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ACTIVITY PATTERNS AND POPULATION BIOLOGY IN THE TERRESTRIAL  
SALAMANDER COMMUNITY AT SADDLE MOUNTAIN,  
NORTH CAROLINA

A Thesis

by

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Submitted to the Graduate School

Appalachian State University

in partial fulfillment of the requirements for the degree of

MASTER OF SCIENCE

December 1998

Major Department: Biology

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ABSTRACT

ACTIVITY PATTERNS AND POPULATION BIOLOGY IN THE TERRESTRIAL  
SALAMANDER COMMUNITY AT  
SADDLE MOUNTAIN, NORTH CAROLINA. (December 1998)

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Thesis Chairperson: R. Wayne Van Devender

The present research was performed to learn about activity patterns and population characteristics of salamanders at Saddle Mountain in Surry County, NC. Saddle Mountain was chosen due to the presence of the threatened *Plethodon wehrlei*, which had never been studied in North Carolina. Two transects (A = 500m X 3m and B = 90m X 3m) were established at Saddle Mountain and sampled at night. Transect A was sampled 50 times and transect B was sampled 42 times between July 9, 1996 and December 3, 1997. A total of 519 salamander encounters were recorded.

Of eight species of salamanders found on the site, only *Plethodon cylindraceus*, *P. wehrlei*, and *P. yonahlossee* were common. Schnabel estimates of number per hectare and 95% confidence intervals were 5182.7 (2318.7-13154.0) *P. cylindraceus*, 3476.0 (2121.3 - 6006.7) *P. wehrlei*, and 6248.7 (3177.3 -13315.3) *P. yonahlossee*. Schumacher – Eschmeyer estimates and 95% CI per hectare were 5167.3 (2881.3 - 24995.3) *P. cylindraceus*, 4022 (3202.7 - 5400) *P. wehrlei*, and 7111.3 (4365.3 - 19167.3) *P.*

*yonahlossee*. Ranges for several estimates of biomass (kg/ha) were 14.1 - 20.2 *P. cylindraceus*, 3.3 - 5.4 *P. wehrlei*, and 32.0 – 56.9 *P. yonahlossee*. Total *Plethodon* biomass at the site was estimated to be between 49.4 and 82.6 kg/ha.

Along transect A all salamanders had clumped distributions which were not related to canopy closure, herbaceous cover, loose rock cover, bedrock exposure, or soil exposure, or any combination of these characteristics. *P. cylindraceus* showed a weak, negative correlation with herbaceous cover. Movements between captures were 0 – 20 m ( $\bar{x}$  = 5.8) for *P. wehrlei*, 0 – 23m ( $\bar{x}$  = 9.0) for *P. cylindraceus*, and 2 – 20m ( $\bar{x}$  = 8.43) for *P. yonahlossee*. Species composition of the three *Plethodon* differed between south and east aspects ( $\chi^2$  = 22.309, df = 2, P < 0.001). *P. yonahlossee* was most common on the east slope and least common on the southern slope.

Seasonal activity patterns varied among the three *Plethodon* ( $\chi^2$  = 155.325, df = 6, P < 0.001). *Plethodon wehrlei* was active during fall, winter, and spring. *P. cylindraceus* was active spring, summer, and fall. *P. yonahlossee* was active primarily in late spring, summer, and early fall. Species were active at different air temperatures (Kruskal-Wallis test, H = 86.06, df = 2, P < 0.001). Mean temperatures of activity were: 12.4°C (*P. wehrlei*), 14.5°C (*P. cylindraceus*), and 16.2°C (*P. yonahlossee*). Activity varied with surface litter moisture category ( $F_{2,510}$  = 3.3, P = 0.038). *P. wehrlei* was active under the wettest conditions and *P. cylindraceus* was active under the driest conditions.



## ACKNOWLEDGEMENTS

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I want to thank my parents for all of their support and confidence. I would also like to thank my better half, Kiersten Bashor, for her assistance as well as her unwavering support and confidence. Without these people, this thesis couldn't have happened.

## DEDICATION

This work is dedicated to those who study endangered species. There is no other way to learn how to protect them.

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## INTRODUCTION

Wehrle's salamander, *Plethodon wehrlei*, is a terrestrial, lungless salamander of the Family Plethodontidae (Highton, 1972). *P. wehrlei* is a member of the eastern large *Plethodon* (Highton, 1972). Adults range from 45-70 mm snout to vent length (SVL) and 100-160 mm total length. This salamander ranges along the Appalachians from New York in the north barely in to North Carolina and Tennessee (Highton, 1987). It has been found in caves (Pope and Fowler, 1949), montane spruce forests, and deciduous forests (Netting, 1936). *P. wehrlei* occupies a relatively large and northerly range (Hall and Stafford, 1972). This salamander has many color variations throughout its range. Salamanders in northern populations frequently have a patternless gray dorsum but brassy flecking or areas of lateral spotting are also common. Juveniles often have dorsal red spots. This character is retained in adults of some southern populations. Dorsal yellow spotting is present in Tennessee, Kentucky, and some West Virginia populations (Highton, 1987; Hoffman, 1967). There is usually lateral creamy or white spotting and the chin is often lighter than the venter (Highton, 1987; Hoffman, 1967).

This salamander is Threatened in North Carolina. Until recently it was known on the basis of only two specimens from Hanging Rock State Park in Stokes County. Two populations are now known, one on Saddle Mountain (Beane and Somers, 1994) and the other at the base of Hanging Rock, situated far from the original site (Jackan, personal



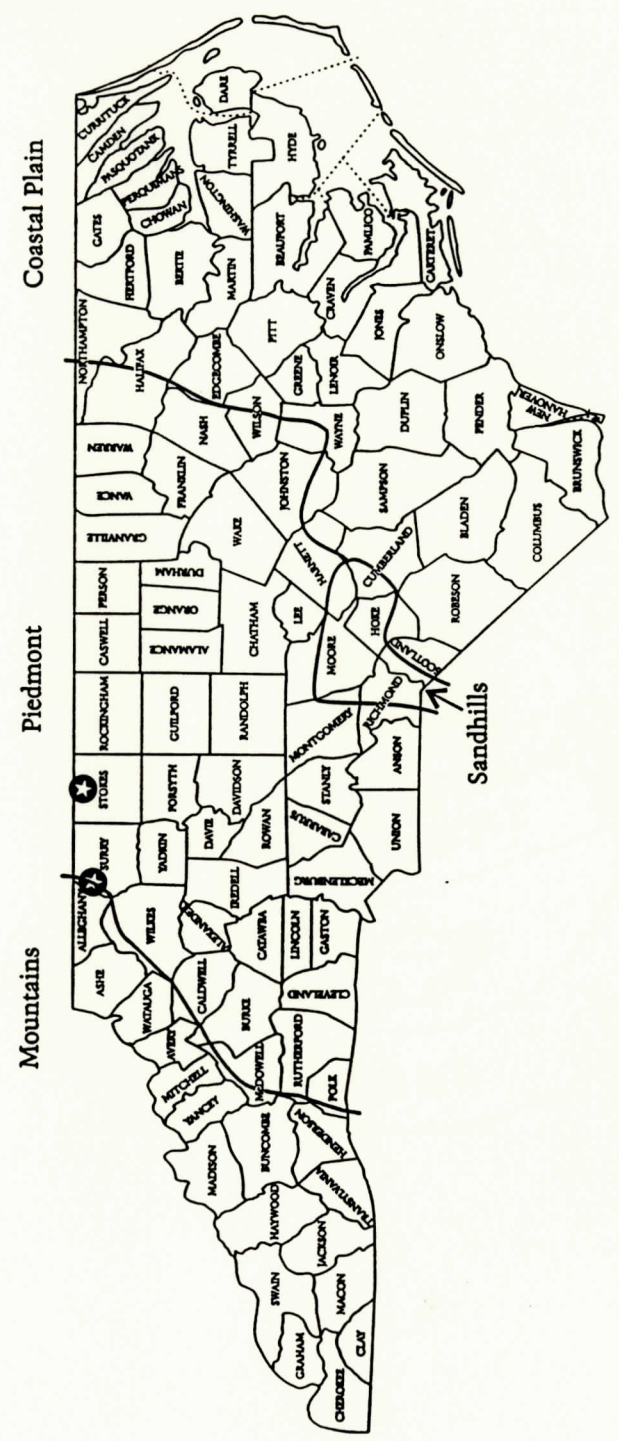


Figure 1. General location of Saddle Mountain (Surry and Alleghany County border) and Hanging Rock State Park (Stokes County) in northwestern North Carolina. (modified from Palmer and Braswell, 1996)

communication, 1996). Saddle Mountain (Fig. 1) sits on the border of Surry and Alleghany County in northwestern North Carolina. The North Carolina populations represent the southernmost portion of the species' range.

Oak-hickory and mixed pine hardwood communities occupy the Saddle Mountain site. These forests were last logged between 1900 and 1930. There are also abundant rock outcroppings and boulders throughout the area (Taggart and Peacock, 1978; Weakley, 1984). Early surveys report no plants or animals with special status at the site and indicate that Saddle Mountain is rather representative of middle elevation forest (Taggart and Peacock, 1978; Weakley, 1984). The soils and geology at Saddle Mountain are similar to much of the surrounding Blue Ridge escarpment. Predominant soil types are infertile loams developed from mica gneisses and schists of Precambrian age (Weakley, 1984).

The present study was designed to learn basic information about the activity patterns and population biology of *Plethodon wehrlei* and the other terrestrial salamanders in this community. A mark and recapture study was initiated on Saddle Mountain to obtain information about the density of *P. wehrlei* and other salamanders. This study also resulted in information on dispersion patterns, movements, and habitat preferences of each species.



## REVIEW OF LITERATURE

An overview of the biogeographical history of the Genus *Plethodon* is necessary for understanding the ranges of many species. Information about *Plethodon* life history and ecological interactions also allow a better understanding of how populations at Saddle Mountain compare to those in other areas.

### *Biogeography*

The Appalachian Mountains are well known for high salamander diversity, primarily in the lungless salamander family, Plethodontidae (Hairston, 1949). Plethodontidae probably arose in the Appalachian Mountains and dispersed from there to other parts of North America, Central America and even Europe (Hairston, 1949; Highton, 1972; Wake, 1966). Mountain brooks in the region are thought to be ancestral habitats for the family and many aquatic forms are still native to the region (Wake, 1966; Highton, 1972). Today, thirteen genera (Wake, 1966) and over 70 species in this family live in Eastern North America (Conant and Collins, 1991). Plethodontidae also includes over 20 species in western North America (Stebbins, 1985). Both subfamilies (Plethodontinae and Desmognathinae) and two of three tribes of Plethodontinae (Hemidactylini and Plethodontini), including all “primitive” genera, occur in Appalachia (Wake, 1966). Other centers of diversity for this family are highland areas of Mexico, Guatemala, and eastern Costa Rica and western Panama (Pough et al., 1998).

The stable environment of the Appalachian highlands has been important in developing the current biota. Formation of the mountains began during the Ordovician and continued throughout the Paleozoic, ending at the close of the Permian (265 MYA). The environment has been relatively stable since the end of the Permian (Wake, 1966). Salamanders with characteristics of the family Plethodontidae have probably been in existence since at least the early Cretaceous (125 MYA) (Wake, 1966). The ancestral stock of Subfamily Plethodontinae was already present in early Tertiary (ca. 60 MYA). This stock had three main divergence periods, the second of which may have led to Tribe Plethodontini. This divergence included loss of aquatic larvae and occupation of terrestrial niches and the group was well established by the Oligocene epoch (25-35 MYA). Differentiation of Genus *Plethodon* probably occurred in the Oligocene or early Miocene (Wake, 1966) when this tribe of salamanders was probably widespread in the North America. The group was eliminated in what is now central United States following the uplift of the Rocky Mountains and the development of its rainshadow during the Miocene. Formation of the Rocky Mountains produced savannas and grasslands (unfavorable for plethodontines) in central North America. This separation generated the eastern and western “species groups” recognized today.

Many species of *Plethodon* are endemic in the southern Appalachians. These narrow ranges are possible results of recent range contractions (Highton, 1972) and/or isolation events during the Pleistocene or Pliocene (Larson et al., 1984). Narrow ranges are more prevalent in the southern U.S. (Highton, 1972). Some species, such as *P.*



*cinereus*, *P. wehrlei*, and *P. glutinosus*, expanded their range into previously glaciated areas since the retreat of the glaciers 18,000 years ago (Larson et al., 1984). Present salamander distributions may be results of interspecific competition (Hairston, 1951; Hairston, 1980; Hairston, 1981, Jaeger, 1971; Jaeger, 1974).

#### *Natural history*

*Plethodon* is a genus of lungless, terrestrial salamanders in the Family Plethodontidae. Gas exchange in this family occurs over skin and buccopharyngeal mucosa. Cutaneous gas exchange may account for over 90% of the exchange in these salamanders, and is dependent on capillary number and proximity to the skin surface, affinity of the hemoglobin to oxygen, and a moist skin surface (Duellman and Trueb, 1986). *Plethodon* are terrestrial animals and hatch from eggs laid in rotten logs, under cover objects (Pfungsten, 1989a), or underground (Pfungsten, 1989b). Throughout most of its range, *P. cinereus* lays its eggs underground as do the larger *P. jordani*, *P. glutinosus*, *P. wehrlei*, and *P. yonahlossee* (Hairston, 1987; Hall and Stafford, 1972; Pfungsten, 1989a,b; Pope, 1950). Nests under surface objects are most common in the most northerly portion of the range of *P. cinereus* (Pfungsten, 1989a). Individual clutch sizes in Ohio *Plethodon* range from four to ten in *P. cinereus* (Pfungsten, 1989a) and 15 for *P. glutinosus* (Pfungsten, 1989b). Females remain with developing eggs and hatchlings for 10-12 weeks after egg deposition. Actual incubation takes six to eight weeks. Both *P. glutinosus* and *P. cinereus* remain in the nest until gill buds are completely absorbed (Pfungsten, 1989a,b). Surface emergence of hatchlings varies

according to location and species. Juveniles may emerge in the same season they hatch or up to a year later (Pfungsten, 1989a,b).

Maturation time and reproductive frequency in females also vary according to species and location. Maturation times for *Plethodon* range from two to 9.79 years (Fraser, 1976; Hairston, 1987; Hall and Stafford, 1972; Pauley and England, 1969; Pfungsten, 1989b; Semlitsch, 1980). Oviposition can be annual for some species in some areas or occur at longer intervals (Hall and Stafford, 1972; Pauley and England, 1969; Pfungsten, 1989a; Pungsten, 1989b).

Leaf litter is but a small segment of the total habitat for these salamanders. However, leaf litter is the most commonly sampled portion of their habitat because it happens to be the most convenient for researchers (Taub, 1961). Few salamanders are observed on the surface at any one time. In natural settings two to 32% of all salamanders present were observed in the top inch of soil and even smaller proportions were observed in controlled settings (Taub, 1961) except in northern Michigan where over 60% of the population occur above the soil layer (Kleeberger and Werner, 1982). Surface activity depends on temperature, water table level, and types of surface shelter available. Salamanders avoid dry soil, areas inundated by water, and extreme temperatures (Taub, 1961). Egg clutches are found more frequently in northern Michigan than in southern Michigan and Ohio, where they are thought to be laid deep underground (Pfungsten, 1989a). It is not clear how *Plethodon* find, occupy, or construct their burrows. Natural burrows of *Plethodon (jordani) metcalfi* are ten to twelve feet in depth



(Chadwick, 1940). Salamanders probably do not construct the burrows but may extend or improve them (Chadwick, 1940; Pope, 1950). Burrows of insects and small mammals, rock fissures, and decayed roots probably provide the start for most salamander burrows.

#### *Plethodon ecology*

*Plethodon* species have rather restricted home ranges, which may vary with gender. *P. jordani* males have larger home ranges (39-64m<sup>2</sup>) than do females (4-24m<sup>2</sup>) (Madison and Shoop, 1970). In Great Smoky Mountains National Park, N.C., males of the same species have significantly larger mean home ranges (11m<sup>2</sup>) than do females (2.8m<sup>2</sup>) (Merchant, 1972). Male *P. glutinosus* have larger mean home ranges (14.2m<sup>2</sup>) than do females (6.4m<sup>2</sup>). *P. jordani* juveniles have smaller home ranges ( $\bar{x} = 1.7\text{m}^2$ ) than do *P. glutinosus* juveniles ( $\bar{x} = 7.4\text{m}^2$ ) (Merchant, 1972). In an early study in N.C., it was found that male and female *P. glutinosus* moved similar distances but juveniles move significantly less (4.2m, SE = 0.9) than adults (15.4m, SE = 2.8) (Wells and Wells, 1976). Water conservation might play a role in limiting movements of juveniles, which are likely more susceptible to dehydration. In addition, adults probably require larger foraging areas (Wells and Wells, 1976). *P. jordani* appears to possess a well-developed homing mechanism and exhibits homeward movements after displacement, probably using olfactory cues to find home (Madison and Shoop, 1970).

Local community structures of *Plethodon* are complex. In some areas several *Plethodon* species are sympatric and even syntopic. In other areas species have allopatric or parapatric distributions. Competitive exclusion also seems to occur between some

salamanders in selected locales. Hairston (1951, 1980, 1981) suggests that *Plethodon jordani* limits the upward distribution of *P. glutinosus* on some mountains where the two occur, since the altitudinal overlap between the two species is small in the Black and Great Smoky Mountains of North Carolina. There is greater overlap in the Balsams, and *P. glutinosus* actually is found at higher elevations than *P. jordani* in the Blue Ridge of South Carolina (Hairston, 1987). Hairston (1980) concludes that the two species are in intense competition in the Smoky and Black Mountains, and that weaker competition occurs in the Balsams where the species are more broadly sympatric. In these areas removal of either *P. jordani* or *P. glutinosus* caused the abundance of the other species to increase. Since removals of neither species has an effect on the smaller congener, *P. serratus*, it seems the larger *P. glutinosus* and *P. jordani* are not competing for the same resources with *P. serratus* (Hairston, 1981). Food does not appear to be the limiting resource since five other sympatric species of terrestrial salamanders did not respond to removal of either *P. jordani* or *P. glutinosus*. All species utilize the same prey base, thus, some other resource (eg. nest sites) may limit salamander populations (Hairston, 1981).

A series of experimental studies of *Plethodon cinereus* and *P. shenandoah* suggest that interspecific competition causes the mutually exclusive local distributions seen at Hawksbill Mountain, Virginia. *P. cinereus* appears to prevent *P. shenandoah* from entering areas of deeper soil, limiting this species to suboptimal habitat in talus slopes (Jaeger, 1971). The mechanism for this distribution may be competition for space (Jaeger, 1974; Wrobel et al., 1980, Jaeger et al., 1982).



Many *Plethodon* species show aggressive behavior towards other species when establishing and defending territories under laboratory conditions (Thurrow, 1975, Wrobel et al., 1980). Salamanders appear to establish territories in the field as well. Individuals are observed repeatedly in a small area and return to their home area when displaced (Madison and Shoop, 1970). Salamanders seem to recognize home areas by identification of their own secretions. Pheromones are effective means of designating territory in *P. cinereus*, since their presence causes intruders to avoid an area (Jaeger et al., 1982). Salamanders can also determine from these pheromone secretions whether an unseen individual is a stranger (Jaeger, 1981). *P. cinereus* was more aggressive towards strangers than toward individuals it recognized (Jaeger, 1981) but adult members of the species were more tolerant of juveniles than other adults (Faragher and Jaeger, 1997). Adult *P. cinereus* also defend cover objects from other salamanders. These cover objects are important to salamanders because they may allow foraging during dry periods when surface foraging is otherwise precluded by desiccation (Hairston, 1987, Faragher and Jaeger, 1997)).

Often several species of *Plethodon* salamanders coexist in a given habitat. Several characteristics may allow these species to minimize competition. One way to avoid competition is to be active when other species are not (Highton, 1972). In Virginia, *P. hoffmani* is active earlier in the spring and later in the fall than is the sympatric *P. punctatus*. *P. hoffmani* is also less active in the summer than is *P. punctatus* (Fraser, 1976). Generally, large *Plethodon* species are active during warm weather and retreat

from the surface in cooler temperatures. Small *Plethodon* species are generally active during the cooler months at lower temperatures (Hairston, 1972). This seasonal activity pattern is one aspect that enabled the small *P. cinereus* to colonize northeastern North America after the retreat of the Wisconsin glacier. *P. cinereus* survives in areas with short growing seasons as well as in more southerly areas where more species of *Plethodon* occur. In *P. cinereus* assimilation efficiency is inversely related to ambient temperature so the species has difficulty maintaining a positive energy budget at higher summer temperatures. It avoids the problem by remaining underground during the summer (Bobka et al., 1981).

Choice of microhabitat may also reduce competition between species. In Oregon *P. dunni* prefers wetter substrates than does *P. vehiculum* (Dumas, 1956). Despite the fact that the two species prefer the same relative humidity, *P. vehiculum* is more tolerant of variation in humidities. These species also differ in temperature preferences, with *P. dunni* preferring lower temperatures (Dumas, 1956). In West Virginia the larger *P. wehrlei* is more common in warmer, drier habitats than is the smaller *P. cinereus* (Pauley, 1978).

#### *Human impacts*

Although many salamander species are common locally, they are not immune to the pressures man exerts on all other living organisms. As human populations grow, so do several measures of environmental stress. Natural habitats are destroyed and the production of various, harmful pollutants increases. Petranka et al. (1994) estimated that



earlier timbering on a site in North Carolina caused a 70% reduction of salamander populations during the last century. The richness and density of salamander species are highest in mature forests and fall dramatically after a clearcut (Petranka et al., 1994). It may take a century, or more, after logging for salamanders to return to high densities. Timbering practices typically eliminate the moisture-retaining potential of the soil and leaf litter. Insolation also increases soil temperature while the open canopy causes greater erosion (Buhlmann et al., 1988). Introduction of exotic species can be harmful to native amphibian populations as well (Duellman and Trueb, 1986).

Amphibians such as salamanders are important middle- and upper-level predators of invertebrates (Petranka et al., 1994) and serve as prey for selected snake and shrew species (Buhlmann et al., 1988; Hall, 1976). In New Hampshire, biomass of five species of salamanders equals that of mammals and is twice that of birds during the height of the breeding season (Burton and Likens, 1975). Hairston (1987) estimates that salamander biomass in the Southern Appalachians exceeds that of birds and mammals combined and argues that these animals must constitute important components of the forest floor ecosystem. Petranka et al. (1994) recommended ecosystem management strategies that allow forests to mature more before harvest. These strategies would help restore salamander populations to pre-cut levels.

Loss of biodiversity at all levels affects the ways ecosystems function and impairs our ability to understand natural systems. Certain physiological traits make amphibians excellent indicators of environmental health. Since amphibian declines are evident in

many areas, it is imperative that we assess the current status of amphibian populations and use this information to evaluate changes in our environment (Heyer et al., 1994). Endangered species also represent urgent situations for further study. It is important to understand why each species becomes protected. Listing often follows declines in population sizes and/or decreases in the species' range. On the other hand, some species historically may have existed as small, isolated populations or may have always occurred in low densities, making them susceptible to human pressures. Determining a species' historical range and abundance is important in making decisions about management.

The rationale for the present project was to provide information for scientific and management groups, helping them understand the biology of *Plethodon wehrlei* and its associated species at Saddle Mountain. Information about densities of these salamanders should also prove helpful as a comparison with studies of other *Plethodon* and as a historical baseline for future studies.



## MATERIALS AND METHODS

### *Transect establishment*

In order to find an appropriate study site, Saddle Mountain was visited 7 times between May 5 and July 2, 1996. During these visits only species, snout-vent length (SVL), tail length (TL) and time of capture were recorded for each salamander encountered. Air temperature was recorded intermittently during each visit throughout this survey period.

On July 9, 1996, Transect A (500 X 3m) was established along the upper border of an old logging road on the eastern slope of Saddle Mountain (Fig. 2). This transect was marked with a lettered flag (A to Z) every 20 meters to provide visual aids for locating capture sites of individual salamanders. A smaller site, Transect B (90m X 5m) was established on September 17, 1996 on a southern slope in older second-growth forest with considerable coverage of talus substrate (Fig. 2). Both transects were at approximately 850m (2800 feet) elevation. The site was visited fifty times from July 9, 1996 until December 3, 1997.

Transects were visited at night to capture maximum numbers of salamanders with minimal habitat destruction. Both transects were searched during each site visit. Depending on salamander activity, each site visit required two to five hours. Search order alternated between Transect A first and B first to minimize bias related to time of

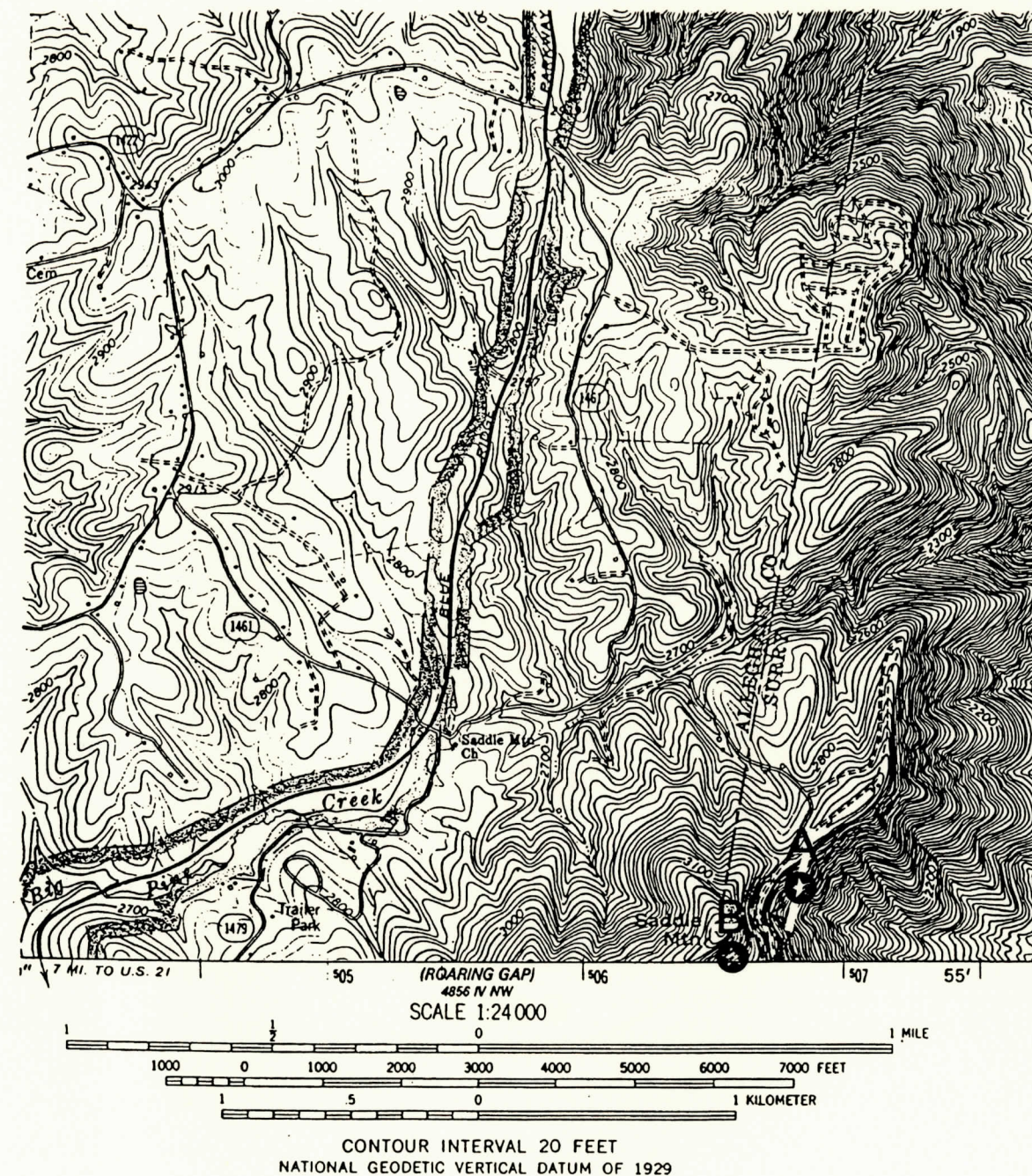


Figure 2. Topography of Saddle Mountain and approximate location of transects A and B on USGS Cumberland Knob quadrangle. Note extreme relief on eastern escarpment.



day and fatigue. In addition, the search on Transect A was begun alternately from the top (A) or bottom (Z) to provide unbiased information on activity.

#### *Field data collection*

Salamanders were captured on surface litter or in crevices. Time, species, and location were recorded for each salamander sighted. Each salamander was placed in a clear plastic sandwich bag to facilitate measurement of SVL, TL, mass, presence of an enlarged mental gland or eggs, and distinguishing marks. Salamanders were weighed with a Pesola spring scale while in the plastic bag. Two types of bags were used in weighing salamanders. Type of bag used in weighing the salamander was recorded each night. Average weight of the appropriate bag type ( $n = 17$  and  $7$  for the two bag types) was used as tare weight. Each salamander was marked by clipping a unique combination of toes, and released at the site of capture.

Early in the study air temperature was recorded periodically throughout the visit. After March 13, 1997, temperature was recorded at time of each capture. Starting on March 26, 1997, relative humidity was recorded periodically throughout each night using a Radio Shack digital thermometer/hygrometer. Surface litter wetness was evaluated on a scale of 1 to 3 each time the site was visited. Level 1 indicated a dry surface leaves which were dry to the touch. Level 2 indicated leaves that were moist to the touch and appeared darkened due to absorbed water. Level 3 indicated standing water on the litter surfaces.

#### *Activity patterns*

Impacts of relative humidity, surface moisture, air temperature, time, and seasonality on salamander activity were assessed using a series of tests. Data were pooled from both sites to give a better overview of activity patterns. This set of data included salamanders captured inside and outside of the two transects. Samples were tested for homogeneity of variance using Levene's test. If there was no significant heterogeneity, data were included in a series of one-factor analysis of variance tests (ANOVA). In cases with significant heterogeneity, frequency data were log or square root transformed. If transformed data were not heterogeneous, they were analyzed using ANOVA. If variances remained heteroscedastic, data were analyzed further using the non-parametric Kruskal-Wallis test. Salamanders were grouped according to species and season of capture to study seasonal activity. These data were analyzed by a chi-square contingency table for similarity in seasonal activity.

#### *Population characteristics*

Abundance of each species along the two transects was compared by a chi-square contingency table. Since Transect B was established later than Transect A, inclusion of all data in this analysis would have produced an invalid comparison. All animals observed or captured between September 16, 1996, when Transect B was established and the end of the study on December 3, 1997 were included in the analysis.



Population estimates (N) were made for each species using both the Schnabel and Schumacher-Eschmeyer methodologies described by Krebs (1989). Ninety-five percent confidence intervals were calculated from the Poisson distribution for the Schnabel estimates and from the normal approximation for the Schumacher-Eschmeyer estimates, as described by Krebs (1989). All estimates were extrapolated to number per hectare by simple scaling ( $10,000\text{m}^2/\text{ha} \div \text{transect area in m}^2$ ) and compared with previously published data for salamanders.

Spatial distribution within each site was analyzed for each species by determining the numbers of salamanders encountered in each one-meter interval along each transect. To determine if salamanders were randomly distributed, numbers of individuals per interval were tabulated for each species and compared to values expected in a Poisson distribution (Krebs, 1989) with a G test (Sokal and Rohlf, 1969). Mean values for these Poisson distributions were total number of encounters divided by number of intervals. Significant values in this test indicated a nonrandom distribution. A second G test (Sokal and Rohlf, 1969) was performed to determine if the salamanders were distributed evenly along each transect. For this test, each transect was divided into linear quarters so expected values were 25% of total captures per species.

Descriptive statistics of SVL and mass for all captures of each species and population estimates were used to estimate salamander biomass. Three original methods for estimating biomass utilized mean SVL (Method 1), mean mass (Method 2), and

projected mass for all salamanders captured (Method 3). Alternate values were calculated using Schnabel and Schumacher-Eschmeyer estimates and their 95% confidence intervals (CI). Method 1 began with least square regressions of log (mass) against SVL for each species. These regressions provided predicted mass for mean SVL's for each species. This estimate of "average mass" was multiplied by estimated density to determine salamander mass in the  $1500\text{m}^2$  transect or in a hectare of similar habitat:

$$\text{Method 1} \quad \text{kg/ha} = \text{N/hectare} \times \text{Mass/average SVL animal.}$$

In method 2, the average mass of all salamanders weighed was calculated for each species and multiplied by the population estimates:

$$\text{Method 2} \quad \text{kg/ha} = \text{N/hectare} \times \text{Average Mass/animal.}$$

Method 3 used the regression equations to estimate mass of all salamanders captured on the plot. The average of these estimates was used in place of actual mean mass used in method 2:

$$\text{Method 3} \quad \text{kg/ha} = \text{N/hectare} \times \text{Average Estimated Mass/animal.}$$



Recaptures provided information on salamander movements and growth. Means and 95% CI were calculated for distance moved in each species. Regression analysis was used to determine relationship between distance moved and time between captures. Growth was also studied using regression analysis of change in SVL against time at risk or average (first and last capture) SVL and growth rate ( $\Delta\text{SVL}/\Delta\text{T}$ ) against average SVL.

#### *Habitat relationships*

Several potentially important aspects of the site were quantified and used to analyze habitat use by each species. Canopy closure was measured with a spherical densiometer at 10m intervals along the downhill boundary of Transect A and from the middle of Transect B. Small (0.5m X 0.5m) quadrats were located at 3m intervals 1 m uphill from lower boundaries of each transect. Visual estimates were made of proportional coverage in each quadrat of exposed bedrock, loose rock with diameter  $\geq 5$  cm, bare soil, and herbaceous vegetation. Each three-meter interval was assigned the nearest canopy closure value for correlation and regression analyses. Correlation analyses between these percentages and numbers of salamanders encountered in each three meter segment of the each transect were used to detect habitat preferences for each species. In addition, stepwise multiple regression was used to detect combinations of habitat characteristics that might explain salamander abundance.

The primary statistical source was Sokal and Rohlf (1969). Most statistical calculations were performed using MINITAB for WINDOWS 11 (Minitab, Inc., 1996) licensed to Appalachian State University.

## RESULTS

Sixteen species of reptile and amphibian were observed at Saddle Mountain during the study (Table 1). Eight species of salamander were found on the Saddle Mountain sites but only three *Plethodon* species were common enough to provide population information. The numbers of common species encountered were 150, 176, and 193 for *Plethodon cylindraceus*, *Plethodon wehrlei*, and *Plethodon yonahlossee*, respectively. Geographic ranges for these species (Fig. 3-5) varied greatly.

*Plethodon wehrlei* was much the smallest common species (Table 2) both in overall size (SVL) and size at which males developed visible mental glands (MG). This species seemed more stressed from being captured than the other two species and exhibited two characteristic behaviors. Occasional individuals would bite upon capture, but more commonly they would begin spinning in hand, a defensive tactic seen during marking. Spinning was most prevalent on "dry" nights. These types of behaviors were not seen in other species of *Plethodon* at the site or elsewhere. Several adults regurgitated the only documented prey items, small earthworms.

### *Activity patterns*

Examination of seasonal encounters with salamander species indicated seasonal and species differences in activity (Fig. 6). Classification of these data into seasons (Table 3) revealed highly significant differences among the species in seasonal activity

Table 1. Species of reptile and amphibian encountered (+) along each transect (A or B) and outside the study area (O) at Saddle Mountain, NC (Common names obtained from Conant and Collins, 1991).

Species	Common Name	Site A	Site B	O
<i>Bufo americanus</i>	American Toad	-	-	+
<i>Crotalus horridus</i>	Timber Rattlesnake	-	+	-
<i>Desmognathus fuscus</i>	Northern Dusky Salamander	-	-	+
<i>D. monticola</i>	Seal Salamander	+	-	+
<i>D. quadramaculatus</i>	Blackbelly Salamander	-	-	+
<i>Diadophis punctatus</i>	Ringneck Snake	+	-	+
<i>Eurycea wilderae</i>	Blue-Ridge Two-lined Salamander	+	-	-
<i>Gyrinophilus porphyriticus</i>	Spring Salamander	+	-	-
<i>Nerodia sipedon</i>	Northern Watersnake	-	-	+
<i>Notophthalmus viridescens</i>	Red-Spotted Newt (eft)	+	-	+
<i>Plethodon cylindraceus</i>	White-Spotted Slimy Salamander	+	+	+
<i>P. wehrlei</i>	Wehrle's Salamander	+	+	+
<i>P. yonahlossee</i>	Yonahlossee Salamander	+	+	+
<i>Rana sylvatica</i>	Wood Frog	+	+	+
<i>Regina septemvittata</i>	Queen Snake	-	-	+
<i>Terrapene carolina</i>	Eastern Box Turtle	-	-	+
<i>Thamnophis sirtalis</i>	Common Garter Snake	-	-	+



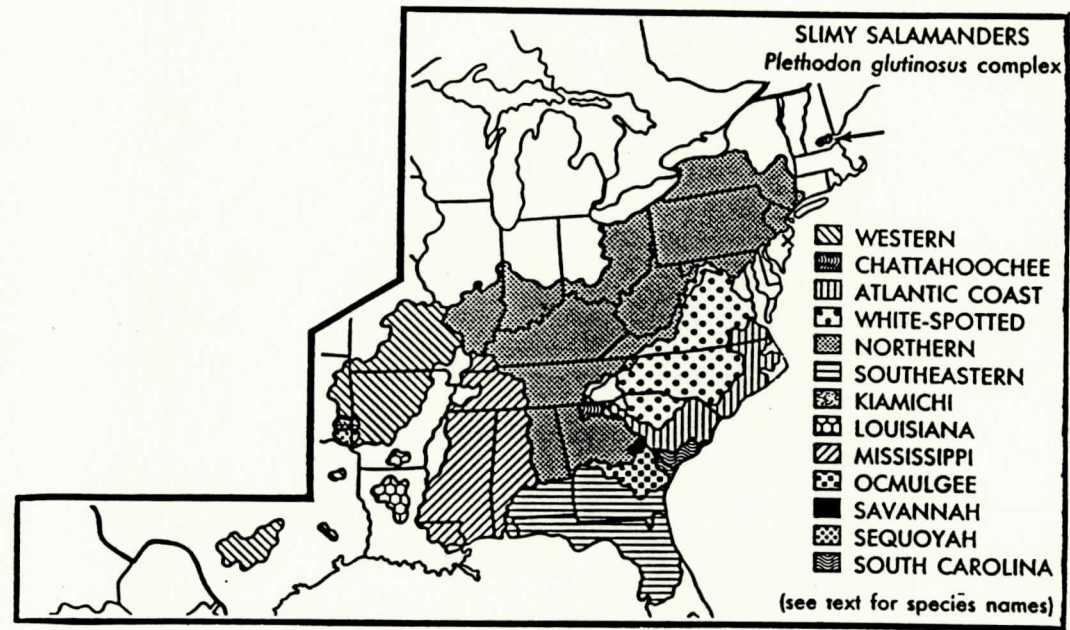


Figure 3. Geographic range of the white spotted slimy salamander, *Plethodon cylindraceus*, in eastern North America. (Reprinted from Conant and Collins, 1991).

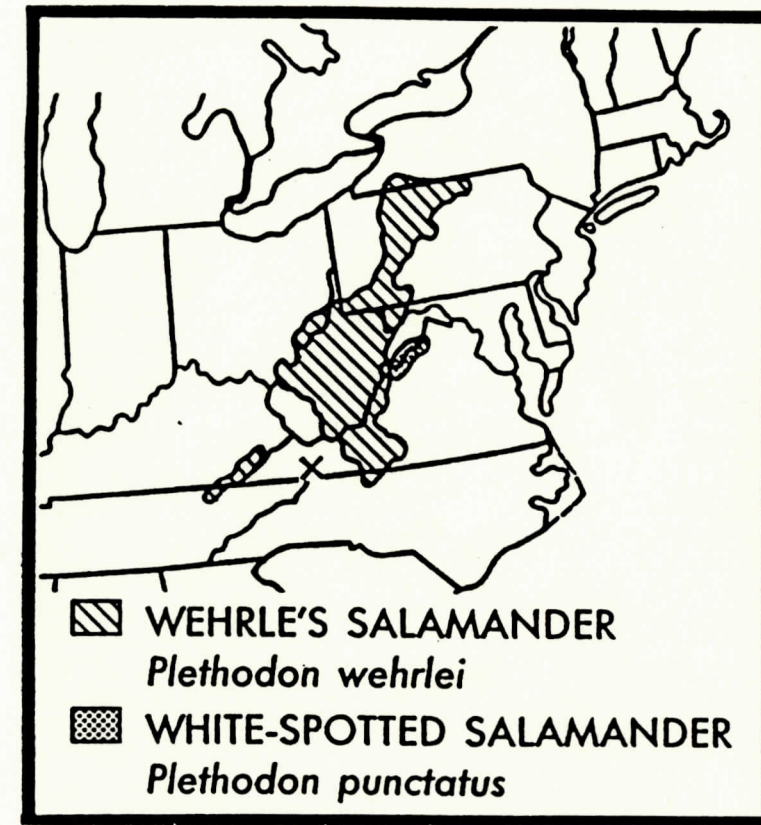


Figure 4. Geographic range of Wehrle's salamander, *Plethodon wehrlei*, in eastern North America. (Reprinted from Conant and Collins, 1991).

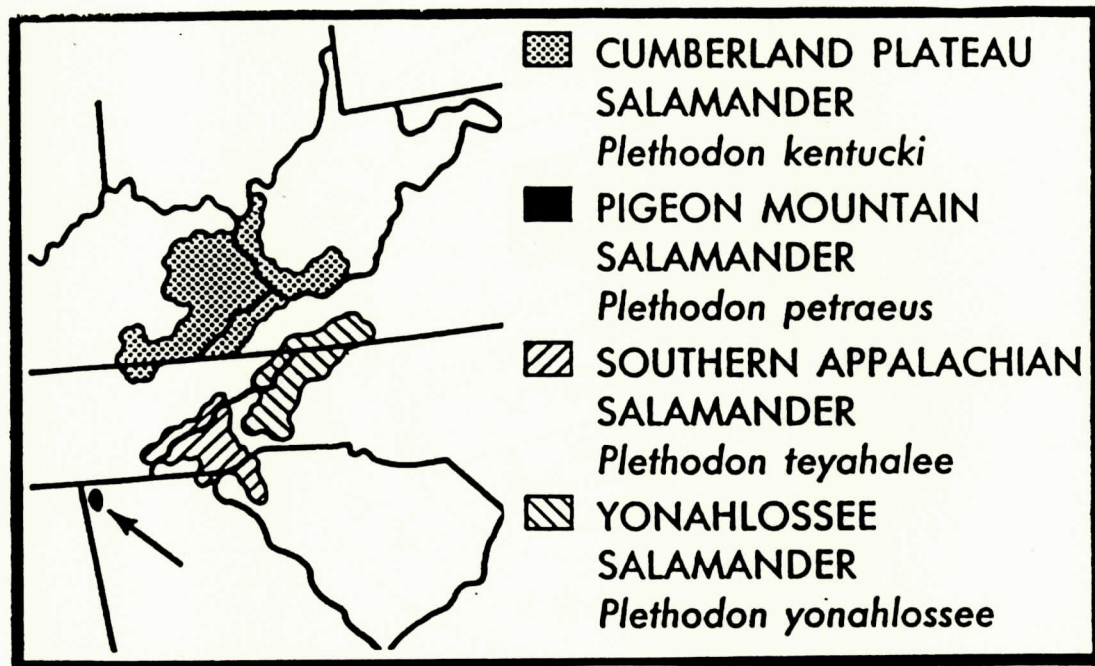


Figure 5. Geographic range of the Yonahlossee salamander, *Plethodon yonahlossee*, in eastern North America. (Reprinted from Conant and Collins, 1991).

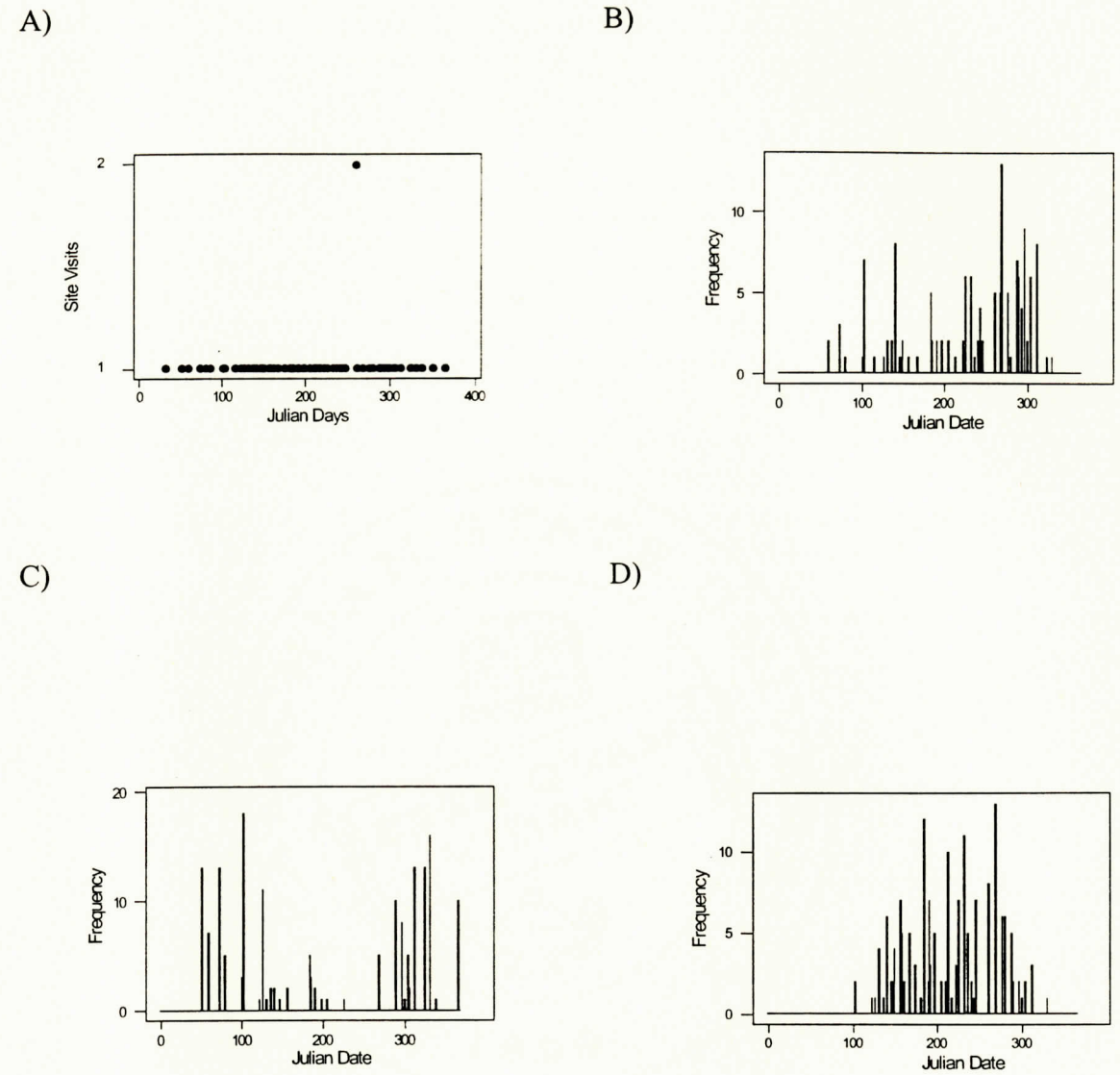


Figure 6. Julian days of site visits (A) and patterns of surface activity in *Plethodon cylindraceus* (B), *P. wehrlei* (C), and *P. yonahlossee* (D). Julian days are days since January 1 each year. (Approximate starting Julian Days for seasons are spring (85), summer (175), fall (265), and winter (355)).



( $\chi^2 = 155.3$ ,  $df = 6$ ,  $P < 0.001$ ). *Plethodon cylindraceus* was active throughout the year (Fig. 6A). Only five *P. cylindraceus* were active during the winter but activity increased through the spring and summer to a peak in fall. The few juveniles encountered were observed in spring and summer. Courtship was observed in this species on September 24, 1996.

Table 2. SVL ranges (in mm) for species and for males with visible mental glands (MG).

Species	N	Mean	Min	Max	MG min	MG max
<i>Plethodon cylindraceus</i>	123	56.4	22	89	65	84
<i>Plethodon wehrlei</i>	169	48.4	21	61	48	61
<i>Plethodon yonahlossee</i>	154	71.1	24	93	55	90

Table 3. Salamanders encountered in each season during the entire study.

	<i>P. cylindraceus</i>	<i>P. wehrlei</i>	<i>P. yonahlossee</i>	Total
Winter	5	43	0	48
Spring	29	46	42	117
Summer	48	13	110	171
Fall	68	74	41	183
Total	150	176	193	519

*Plethodon wehrlei* exhibited a bimodal activity pattern with most activity between Julian days 50 and 120 (late winter and early spring) and 260 and 330 (fall and early winter) (Fig. 6B). Activity observed during the summer consisted primarily of juveniles

with an SVL from 20 – 30 mm. One adult, however, was found during the summer.

Activity of juvenile and adult *P. wehrlei* overlapped in Spring 1996 but not in Spring 1997. Gravid females were found from February 20, 1997 to April 12, 1997. One clutch visible within a female contained 11 eggs three millimeters in diameter.

*Plethodon yonahlossee* had the narrowest active season (Fig. 6C). It was inactive in winter and the last species to emerge in the spring. It was also the first species to return underground for the winter. Juveniles were found during the spring and summer. Courtship was observed in this species on September 17, 1997.

Seasonal air temperature fluctuations influenced salamander activity. Each species responded differently to differences in air temperature (Fig. 7). *Plethodon wehrlei* had the widest thermal range (5 – 23 °C) and lowest mean temperature (12.4 °C). Individual *P. wehrlei* active during the warmer temperatures were primarily juveniles. *P. yonahlossee* had the narrowest thermal range (8 – 21 °C) and highest mean temperature (16.2 °C). *P. cylindraceus* had an almost flat thermal profile except for a peak at 15 °C. The temperature range of *P. cylindraceus* was relatively wide (7 – 21 °C) with the mean temperature (14.5 °C) relatively close to the peak observed in Figure 7C.

Levene's test for homogeneity of variance revealed serious heteroscedasticity for temperature,  $\log(T)$ , and  $\sqrt{T}$ , ( $P = 0.021$ ,  $P < 0.001$ , and  $P < 0.001$  respectively). When

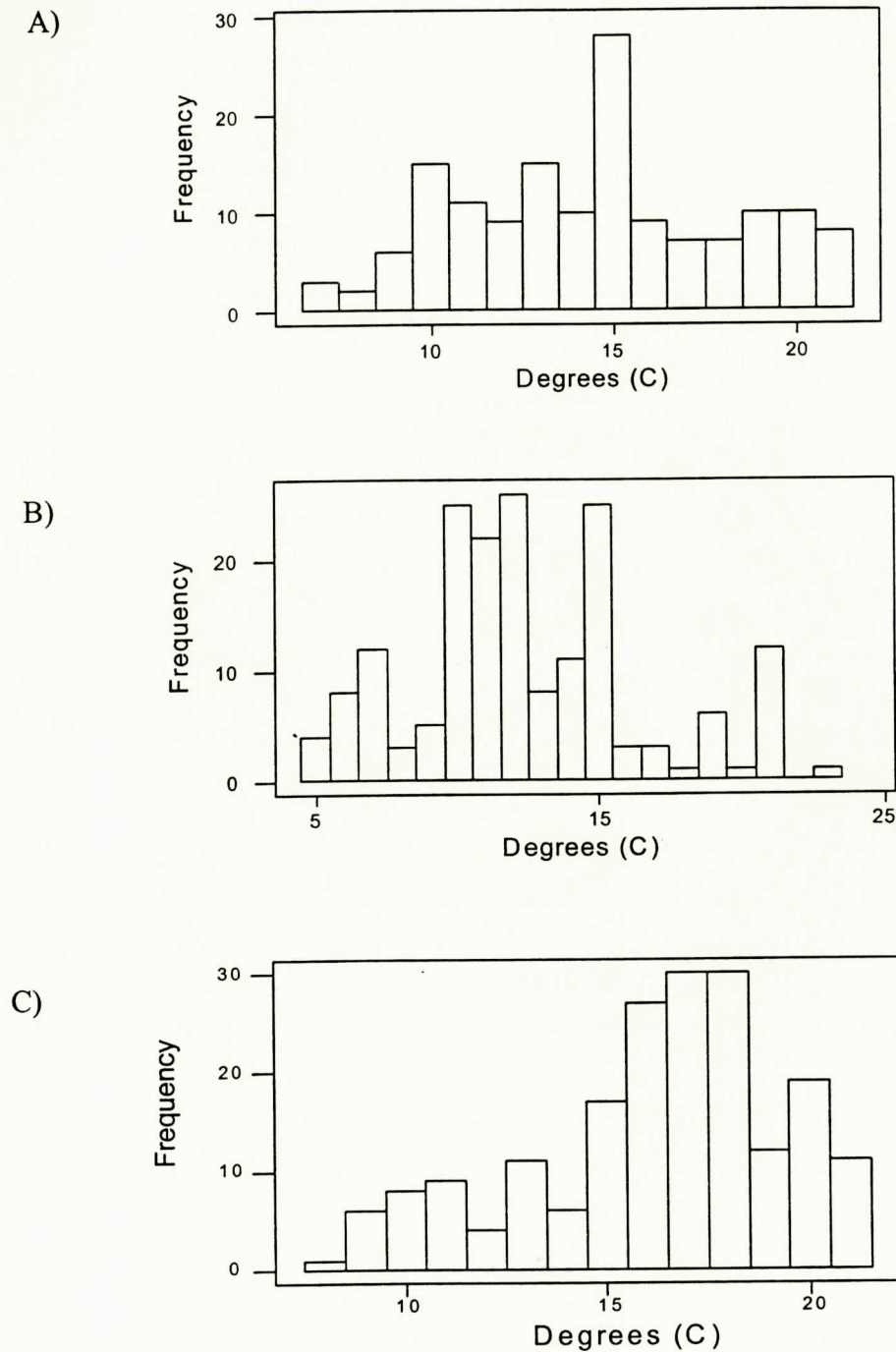


Figure 7. Influence of temperature on encounters (frequency) of *Plethodon cylindraceus* (A), *P. wehrlei* (B), and *P. yonahlossee* (C). Note temperature scales are inconsistent between species.

data were converted to ranks, significant differences among the species were evident using the Kruskal-Wallis test ( $H_{2,517} = 86.06, P < 0.001$ ). As expected, *P. wehrlei* had the lowest ranking for temperature and *P. yonahlossee* had the highest (Sokal and Rohlf, 1969).

Although some salamanders were active throughout the range of surface moisture, the species responded differently to this variable (Fig. 8). *Plethodon cylindraceus* was least affected by litter moisture because almost equal numbers were seen under all conditions. Both *P. wehrlei* and *P. yonahlossee* were observed more frequently when litter was wet (Fig. 8B and 8C, respectively). Litter moisture content at time of capture was significantly different among species ( $F_{2,510} = 3.30, P = 0.038$ ). Overlapping 95% confidence intervals for means for *P. cylindraceus* ( $\bar{x} = 2.13$ ) and *P. yonahlossee* ( $\bar{x} = 2.21$ ) indicated that these two were not different from each other but *P. wehrlei* ( $\bar{x} = 2.36$ ) was active under wetter conditions than the other two species (Table 4).

Table 4. Analysis of variance table for litter moisture levels when *Plethodon wehrlei* (1), *P. cylindraceus* (2), and *P. yonahlossee* (3) were active.

Source	DF	SS	MS	F	P
species	2	4.353	2.176	3.30	0.038
Error	510	336.107	0.659		
Total	512	340.460			

Level	N	Mean	StDev
1	171	2.3567	0.7793
2	149	2.1275	0.7994
3	193	2.2124	0.8487

Pooled StDev = 0.8118

Individual 95% CIs For Mean Based on Pooled StDev

-----+-----+-----+-----+-----  
 (-----\*-----)  
 (-----\*-----)  
 -----+-----+-----+-----+-----  
 2.10      2.25      2.40



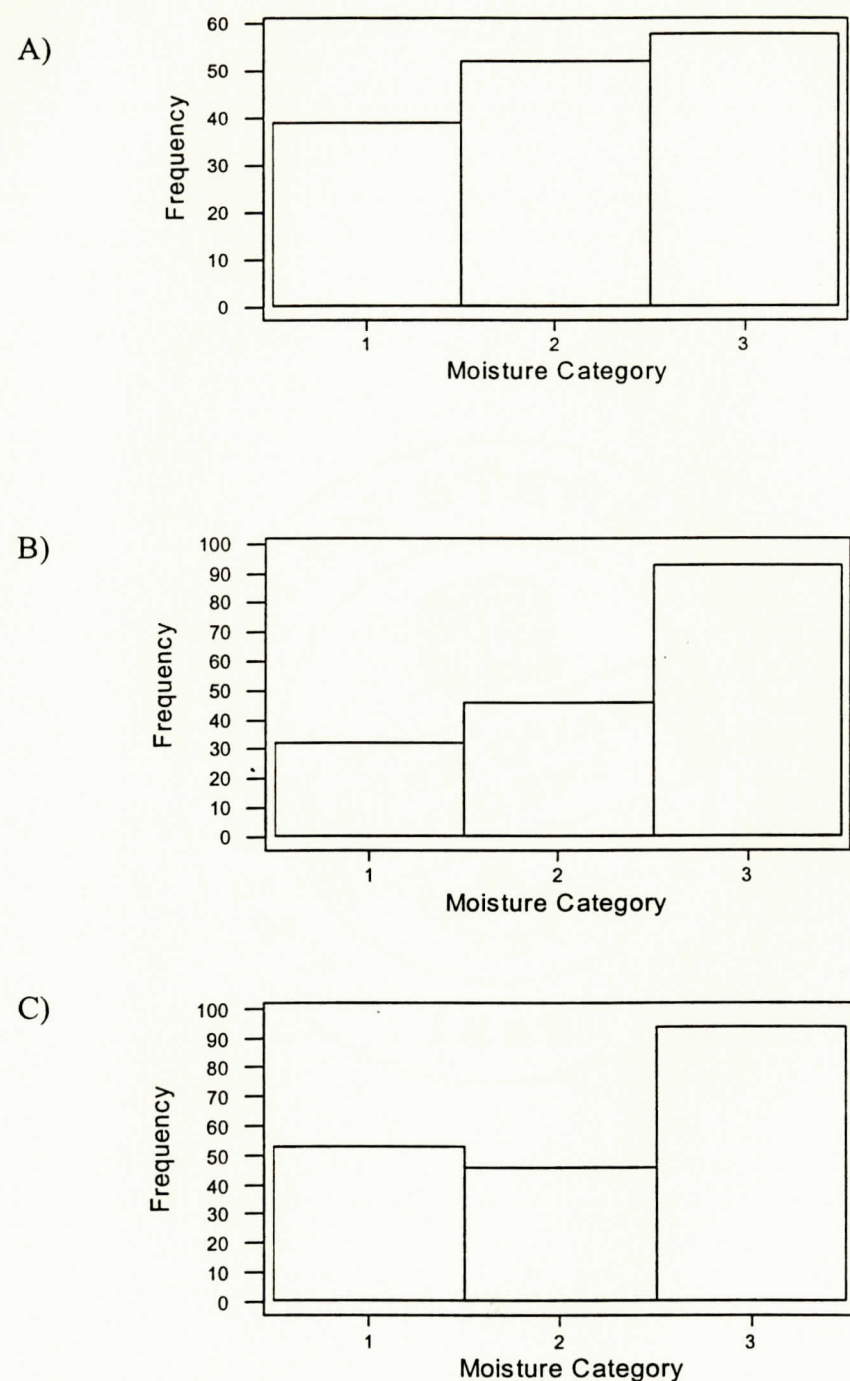


Figure 8. Effect of litter moisture on encounters (frequency) of *Plethodon cylindraceus* (A), *P. wehrlei* (B), and *P. yonahlossee* (C) encountered at Saddle Mountain. Soil moisture categories are dry (1), moist (2), and wet (3).

Salamander species responded similarly to relative humidity ( $F_{2,163} = 0.58, P = 0.561$ , Table 5). A few individuals of each species were active in low relative humidity but the means for all species were similar (Fig. 9). In all species, most individuals were active at higher humidities between 60 and 80% relative humidity.

Table 5. Analysis of variance table for relative humidity levels when three species (sp) of *Plethodon* were active. Levels are *Plethodon wehrlei* (1), *P. cylindraceus* (2), and *P. yonahlossee* (3).

Source	DF	SS	MS	F	P
sp	2	195	97	0.58	0.561
Error	163	27324	168		
Total	165	27518			

Level	N	Mean	StDev	Individual 95% CIs For Mean Based on Pooled StDev
1	31	70.81	17.44	(-----+-----+-----+-----+)
2	61	68.95	12.48	(-----*-----)
3	74	67.84	11.01	(-----*-----)

Pooled StDev = 12.95      66.0      69.0      72.0      75.0

Salamanders were active on the surface from immediately after sunset until well after midnight. The average times (minutes) of activity after sunset for each species were 161.2 for *Plethodon wehrlei*, 128.0 for *P. yonahlossee*, and 130.0 for *P. cylindraceus*. Heterogeneity of variance was found for time but not for log time. Significant differences existed among the species in log time of activity after sunset ( $F_{2,473} = 14.48, P < 0.001$ ). Means for *P. cylindraceus* and *P. yonahlossee* were within each other's 95%

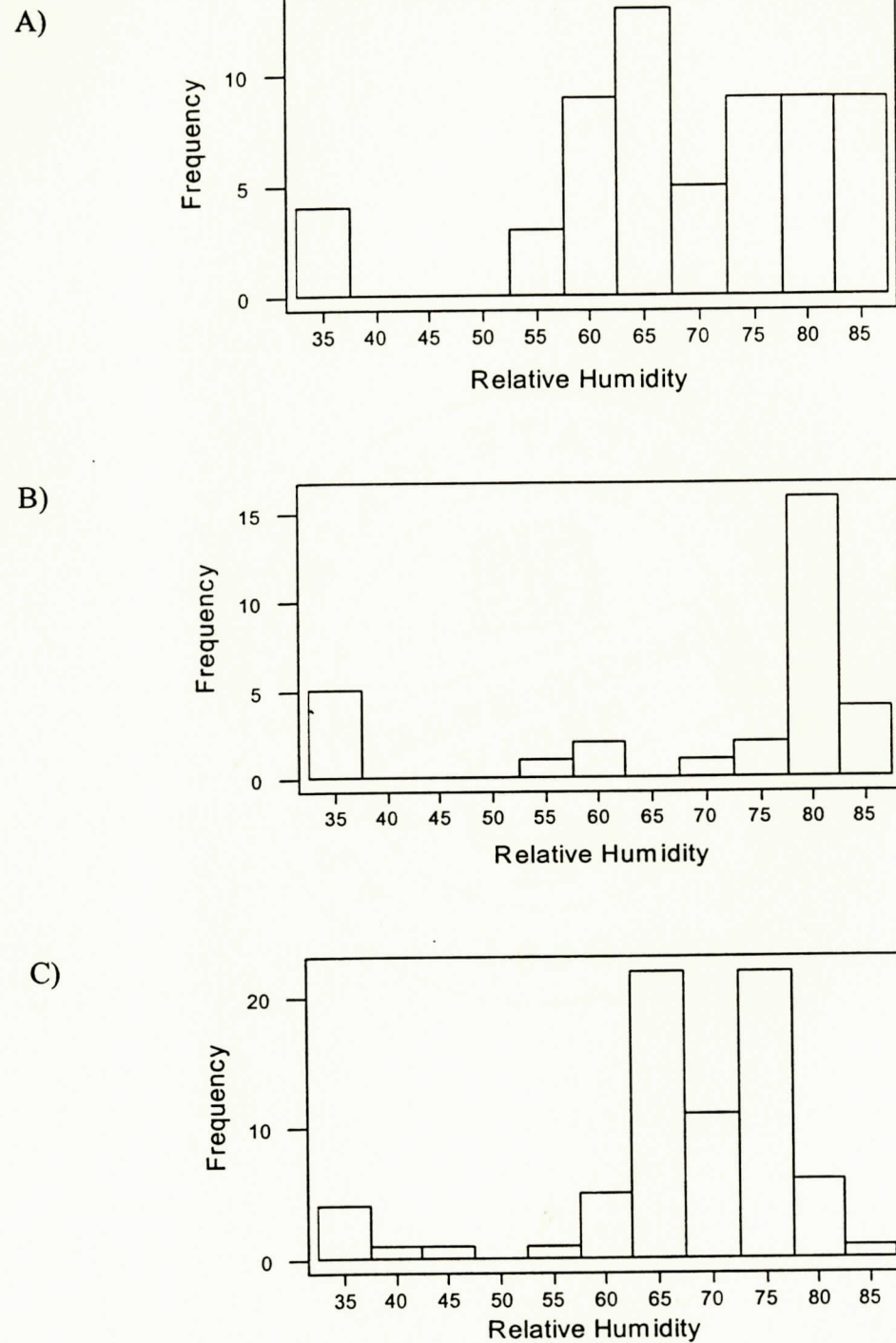


Figure 9. Influence of relative humidity on encounters (frequency) of *Plethodon cylindraceus* (A), *P. wehrlei* (B), and *P. yonahlossee* (C) at Saddle Mountain.

confidence intervals so the two were statistically similar (Table 6). *P. wehrlei* was found on the surface later than were the other two species.

Table 6. Analysis of variance table for log times active after sunset when three species (sp) of *Plethodon* were active. Levels are *Plethodon wehrlei* (1), *P. cylindraceus* (2), and *P. yonahlossee* (3).

Source	DF	SS	MS	F	P
sp	2	1.3571	0.6785	14.48	0.000
Error	473	22.1715	0.0469		
Total	475	23.5286			

Level	N	Mean	StDev	Individual 95% CIs For Mean Based on Pooled StDev
1	159	2.2232	0.2129	(-----*-----)
2	137	2.1139	0.2241	(-----*-----)
3	180	2.1073	0.2137	(-----*-----)

Pooled StDev = 0.2165

2.100      2.150      2.200      2.250

*Population characteristics*

Marking and recapturing of salamanders was performed from July 9, 1996 to December 3, 1997 on Transect A and September 17, 1996 to December 3, 1997 on Transect B. Fifty visits involving marking and/or recapturing of animals were made in this time period. Animals with recognizable marks were free in the population up to 400 days before recapture. Total numbers of *Plethodon* species measured at the sites before and during the mark and recapture study were 169 *P. wehrlei*, 123 *P. cylindraceus*, and 154 *P. yonahlossee*. These captures revealed one interesting pattern of abundance. *P. yonahlossee* was most common on east-facing Transect A while *P. cylindraceus* was most common on the south-facing Transect B. Conversely, *P. cylindraceus* was least



common on Transect A and *P. yonahlossee* was least common on Transect B (Table 1).

These differences in relative abundance differed significantly ( $\chi^2 = 22.309$ ,  $df = 2$ ,  $P < 0.001$ ).

Population estimates were obtained only from Transect A due to the low number of recaptures on Transect B. Schnabel and Schumacher-Eschmeyer population estimates and their 95% confidence intervals were calculated for *Plethodon cylindraceus*, *P. wehrlei*, and *P. yonahlossee* in the 1500 m<sup>2</sup> transect and extrapolated to values for a hectare of similar habitat (Table 7). Lowest population estimates were found for *P. wehrlei* and highest estimates were for *P. yonahlossee* using both methods. Numbers of animals marked for each species over an 18-month period represented between 11 and 22% of the populations at hand. More recaptures produced a narrower 95% confidence interval while fewer recaptures produced wider confidence intervals in both techniques. With few recaptures (*P. cylindraceus* and *P. yonahlossee*) Schumacher-Eschmeyer methodology produced larger confidence intervals than Schnabel methodology. This trend was reversed in *P. wehrlei* with over 10% of the marked animals recaptured.

Salamander distribution was clumped for each species along Transect A. Counts of each species seen per 1m length of Transect A (Fig.10) differed significantly ( $P < 0.001$ ) from those expected for a random or Poisson dispersion pattern for *P. wehrlei* ( $G = 40.78$ ,  $df = 2$ ), *P. cylindraceus* ( $G = 15.66$ ,  $df = 2$ ), and *P. yonahlossee* ( $G = 28.02$ ,  $df = 2$ ). Similar comparisons with counts predicted from a uniform dispersion among quarters

Table 7. *Plethodon* population estimates along Transect A using Schumacher – Eschmeyer and Schnabel methods.

	<i>P. cylindraceus</i>	<i>P. wehrlei</i>	<i>P. yonahlossee</i>
# Marked	87	117	116
# Recaptured	5	14	7
Population estimate (Schumacher – Eschmeyer)			
Lower 95% CI	775.1	603.3	1066.7
Upper 95% CI	432.2	480.4	654.8
CI width	3749.3	810	2875.1
#/ hectare	3317.1	329.6	2220.3
Lower estimate/ ha	5167.3	4022	7111.3
Upper estimate/ ha	2881.3	3202.7	4365.3
	24995.3	5400	19167.3
Population estimate (Schnabel)			
Lower 95% CI	777.4	521.4	937.3
Upper 95% CI	347.8	318.2	476.6
CI width	1973.1	901.0	1997.3
#/ hectare	1625.3	582.8	1520.7
Lower estimate/ ha	5182.7	3476.0	6248.7
Upper estimate/ ha	2318.7	2121.3	3177.3
	13154.0	6006.7	13315.3

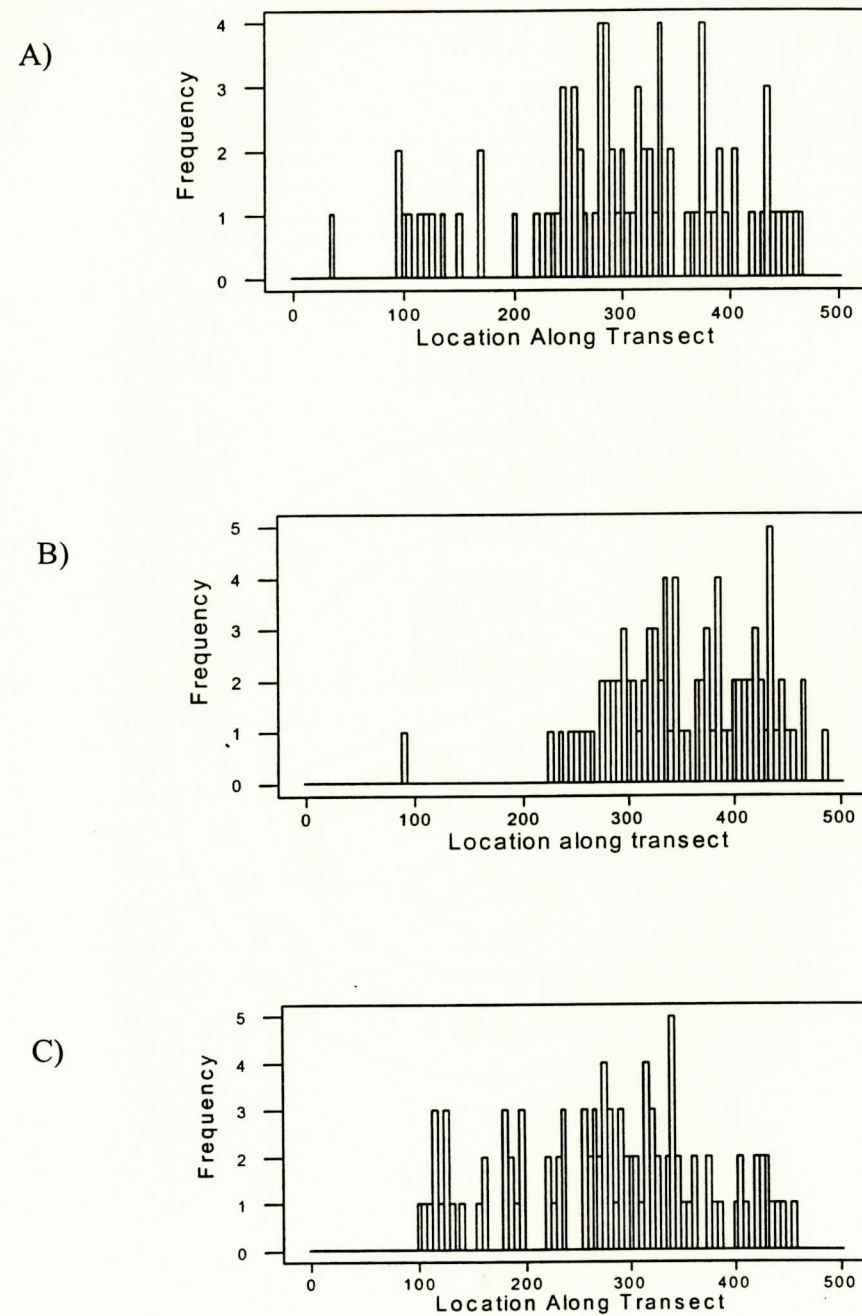


Figure 10. Location of *Plethodon cylindraceus* (A), *P. wehrlei* (B), and *P. yonahlossee* (C) along Transect A.

of the transect showed significant differences ( $P < 0.001$ ) for *P. wehrlei* ( $G = 77.129$ ,  $df = 3$ ), *P. cylindraceus* ( $G = 50.561$ ,  $df = 3$ ), and *P. yonahlossee* ( $G = 90.009$ ,  $df = 3$ ). Each species distribution was significantly different in location (quarters) along Transect A ( $\chi^2 = 49.7$ ,  $df = 6$ ,  $P < 0.001$ ). Too few encounters were made along Transect B (*P. cylindraceus* = 26, *P. wehrlei* = 14, and *P. yonahlossee* = 3) to perform these comparisons.

Estimates of body size and weight were essential for all estimates of biomass. Regressions of mass against SVL were curvilinear, so mass was transformed to log mass to obtain a linear relationship (Fig. 11). All of these regressions were highly significant ( $P < 0.001$ ) and had high  $r^2$  values. Method 1 of biomass estimation resulted in consistently lower values ( $\pm 30\%$ ) than did methods 2 and 3 (Table 8). Methods 2 and 3 required the input of more information about the captured salamanders and yielded nearly equal values. *Plethodon wehrlei* had the lowest biomass estimates (3.3 – 5.4 kg/ha) and narrowest confidence intervals. Biomass estimates for *P. cylindraceus* (14.1 – 20.2 kg/ha) and *P. yonahlossee* (32.0 – 56.9 kg/ha) were larger and had wider confidence intervals. Upper confidence intervals indicated the incredible biomass of 110.4 - 251.3 kg of salamanders in one hectare.

Recaptures provided limited information on salamander movements (Table 9). Only one *P. cylindraceus* was recaptured twice. Salamanders of each species displayed a wide range of movements, but sample sizes were relatively small for *Plethodon*







*cylindraceus* and *P. yonahlossee*. Individuals in all species had movements from near zero up to around 20 meters from the site of first capture and similar means. Salamanders moved between six and nine meters on average over intervals up to 401 days.

Table 9. Movement distances and intervals for recaptured salamanders.

	<i>P. cylindraceus</i>	<i>P. wehrlei</i>	<i>P. yonahlossee</i>
N	5	15	7
Minimum distance (m)	0	0	2
Maximum distance (m)	20	23	20
Mean distance (m)	9.00	5.80	8.43
Two standard errors	10.03	3.24	5.85
Minimum interval (days)	21	6	3
Maximum interval (days)	248	200	401
Mean interval (days)	140.8	65.7	142.3

Recaptures also provided information on salamander growth. The largest changes in SVL occurred after long time periods between captures. One *P. wehrlei* increased 11 mm in SVL in 200 days while a *P. yonahlossee* grew 6 mm in SVL in 401 days. One *P. cylindraceus* experienced a nine-millimeter increase in SVL over 248 days. Periods of little, or no, growth were observed in all three species as well, e.g. zero change in SVL was seen in one *P. wehrlei* recaptured after 7 and 87 days. This pattern was more pronounced in some *P. yonahlossee*, which exhibited 0 - 1 mm increase after 3 to 330 days. Several *P. cylindraceus* also experienced SVL increases of 2 - 3 mm in 21 to 239 days after marking.

Growth was analyzed as a function of time between captures (Fig. 12) and animal size (mean SVL, Fig. 13). Change in SVL was negatively correlated with mean SVL for

*P. wehrlei* ( $r = -0.600$ ,  $r^2 = 0.361$ ,  $P = 0.018$ ) but not for *P. cylindraceus* ( $r = -0.219$ ,  $r^2 = 0.048$ ,  $P = 0.724$ ) or *P. yonahlossee* ( $r = 0$ ,  $r^2 = 0$ ,  $P = 0.964$ ). Similarly, only *P. wehrlei* had a significant increase in  $\Delta$  SVL with time between captures ( $r = 0.666$ ,  $r^2 = 0.443$ ,  $P = 0.007$ ), whereas *P. cylindraceus* ( $r = 0.424$ ,  $r^2 = 0.18$ ,  $P = 0.476$ ) and *P. yonahlossee* ( $r = 0.475$ ,  $r^2 = 0.226$ ,  $P = 0.281$ ) did not. Growth rate was unrelated to SVL in all species (Fig. 14).

#### Habitat relationships

The canopy of Transect A was relatively open for the first 15 meters (58.9–68.3% closure) but the remaining areas ranged from 74.0-95.6% closure. Average canopy closure for the plot was 87.8%. Loose rock cover along this transect was minimal with an average of 3.35 % and a range from 0 to 100%. One hundred percent cover was found only at 174 meters. Rock cover was most prominent at 110-125 meters and 170-205 meters. Bedrock exposure along transect A varied from 0 to 100% coverage, averaging 9.6%. Two major outcrops were at 90-120 and 265-300 meters. Soil exposure was primarily limited to two general areas along the transect: 0-100 and 375-500 meters. Average soil exposure for the entire plot was 22.7%. Herbaceous cover ranged from 0-100% along the transect and averaged 31.2%.

Transect B was somewhat different in that there were no open areas. Canopy closure in B ranged from 90.9-96.4% with an average of 93.7%. Loose rock cover was again minimal, 0 - 30% cover with an average of 5.6%. Bedrock was a minor component

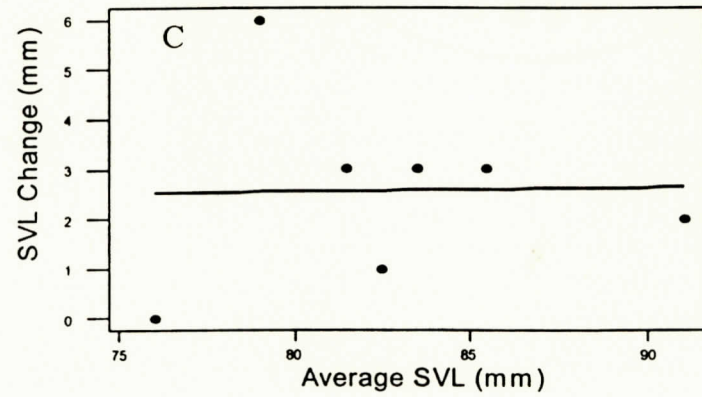
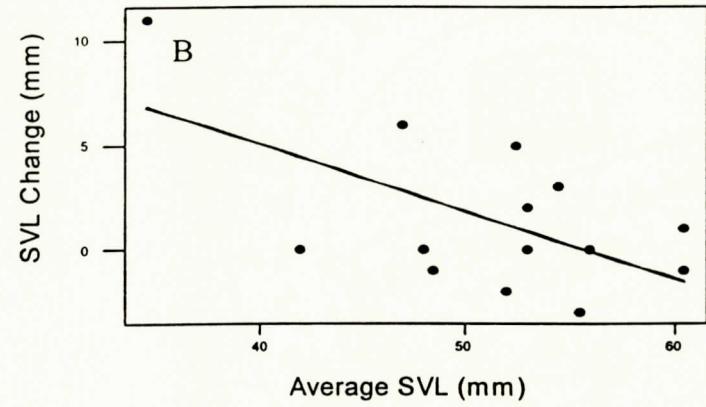
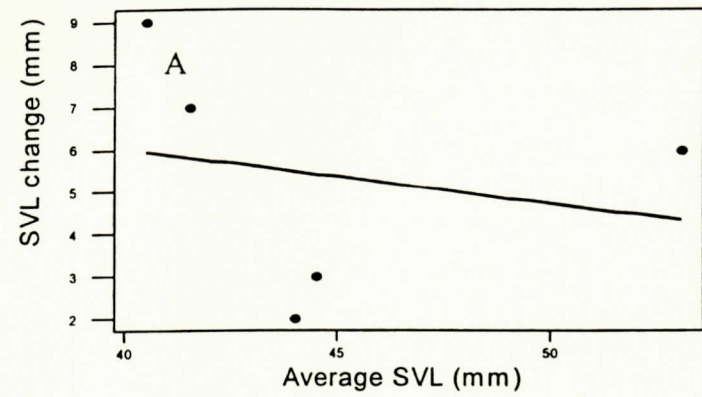


Figure 12. Relationship between growth and size (average SVL) in *Plethodon cylindraceus* (A), *P. wehrlei* (B), and *P. yonahlossee* (C).

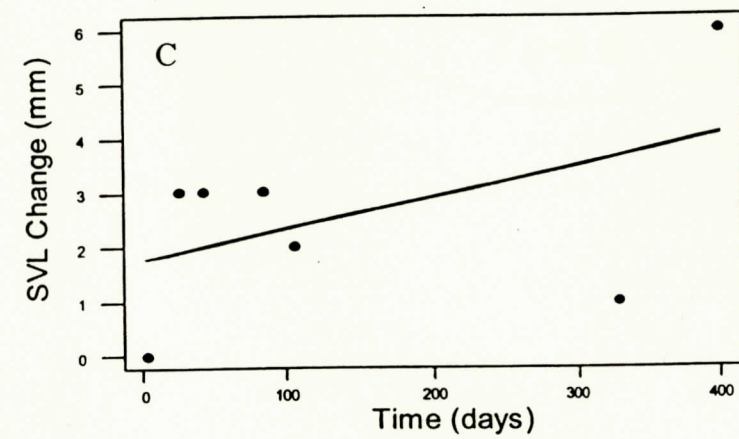
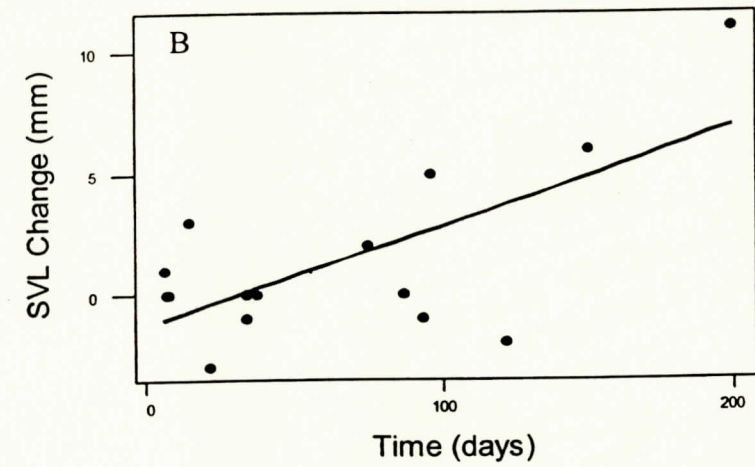
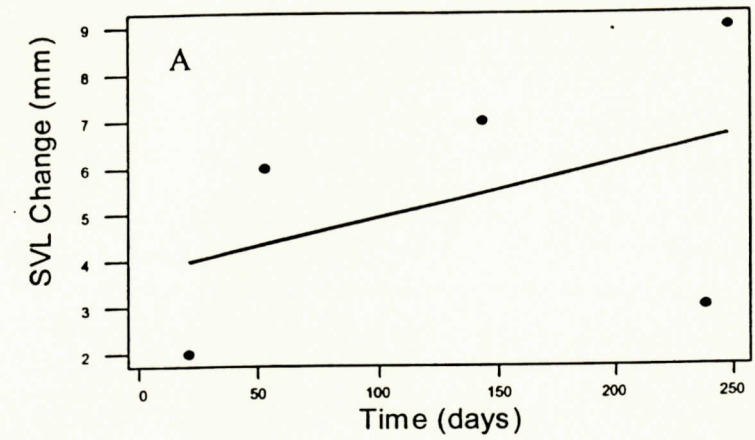
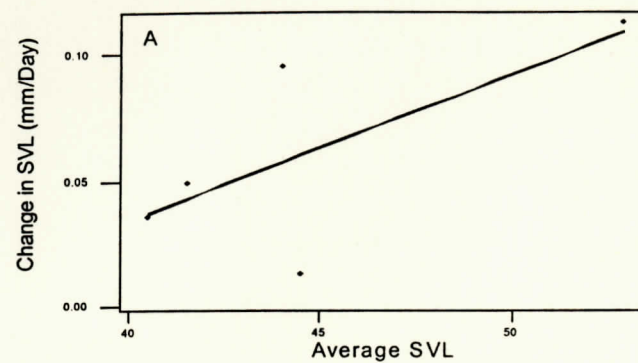


Figure 13. Relationship between time and growth in *Plethodon cylindraceus* (A), *P. wehrlei* (B), and *P. yonahlossee* (C).



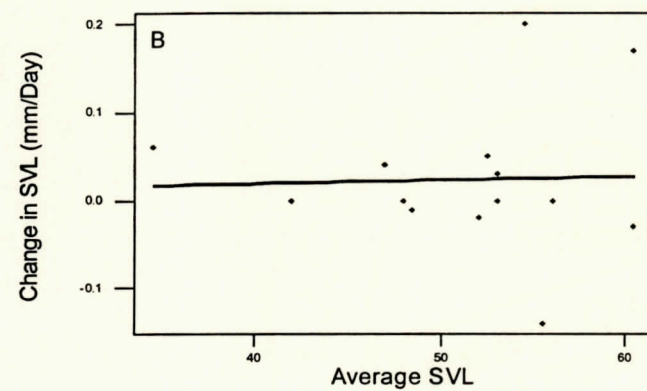


$$Y = -0.196 + 0.006X$$

$$r^2 = 0.466$$

$$N = 5$$

$$P = 0.204$$

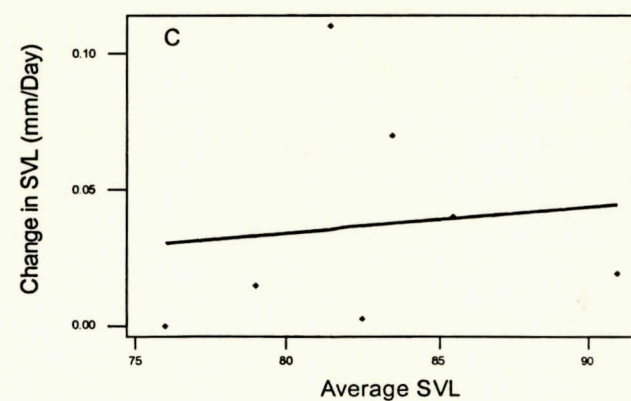


$$Y = .002 + 0.0004X$$

$$r^2 = 0.0001$$

$$N = 15$$

$$P = 0.903$$



$$Y = -0.04 + 0.001X$$

$$r^2 = 0.013$$

$$N = 7$$

$$P = 0.805$$

Figure 14. Relationship between SVL and growth rate in *Plethodon cylindraceus* (A), *P. wehrlei* (B), and *P. yonahlossee* (C).

of this transect. Average coverage was 1.6% with only one area of outcropping (50%) at approximately the 65m point. Soil exposure was less prominent along this transect and ranged from 0-95% with an average of 12.3%. Approximately half of the transect had no soil exposure, but two areas with higher exposure occurred at 35 and 90 meters along the transect. Herbaceous cover was also less prominent (0 – 40%,  $\bar{x}$  = 10.6%) along B. Highest values for herbaceous cover were from 0-30 meters.

Only habitat measurements of Transect A were compared to salamander abundance due to the small number captured in Transect B. All habitat variables were essentially useless as predictors of salamander abundance (encounters per 3 m interval). Only one species, *Plethodon cylindraceus*, had a weakly negative response to herbaceous cover (Pearson's  $r = -0.172$ ,  $P = 0.05$ ). No regression models (single factor or stepwise multiple factor) contributed significantly to explaining variation in numbers of salamander present. Correlation analysis did show that all salamander species co-occurred with one another at this scale. In 167 three-meter intervals, frequency of *P. wehrlei* positively correlated with that of *P. yonahlossee* ( $r = 0.329$ ,  $P < 0.01$ ) Abundance of *P. cylindraceus* correlated positively with that of *P. wehrlei* ( $r = 0.497$ ,  $P < 0.01$ ) and numbers of *P. yonahlossee* were correlated positively with *P. cylindraceus* ( $r = 0.387$ ,  $P < 0.01$ ).



## DISCUSSION

One goal of community ecology is to understand how communities are organized and function. In order to understand these aspects of a community, it is important to gather as much data as possible for all species present. In the case of a community of salamanders, these data would include annual, seasonal, and daily behavioral patterns of every species as well as characteristics of their population structures. Such concerted studies should provide essential data about how these animals interact with each other and their environments. These data are also needed to understand local distributions of rare species and the biotic and abiotic factors generating them.

The terrestrial salamander community at Saddle Mountain includes only eight species, and five of them were quite rare at the study sites. The three remaining species are sufficiently abundant to provide meaningful ecological and behavioral data. The focal species of the study, *Plethodon wehrlei*, is an animal at the southern end of its range where it seemingly occurs in widely isolated populations. The other two common species, *P. cylindraceus* and *P. yonahlossee*, are abundant over a much larger area in N.C. Saddle Mountain is the only documented site in the range of *P. yonahlossee* where it co-occurs with *P. wehrlei* (Hoffman, 1992). A study at this unique site will enable us to understand better the ecology of *P. wehrlei* and other

members of the community. Data from this study will enable us to answer some important questions about the community. Important issues about this salamander community include those aspects of the environment that determine the abundance, distribution, and behavior of each species. It is important to determine, as well, whether interspecific competition is an important factor in this community.

### *Activity patterns*

In a mark-recapture study, it is rarely possible to monitor any single individual through a whole day, season, or year. Nevertheless, frequency of encountering members of each species under different conditions throughout the study provides useful activity profiles. Each of the common species at Saddle Mountain had its own unique pattern of activity in time and space.

*Plethodon wehrlei* is active throughout the year at Saddle Mountain; but activity is reduced to a few juveniles in the summer. Adults are most abundant in October, March, and April and nearly absent in summer. This absence during the summer and coldest parts of winter is similar to other studies of *P. wehrlei* observed at lower elevations (Green and Pauley, 1987 *vide* Petranka, 1998). At higher elevations in West Virginia individuals were active on the surface from April until October (Green and Pauley, 1987 *vide* Petranka, 1998). Retreating from the surface during the summer is common in smaller *Plethodon* species, such as *P. cinereus*, *P. richmondi*, and *P. dorsalis* (Highton, 1972; Pfingsten, 1989a). *P. wehrlei* are found foraging later in the evening and under cooler conditions than the other species. Courtship in *P. wehrlei*



apparently takes place in the fall and oviposition probably occurs in late spring based upon finding gravid females in late winter and early spring. The small juveniles encountered in May and June were probably hatched from eggs laid the previous year.

Some *P. cylindraceus* were active throughout the year but few were on the surface during the colder parts of the year. This retreat appears to be real since numerous *P. wehrlei* were active during the winter months. *P. cylindraceus* emerges onto the surface to forage earlier in the evening than *P. wehrlei*. This species appears to be more common during drier conditions than the other two species. Small juveniles were seen in spring and summer. Courtship occurred in September, which was comparable to mid-August courtship seen in *P. glutinosus* at Mountain Lake, Virginia (Pope, 1950).

*Plethodon yonahlossee* exhibited the most restricted seasonal activity pattern and was absent during the cooler months from November to April. Peak abundance occurred from July through October. *P. yonahlossee* was active at about the same time of night as *P. cylindraceus*. *P. yonahlossee* was also active under drier conditions than *P. wehrlei*. Courtship in this species also occurred in September. Juveniles were found in the spring and summer as with the other two species.

The three species studied here had different activity patterns which were similar to observations already published for each species. *P. yonahlossee* and *P. cylindraceus* exhibited activity patterns typical for the eastern large *Plethodon* species

group (Highton, 1972). *P. wehrlei* has an activity pattern similar to many "small" species of *Plethodon* such as *P. cinereus*, *P. richmondi*, and *P. dorsalis* (Highton, 1972; Pfingsten, 1989a). This activity pattern was similar to that described for low elevation populations, while high elevation populations of *P. wehrlei* exhibited activity similar to the eastern large *Plethodon* species group (Green and Pauley, 1987 *vide* Petranka, 1998). Differences in assimilation efficiency may cause the different seasonal activity patterns. Assimilation efficiency is inversely related to ambient temperature in *P. cinereus* and *P. shenandoah* but metabolic rate of *P. cinereus* is directly related to ambient temperature. Salamanders in cold temperatures have high assimilation efficiency and low metabolic costs while those at warm temperatures have low assimilation efficiency and high metabolic costs. Thus, a salamander might not maintain a positive energy budget in the summer when temperature is highest (Bobka et al., 1981). The activity pattern and distribution of *P. wehrlei* suggest that it may share these traits. The species has a northerly distribution exceeded only by *P. cinereus* and *P. glutinosus* in the East (Highton, 1972). The separate emergence of juveniles in early summer is an unusual result that has not been documented and warrants further study.

*Plethodon* species are more likely to be on the surface when conditions are wet and retreat to deeper layers as the soil dries (Heatwole, 1962; Burton and Likens, 1975; Hairston, 1987). These salamanders apparently require wet conditions to



forage since animals have more prey in their stomachs during wet periods (Jaeger, 1972). All three species were most abundant when surface litter is wet. Of the three species, *P. cylindraceus* was active under the driest conditions. The species may be more resistant to drier conditions. However, the three species of *Plethodon* responded identically to relative humidity. All three species were most common on the surface when the humidity was highest. Under conditions of low relative humidity salamanders are often seen with their heads protruding from crevices (Spotila, 1972).

Data collected at Saddle Mountain allows examination of different models about how communities are structured. Differences in abundance of species may result from environmental or interspecific interactions. Differences in moisture preference may dictate the widely differing relative abundance of the three species seen on the eastern and southern aspects. South-facing slopes are typically warmer and drier than north-, east-, and west-facing slopes due to increased solar radiation. The amount of solar radiation on a given aspect varies with slope steepness, latitude, and season (Perry, 1994). The different proportions of salamanders observed on the two slopes may partially be a product of insolation-related environmental differences in early spring or late fall. There were slight differences in how species of *Plethodon* responded to moisture, but it seemed unlikely that these differences were large enough to serve as a basis for competition avoidance. Even differences in salamander abundance on different slopes were inconsistent with the hypothesis of interspecific competition

since numbers of all species were positively correlated on Transect A.

Another possible means of avoiding or reducing competition would involve separate temporal foraging niches among species. On Saddle Mountain *P. wehrlei* forages significantly later in the evening than do the other two species. Without information on temporal occurrence of food, it is unclear if the time separation would be beneficial or costly for this species. Later foraging may decrease metabolic costs since temperature is lower later (Bobka et al., 1981). Evidence on activity times was seemingly contradictory in regard to *P. yonahlossee*. At Saddle Mountain *P. yonahlossee* and *P. cylindraceus* emerged early after sunset. In Boone, NC, *P. yonahlossee* emerged later in the evening than congeners, *P. jordani* and *P. cylindraceus* (Harris, 1981). In another study in the same general area, *P. yonahlossee* had a relatively early peak of activity (Gordon et al., 1962). If temporal niche partitioning was occurring, it was different among these sites. A more careful study of this subject is warranted to document the extent of this phenomenon. None of these activity patterns suggests any definitive means of niche partitioning or even the existence of interspecific competition.

#### *Population characteristics*

Estimating numbers or densities of vertebrates living in any particular area is replete with problems. Some problems are associated with the creatures, themselves, while others are associated with the methodology. Both difficulties are evident for



Saddle Mountain *Plethodon* species. Salamanders were abundant at the site, but very few recaptures were recorded. Population estimates using the Schnabel methodology were similar to those using Schumacher-Eschmeyer methods. Different numbers of recaptures for the three common *Plethodon* species mean that population estimates are better (narrower confidence interval) for the species with the most recaptures (*P. wehrlei*, n = 14) and worse (widest confidence interval) for the species with the fewest recaptures (*P. cylindraceus*, n = 5). The estimates were similar from method to method, but the widths of the 95% confidence intervals were not. Confidence intervals were narrower for species with few recaptures (*P. cylindraceus* and *P. yonahlossee*) when using the Schnabel method. Conversely, the confidence interval using the Schumacher-Eschmeyer method was narrower for *P. wehrlei*, the species with the most recaptures. No confidence interval includes zero, and the minimal estimate for salamanders on Transect A was 1142.6 salamanders.

Both Schnabel and Schumacher-Eschmeyer estimators assume closed populations which was not the case at Saddle Mountain. A study extending 18 months certainly includes births and deaths. These changes in the populations probably resulted in an underestimate of the actual population sizes at the site. Differences in “catchability” and survivorship across age classes and species probably occurred as well but remained undetected in most studies, including the present one. The assumptions that markings applied by investigators do not impact survivorship or

behavior cannot be addressed in this study any more than in previous studies of *Plethodon* populations. Markings were apparent on some animals over 400 days and only minimal swelling was evident on some recaptures. In fact, one salamander’s recapture less than a week after marking suggests rapid return to normal behavior. These observations indicate that toe-clipping had a negligible effect on the individual.

The Saddle Mountain study was similar to several earlier studies of salamander density and biomass (Table 10). The estimates of 3476 and 4020 *P. wehrlei* per hectare at Saddle Mountain are much higher than the only published estimate of 1000/ha in Pennsylvania (Hall and Stafford, 1972). Despite this large difference in apparent density, biomass estimates for the two areas are much closer: 3.3-5.4 kg/ha at Saddle Mountain and 1.5-3.0 kg/ha in Pennsylvania (Hall and Stafford, 1972). Differences between the two sites were related to geographic variation in body size and density. Average SVL of *P. wehrlei* at Saddle Mountain was only 48.4 mm. The largest *P. wehrlei* at Saddle Mountain (61 mm) was about the same size as average animals in West Virginia (61.98 mm) and New York (60.39 mm) and considerably smaller than average individuals from Pennsylvania (66.12) (Hall and Stafford, 1972). The lower densities and larger animals farther north result in biomass estimates only half of those at Saddle Mountain. *P. wehrlei* density estimates at Saddle Mountain are similar to those for the similar-sized *P. jordani* farther south and west (Merchant, 1972; Howard, 1987; Table 10).



Table 10. Density estimates of *Plethodon* species in Eastern United States. (Values are extrapolated to salamanders/hectare if authors did not do so.)

Species	Estimate	Method Used	State	Author
<i>P. cinereus</i>	2583	Surface census	MI	Test and Bingham, 1948
<i>P. cinereus</i>	2118	Mark-recapture	PA	Klein, 1960
<i>P. cinereus</i>	496	Surface census	NH	Burton and Likens, 1975
<i>P. cylindraceus</i>	5167-5183	Mark-recapture	NC	Lapp, 1998
<i>P. cylindraceus</i>	40	Surface census	NC	Gordon <i>et al.</i> , 1962
<i>P. cylindraceus</i>	2300	Mark-recapture	NC	Merchant, 1972
<i>P. glutinosus</i>	4180	Mark-recapture	MD	Semlitsch, 1980
<i>P. glutinosus</i>	8440	Mark-recapture	PA	Semlitsch, 1980
<i>P. jordani</i>	220	Surface census	NC	Gordon <i>et al.</i> , 1962
<i>P. jordani</i>	8600	Mark-recapture	NC	Merchant, 1972
<i>P. jordani</i>	5168	Mark-recapture	NC	Howard, 1987
<i>P. wehrlei</i>	1000	Mark-recapture	PA	Hall and Stafford, 1972
<i>P. wehrlei</i>	3476-4022	Mark-recapture	NC	Lapp, 1998
<i>P. yonahlossee</i>	6249-7111	Mark-recapture	NC	Lapp, 1998
<i>P. yonahlossee</i>	70	Surface census	NC	Gordon <i>et al.</i> , 1962

Comparison of Saddle Mountain *P. cylindraceus* with those described in previous studies is not simple. *P. cylindraceus* is one of 13 species in the “*P. glutinosus* complex” (Highton, 1989). All previous ecological studies involved *P. glutinosus*, but most were from locales where only one species of the complex occurred. Data presented in Table 10 were assigned to the “species” most likely at the study sites. Morphological and ecological similarities among species suggest that comparisons are possible and meaningful across species. Estimates of *P. cylindraceus* were higher at Saddle Mountain (5129-5167/ha) than in the Great Smoky Mountains (2300/ha; Merchant, 1972). Density of *P. cylindraceus* at the site was comparable to *P. glutinosus* in Maryland (4180/ha) but lower than *P. glutinosus* in Pennsylvania (8440/ha; Semlitsch, 1980) or *P. jordani* farther south in North Carolina (Merchant, 1972; Howard, 1987; Table 10). All other density estimates for *P. cylindraceus* and *P. glutinosus* fell within the wide 95% confidence intervals of both Schumacher-Eschmeyer and Schnabel estimates from Saddle Mountain. The biomass estimate for *P. cylindraceus* at Saddle Mountain (14.1-20.3 kg/ha) is not comparable to any other estimates but certainly indicates that this species comprises a large and important portion of its local community.

*Plethodon yonahlossee* is the largest and most common (6249-7111/ha) *Plethodon* species at Saddle Mountain and contributes the greatest component (32-57 kg/ha) to the local salamander biomass. Unfortunately, there are no similar studies on



this species for comparison. This species is seemingly the most successful species on at least one slope on Saddle Mountain.

Salamander biomass has been reported in very few field studies. The few in which it was done used different techniques that are not exactly equivalent to those used here. In the Saddle Mountain study, several estimates of population and several methods of extrapolating those populations to biomass were compared. The range of estimates for total salamander biomass was from 24.7 kg/ha to 251.5 kg/ha. Hairston (1987) estimated that biomass for *P. jordani* and *P. glutinosus* averaged 8.3 kg/ha and ranged from 3.9 kg/ha to 12.5 kg/ha in the Great Smoky Mountains. Another estimate of salamander biomass (1.77 kg/ha) was for *P. cinereus* at the Hubbard Brook Forest in New Hampshire (Burton and Likens, 1975). Burton and Likens (1975) argue that *P. cinereus* represented a proportion of standing crop biomass in that forest more than two times that of passerine birds and equal to that of small mammals. *P. cinereus* must be an important component of the forest ecosystem in New Hampshire. Biomass estimates of *Microtus* species and *Mustella* species per hectare combined (4.1 kg/ha), in Michigan (Golley, 1960) were much smaller than the total salamander biomass at Saddle Mountain. Biomass estimates for the mouse, *Peromyscus polinotus* in Aiken, South Carolina are only .3 kg/ha (Odum et al., 1962). All three species of *Plethodon* at Saddle Mountain comprise biomass estimates at least an order of magnitude larger than these estimates of small mammals, *P. cinereus*, or combined *P. jordani* and *P.*

*cylindraceus*. This large salamander biomass indicates that terrestrial salamanders play an immensely important role in the Saddle Mountain ecosystem.

Salamanders on Saddle Mountain occurred in non-random, clumped distributions. This pattern was demonstrable statistically for the larger transect due to its larger sample size. Animals at the smaller site may have had a similar pattern but the effects could not be tested statistically. All three common species of *Plethodon* have correlated distributions so local areas within the plots have varying density ranges of salamanders. Overall estimates of density and biomass would have been sensitive to the relative amount of high and low-density areas. The large study site at Saddle Mountain may override the effect of preferred and avoided microhabitats. When information on patch size and distribution becomes available, it will be possible to produce better estimates of the actual numbers of salamanders in an area as large as a hectare. Patch size is not evident from the Saddle Mountain data. Individual salamanders do not move far between captures (5.8- 9.0 m means for the three species) thus, home ranges are rather small. Small home range sizes were also reported for *P. wehrlei* (Hall and Stafford, 1972), *P. cinereus* (Taub, 1961; Test and Bingham, 1948), *P. cylindraceus* (Merchant, 1972), and *P. jordani* (Madison and Shoop, 1979; Merchant, 1972).

Hall and Stafford (1972) noted that *P. wehrlei* in Pennsylvania preferentially occupied half of the study area where trees and/or exfoliating rocks were more



common. *P. glutinosus* and *P. jordani* had home ranges centered around large objects like rocks, logs, or stumps (Merchant, 1972). Other factors thought to be important aspects of habitat selection were moisture (Pauley, 1978) and competitive exclusion (Jaeger, 1971). Study sites were typically selected in areas that had high salamander densities, so it is uncertain how applicable the conclusions of these studies may be to larger areas.

At Saddle Mountain, the sites were selected because the rare and threatened *P. wehrlei* occurs there. Observed densities of the other species are not the result of preselection of "hot spots" and were higher than those for the selected species. Distributions of salamanders at this site are not explained by any habitat variables measured. It seems likely that additional, unmeasured aspects of the site produced the patchy distribution of salamanders. Unfortunately, the list of unmeasured variables was large. Differences in burrow number, size and presence of ovoposition sites may have been important as suggested by Hairston (1987). Evidence of niche differences among the species at Saddle Mountain was minimal. The only possibilities may have included differences in distribution or temporal and seasonal activity.

#### *Habitat Relationships*

Spatial distributions in plethodontid salamanders may be influenced by the dispersion of suitable microhabitats as well as by interactions among individuals (Wells, 1980). Salamander occurrence and density at Saddle Mountain was unrelated

to most physical aspects of the site (bedrock exposure, loose rock exposure, canopy closure, herbaceous plant cover, and soil exposure). *P. cylindraceus* was slightly less common when herbaceous cover was more common. *P. wehrlei* was not especially common in rocky areas at Saddle Mountain as they were in Pennsylvania (Hall and Stafford, 1972). As for *P. cinereus* in New Hampshire (Burton and Likens, 1975), salamander densities at Saddle Mountain were unrelated to any obvious environmental measures. Salamanders were neither randomly nor uniformly distributed at Saddle Mountain but demonstrated clumped distribution patterns in certain areas regardless of species. The suggestion that salamanders may be distributed according to availability of burrows, underground retreats, or oviposition sites (Hairston, 1987) cannot be easily tested. If *Plethodon* species partition spatial niches to reduce competition, the bases for this partitioning at Saddle Mountain are unclear since observations of all species were significantly correlated.

Knowledge about natural history of endangered species is important in making management decisions. This study provides basic biological information about *P. wehrlei*, a species protected in North Carolina. *P. wehrlei* is similar in habits to most other *Plethodon* in the region. It is smaller at the southern limit of its range and is active primarily during spring and fall. This knowledge is important because it allows managers to choose appropriate survey periods. *P. wehrlei* was not restricted to rock outcrops but occurred in habitats similar to other more widespread *Plethodon* in the



region. Further searches in the vicinity of Saddle Mountain and Hanging Rock should provide essential information on abundance and distribution of the species in the state. Hopefully, *P. wehrlei* will prove to be more widespread than initially thought.

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