked on scanned images of each rock to map green salamander movements.

**Figure 18**. The four tagging locations are represented on salamander A. Salamander B has the tagging code 1R,2Y (location 1 has red tag and location 2 has yellow tag). Every salamander was given at least two tags of three possible colors (red, yellow, and orange).

**Figure 19**. A cave salamander in the process of being tagged with VIE tags. Photo by Andrew Longenecker.

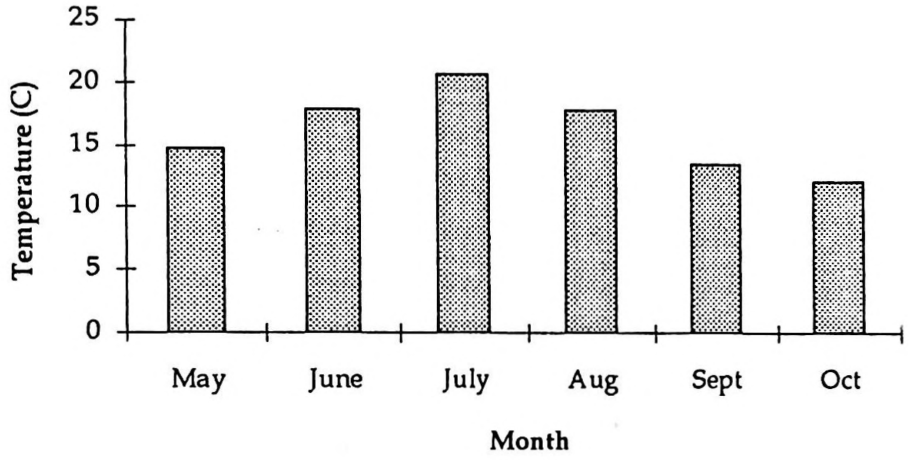

**Figure 20**. Average monthly air temperature at the study site in the WWERF, Randolph County, West Virginia, during the summer of 1999.

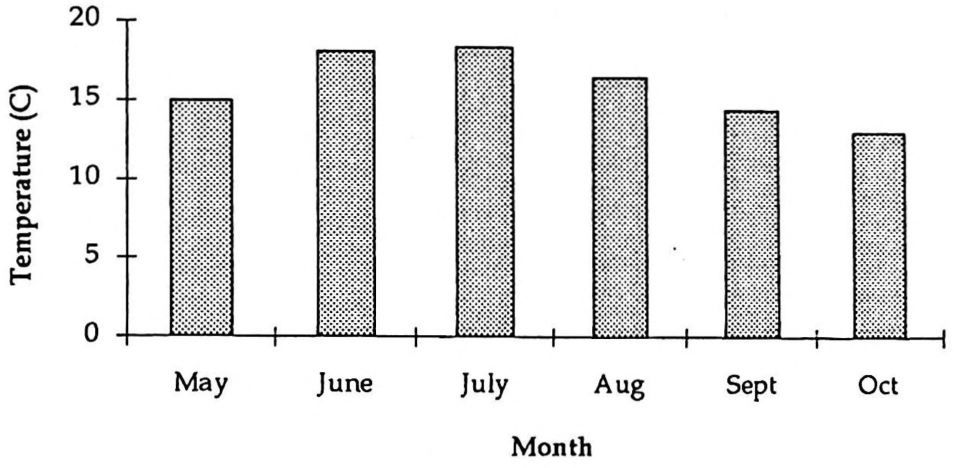

**Figure 21**. Average monthly crevice air temperature at the study site in the WWERF, Randolph County, West Virginia, during the summer of 1999.

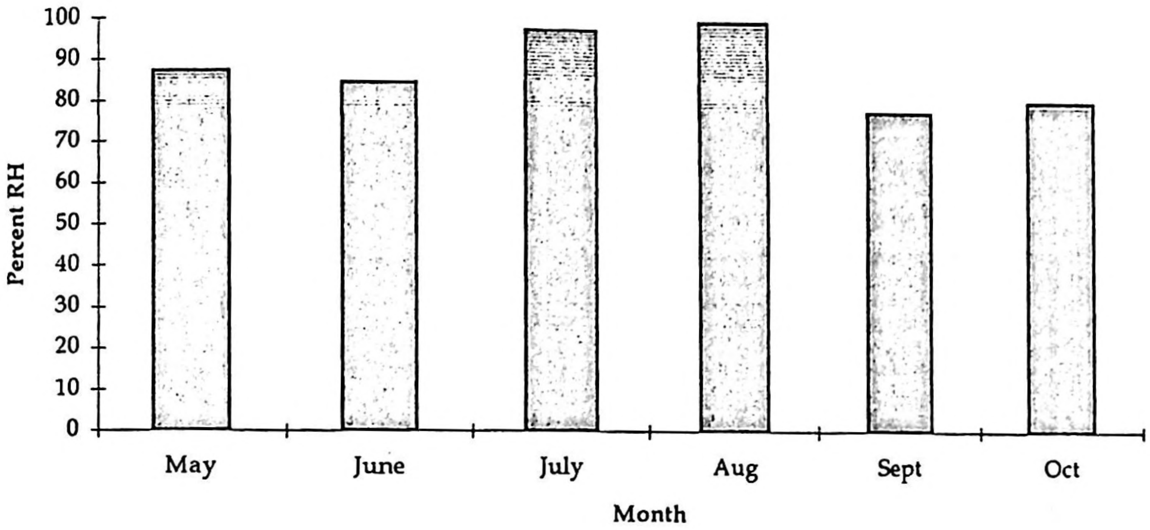

**Figure 22**. Average monthly relative humidity at the study site in the WWERF, Randolph County, West Virginia, during the summer of 1999.

**Figure 23**. Typical red eft, *Notophthalmus viridescens viridescens*, in West Virginia. Photo courtesy of Jeff Humphries.

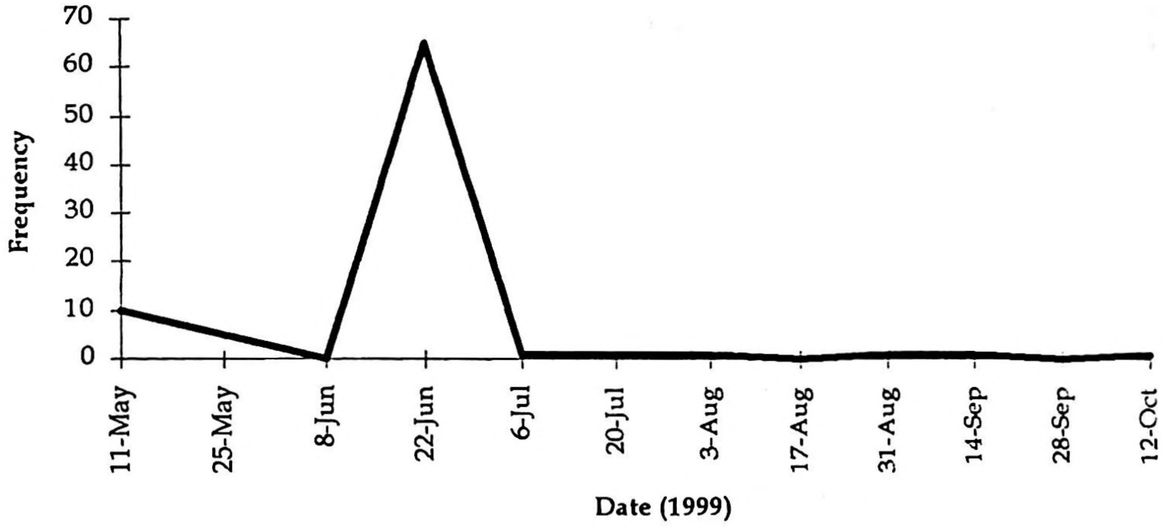

**Figure 24.** Plot of green salamander population size during the summer of 1999 within the study site in the WWERF, Randolph County, West Virginia, using an open population model based on Jolly, 1965.

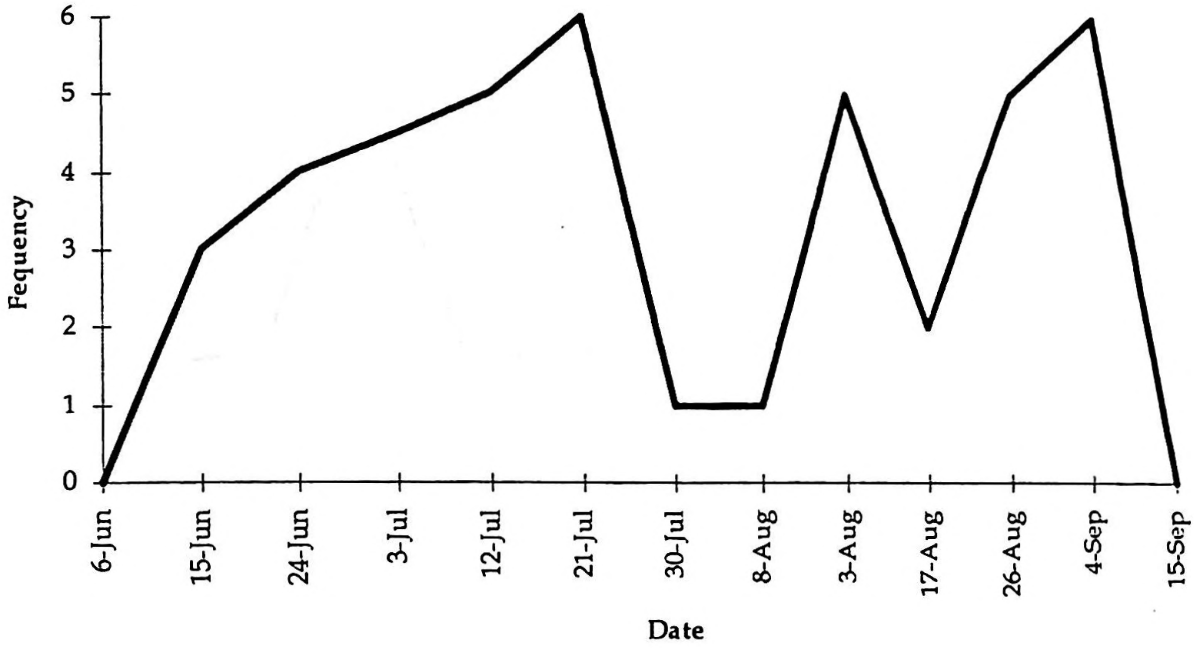

**Figure 25**. Plot of mountain dusky salamander population size during the summer of 1999 within the study site in the WWERF, Randolph County, West Virginia, using an open population model based on Jolly, 1965.

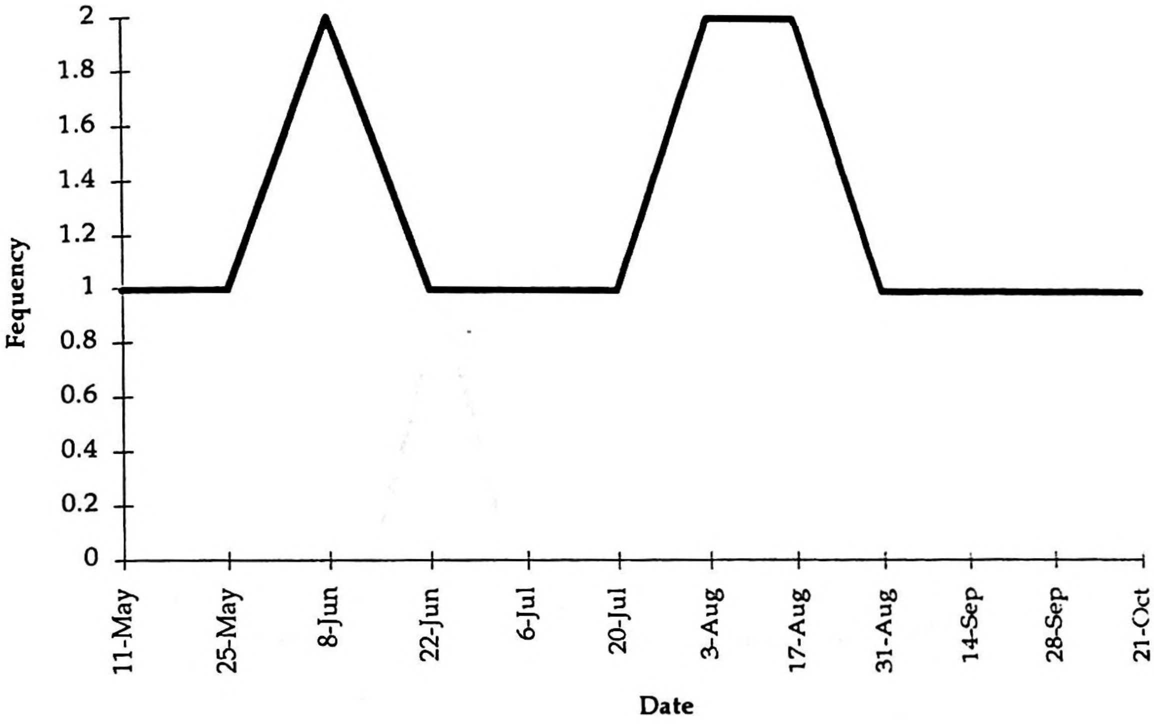

**Figure 26**. Plot of slimy salamander population size during the summer of 1999 within the study site in the WWERF, Randolph County, West Virginia, using an open population model based on Jolly, 1965.

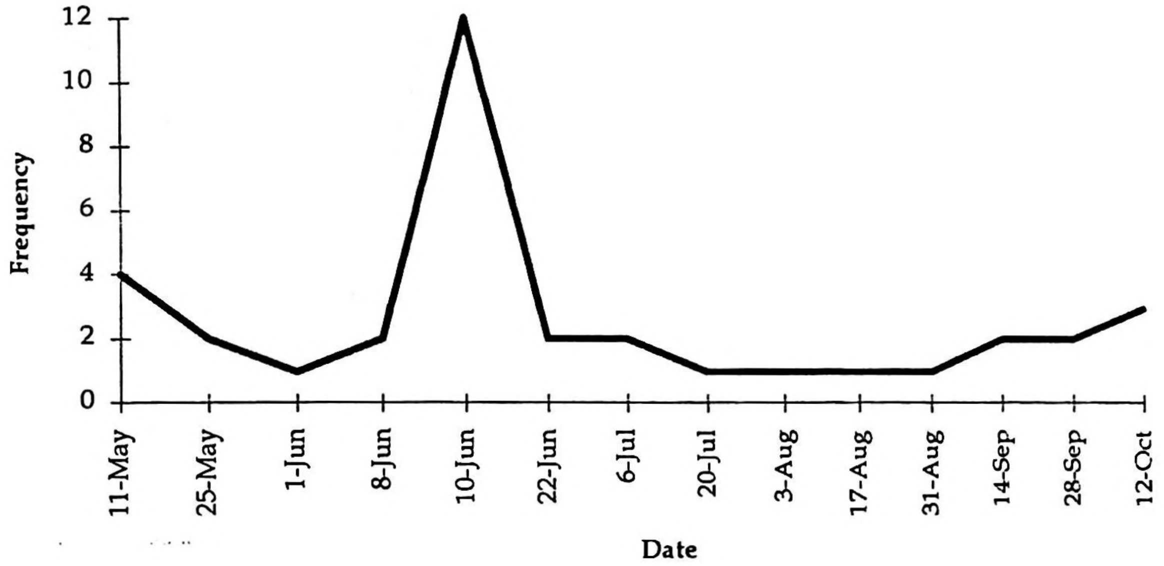

**Figure 27**. Plot of green salamander population size on rock number R1 during the summer of 1999 in the study area in the WWERF, Randolph County, West Virginia, using an open population model based on Jolly, 1965.

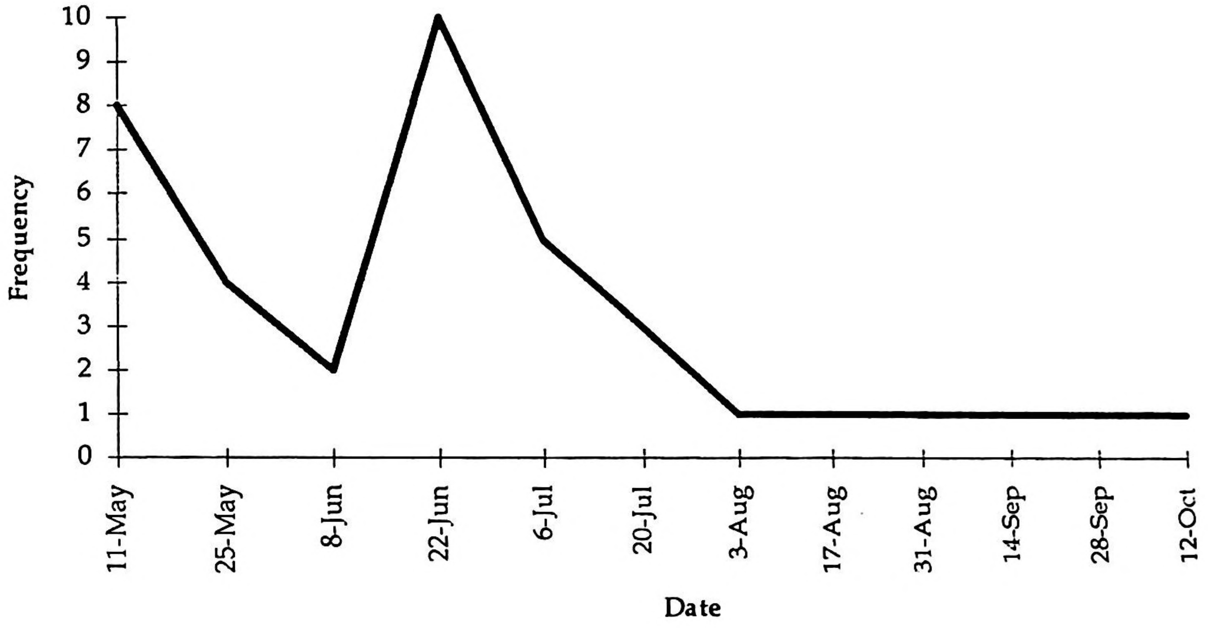

**Figure 28**. Plot of green salamander population size during the summer of 1999 on rock number R2 in the study area in the WWERF, Randolph County, West Virginia, using an open population model based on Jolly, 1965.

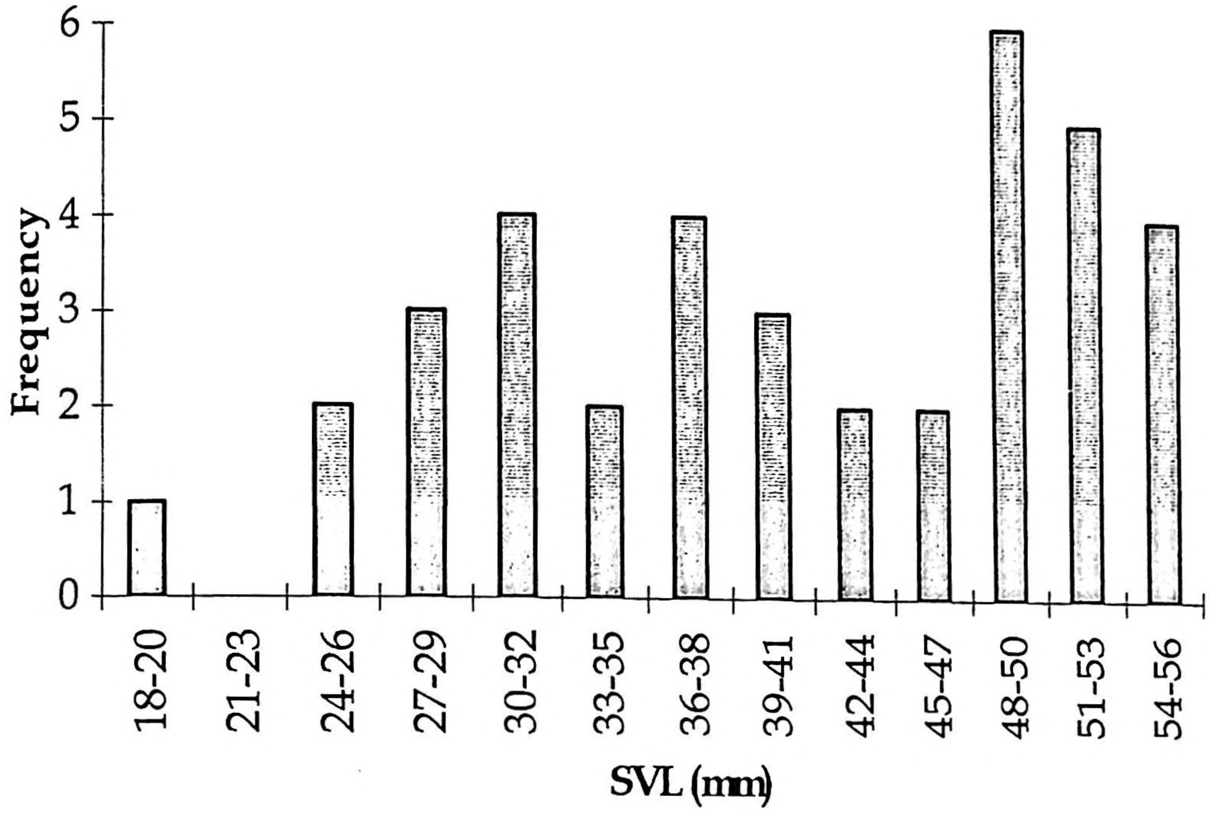

**Figure 29**. Size distribution of all green salamanders captured in the study area in the WWERF, Randolph County, West Virginia (N = 38).

**Figure 30**. Female green salamander with eggs in the study area in the WWERF, Randolph County, West Virginia. Photo by Zach Felix.

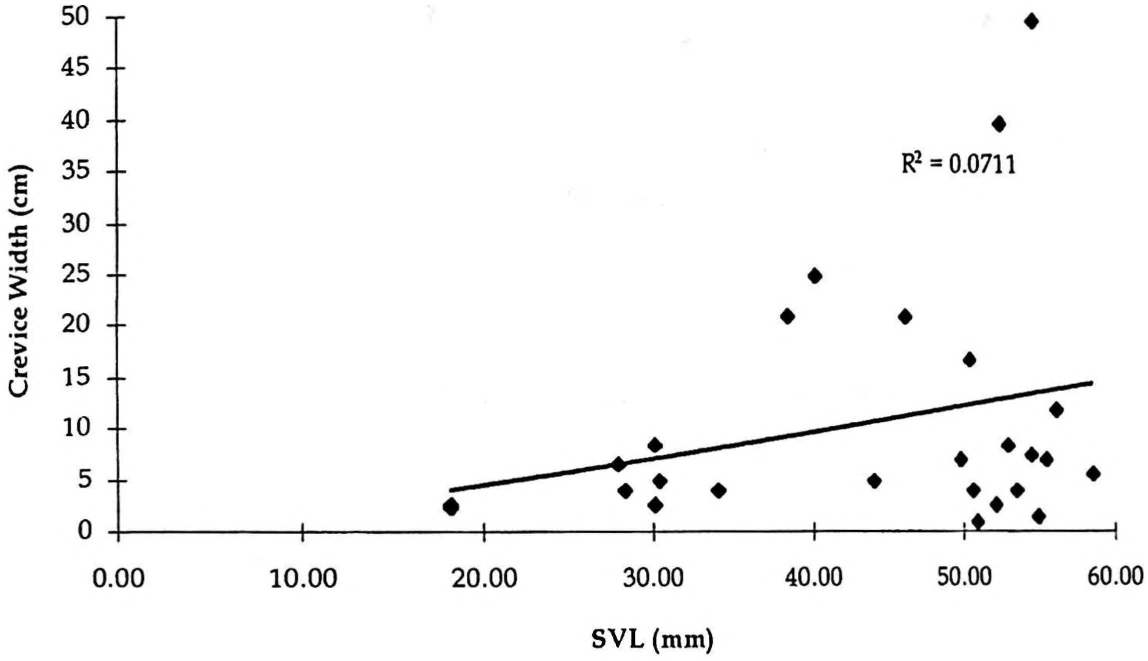

**Figure 31**. Relationship between width of crevices occupied by green salamanders and SVL.

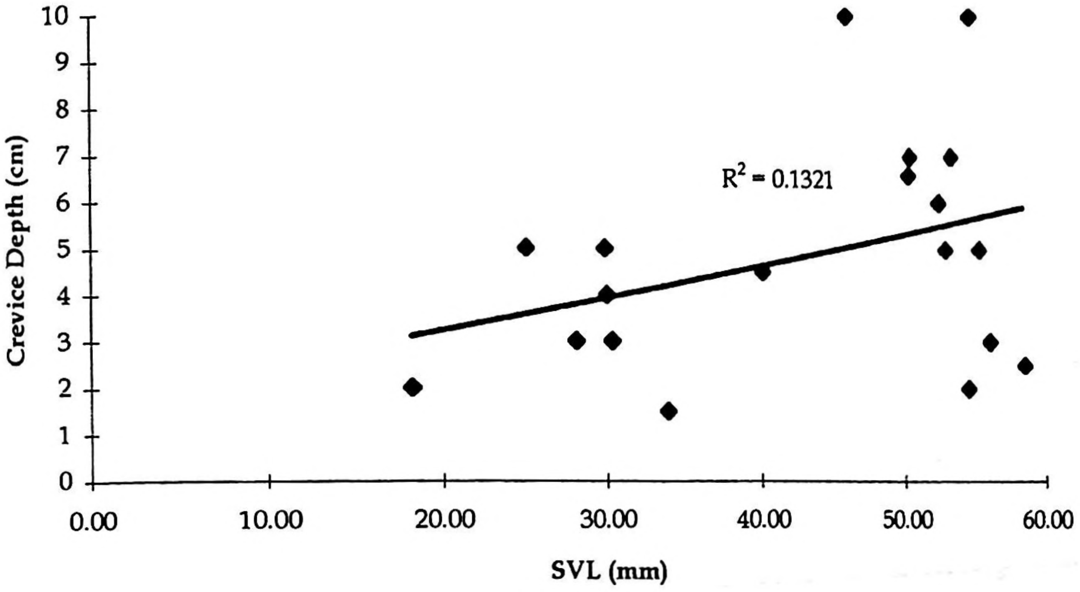

Figure 32. Relationship between depth of crevices occupied by green salamanders and SVL.

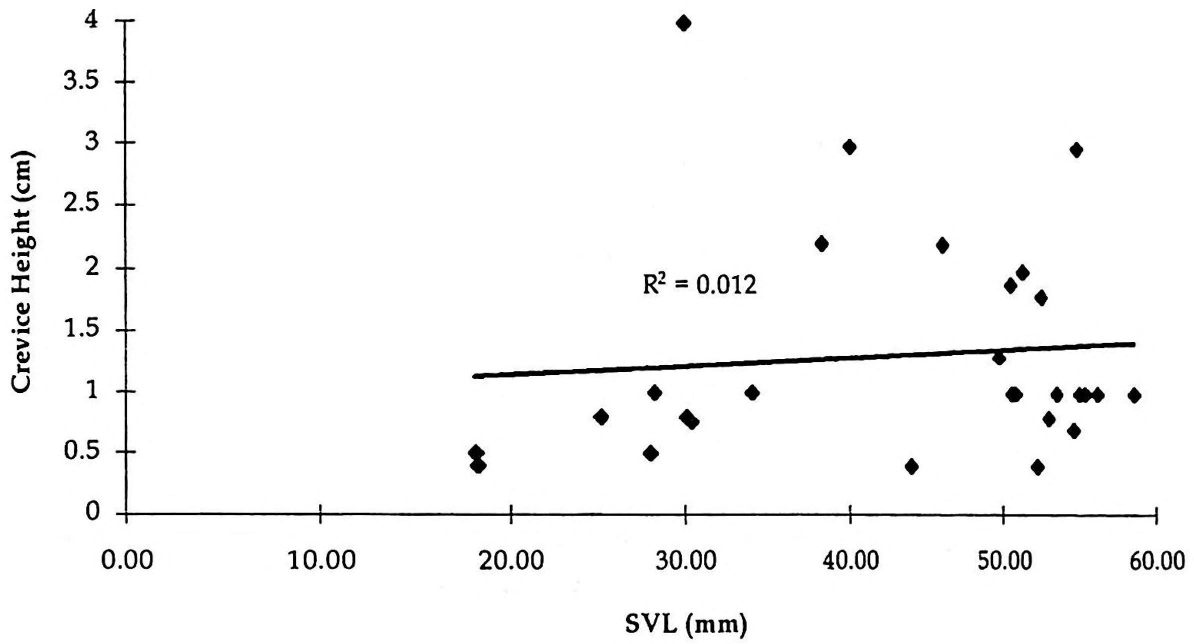

**Figure 33**. Relationship between height of crevices occupied by green salamanders and SVL.

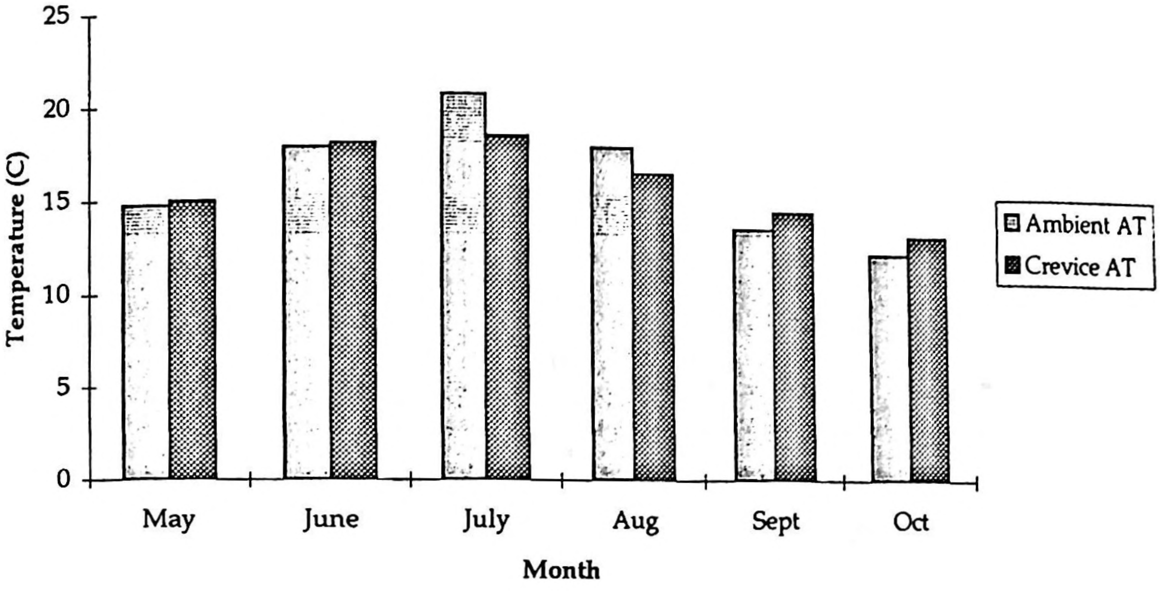

**Figure 34**. Average monthly ambient and crevice air temperature at the study site in the WWERF, Randolph County, West Virginia.

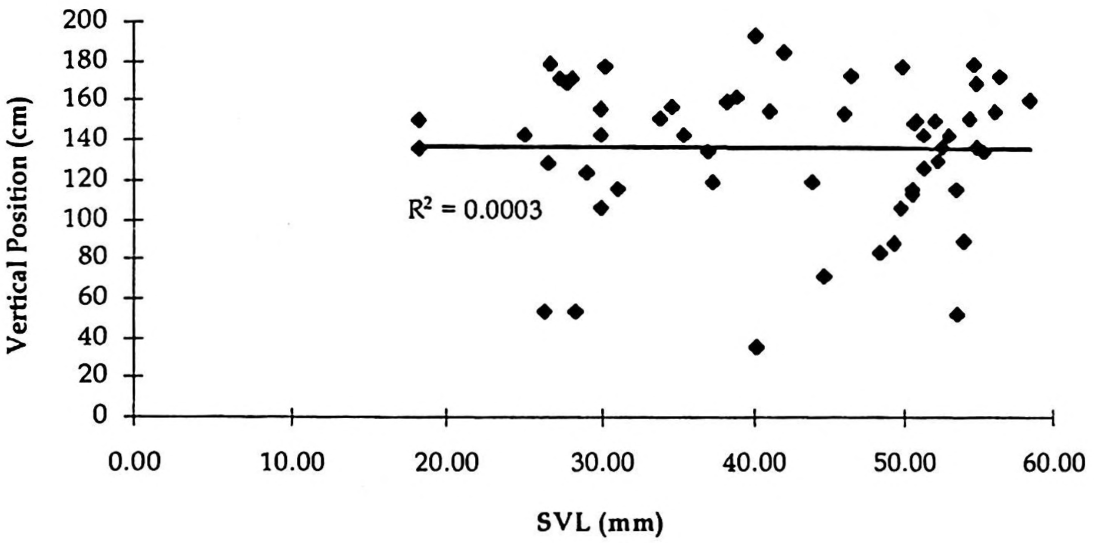

**Figure 35**. Relationship between green salamander SVL and vertical positions occupied on rockfaces.

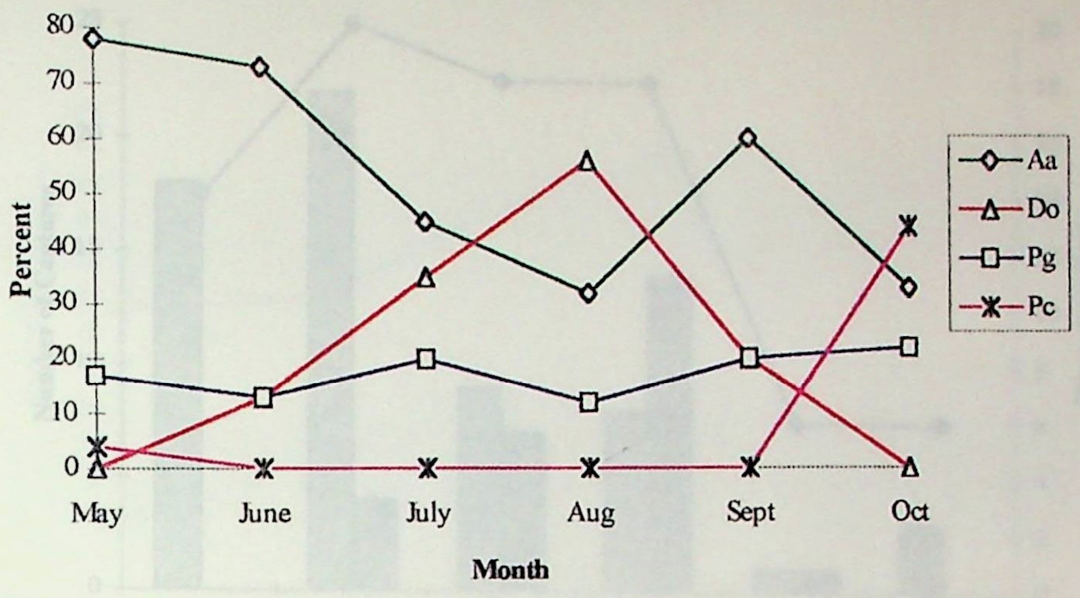

**Figure 36**. Relative seasonal occurrence of *Aneides aeneus* (Aa), *Desmognathus ochrophaeus* (Do), *Plethodon glutinosus* (Pg), and *P. cinereus* (Pc).

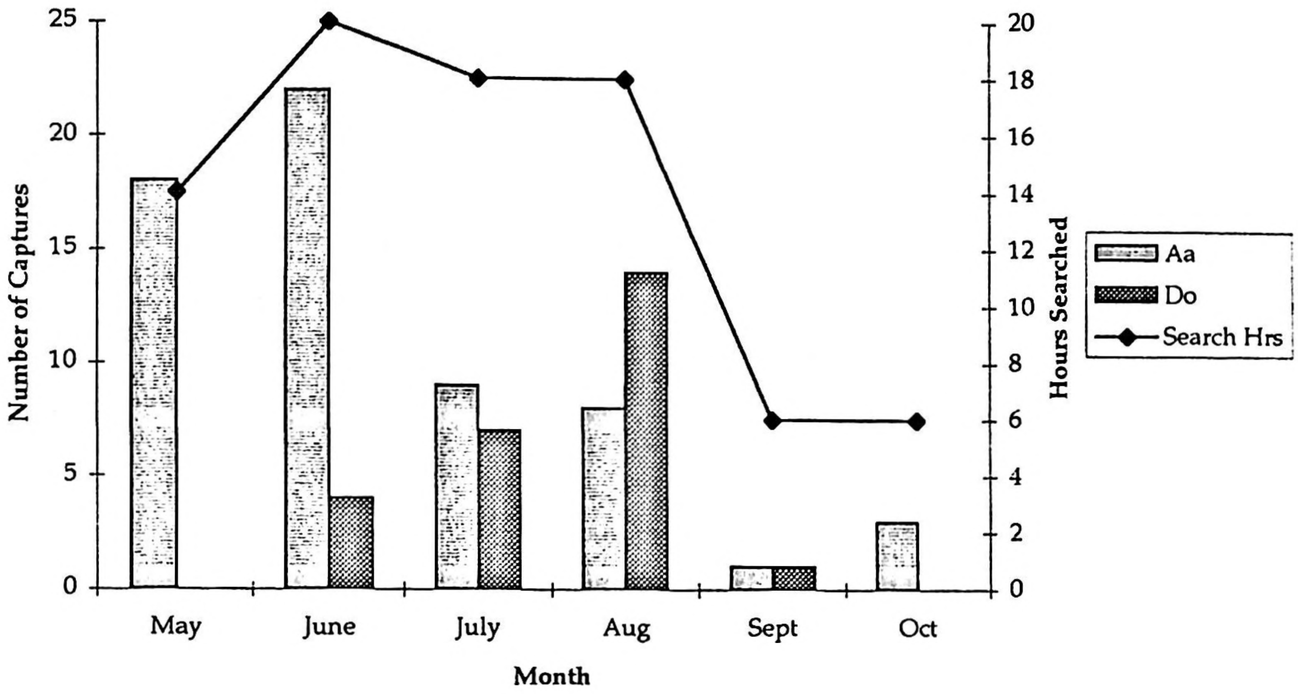

**Figure 37**. Number of captures of *Aneides aeneus* (Aa) and *Desmognathus ochrophaeus* (Do) in relation to the number of person-hours (search hrs) spent searching the study area in the WWERF, Randolph County, West Virginia.

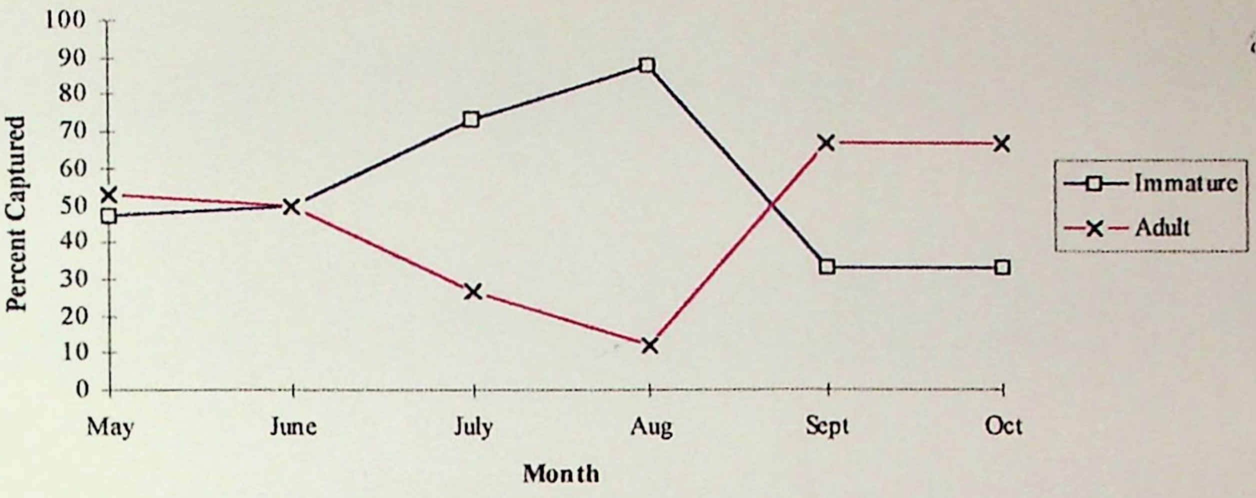

**Figure 38**. Percent capture of adult and sexually immature green salamanders in the study area in the WWERF, Randolph County, West Virginia.