

POPULATION FLUCTUATION, DISPERSION, AND DIEL ACTIVITY OF
THE CAVE
SALAMANDER, EURYCEA LUCIFUGA, IN SELECTED
TENNESSEE AND KENTUCKY CAVES

COLLEEN M. WHITE

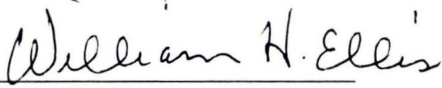
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I am submitting herewith a thesis written by Colleen M. White entitled "Annual Population Fluctuation, Dispersion, and Diel Activity of the Cave Salamander, *Eurycea lucifuga*, in Selected Tennessee and Kentucky Caves." I have examined the final copy of this thesis for form and content and recommend that it be accepted in partial fulfillment of the requirements for the degree of Master of Science, with a major in Biology.


A. Floyd Scott, Major Professor

We have read this thesis
and recommend its acceptance:


David H. Snyder
Second Committee Member


William H. Ellis
Third Committee Member

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POPULATION FLUCTUATION, DISPERSION, AND DIEL ACTIVITY OF THE CAVE
SALAMADER, *EURYCEA LUCIFUGA*, IN SELECTED
TENNESSEE AND KENTUCKY CAVES

A Thesis
Presented for the
Master of Science
Degree
Austin Peay State University

Colleen M. White

December 1997

DEDICATION

This thesis is dedicated to my good friends

Madeline and John Howard

whose loving care of my children has allowed me to complete this work.

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ABSTRACT

A year-long study of cave populations of *Eurycea lucifuga* was conducted from September 1994 through August 1995. Six caves (three in Montgomery County, Tennessee and three in Edmonson County, Kentucky) were studied. Abiotic conditions and physical descriptions of each cave and its adjacent epigeal habitat were recorded. Individual cave salamanders encountered within the survey zone of each cave were counted, measured, and assessed for the following: distance from entrance, height above floor, side of cave on which found, vertical and horizontal orientation, and microhabitat. Population changes recorded monthly throughout the year were nonrandom. In both regions populations peaked in early spring, declined in summer, and peaked again in either late summer or early fall. After this secondary peak, numbers of visible individuals declined gradually to a low in January and February. In both regions significant correlations were detected between monthly fluctuations in population size and monthly means of the following cave variables: relative humidity, air temperature, and available surface moisture. Of these factors, relative humidity correlated most strongly, followed in order by surface moisture and air temperature. Of the 421 individuals observed, 291 were on walls, 129 on the floor, and only one on the ceiling. When observed on vertical surfaces, salamanders were usually oriented horizontally (68%) with their directional heading (in or out of the cave) divided equally. Of those oriented vertically, 85% were observed with the head pointing upward. Surface moisture seemed to be the most important factor affecting both dispersion and choice of microhabitat.

To document diel activity, one cave from each region was selected and surveyed seasonally (once each in November 1994 and in February, May, and August 1995, all at mid-month during a 2-day period). Data, recorded at 2-h intervals, included the number of cave salamanders detected, inside and outside air temperature and relative humidity, and light intensity at the cave entrances. The number of individuals peaked at sunrise and sunset in what appeared to be a response to changes in light intensity.

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CHAPTER I

INTRODUCTION

The cave salamander, *Eurycea lucifuga* Rafinesque, was described in 1822 (Rafinesque, 1822). Although common throughout its range, relatively little field work has been done on this salamander. Only two comprehensive studies have been done to date. Banta and McAtee (1906) studied the life history of this troglophile, making detailed observations on its distribution, habits, habitat, development, coloration, and larvae within caves. However, this paper was descriptive only, and it was not until Hutchison's study (1956) that any attempt was made to quantitatively describe the ecology of *E. lucifuga*. In two studies, Hutchison (1956 and 1958) examined virtually all aspects of the species' ecology. Since Hutchison's work, additional observations have been made by several investigators concerning various aspects of the cave salamander's life history. Much of the resulting information, however, is incomplete or misleading and needs clarifying through further research. The purpose of this investigation was to document seasonal and daily fluctuations in the size of the visible populations of *E. lucifuga* occupying the twilight zones of caves, and to analyze the distribution, orientation, and microhabitat selection of the individuals encountered.

Literature Review

Distribution

Eurycea lucifuga occurs primarily in limestone areas from southern Missouri, Illinois, Indiana, and southwestern Ohio to northwestern Georgia and central Alabama, and from western Virginia west through southeastern Kansas and northwestern Oklahoma (Conant and Collins, 1991.) It is unclear whether its restriction to limestone areas is a result of some chemical property of the substrate itself, or as Hutchison (1958) suggests, that limestone's high solubility rate makes it the most likely substrate to produce caves attracting the species. Vernberg's (1955) study examining the reactions to pH of *Plethodon cinereus* and *P. glutinosus* in the field indicated that in these plethodontids pH was of little or no importance in substrate choice. Based on the documentation of two individuals collected in Georgia in an

area of crystalline rock far removed from any limestone area. Hutchison (1958) suggests *E. lucifuga* may be found on other rock types, providing favorable ecological conditions are met (any cave formed by means other than solution). I have found only one account of *E. lucifuga* documented on a substrate other than limestone. In this account (Pauley and Bailey, 1993) cave salamanders, previously thought to be restricted to natural caves in limestone areas in West Virginia, were found in nine abandoned coal mines in sandstone formations. In addition to being found in caves, *E. lucifuga* populations exist in adjacent terrestrial epigean habitats where they are often found under logs, leaf litter, and piles of debris (Guttman, 1989; Redmond and Scott, 1996). In fact, in some localities such as West Virginia, they are most often encountered away from caves (Green et al., 1967). A notable exception is in Mississippi, where Cliburn and Middleton (1983) found no individuals in surface habitats. They suggested *E. lucifuga* populations in the region are relics of a larger Pleistocene distribution, and that the species took refuge in caves as the local climate became warmer following northward retreat of the glaciers..

Seasonal Population Fluctuations

Although several authors have recorded the dates of individual observations, Ives (1951b), who studied a Tennessee cave for a full year, was the first to note seasonal changes in the size of the visible population of *E. lucifuga*. He recorded between one and ten cave salamanders for each month except in February, when the population peaked at between 10 and 20 individuals. An abstract describing a more recent study of 5 caves in Trigg County, Kentucky (Walston and Wilder, 1977) states data were collected on the seasonal abundance of *E. lucifuga*, but gives no details. Results published by Hutchison (1958) and Williams (1980), describing seasonal abundance of *E. lucifuga* in caves, state that the visible populations of *E. lucifuga* peaked from April through June, declined during July and August, and remained low throughout the winter and fall months.

Although observations by Hutchison (1958) and Williams (1980) may represent the true nature of *E. lucifuga*'s population fluctuations and distribution within caves, they probably represent also local behaviors driven by conditions that vary across the range of the species. Hutchison's (1958) study was confined to Giles County, Virginia, and Williams' (1980) study dealt with one cave in Carbondale, Illinois. In addition, design flaws (discussed in detail later) in these studies make their conclusions suspect.

Distribution, Orientation, and Microhabitat

When found in caves, *E. lucifuga* is observed most often in the twilight zone (Ives, 1951a; Myers, 1958; Barr, 1961; Williams, 1980). Green et al. (1967) suggest this may simply reflect the twilight zone's accessibility rather than any preference for this zone. Several authors have observed *E. lucifuga* beyond the twilight zone (Lawhon, 1969; Knight, 1969; Cliburn and Middleton, 1983). Peck and Richardson (1976) observed individuals throughout caves, but noted that population densities peaked in the twilight zone during spring and summer.

Documentation of microhabitat selection of *E. lucifuga* within caves has been limited to nonquantitative, anecdotal accounts. They have been observed under rocks, in crevices, on walls and ceilings, and around pools (Guttman, 1989).

Diel Activity

Literature accounts of diel activity patterns for cave populations of *E. lucifuga* also conflict. Hutchison (1958) determined that under laboratory conditions, *E. lucifuga* is arrhythmic. Field observations by both Hutchison (1958) and Sinclair (1950) seem to support these findings. Other investigators disagree, stating that cave populations of *E. lucifuga* are nocturnal (Green et al., 1967) or crepuscular (Besharse and Brandon, 1974). Again the lack of controlled field studies indicates that further research in this area is warranted.

Goals and Objectives

The goals of this study were to: 1) document and compare monthly fluctuations in the size and distribution of the visible populations of *E. lucifuga* in the twilight zones of selected Tennessee and Kentucky caves; 2) determine microhabitat preferences of individuals encountered; and 3) monitor, on a quarterly schedule, the diel activity of individuals in one cave from each of the two regions.

These goals involved the following specific objectives:

- 1) Obtain all existing published information on the life history of *E. lucifuga*.
- 2) Locate for study three caves in each region that support visible populations of *E. lucifuga*.
- 3) Characterize each cave and surrounding area in terms of physiography, geology, vegetation, and human use (historical and current).
- 4) Visit each study cave monthly for one year to obtain data on:
 - air temperature, relative humidity, and type of precipitation occurring (if any) outside each cave
 - air temperature, relative humidity, pH, and relative moisture level inside the twilight zone of each cave
 - the number, sex, snout-vent-length, location within the cave, orientation (horizontal, vertical, facing in or out of cave), and microhabitat (ledge, crevice, under rock) of visible individuals.
- 5) Select one cave from each study area and conduct quarterly surveys of *E. lucifuga*'s diel activity in each cave.
- 6) Analyze the data for general trends and differences in population fluctuations, distribution, and microhabitat use within and between caves of the two regions.
- 7) Compile additional noteworthy observations of *E. lucifuga* and the cave environment to support and augment existing knowledge.

Significance of Study

Renewed interest in amphibian monitoring has emerged as a result of speculation about worldwide amphibian declines (Wake, 1991; Sarkar, 1996). Long-term amphibian monitoring efforts are now being implemented to assess the validity of decline claims, and to determine, if possible, the factors causing the decline (Crump et al., 1992; Blaustein and Wake, 1995). The Center for Field Biology at Austin Peay State University was contacted by the University of North Carolina at Asheville to participate in a federally funded project aimed at implementing long-term amphibian monitoring programs at selected national parks in the southeastern United States. Mammoth Cave National Park (MCNP) was the focal point of the Center's efforts. One of the study's objectives was to locate, and monitor annually, stream-side salamander populations. Despite an exhaustive search for salamanders in several streams located within the park, researchers were unable to find populations large enough for study (Petranka et al., 1995). Given the karst nature of the terrain and the vast network of caves that exist within the park, monitoring cave amphibian species was suggested as an alternative, since caves are eventually subjected to many of the same factors that affect terrestrial and stream-side species. This study was designed and conducted to serve as a pilot project for the long-term monitoring of cave amphibians at MCNP.

Caves are relatively simple ecosystems and as such are excellent natural laboratories, characterized by few variables, simplified food webs, and minimal physiochemical fluctuations (Hobbs, 1992). An understanding of *E. lucifuga* population fluctuations, distribution, microhabitat selection, and diurnal activity patterns is needed before efficient monitoring of this species can occur. Determining how epigean and cave conditions affect populations will help resource managers ensure the continued existence of *E. lucifuga* as an integral part of cave fauna.

In addition to the general significance mentioned above, results of this study may prove valuable in understanding the influence of entrance air-locks on cave-dwelling populations of *E. lucifuga*. Since the completion of my study, air-locks have been installed in several cave entrances at MCNP. Two of the caves in my study (Great Onyx Cave and Austin Cave) now have these structures. As part of the long-term study mentioned above, data are still being collected at these two caves. The information in my

study will serve as baseline data in comparing population fluctuations and dispersal within these caves both before and after installation of the air-locks. An understanding of these effects may in turn have far-reaching implications for management of caves in general.

CHAPTER II

THE STUDY AREA

Selection of Study Caves

Six caves-- three in Montgomery County, Tennessee, and three in Edmonson County, Kentucky-- were selected for study. This followed a preliminary survey of caves in the two regions for viable populations of *E. lucifuga*. Choice of number and location of caves was intended to provide an adequate sample size and data for comparison between the two widely separated (ca. 135 km) locations. By comparing results from the two localities, something of the geographical dependence on visible population trends might be revealed.

Caves within each of the two areas were chosen based on whether they supported a population of *E. lucifuga*, their accessibility, and their comparative uniformity. An accessible cave was one whose entrance could be reached alone safely without special equipment or undue hardship. Comparative uniformity meant that caves should have similar tunnel-type entrances, and twilight zones. This helped minimize the variability of entrance type, and maximize the likelihood of a more thorough census. Although entrances and twilight zones of study caves varied in width, height, and length, all could be searched quickly and thoroughly, ensuring uniformity throughout the year-long study.

Description of Study Caves and Their Environs

Tennessee Region

The Tennessee study caves (Barnett, Dunbar, and Woodson), were in Montgomery County, on the north central border of Tennessee (Fig. 1). Physiographically, Montgomery County is part of the Interior Low Plateaus Province, Highland Rim Section, Pennyroyal Plain and Western Highland Rim Subsections (Fenneman, 1938). My study caves were in the southern portion of the Pennyroyal Plain subsection, underlain primarily by St. Louis and Warsaw limestones of Mississippian Age (Hardeman et al., 1966).

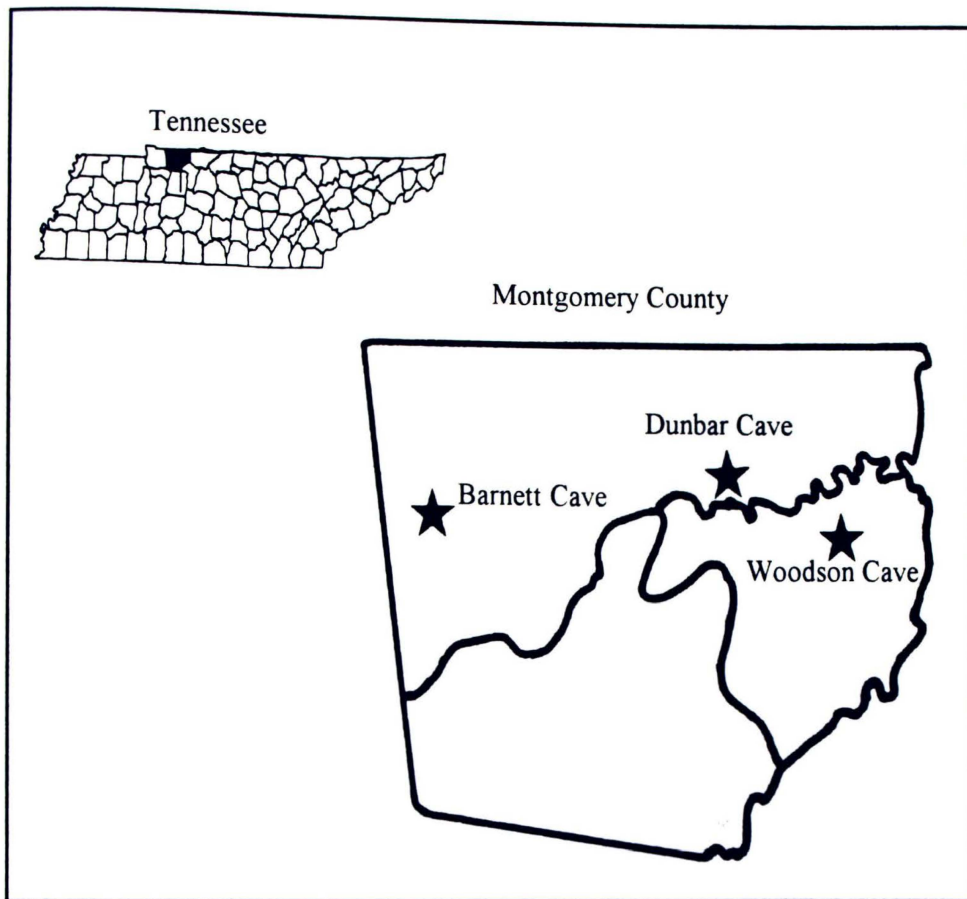


Figure 1. Montgomery County, Tennessee, showing locations of study caves.

In this area, which is just south of an area of sinkhole plains, karst features and caverns are common (Quarterman and Powell, 1978).

Montgomery County is drained by two rivers: the Cumberland River which enters from the southeast and flows northwest, and the Red River, which enters from the northwest and joins the Cumberland River near the county's center.

The county is within the Western Mesophytic Forest Region as described by Braun (1950). The woody vegetation consists primarily of oaks and hickories. Stream banks, bottomlands, ravines, and moist slopes support such species as American beech, yellow-poplar, boxelder, sugar maple, green ash, sycamore, eastern cottonwood, and various elms (Duncan and Ellis, 1969 and Chester, 1986).

All of the Interior Low Plateaus Province is located within the humid mesothermal climate region of Koppen (Trewartha, 1954). Although the entire province is considered a warm, temperate rainy area with rainfall distributed evenly throughout the year, both middle Tennessee and the southern portion of Kentucky experience both winter and summer temperature extremes, with heaviest rainfall occurring during the winter months. The local climate is characterized as humid and mesothermal in nature (Thornwaite, 1948). Average total yearly rainfall at Clarksville (county seat of Montgomery County) is 126 cm with a mean yearly temperature of 14.67°C. Coldest average temperatures occur in January (2.05°C), and the warmest (25.9°C) in July (NOAA, 1983).

Caves in Tennessee

Barnett Cave. Barnett Cave occurs within the Warsaw Limestone and is located at 36°31'04"N latitude by 87°33'35"W longitude (USGS Topographic Quadrangle: Woodlawn, TN). It is 2.25 km south of U.S. Hwy. 79 on Cooper Creek Rd., approximately 91.4 meters west of Cooper Creek and 91.4 meters east of Cooper Creek Road, at an elevation of 134 meters (Barr, 1961).

Barnett Cave (also known locally as Cooper Creek Cave, Barnett Woods Cave, and Foster Cave) is in Barnett Woods Natural Area, a 28-hectare tract purchased by the Barnett family in 1925 and sold to the Tennessee Nature Conservancy in 1981 (Chester, 1986). In the past the cave was mined for saltpeter,

as evidenced by the extensive digging and many niter vat casts (Barr, 1961). Currently, the cave is a favorite of amateur spelunkers. Vandalism has occurred and continues to occur. Recent evidence of regular human gatherings was visible monthly, in the form of beer cans, newly painted graffiti, and campfire remains.

The entrance to Barnett Cave consists of a large, east-facing arch 3 m high and 11 m wide. Upon entering there is a large, semicircular room that extends for approximately 8 m. Here, the room ends and branches into two narrow passages, one on either side. The left branch, a crawl-way only, eventually connects by way of a wet-weather stream to the right branch (Barr, 1961). The right branch continues northwest, then southwest, for 74 m. There it fills with mud and joins the stream, with a ceiling height of about 0.7 m. The survey zone of this cave consisted of the entrance area directly below the arch, the large semicircular room, and the right branch to where it meets the stream. Total strait-line distance of the survey zone was 82 m (Fig. 2).

Dunbar Cave. Dunbar Cave is located within the St. Louis Limestone and is located at 36°33'11"N latitude by 87°18'22"W longitude (USGS Topographic Quadrangle: Clarksville, TN). It is in Dunbar Cave State Park, on Dunbar Cave Rd. 1.76 km east of that road's junction with U.S Hwy. 79. The entrance to Dunbar Cave is at an elevation of 131 meters, located at the base of a limestone bluff, above a spring that forms a tributary to the Red River.

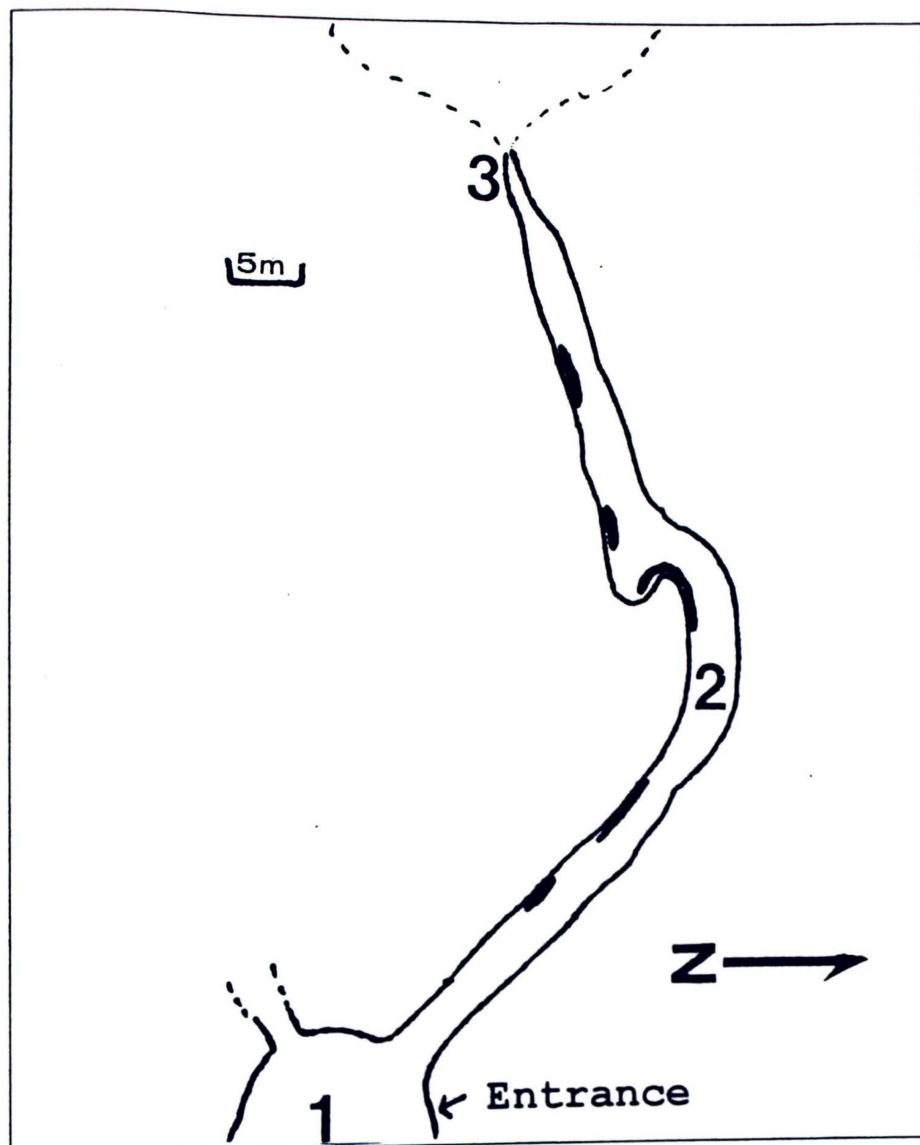


Fig. 2. Map of Barnett Cave survey zone. Abiotic data stations are numbered 1 through 3.

The following historical data were obtained from Ellen Finnety (pers. comm.) of Dunbar Cave State Park. The cave area was purchased by Isaac Peterson in 1790. From 1843-1868 it was used as a food storage facility, and during the Civil War was occupied by Union troops. Commercialization of the cave began in 1880, and it hosted its first dance in 1883. By 1884 a hotel existed in association with the cave, and nearby Idaho Springs Resort Area was being leased. Its most famous owner, Roy Acuff, owned the cave during the 1960s when socialization at the cave was in its heyday. The cave changed ownership and eventually went into probate. It was acquired by the state in 1973. The electric lighting that had been installed was destroyed by vandalism sometime between 1961 and 1973. Since becoming property of the state, attempts have been made to restore the cave to a more natural condition. The entrance was fitted with a locked steel gridwork gate. The park hosts weekly guided tours throughout most of the year.

The cave is located at the bottom of a limestone bluff, directly above an emerging stream which has been dammed to form Swan Lake. The large, semicircular entrance below the bluff overhang is 3.0 m high and 10.7 m wide. Towards the rear of the entrance a tunnel-like passageway leads to the main cave. This beginning of the passageway is fitted with the locked gate of steel gridwork. The passageway to the natural level of the cave runs straight for 10 m, at which point it widens and turns 30° left, descending gradually for an additional 10 m where it opens into a large room. The survey zone of this cave consisted of the first 20 m beyond the entrance arch, beginning at the gate and ending just prior to the large open room (Fig. 3).

Woodson Cave. Woodson Cave is located 1.9 km northeast of Sango, on the east side of North Woodson Road in a sink at an elevation of 167.6 meters. It occurs within the St. Louis Limestone at 36°31'01"N latitude by 87°12'12"W longitude (USGS Quadrangle: Sango, TN).

The mouth of the cave is located in a sink directly under North Woodson Road. This cave is the private property of Mr. Harlin Edwards, a member of the Woodson family by marriage.

A wet-weather stream draining the surrounding sink runs directly into the cave. The entrance is 3.7 m high and 7.6 m wide. The entrance narrows to a tunnel 2m wide by 2.5 m high. Continuing to

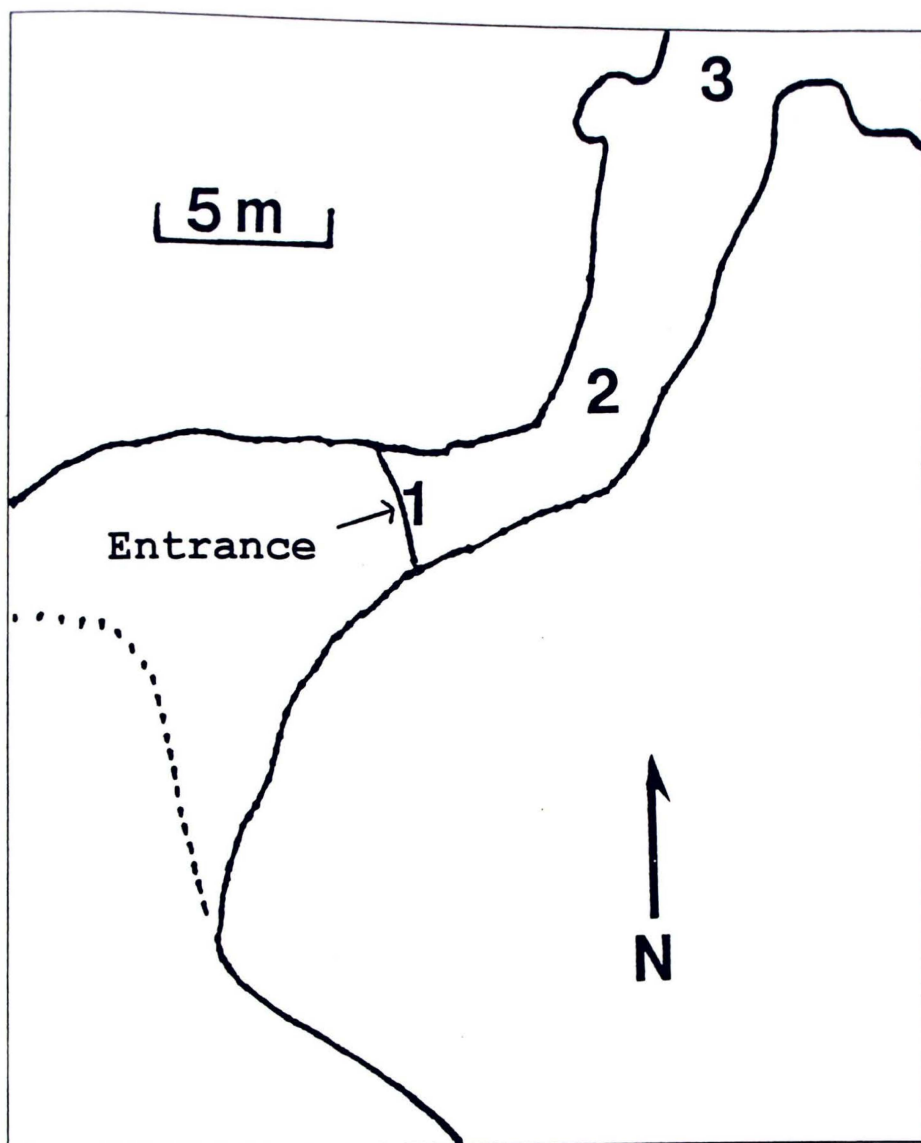


Fig. 3. Map of Dunbar Cave survey zone. Abiotic data stations are numbered 1 through 3.

narrow as it runs westward, this tunnel eventually becomes choked with stream fill and carried debris. The survey zone began at the entrance just below the rock overhang, and continued for a straight-line distance of 32 m to the choke point (Fig. 4).

Kentucky Region

All three Kentucky caves (Austin, Great Onyx, and Crystal) were in Edmonson County, just south of the Green River in Mammoth Cave National Park (Fig. 5).

Edmonson County is located in the Interior Low Plateaus Province, Shawnee Hills Section, Mammoth Cave Plateau Subsection (Fenneman, 1938). Area ridges are capped with Big Clifty and Hardinsburg sandstones located between dry, karst valleys that have downcut into the Girkin Formation (Quarterman and Powell, 1978). Many intact and large collapsed sinkholes occur in the karst valleys (Quarterman and Powell, 1978).

The Green River runs through the center of the county from east to west. The area south of Green River, where all three study caves were located, has no natural surface drainage; instead the surface water runs into numerous sinkholes to be carried to the Green River by subterranean streams (Hibbard, 1936).

The vegetation of some areas in Edmonson County are described as mixed mesophytic (Quarterman and Powell, 1978). Cover types on the south side of Green River are sugar maple, post oak, blackjack oak, scarlet oak-black oak, southern red oak-red oak, beech-sugar maple, beech, and river birch-sycamore.

Like Montgomery County, the general climate of Edmonson County is of the humid, mesothermal type (Trewartha, 1954). The Mammoth Cave area receives an average of 131 cm of rain annually, and has a mean air temperature of 13.67°C. The coldest (1.33°C) month is January and the warmest (24.39°C) is July (NOAA, 1983).

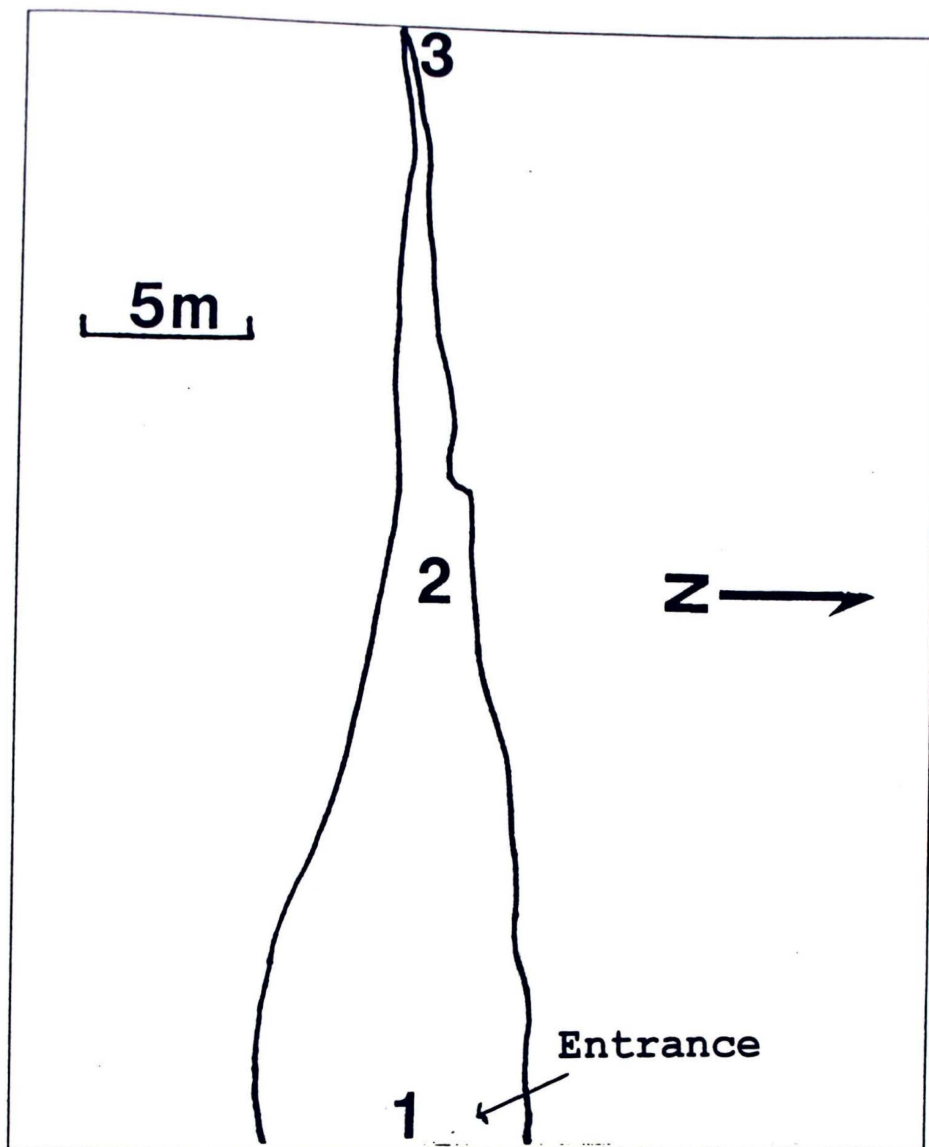


Fig. 4. Map of Woodson Cave survey zone. Abiotic data stations are numbered 1 through 3.

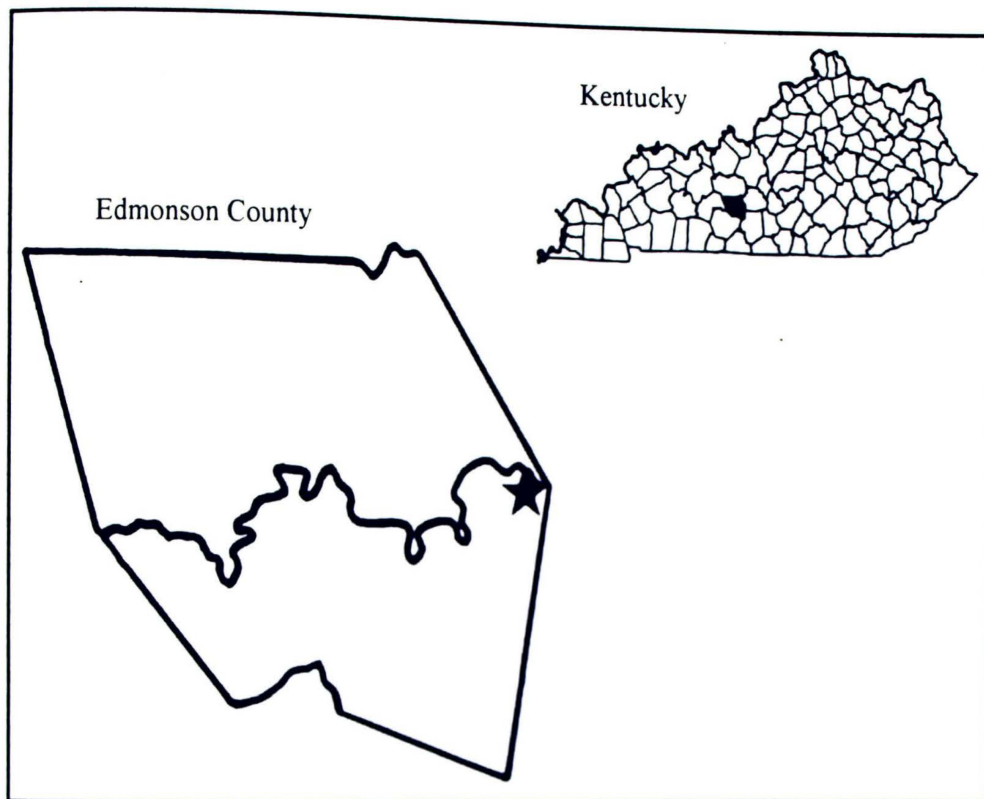


Figure 5. General location of Kentucky study caves (Austin, Great Onyx, and Crystal) in Edmonson County.

Caves in Kentucky

Austin Cave. Austin Cave is at 37°12'21"N latitude by 86°03'48" W longitude (USGS Topographic Quadrangle: Mammoth Cave, KY). It is just south of the Green River on the east slope of Three Sisters Hollow, 0.8 km northwest of Flint Ridge Ranger Station, at an elevation of 158.5 meters.

The following historical information was obtained from Mammoth Cave National Park Ranger John Frye (pers. comm.). The entrance to Austin Cave is manmade, having been blasted and drilled in 1956 to facilitate exploration of the Flint Ridge Cave System. The location was chosen through detailed subsurface and surface closed survey loops. The cave, intended for research purposes only, has never been open to the general public.

The entrance is at the top of a "ramp-type" ascent from the trail. Beneath the overhang the entrance is 1.9 m high and 2.0 m wide. Just inside the entrance a fairly uniform tunnel, with a height of 1.7 m and width of 1.0 m, extends 14.0 m to where a solid steel door is set in the stone wall. In the door is a 10-cm diameter hole for reaching the lock that allowed limited airflow. Beyond the door, the tunnel continues for another 12.0 m, where it ends abruptly at a shallow pit. From the bottom of the pit one level of the cave can be reached; another can be reached by crossing over the pit. My survey zone in this cave began directly under the overhang at the entrance and extended to the edge of the pit, a distance of 26 m (Fig. 6).

Great Onyx Cave. Great Onyx Cave is at 37°13'08"N latitude by 86°04'43" W longitude (USGS Topographic Quadrangle: Mammoth Cave, KY). It is just south of the Green River at the end of Great Onyx Cave Road, off of Flint Ridge Rd., on a steep slope at an elevation of 182.9 m. The following historical data were obtained from Mammoth Cave National Park Ranger John Frye (pers. Comm.). The artificial entrance was opened in 1915 after owners suspected the existence of a cave in that area. This first entrance was soon filled, and a second entrance opened, presumably to facilitate access by tourists. Later the cave was owned and shown by the Cox family. In 1961 it was acquired by Mammoth Cave National Park, and the electrical wiring was removed. During the tourist season the cave is a scheduled "lantern tour" and may also be toured by special request.

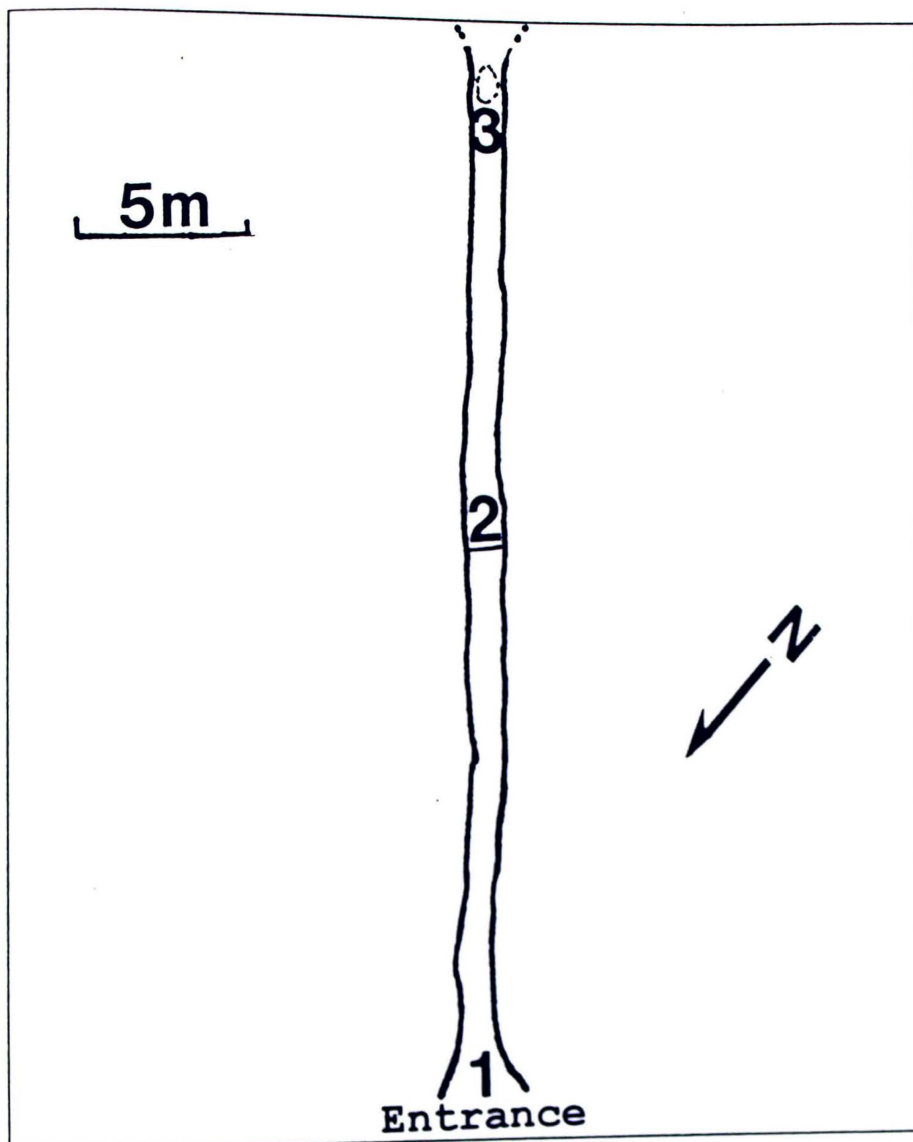


Fig. 6. Map of Austin Cave survey zone. Abiotic data stations are numbered 1 through 3.

The entrance is in an above-ground building with a solid steel door. Gaps around the door allow for limited airflow and passage of small animals. The entrance room is 2.3 m high and 5.0 m square. A narrow concrete stairwell descends steeply from the back of the room for about 8 m. There the stairs stop at a wide platform where the cave opens up. In this cave, my survey zone extended from a just inside the entrance room door to the bottom-most stair, a distance of 13 m (Fig. 7).

Crystal Cave. Crystal Cave is at 37°12'42"N latitude by 86°03'18"W longitude (USGS Topographic Quadrangle: Mammoth Cave, KY). It is south of the Green River, at the end of trail leading north from Flint Ridge Ranger Station, at an elevation of 221 m.

Little is known of the history of Crystal Cave. According to John Frye (pers. Comm.), the cave was opened and shown by the Collins family in the late 1910s and early 1920s. It was later owned by Bill Austin, from whom it was acquired by the park in 1961.

The entrance is at the bottom of a small sink and is approximately 1.9 m high and 1.1 m wide. From the entrance a passage continues for 3.8 m where it is blocked by an unlocked, solid steel door. Beyond the door lies a large rectangular room, 3.6 m high and 5.8 m wide, that extends back another 15 m to where a solid steel wall and locked door cross the width of the room. My survey zone for this cave began at the entrance just under the overhang, and extended 19 m to the solid steel wall (Fig. 8).

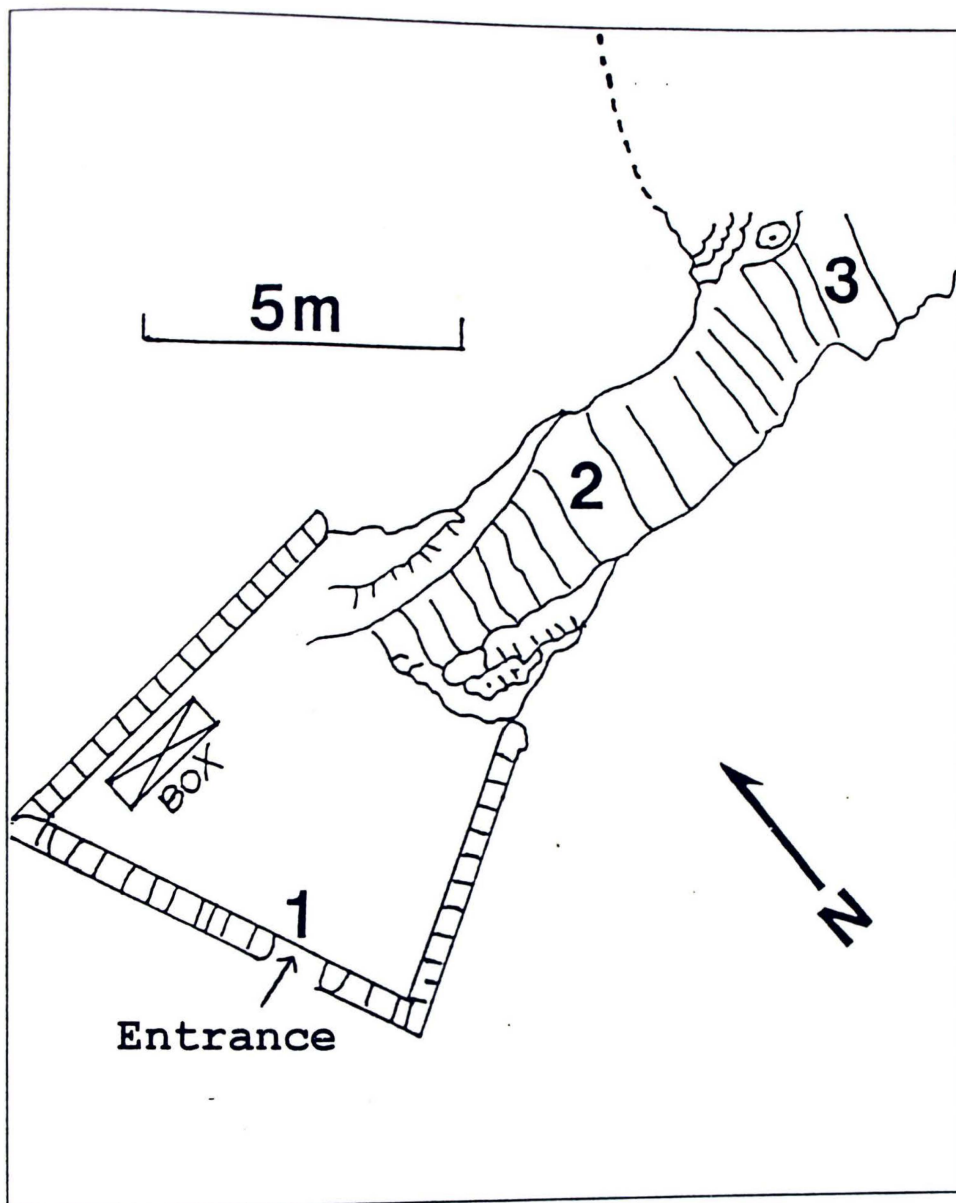


Fig. 7. Map of Great Onyx Cave survey zone. Abiotic data stations are numbered 1 through 3.

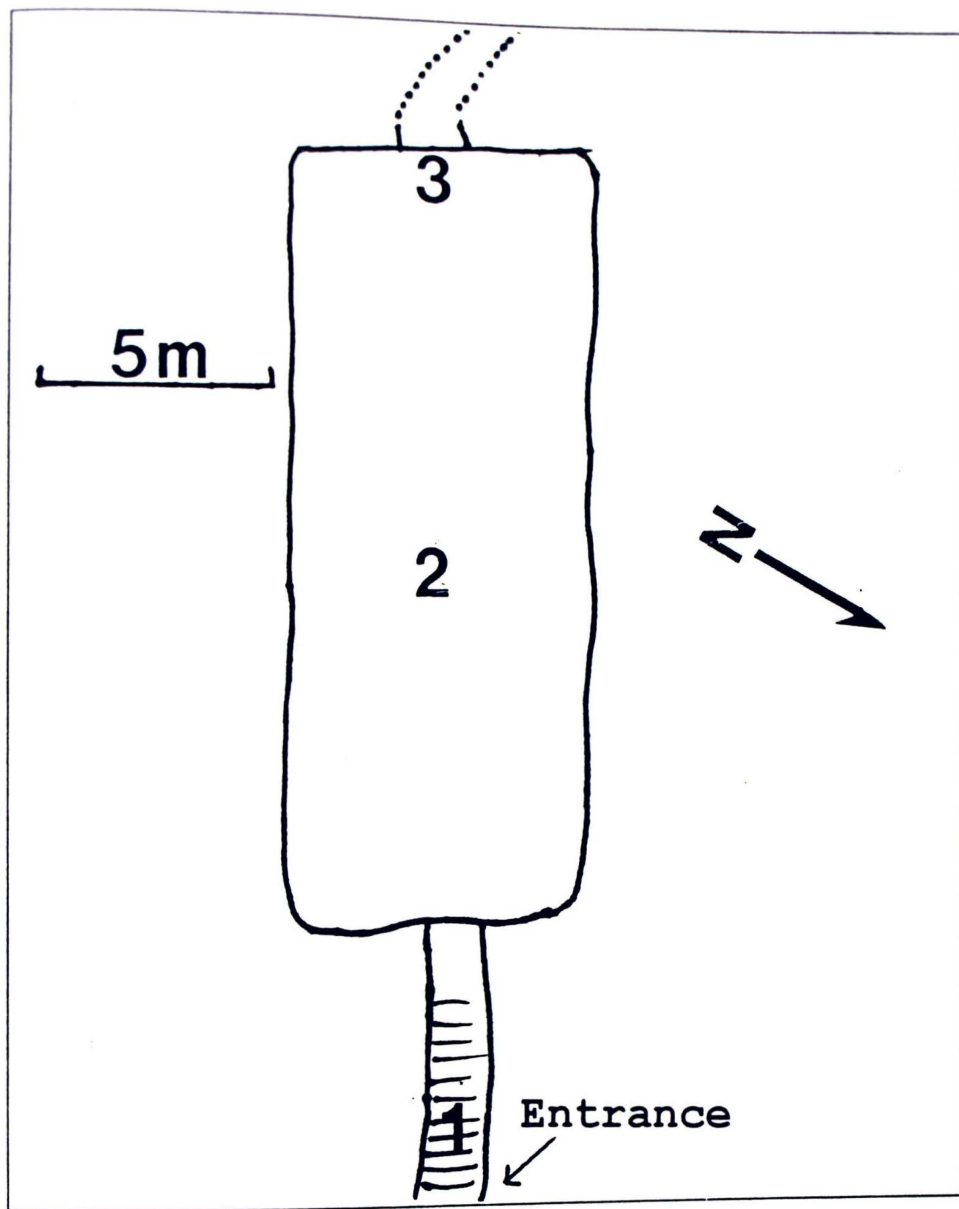


Fig. 8. Map of Crystal Cave survey zone. Abiotic data stations are numbered 1 through 3.

CHAPTER III

METHODS

Monthly Surveys

Duration and Frequency

Beginning in September 1994, all six caves were visited once a month for twelve months. All visits occurred during the first full week of each month. The Tennessee caves were surveyed first, followed by the Kentucky caves one day later. The caves in each region were always surveyed in the same order at approximately the same time of day. An example of the data sheet used in this portion of the study is in Appendix A.

Abiotic Data

At a fixed location outside each cave, air temperature and relative humidity were measured immediately before and after each survey. Readings were taken with a mercury bulb thermometer and wheel hygrometer, which were allowed to acclimate prior to the initial readings and left in place while the surveys were being conducted. Precipitation (rain or snow) at the time of the survey was described as light, moderate, heavy, or none. Monthly rainfall data were obtained from the nearest official weather station (Clarksville Sewage Plant, Clarksville, TN; and Mammoth Cave National Park Weather Station, Mammoth Cave, KY) in each region.

Inside each cave, replicate readings of abiotic data were taken at three locations during each survey. Their locations, designated stations 1-3, were at the beginning, midpoint, and end of each survey zone, and differed in length from cave to cave. Air temperature and relative humidity were read with a digital thermometer/hygrometer. Chemical test strips were used to estimate pH of any running, dripping, or pooled water. Surface moisture was rated using a scale of 1 to 4, with 0 being dry, 1 damp, 2 moist, 3 wet, and 4 dripping and/or standing water.

Biotic Data

Beginning at Station 1 and working slowly in to Station 3, all accessible parts of the survey zone in each cave were systematically searched for *E. lucifuga*. The following data were recorded for each individual encountered: snout-vent-length (SVL); straight-line distance from entrance; side of cave on which found (left or right, looking inward); orientation of body (horizontal or vertical); orientation of head (up, down, outward, or inward); and microhabitat (floor, ceiling, wall, under rock, in crevice, etc.). In order to minimize any negative impacts that might result from handling the specimens (as described by Hutchison, [1958] and Williams, [1980]), all data on individuals were collected without actually touching the salamander. Snout-vent-length was recorded to the nearest 0.5 cm by placing a millimeter rule as close to the animal as possible. This was usually easy, and I believe accurate, but some individuals were curled up or partially hidden. In these cases the recorded SVL was annotated as an estimate only. Straight-line distance from entrance was measured with a tape to the nearest 0.1 m. I had intended to determine the sex of each individual, using the male characteristics as stated by Guttman (1989). This proved to be impractical without touching the animal, and I therefore abandoned the effort after the first few cave surveys. Miscellaneous observations (regenerating tail, unusual pigmentation, feeding behaviors, etc.) of each individual were also recorded when appropriate.

Statistical Analyses

In addition to plotting frequency histograms of all nominal data sets, and calculating descriptive statistics (mean, mode, median, range, standard deviation, and standard error) for all continuous data, two inferential tests were used. The Chi Square One-Sample Goodness of Fit Test was used to determine if the monthly frequencies of individuals over the 12-month period in each region deviated significantly ($p=0.05$) from a null hypotheses assumption of equal numbers per month. The Spearman Rank Correlation Coefficient (r_s) was used to correlate monthly population fluctuations in each region with corresponding changes in selected abiotic factors, and to compare various abiotic factors to each other.

Twenty-Four Hour Surveys

Duration and Frequency

Four 24-hour surveys, one in each season (November 1994, and February, May, and August 1995) were conducted at Dunbar and Great Onyx caves. Since all six caves remained relatively undisturbed during any 24-hour period, these caves were chosen because of their ease of access and known numbers of *E. lucifuga* present. The surveys occurred mid-month in order to maximize the population's recovery time between the monthly surveys. Dunbar Cave was always surveyed first, followed by Great Onyx Cave 24 hours later. Searches for *E. lucifuga* were made and data recorded every two hours, beginning at 0600 and ending at 0400 the following day. A sample data sheet used in this phase of the study is presented in Appendix A.

Abiotic Data

Before each 2-hour check, a mercury thermometer and wheel hygrometer were used to record air temperature and relative humidity at a fixed location outside each cave. Instruments were allowed to acclimate for 30 minutes prior to the initial readings, and left in place for the entire 24-hour period. General weather conditions occurring during the survey were also recorded. Because checks were made of the caves every 2 hours, I felt it was necessary to minimize any effects my presence might have on the *E. lucifuga* in the two caves. Therefore, abiotic data were collected from Stations 1 and 3 only. These data consisted of air temperature, relative humidity, and light intensity (at station 1 only). Air temperature and relative humidity were obtained with a digital thermometer/hygrometer. Light intensity was measured on the first survey with a General Electric Light Meter (Type 214). This instrument was replaced on subsequent surveys with a LI-COR Quantum/Radiometer/Photometer (Model LI-189), which was more sensitive and better able to detect the minor changes in light levels occurring in the entrance area of each cave.

Biotic Data

Moving quietly and quickly (average 7 to 15 minutes, depending on the cave) through the survey zone, visible *E. lucifuga* were tallied and any unusual or otherwise noteworthy observations recorded. Notes on the number of *E. lucifuga* just beyond the survey zone (in and out) were also taken. To minimize disturbance, no measurements of individuals or their positions in relation to cave entrance, floor, ceiling, or walls, were taken.

Statistical Analyses

Results from the 24-hour surveys were analyzed in two ways. The Chi Square Goodness of Fit Test was used to determine if numbers of individuals observed every 2 hours over each 24-hour period deviated significantly ($p=0.05$) from a null hypothesis assumption of equal numbers per check. The Spearman Rank Correlation Coefficient (r_s) was used to determine the type and strength of relationship between changes in population size and selected abiotic factors.

CHAPTER IV

RESULTS AND DISCUSSION

Monthly Surveys

Eurycea lucifuga populations

Monthly surveys to each of the six study caves resulted in 421 *E. lucifuga* sightings. The data by cave and month appear in Table 1. Numbers from the combined Kentucky caves (N=327) represent 78% of the total as compared to the 22% for the Tennessee caves (N=94). Great Onyx Cave had the largest yearly total at 225, comprising 53% of the grand total. Following it, in descending order, were Austin Cave 94 (22%), Dunbar Cave with 56 (13%), Barnett Cave with 23 (6%), and Crystal Cave with 8 (2%). A description of each cave and its available microclimates and microhabitats is discussed in detail later.

Populations in the caves of both regions (Tennessee and Kentucky) reached peak numbers in the spring, declined dramatically in July, and peaked again in late summer or fall (Figure 9). In Tennessee this secondary peak occurred in August, with numbers close to those recorded in June. In Kentucky the secondary peak occurred during the period of October through November, when numbers were approximately half those recorded during the May survey. In both regions there was a gradual decline following the secondary peak, with population sizes being smallest in January and February.

Seasonal fluctuations of population size of terrestrial salamanders within caves have been reported for *E. longicauda* (Mohr, 1944), *Plethodon dixi* (Fowler, 1951), and *P. cinereus dorsalis* (Mohr, 1952). None of these three species occur regularly in caves, making comparisons with *E. lucifuga* meaningless. Brandon (1971) studied seasonal fluctuations in populations of the grotto salamander, *Typhlotriton spelaeus*, and found peak abundance during the period of April through July. In their studies of *E. lucifuga*, Hutchison (1958) and Williams (1980) recorded peak population sizes during the months of April through June, with numbers declining and remaining low throughout the late summer, fall, and winter months. Neither study mentions a secondary peak as reported here, but in three of the four caves

Table 1. Numbers of *Eurycea lucifuga* individuals detected per observational man hour each month in each of the study caves.

MONTH	TENNESSEE CAVES				KENTUCKY CAVES				Grand Totals
	Dunbar	Woodson	Barnett	Totals	G. Onyx	Austin	Crystal	Totals	
January	2	0	0	2	0	0	0	0	2
February	0	0	0	0	1	0	0	1	1
March	1	0	0	1	6	7	0	13	14
April	0	0	2	2	19	0	0	19	21
May	7	1	1	9	56	19	0	75	84
June	19	1	5	25	38	24	2	64	89
July	5	0	0	5	4	10	1	15	20
August	10	5	8	23	6	4	5	15	38
September	4	5	3	12	21	8	0	29	41
October	5	2	3	10	31	7	0	38	48
November	3	1	0	4	36	2	0	38	42
December	0	0	1	1	7	13	0	20	21
Totals	56	15	23	94	225	94	8	327	421

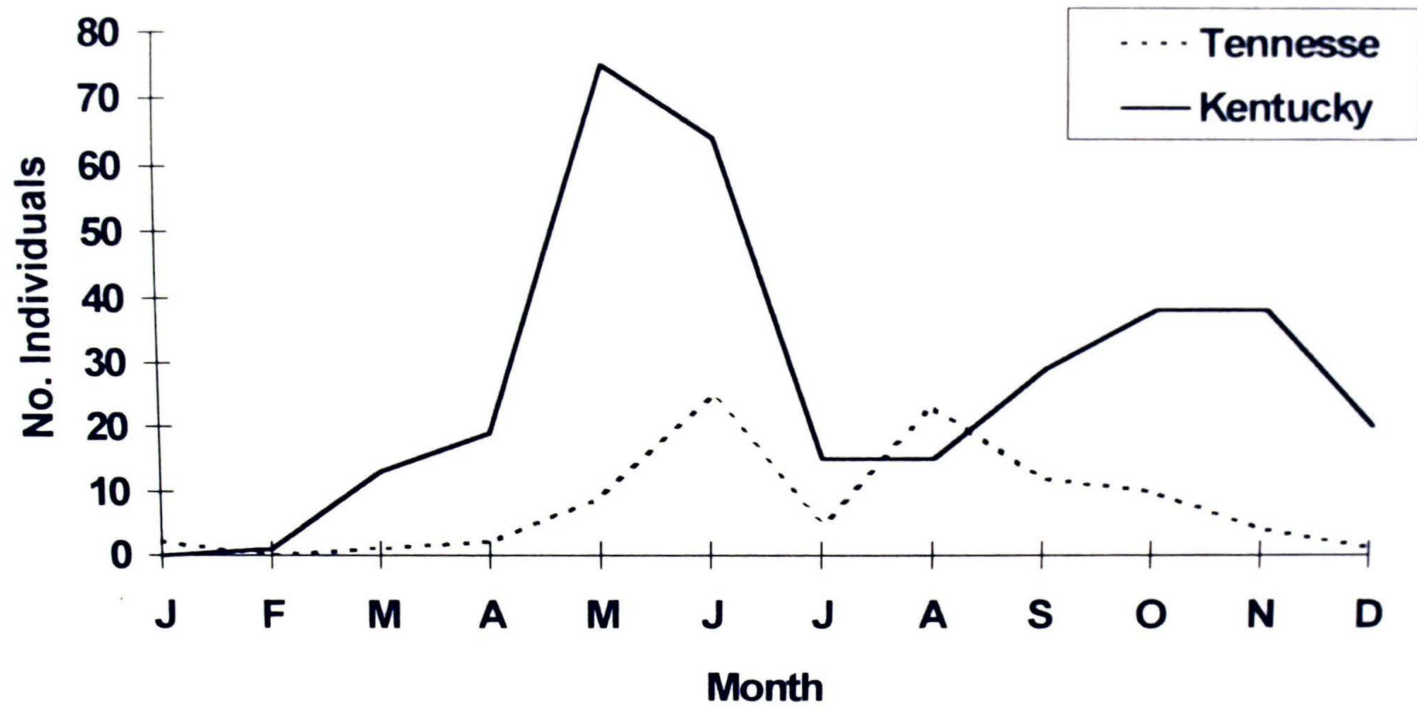


Figure 9. Numbers of *Eurycea lucifuga* individuals detected each month in the Tennessee and Kentucky caves.

Hutchison (1958) surveyed population sizes dropped dramatically in July, followed by an increase sometime during the fall months. Because no such decline was recorded in the control caves of Hutchison's (1958) study, he attributed the July decline in numbers to sampling bias (increased sampling and subsequent disturbance). My data indicate that this decline may in fact be "real," and a response to some abiotic factors found within caves (as discussed below). Williams' (1980) study ended in August, so there is no way to know if his population exhibited a secondary peak.

Other Species

In addition to *E. lucifuga*, four other amphibian species and one reptile species were observed at various times in one or more of the study caves. In order of abundance, these were *Rana palustris* (N=21), *Plethodon glutinosus* (N=9), *E. longicauda* (N=7), *P. dorsalis* (N=3), and *Diadophis punctatus* (N=1). Table 2 shows the number and percent of total for all herptiles detected.

The number, month, and cave of other species detected are shown in Table 3. *Rana palustris* occurred in all six study caves, with the highest number observed in late summer and early fall. *Plethodon glutinosus* occurred in three of the six caves, with equal numbers observed in August and September. *Eurycea longicauda* were observed only in Barnett Cave and were most abundant in April. *Plethodon dorsalis* was found in just two caves (Austin and Great Onyx). The only reptile, *D. punctatus*, was recorded in Great Onyx Cave in October.

The occurrence of *R. palustris* in all six study caves was not surprising as it has been reported by several authors as commonly inhabiting caves (Myers, 1958; Cliburn and Middleton, 1983). Based on an analysis of stomach contents, Smith (1948) suggested that this ranid wanders frequently into and out of caves. It has been reported from Tennessee caves by Scott (1991), Dearolf (1956), and Barr (1953) and in Kentucky caves in Mammoth Cave National Park by Hibbard (1936). Although Barr (1953) suggested that ranids enter caves to avoid desiccation in summer, rather than to avoid winter cold as suggested by Rand (1950) and Blair (1951), my data and that of Myers (1958) document *R. palustris* in caves during all months except July and January, suggesting they are year-round inhabitants. *Rana clamitans* has been

Table 2. Numbers of individuals and percentages of total for the six species of herpetofauna observed during the study.

Species	No. Observed	% of Herpetofauna
<i>Eurycea lucifuga</i>	421	91.1
<i>Rana palustris</i>	21	4.6
<i>Plethodon glutinosus</i>	9	2.0
<i>Eurycea longicauda</i>	7	1.5
<i>Plethodon dorsalis</i>	3	0.6
<i>Diadophis punctatus</i>	1	0.2
Total	462	100

Table 3. Numbers of individuals of amphibian species, other than *Eurycea lucifuga*, observed each month at each cave.

CAVE	MONTH												TL
	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	
<i>Rana palustris</i>													
Barnett	-	-	-	2	-	-	-	3	-	1	-	1	7
Dunbar	-	-	-	-	-	-	-	-	-	1	-	-	1
Woodson	-	-	-	-	-	-	-	2	-	2	-	1	5
Austin	-	-	-	-	-	-	-	1	2	2	-	-	5
Great Onyx	-	1	-	-	-	-	-	-	-	-	1	-	2
Crystal	-	-	-	-	-	-	-	-	1	-	-	-	1
TL	0	1	0	2	0	0	0	6	3	6	1	2	21
<i>Plethodon glutinosus</i>													
Barnett	-	-	-	-	-	-	-	-	-	-	-	-	0
Dunbar	-	-	-	-	-	-	-	4	-	-	-	-	4
Woodson	-	-	-	-	-	-	-	-	-	-	-	-	0
Austin	-	-	-	-	-	-	-	-	4	-	-	-	4
Great Onyx	-	-	-	-	-	-	1	-	-	-	-	-	1
Crystal	-	-	-	-	-	-	-	-	-	-	-	-	0
TL	0	0	0	0	0	0	1	4	4	0	0	0	9
<i>Eurycea longicauda</i>													
Barnett	-	-	-	5	-	-	-	1	1	-	-	-	7
Dunbar	-	-	-	-	-	-	-	-	-	-	-	-	0
Woodson	-	-	-	-	-	-	-	-	-	-	-	-	0
Austin	-	-	-	-	-	-	-	-	-	-	-	-	0
Great Onyx	-	-	-	-	-	-	-	-	-	-	-	-	0
Crystal	-	-	-	-	-	-	-	-	-	-	-	-	0
TL	0	0	0	5	0	0	0	1	1	0	0	0	7
<i>Plethodon dorsalis</i>													
Barnett	-	-	-	-	-	-	-	-	-	-	-	-	0
Dunbar	-	-	-	-	-	-	-	-	-	-	-	-	0
Woodson	-	-	-	-	-	-	-	-	-	-	-	-	1
Austin	-	-	-	-	-	-	-	1	-	-	-	1	2
Great Onyx	-	-	-	1	-	-	-	-	-	-	-	-	0
Crystal	-	-	-	-	-	-	-	-	-	-	-	-	0
TL	0	0	0	1	0	0	1	0	0	0	1	0	3

found in the cave environment (Banta, 1907), but I found none during my study. However, I did see this species in Long Cave (Mammoth Cave National Park) during preliminary work done for this study.

The occurrence of *P. glutinosus* in caves is well documented. Outside Tennessee and Kentucky it has been reported from caves by Mohr (1950), Myers (1958), and Knight (1969). In Tennessee it has been documented by Scott (1991), and in Kentucky by Dearolf (1956) and Hibbard (1936). Although Scott (1991) reported four individuals in the entrance to Barnett Cave, I did not find it there during this study. Hibbard (1936) reported the species as abundant in cave entrances throughout Mammoth Cave National Park, an observation corroborated by my results (Table 3). Although *P. glutinosus* has been observed in both the twilight and constant dark zones of caves (Cliburn and Middleton, 1983), Mittleman (1950) noted that this species normally occurs in above-ground habitats and resorts to caves during hot, dry periods only. My data appear to support this claim as all nine individuals observed were recorded in July, August, and September (Table 3).

Plethodon dorsalis has been recorded in caves outside Tennessee and Kentucky by Banta (1907) and Mittleman (1950). In Tennessee caves, it has been reported by Barr (1949, 1961) and Scott (1991). Scott reported one individual from Barnett Cave, but my surveys did not detect it there. Hibbard (1936) reported *P. dorsalis* from Mammoth Cave National Park, but he never found it in caves. He reported *P. dorsalis* as abundant in terrestrial habitats in October, but that it then disappeared until March, then disappeared again in April until the next fall. Although the appearance of *P. dorsalis* in Austin and Great Onyx caves suggest some individuals seek cave refuge during periods of epigeal abiotic extremes, my numbers are too low to justify any generalized statement concerning cave use by this species.

The occurrence of *E. longicauda* in Barnett Cave was expected, as they had been documented in its cave entrance by Scott (1991). However, their absence from the other caves was somewhat surprising as they have been well documented in caves by others (Dearolf, 1956; Mittleman, 1950). Some investigators have indicated *E. longicauda* is common in caves with flowing streams (Hibbard, 1936; Knight, 1969). Of the six caves I studied, only two (Barnett and Dunbar) had permanent flowing streams. Myers (1958) noted that in Missouri the only two caves where *E. longicauda* had been documented were

caves in which *E. lucifuga* did not occur, suggesting competitive exclusion of *E. longicauda* by *E. lucifuga*. Among the Tennessee study caves, Dunbar Cave supported the largest visible population of *E. lucifuga* (Table 1), a finding which is in agreement with Myers' suggestion.

Interspecific competition between *E. longicauda* and *E. lucifuga* was first proposed by Hutchison (1958). He noted that when both occurred in a cave, *E. lucifuga* was more prevalent. This appears to have been true in Barnett Cave which had a yearly total of 23 *E. lucifuga* (Table 1) compared to 7 *E. longicauda* (Table 3). In a study of 105 Missouri caves by Woolley (1971), 87 caves exhibited segregation, supporting either *E. longicauda* or *E. lucifuga*. In the 18 caves that supported both species, interspecific competition for food occurred in the early spring. At that time 60% of the *E. longicauda* were observed migrating to areas of higher food density and, supposedly, less competition outside the cave; they were followed later by *E. lucifuga*. My data on Barnett Cave appear to support Hutchison's (1958) study, with the highest number of *E. longicauda* observed in April (Table 3), followed by highs of *E. lucifuga* in June and August (Table 1).

The single *D. punctatus* observed was within 5 m of the entrance to Great Onyx Cave during November. Although infrequent, *D. punctatus* has been reported as occurring in caves (Hutchison, 1958; Cliburn and Middleton, 1983). Although Hibbard (1936) states they were common on wooded slopes and ridges of Mammoth Cave National Park, he did not document it in caves. Scott (1991) failed to find *D. punctatus* in the entrance to Barnett Cave, although he reported them as common throughout the surrounding epigeal environment.

Abiotic Conditions and Their Relationships

Raw data collected during visits to the study caves can be found in Appendix B. The results shown here, and the following discussion, are based on descriptive statistics calculated on each data set.

Air Temperature. Of the caves in each region, Woodson Cave (Tennessee) and Crystal Cave (Kentucky) had the highest mean annual outside temperatures during my visits (Table 4). This was expected as both caves were the last to be visited during each survey. The Tennessee caves had the lowest

monthly mean air temperatures during January, February, and March, and the highest during June, July, and August. Kentucky caves had the lowest monthly mean air temperatures in January, February, March, and April, with the highest also in June, July, and August.

Table 5 shows the monthly and yearly means of air temperature inside each cave, and the combined monthly means for all three caves in each region. In both regions cave air temperatures peaked in July and then gradually declined through December, before plummeting in January. Air temperatures remained low throughout the winter months, then began climbing in April. All six study caves had the lowest mean air temperatures during January, February, and March, and the highest during July, August, and September.

A significant statistical correlation exists ($r_s > .587$, $N=12$) between monthly mean outside air temperatures and monthly mean cave air temperatures in both regions (Fig. 10). In general, cave air temperatures increased or decreased with changes in outside air temperatures. In both regions inside and outside air temperatures approached each other more closely in winter. It was during this time that outside air was detected moving into the caves. During the summer months however, cooler, moisture laden air was detected moving out of the caves, protecting the twilight zone somewhat from external temperature extremes. This air flow pattern has been reported previously by several investigators (Banta, 1907; Hutchison, 1958; Williams, 1980). Banta (1907) describes very little increase in summer cave temperatures (highest 12.2°C), with winter temperatures dropping more in accordance with fluctuations in outside temperatures. Cooler air moving out of caves has been documented during the months of April through September (Banta, 1907) and March through August (Williams, 1980). As in previous cave studies (Hutchison, 1958; Williams, 1980) air temperature fluctuations were greatest just inside the entrance (Station 1), less variable midway in the survey zone (Station 2), and was relatively constant at its terminus (Station 3) (Tables B-1 through B-6).

Table 4. Mean monthly outside air temperatures (°C) at each cave.

CAVE	JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC	YEAR
<i>Tennessee Caves</i>													
Barnett	4.0	-1.0	5.0	21.5	23.0	30.5	26.3	35.0	20.0	20.0	12.5	12.0	17.4
Dunbar	1.0	0.0	5.5	26.5	13.3	31.5	27.0	28.0	24.0	28.0	11.0	12.0	17.3
Woodson	2.5	0.0	5.5	26.5	23.3	32.0	29.5	29.5	23.0	23.0	9.5	11.0	18.0
Means	2.5	-0.3	5.3	24.8	19.9	31.3	27.6	30.8	22.3	23.7	11.0	11.7	17.6
<i>Kentucky Caves</i>													
Austin	-10.5	5.5	2.0	5.0	15.0	26.5	25.5	28.0	19.0	18.0	19.0	6.0	13.3
Onyx	-3.0	8.5	4.5	9.0	15.0	26.0	21.5	32.0	25.0	22.0	21.0	7.0	15.7
Crystal	-3.5	8.5	2.0	7.5	15.0	28.0	38.0	31.0	22.5	20.0	20.5	5.0	16.2
Means	-4.5	7.5	2.8	7.2	15.0	26.8	28.3	30.3	22.2	20.0	20.2	6.0	15.1

Table 5. Mean monthly inside air temperatures (°C) at each cave.

CAVE	JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC	YEAR
<i>Tennessee Caves</i>													
Barnett	6.0	4.0	5.0	9.8	14.7	14.9	16.9	17.6	16.6	14.7	12.9	12.2	12.1
Dunbar	3.7	2.3	5.0	11.8	10.1	13.0	14.2	13.5	14.3	14.0	13.0	12.5	10.6
Woodson	5.5	3.4	6.5	13.1	13.7	18.9	19.0	19.1	17.7	17.5	13.3	13.7	13.5
Means	5.0	3.2	5.5	11.6	12.8	15.6	16.7	16.7	16.2	15.4	13.1	12.8	12.1
<i>Kentucky Caves</i>													
Austin	-2.0	5.4	4.9	4.2	9.7	11.9	13.7	13.3	13.3	12.1	12.3	8.3	8.9
Onyx	4.0	8.1	8.2	9.6	12.6	14.4	15.7	16.0	15.1	15.4	13.1	11.3	12.0
Crystal	0.1	6.4	6.6	7.7	10.8	12.9	14.7	14.2	13.6	12.7	12.4	10.3	10.2
Means	0.7	6.6	6.6	7.2	11.1	13.0	14.7	14.5	14.0	13.4	12.6	10.0	10.4

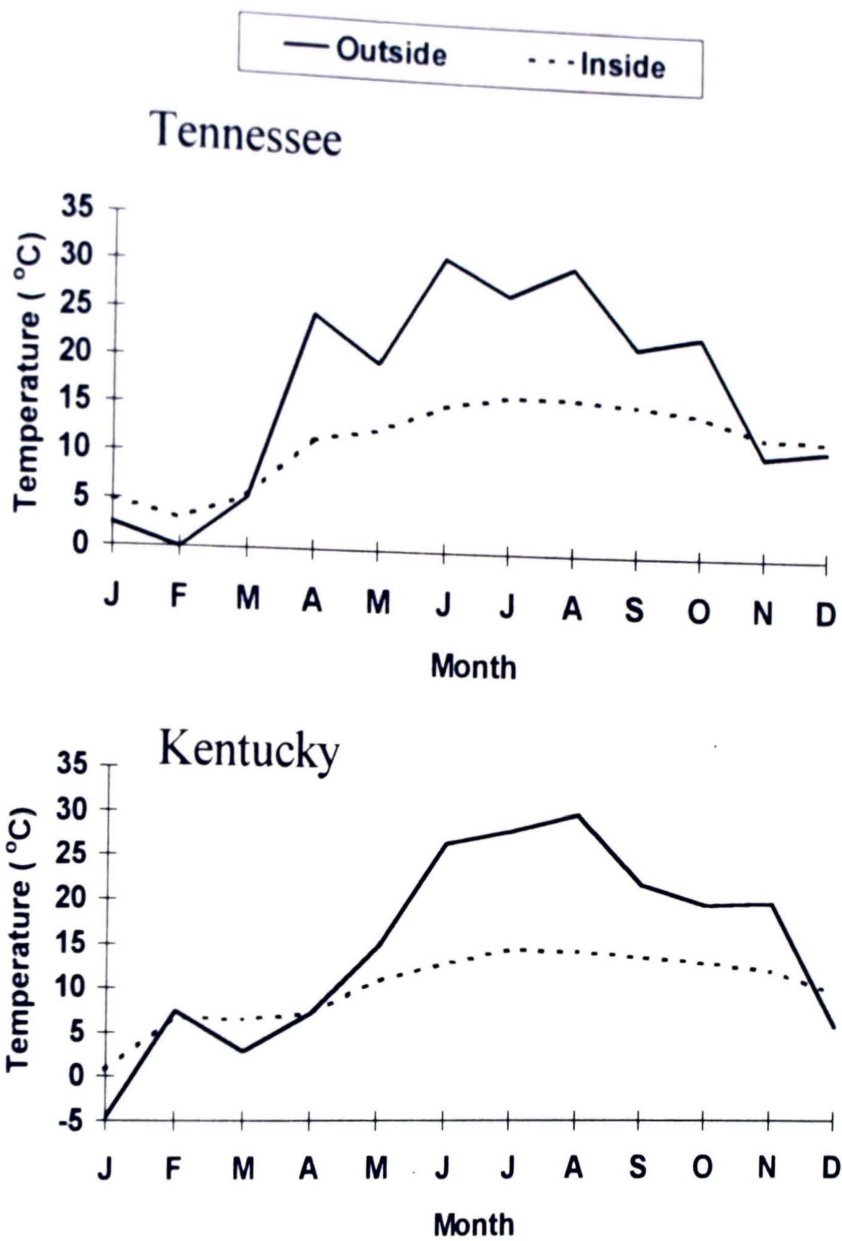


Figure 10. Mean outside air temperatures and mean cave air temperatures recorded throughout the year at the Tennessee and Kentucky caves.

Changes in mean cave air temperature were significantly correlated ($r_s=.610$, $N=12$) with monthly changes in the size of *E. lucifuga* populations (Fig. 11). The role of cave air temperature in influencing population levels appeared to be strongest in the winter months, when temperatures and populations levels correlate most closely. Although Hutchison (1958) stated that air temperature did not appear to be a limiting factor *per se*, his recorded winter temperatures were not as low as those recorded here. Instead, most of the temperatures he recorded fell well within *E. lucifuga*'s activity range. The range of temperatures within which I found salamanders was 8°C to 16°C. This corresponds closely to the range of 8°C to 19°C reported by Hutchison (1958). In both of my study regions, dramatic increases and decreases occurred in population size during periods of relatively constant air temperature (summer and fall)(Fig. 11). As suggested by Hutchison (1958), this indicates that during the warmer months temperature is not the limiting factor. As will be shown below, these highs and lows corresponded directly to changes in relative humidity, the most strongly correlated factor.

Relative Humidity. Relative humidity recorded outside all three caves in both regions, as well as that recorded before and after individual cave surveys, varied greatly, as weather conditions often changed dramatically within a relatively short period of time (Tables B1-B6). The means of relative humidity readings taken outside each cave on each monthly visit are shown in Table 6.

Table 7 gives the means of relative humidity readings taken within each cave during each month, and the 12-month means for the three caves in each region. Taken together, the Tennessee caves had the highest mean relative humidity during the months of June, August, and September, while the Kentucky caves had the highest during May, June, and December. Lows for the Tennessee caves occurred during January, February, March, and April, while the lows in Kentucky were recorded in January, April, July, and August.

As reported by Hutchison (1958) and Williams (1980), I found that relative humidities varied widely from visit to visit, whereas cave relative humidity showed much less variation. As a result, there was no significant correlation between the two factors overall in either region (Fig. 12).

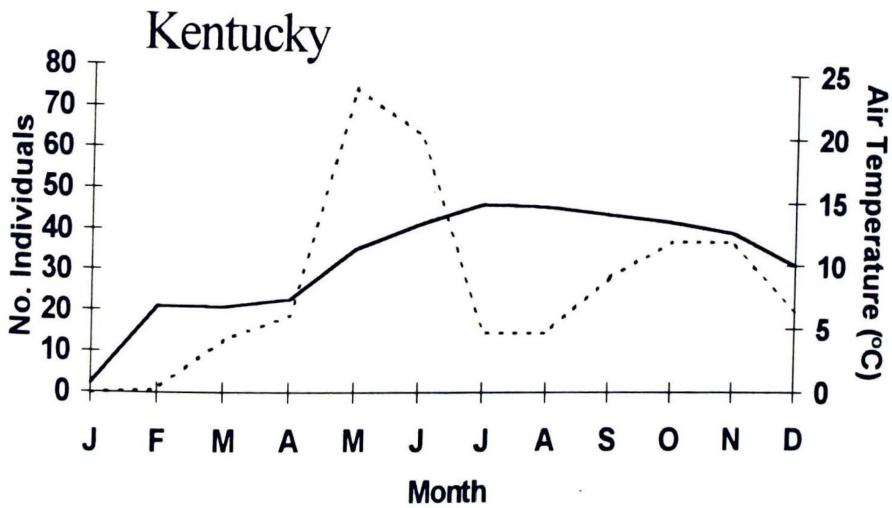
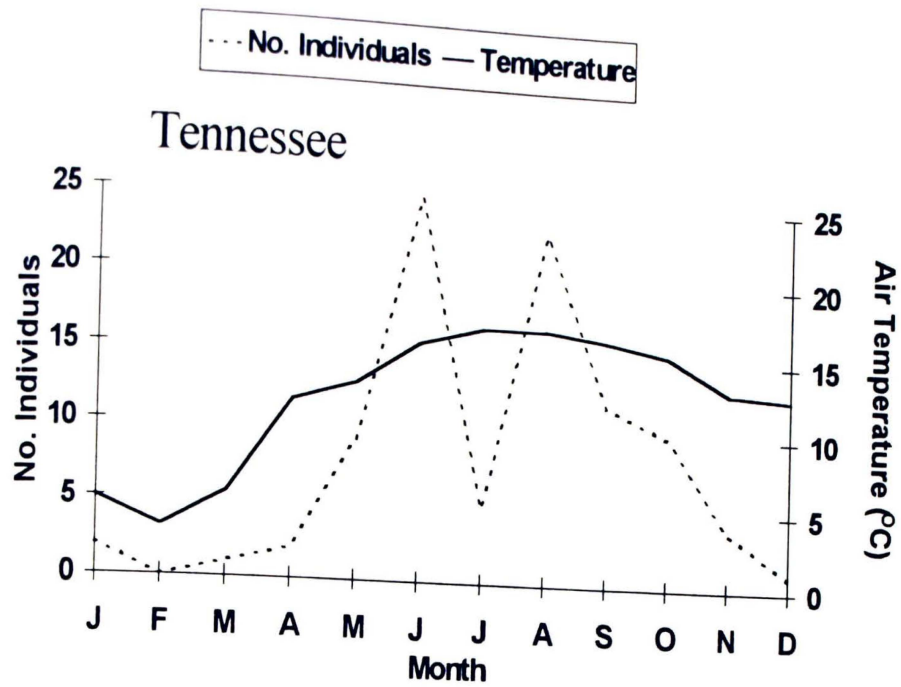


Figure 11. Numbers of *Eurycea lucifuga* individuals detected each month and mean air temperatures in the Tennessee and Kentucky caves.

Table 6. Means of relative humidity readings taken outside each cave on each monthly visit.

CAVE	JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC	YEAR
<i>Tennessee Caves</i>													
Barnett	45	67	41	36	48	61	69	50	81	67	38	84	57
Dunbar	84	69	43	18	72	61	63	63	79	27	43	79	58
Woodson	80	70	44	23	69	58	65	75	79	49	45	78	61
Means	70	68	43	26	63	60	66	63	80	48	42	80	59
<i>Kentucky Caves</i>													
Austin	68	61	64	42	100	72	61	71	90	55	51	71	67
Onyx	49	59	66	38	100	63	87	56	49	49	55	73	62
Crystal	53	57	75	41	100	69	68	64	59	52	52	76	64
Means	56	59	68	40	100	68	72	64	66	52	52	73	64

Table 7. Means of relative humidity readings taken inside each cave on each monthly visit.

CAVE	JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC	YEAR
<i>Tennessee Caves</i>													
Barnett	65	78	71	77	80	90	83	87	89	87	78	88	81
Dunbar	61	64	48	62	90	98	88	98	93	90	63	88	79
Woodson	62	61	64	61	82	79	80	86	88	76	63	84	74
Means	63	68	61	67	84	89	84	90	90	84	68	87	78
<i>Kentucky Caves</i>													
Austin	59	68	83	52	92	93	77	86	88	90	85	84	80
Onyx	80	82	79	70	98	84	76	69	84	81	87	92	82
Crystal	65	79	79	74	93	82	68	72	87	84	80	89	79
Means	68	76	80	65	94	86	74	76	86	85	84	88	80

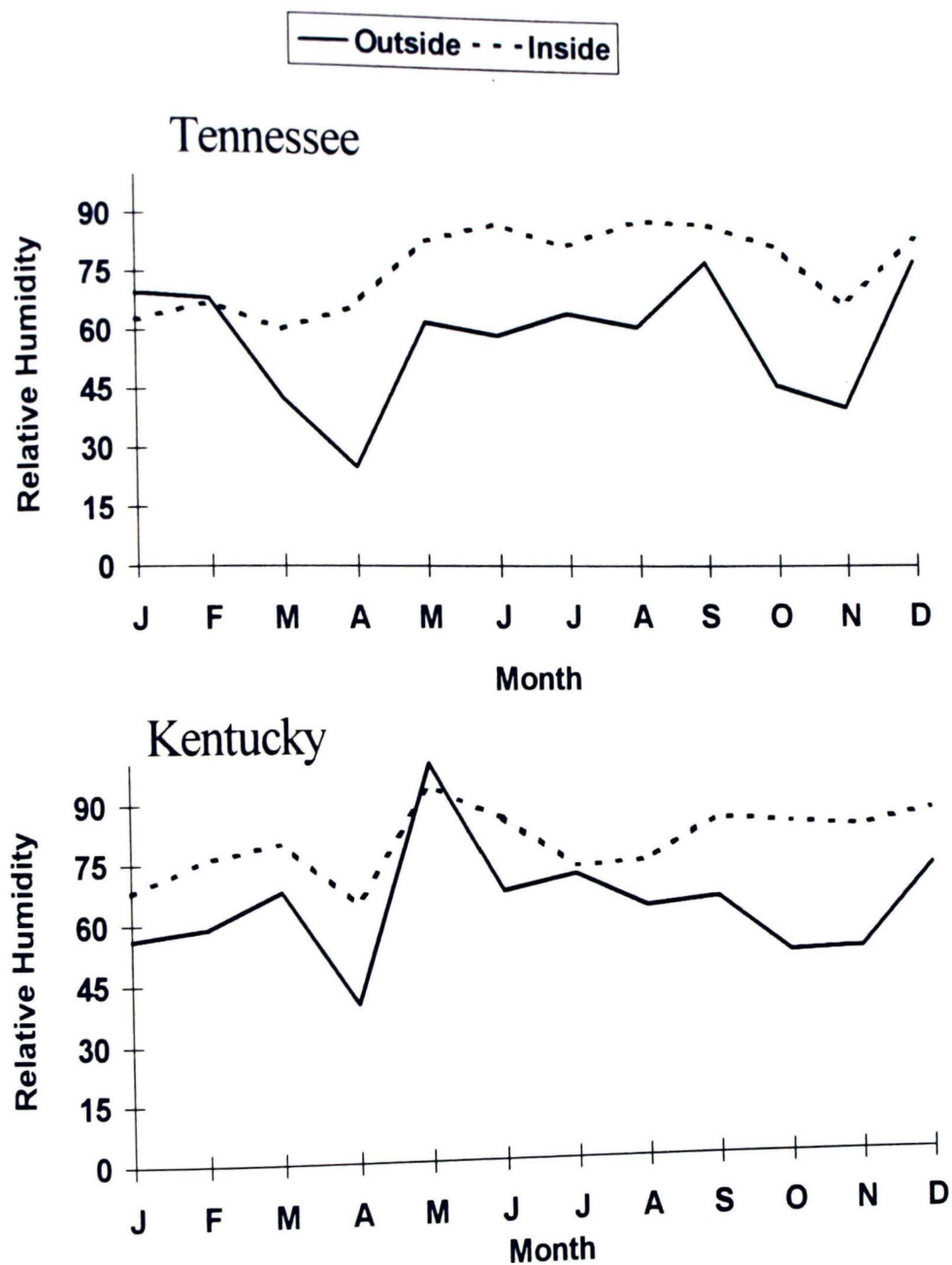


Figure 12. Means of outside cave and inside cave relative humidities recorded each month at the Tennessee and Kentucky caves.

Cave relative humidities generally increased and decreased with corresponding changes in outside relative humidity (Fig. 12). I believe this relationship during the colder months is due to inflow of outside air. In summer, the two factors are inversely related; as outside relative humidities decrease, cave relative humidities increase, and vice versa, due to the outflow of cave air. This phenomenon has been reported previously by both Hutchison (1958) and Williams (1980).

Although overall relative humidities inside and outside the caves were not significantly correlated over the 122 month period, a significant correlation ($r_s = .71$, $N=12$) was found between monthly means for cave relative humidity and the previous month's total rainfall throughout the year, in both regions (Fig. 13). In the Tennessee caves increases and decreases in both factors occur together, but in the Kentucky caves this was not always the case. It seems possible that the solid doors at the entrances to all three Kentucky caves somehow affected this relationship.

Of all the abiotic factors measured in the study caves, relative humidity most strongly correlated ($r_s = .74$, $N=12$) with observed changes in *E. lucifuga* population size (Fig. 14). In the Tennessee caves, corresponding changes in population size was not associated with an changes in cave relative humidities during the months of December, January, February and March. During these months, increases and decreases in population size were coincident with the corresponding changes in cave air temperature. In Kentucky, the exceptions were December, April, and October. April's rise in population size was coincident with a rise in cave air temperature, whereas December's population decline occurred as cave air temperatures were dropping. The slight increase in population size in October is unexplained as cave air temperature, relative humidity, and surface moisture were all dropping. Hutchison (1958) also suggested that population size is a direct result of the available moisture within the cave. He recorded the highest numbers of *E. lucifuga* during periods of low saturation deficit, declining numbers with increasing saturation deficits, and none when saturation deficits were highest. Although cave relative humidity was the strongest abiotic factor measured that correlated with population size, its importance seemed negated when certain other abiotic factors exceeded certain limits (e.g. cave air temperature extremes during winter).

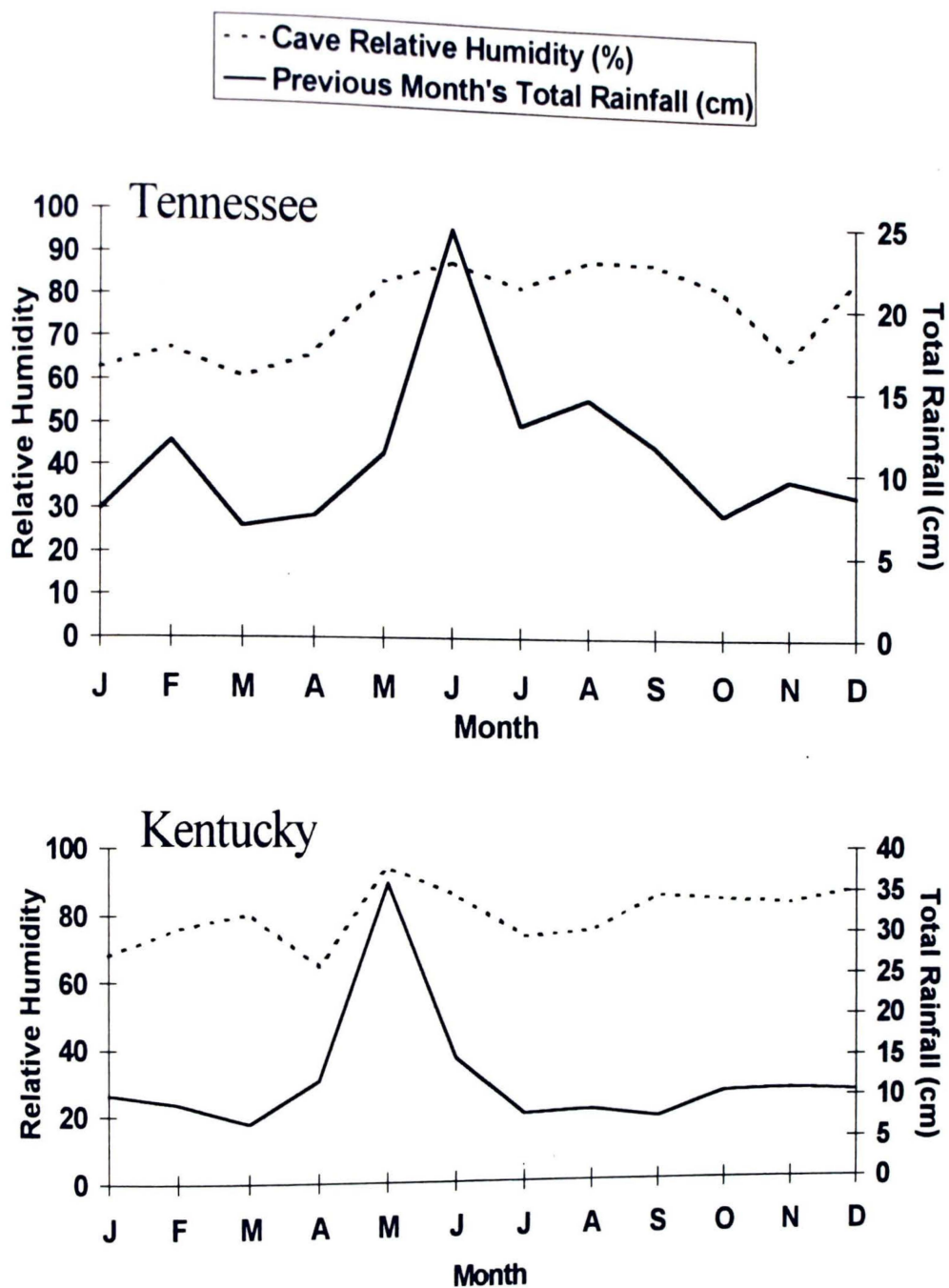


Figure 13. Means of cave relative humidities and previous month's rainfall recorded each month at the Tennessee and Kentucky caves.

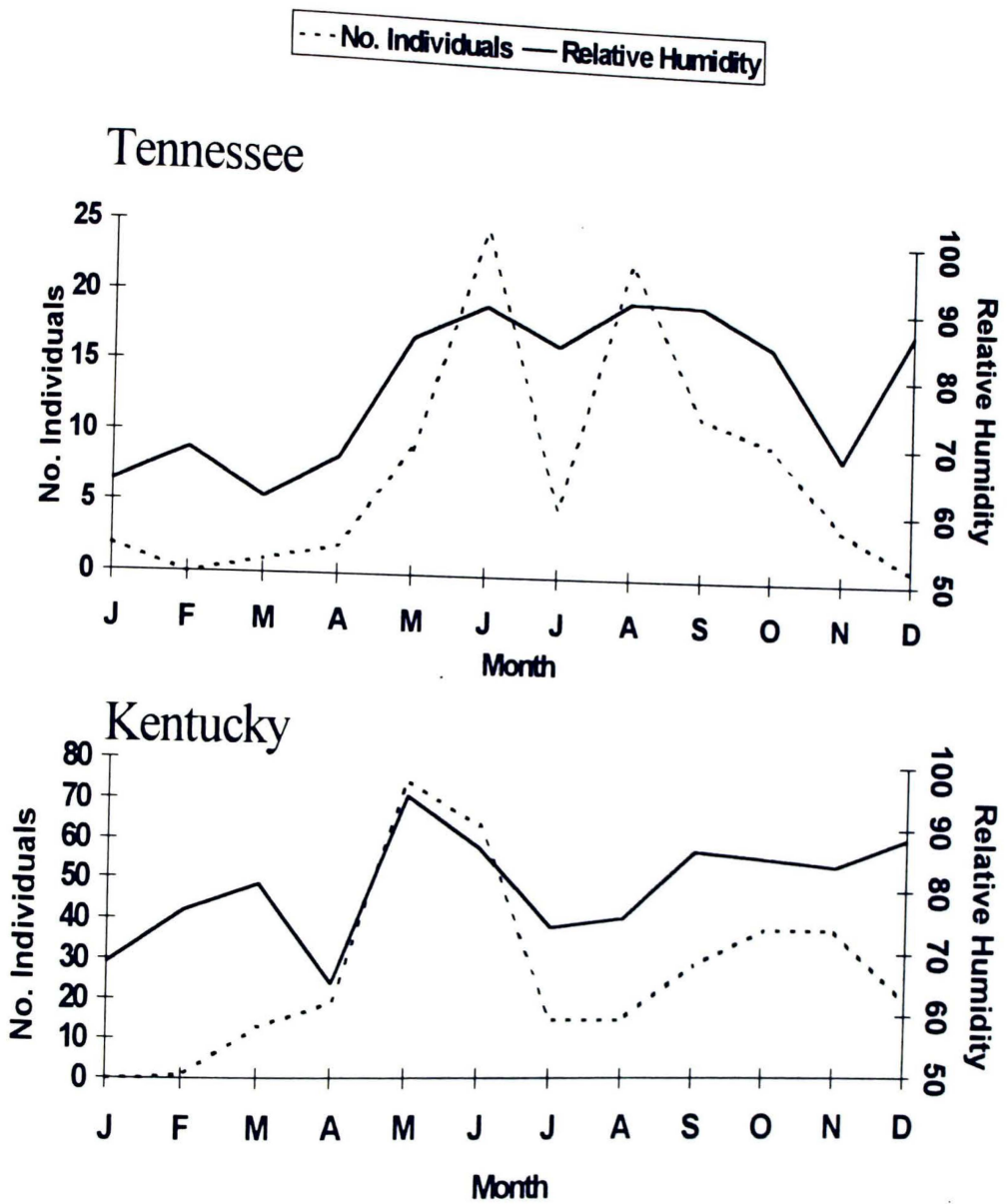


Figure 14. Number of *Eurycea lucifuga* individuals observed and mean relative humidities recorded each month in the Tennessee and Kentucky caves.

Precipitation. Total precipitation over the study period was 132 cm in the area of the Tennessee caves, and 147 cm in the area of the Kentucky caves (Table 8). The Tennessee area had the highest monthly precipitation during May and July, and the lowest during February and March. In the Kentucky area the highest occurred during May and June, and the lowest during March and September. In most cases, no precipitation fell during the actual monthly cave surveys, but there was a light snowfall in the area of the Tennessee caves during the January surveys, and a moderate rain at all three Kentucky caves sites during the May surveys.

Surface Moisture. Table 9 shows the means of surface moisture readings taken at each cave during each monthly survey. As a group, the Tennessee caves had the highest mean surface moisture readings during July and August, and the lowest in January and November. Mean surface moisture recorded in the Kentucky caves was also lowest during January and November, but it was highest during May and June. The progressive "drying" observed from spring to winter in this study was also noted by Hutchison (1958) and Williams (1980).

In the Tennessee (but not Kentucky) caves, a significant positive correlation ($r_s = .64$, $N=12$) was found between available surface moisture and the previous month's total rainfall (Fig. 15). This difference between the two regions may have been due in part to the difference in entrance types, the presence of solid doors in the Kentucky caves may have allowed surface moisture to remain longer by partially blocking airflow. This relationship between rainfall and cave surface moisture was noted by Hutchison (1958), who stated that rainfall directly influenced both the surface moisture and the saturation deficit found in his study caves, and by Brandon (1971) who reported that the dampness of cave walls correlated directly with the season.

Although not statistically significant ($r_s < .578$, $N=12$), my data suggest a relationship between the numbers of *E. lucifuga* observed each month and the means of available surface moisture readings (Fig. 16). The largest population sizes in both regions were detected during periods of highest available surface moisture. Brandon (1971) also reports peak abundance in *Typhlotriton spelaeus* during times when the walls were wettest. Although important, high available surface moisture, in the absence of favorable cave

Table 8. Monthly rainfalls (cm) recorded at the Clarksville, TN, Sewage Plant and the main weather station at Mammoth Cave National Park, Mammoth Cave, KY.

REGION	JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC	YEAR
Tennessee	11.48	6.50	7.14	10.90	24.18	12.65	14.30	11.51	7.49	9.60	8.66	7.47	131.9
Kentucky	10.59	9.42	7.16	12.37	35.84	14.94	8.13	8.64	7.54	10.59	10.95	10.59	146.8

Table 9. Means of surface moisture readings recorded during each monthly survey at the Tennessee and Kentucky caves. Surface moisture recorded on a scale of 0-4, with 0=dry, 1=damp, 3=wet, and 4=standing or running water.

CAVE	JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC	YEAR
<i>Tennessee Caves</i>													
Barnett	2.33	3.00	2.33	2.67	2.67	3.67	3.00	3.33	3.33	2.67	2.67	3.33	2.92
Dunbar	0.00	2.00	1.67	1.67	2.67	3.33	3.00	2.67	2.67	2.00	0.33	1.67	1.97
Woodson	2.67	2.67	4.00	1.33	3.00	4.00	2.00	3.67	2.00	1.33	1.33	3.00	2.58
Means	1.67	2.56	2.67	1.89	2.78	3.67	2.67	3.22	2.67	2.00	1.44	2.67	2.49
<i>Kentucky Caves</i>													
Austin	0.00	0.00	0.00	0.00	2.00	2.00	1.83	1.67	1.00	0.00	0.33	2.00	.90
Onyx	2.33	3.67	3.00	2.33	3.33	3.00	2.00	0.67	1.67	1.67	1.33	2.33	2.28
Crystal	0.00	0.00	1.00	0.33	1.67	1.33	1.33	2.33	2.33	0.67	0.33	0.67	1.00
Means	0.78	1.22	1.33	0.89	2.33	2.11	1.72	1.56	1.67	0.78	0.66	1.67	1.39

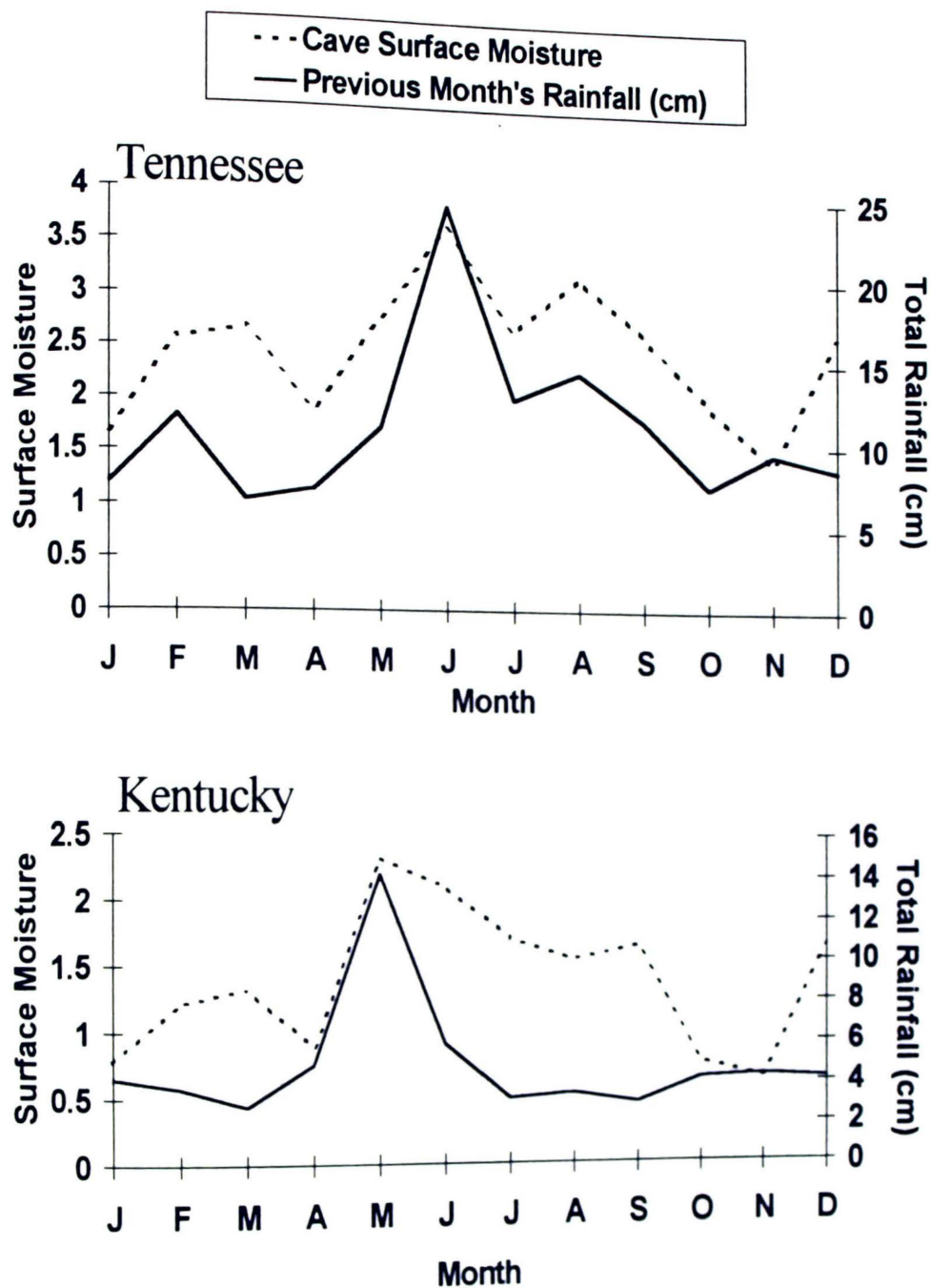


Figure 15. Means of cave surface moisture readings taken each month and the previous month's total rainfall at the Tennessee and Kentucky caves. Available surface moisture recorded on a scale of 0-4, with 0=dry, 1=damp, 2=moist, 3=wet, and 4=standing or running water.

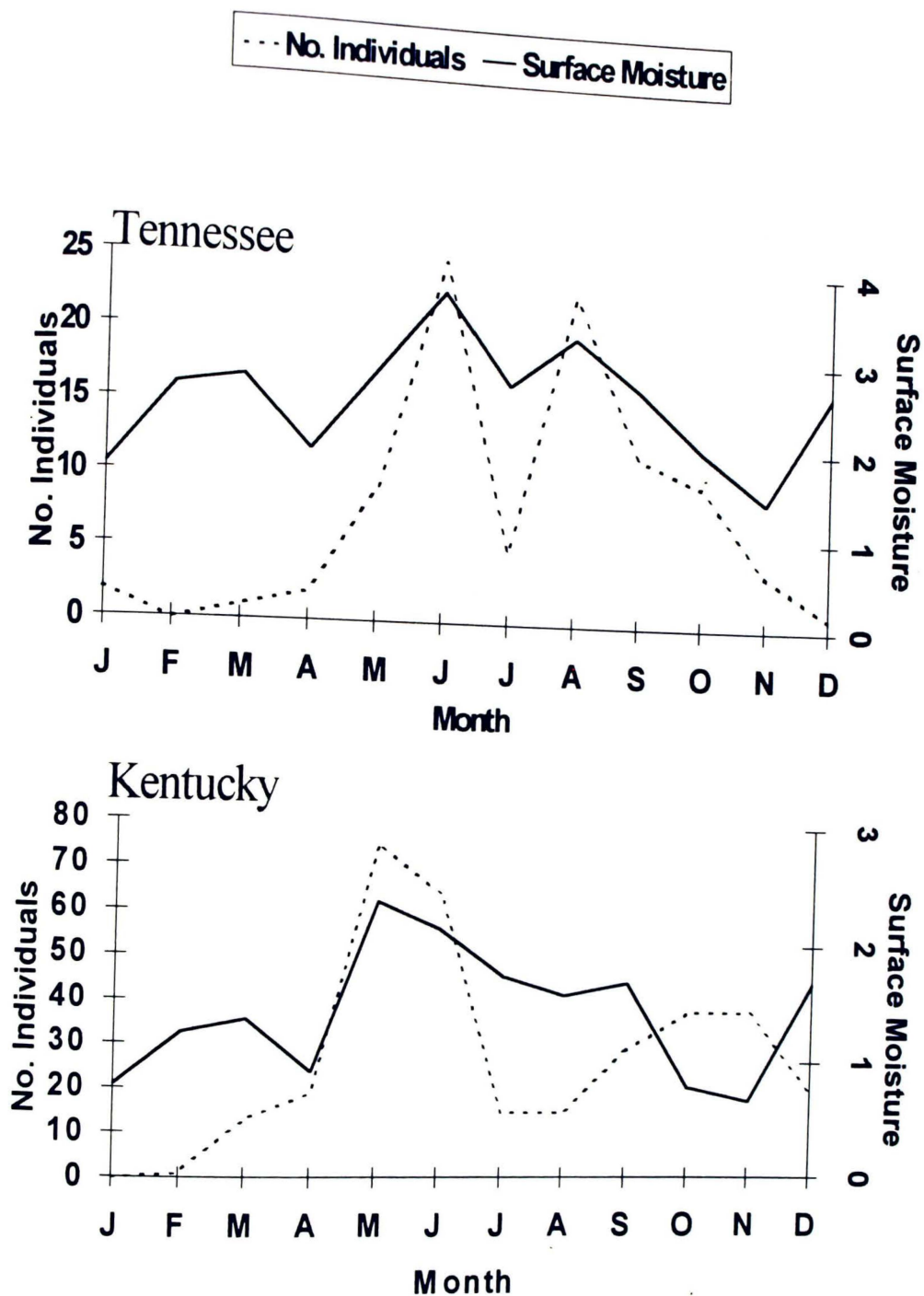


Figure 16. Numbers of *Eurycea lucifuga* individuals observed and the means of available surface moisture data from each monthly survey at the Tennessee and Kentucky caves. Available surface moisture recorded on a scale of 0-4, with 0=dry, 1=damp, 2=moist, 3=wet, and 4=standing or running water.

air temperature or relative humidity, had little influence on population size. Surface moisture, however, did appear to play an important role in determining *E. lucifuga*'s spatial distribution within the survey zones. This relationship will be discussed later.

pH. During each monthly survey, each of the Tennessee caves had at least one station with enough water (either puddles, drips, or run-off) for reading pH with a test strip. Water in all three caves had pHs between 6.5 and 8.5, with no apparent monthly trends. Of the Kentucky caves, only Great Onyx had enough water to test each month throughout the year. Readings there ranged from 6.5 to 8.0. Austin Cave had enough water (drips from slope run-off) for testing only at Station 1 during May and June; readings were 7.0 both times. Crystal Cave could only be tested during March, May, and June at Station 1 (drips at cave mouth). Readings were 7.0 in March, and 6.0 in both May and June.

***Eurycea lucifuga* Distribution, Microhabitat Selection, and Orientation**

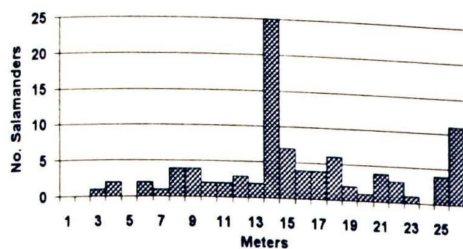
This portion of my study was designed to document the location, orientation, and microhabitat of each salamander detected in each of the study caves. The census zones in each cave differed in terms of size, shape, surface moisture, available cover, etc., making a combined analysis inappropriate. Instead, the data for each cave were analyzed separately. The results are presented and discussed below.

Distribution. Figure 17 shows the number of individuals taken at progressively greater distances into the survey zone of each cave over the study period. Table 10 shows the distribution of *E. lucifuga* observed in each cave in terms of position across the passage (left, right, or center). Because the data appear to be related to individual cave features, they are discussed by cave in the following text.

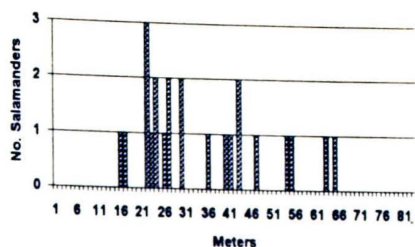
Table 10. Numbers of *Eurycea lucifuga* detected in left, right, and center of survey zone in each cave.

Location	CAVE						TL
	Barnett	Dunbar	Woodson	Austin	Gr. Onyx	Crystal	
Left	15	31	10	44	157	4	261
Right	8	25	5	44	48	0	130
Center	0	0	0	6	3	4	13
Total	23	56	15	94	208	8	404

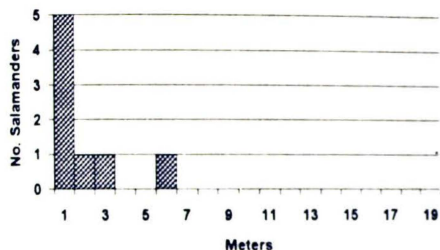
Austin Cave (N=94)



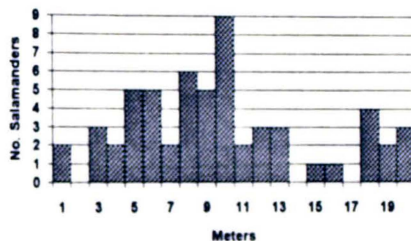
Barnett Cave (N=23)



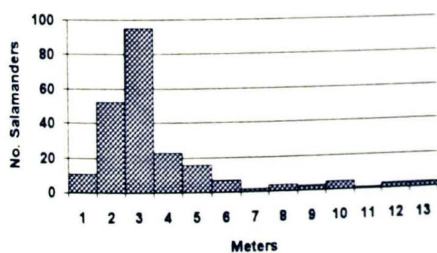
Crystal Cave (N=8)



Dunbar Cave (N=56)



Great Onyx Cave (N=225)



Woodson Cave (N=15)

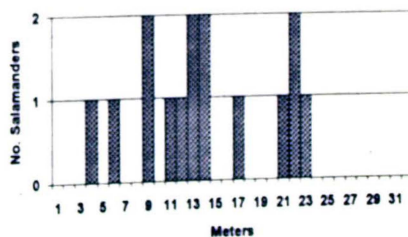


Figure 17. Numbers of individuals detected at different locations (distance from entrance) within each study cave over the entire study period.

At Barnett Cave all salamanders were detected between 16 m and 66 m of the mouth (Fig. 17). The mouth of Barnett Cave is open and large (Fig. 3), giving way to a semicircular room that is flooded with light during daylight. It was here that cave relative humidity and surface moisture were lowest (Table B-1). The tunnel-like passage begins at a straight-line distance of ~10 m from the mouth. Once within the tunnel, light diminished rapidly and conditions were more favorable. Within this tunnel were several persistent pools located to the left of the passageway. Of the 23 *E. lucifuga* detected throughout the year, 65% were detected within 1 m of a pool, but never in the pool. Usually they were on the wall above the pool, although a few were on the floor or the wall just before or beyond the pool. The greatest concentration of salamanders (39%) occurred between 22 and 27 m, within 1 m of a long narrow pool located against the wall (Fig. 17). Most salamanders (65%) were located on the left side of the cave (Table 10). This distribution across the survey zone, like the distribution from front to back, also appears to have been influenced by available surface moisture. As the tunnel curved around to the left from the large entrance, air flow and consequent evaporation were greatest along the right wall. In contrast, the left side of the passage experienced less air flow and evaporation and was where the pools (all permanent) occurred.

Salamanders in Dunbar Cave were detected throughout the survey zone (Fig. 17). Station 1 was beyond the large open mouth and at the beginning of the tunnel-like passage, where conditions were relatively favorable throughout most of the year (Fig. 4). Most salamanders (70%) were detected between 1 and 10 m from the entrance. Beyond that point, at Station 3, the cave was consistently drier and the walls were also smoother, with less available cover in the form of crevices and ledges. Salamanders on the left side (N=31) slightly outnumbered those on the right (N=25) (Table 10). Moisture conditions and available cover in the form of rock debris and wall crevices within the cave varied little between the left and the right. There was no standing water on either side throughout the survey.

In Woodson Cave, no *E. lucifuga* were observed in the last 9 m of the survey zone (Fig. 17). Station 3 was considerably drier than Stations 1 and 2 (Table B-3). Although 66% of the *E. lucifuga* were

detected on the left side of the cave, no obvious differences were detected in surface moisture and cover availability between the two sides.

No salamanders were detected within the first 2 m of the survey zone of Austin Cave (Fig. 17), that was the driest part of the survey zone (Table B-4). Of the 94 *E. lucifuga* detected, 77% were reported just beyond the metal gate at Station 2 (Fig. 17). Relative humidity was much higher at Station 2 than at Station 1. Many (39%) of the salamanders found at Station 2 were observed clinging to the inside of the door, which was often dripping with condensation or covered with a film of water. Equal numbers of individuals was recorded on the left and right sides of the cave (Table 10). This is not surprising as the survey zone in this cave was a straight, narrow tunnel, hewn out of solid rock and virtually identical on both sides.

Of the six caves surveyed, Great Onyx Cave had the most dramatic distribution of salamanders (Fig. 17). Eighty percent of the 208 individuals detected were found in the entrance room (blockhouse) within 3 m of the solid steel access door. This door protected the area around Station 1 from air flow and excluded most of the light, making the blockhouse humid and dark. However, air temperature, relative humidity, and light seem to have been no more favorable here than at the other two stations. The determining factor appears to have been surface moisture. Station 1 was consistently the wettest of the three stations (Table B-5). In fact, a puddle persisted throughout most of the year due to seepage from outside the cave, along both the floor and the left wall. This puddle was sometimes the only wet spot in the survey zone. Of the 180 salamanders detected within the first three meters, 21% were on the left wall, and 51% were submerged in the puddle, sometimes beneath rocks. A second contributing factor to the dense population of salamanders at Station 1 may have been the large metal storage box located on the left side of the blockhouse (Fig. 7). It sat above the puddle on concrete blocks, and as many as 18 salamanders were detected beneath it. The puddle's presence might explain not only the concentration of salamanders near the front of the cave, but also their apparent preference (75%) for the left side of the cave (Table 10). The fact that salamanders were found farther from the door during the colder months, even though the puddle persisted, supports my earlier suggestion that colder temperature extremes may

affect cave population dynamics, even when suitable surface moisture and relative humidity conditions are present.

In Crystal Cave seven of the eight salamanders detected were within the first three meters of the cave (Fig. 17). This was in the rocky entrance (Station 1) before the first steel door (Fig. 8). That area, which received run-off from the hillside above, was consistently the wettest of the three stations (Table B-6). Although some moisture was present beyond the door, it was usually in the form of ceiling drips rather than as moisture on the walls and floor. Beyond the survey zone (beyond the second door) is a narrow, extremely dry passageway bordered on both sides by high piles of dry gravel and rock. During an hour-long excursion deep into the cave no pools, streams, or wet areas were found. Apparently most of the cave salamanders at Crystal Cave inhabited only the entrance and nearby epigean habitats. All eight individuals recorded in Crystal Cave were detected in the center above the door, or to the left of and slightly above it (Table 10). This may have been due to the cover afforded by the numerous crevices in the piles of rock to the left and rocky bluff above the door, as compared to the relatively smooth wall located to the right.

Although Green et al. (1967) suggested that *E. lucifuga*'s apparent preference for the twilight zone of caves is due to sampling bias, all major studies to date indicate that visually detectable adults do in fact inhabit the twilight zone more frequently than the areas beyond which light can be detected (Banta and McAtee, 1906; Hutchison, 1958; Williams, 1980). Those investigators searched well beyond the twilight zone, and except an occasional individual, were unable to detect populations as dense as those found within the twilight zone. Banta and McAtee (1906) report most adults within the first 45.7 m, and Ives (1927) never found an adult beyond 30.5 m.

Hutchison (1958) and Williams (1980) have suggested that salamanders move deeper into the cave as available surface moisture decreases. This suggestion makes sense as plethodontids lack lungs and depend heavily upon cutaneous respiration, which requires a moist skin. Previous studies of *E. lucifuga* in caves have documented this apparent affinity for wet substrates (Banta and McAtee, 1906; Hutchison, 1958; Williams, 1980); with few exceptions, all salamanders detected in those studies were

found resting on rock or earth that was covered by a thin film of water. In Williams' (1980) study, as in mine, many salamanders were also found submerged in water. As first suggested by Hutchison (1958) and later supported by Williams (1980) and by my data, spatial distribution of *E. lucifuga* within the twilight zones of caves seems to be largely influenced by the amount of available surface moisture. If so, one would expect populations occupying the twilight zone to shift toward areas of greater surface moisture, providing other abiotic conditions are favorable, as changes occur throughout the year.

A relationship between the distribution of *E. lucifuga* in caves and available surface moisture appears to be well documented, but more research is needed to determine the spatial nature of shifting distributions within caves. Because of structural differences found among caves, and because of differences in rainfall and drainage, generalizing is hazardous. Not all caves undergo progressive drying toward the mouth. My study design, as it related to surface moisture and the distribution of *E. lucifuga* within caves, was deficient in some respects. Recording available surface moisture at only three stations did not adequately describe conditions found throughout the entire survey zone and proved to be misleading in some cases. Had I recorded surface moisture data for each salamander detected the relationship would likely have been more clearly revealed. A more objective measuring system would also have helped.

Microhabitat Selection. Table 11 shows the data on microhabitat selection by the *E. lucifuga* detected throughout my study period. Considering the combined data for all caves, of the 129 found on the floor, only six were exposed, the remaining 123 were either under some structure (rock, rubble, log, box) or in the corner formed by the floor and wall. Of the 291 detected on walls, 50% were exposed, 26% were in crevices, 22% were on ledges, and 2% were in the corner where wall met ceiling (Table 12). Generalizing from these data seems unwarranted because microhabitat selection depends heavily on the type of microhabitats available and the existing microclimate. For example, crevices are abundant in Great Onyx Cave, yet 57% of salamanders found there were exposed on walls. As mentioned previously, most of these were on the left wall, where surface moisture was greatest. Although this man-made wall is smooth, with no crevices, it was much wetter than were most crevices. In Austin Cave only 6% of salamanders found

Table 11. Number of *Eurycea lucifuga* detected on the floor, ceiling, and wall of each study cave.

Microhabitat	CAVE						TL
	Barnett	Dunbar	Woodson	Austin	Gr. Onyx	Crystal	
Floor	5	4	2	17	101	0	129
Ceiling	0	0	0	1	0	0	1
Wall	18	52	13	76	124	8	291
Total	23	56	15	94	225	8	421

Table 12. Numbers of *Eurycea lucifuga* detected at each of four positions on walls.

Microhabitat	CAVE						TL
	Barnett	Dunbar	Woodson	Austin	Gr. Onyx	Crystal	
ledge	7	25	1	20	10	1	64
crevice	6	10	6	5	45	4	76
exposed	5	13	6	51	68	3	146
corner	0	4	0	0	1	0	5
Total	18	52	13	76	124	8	291

on walls were in crevices. That cave, artificially hewn from solid rock, had few crevices within the first few meters of the cave. Ledges were numerous in Dunbar Cave, accounting possibly for the high number (48%) found there in that microhabitat.

Banta and McAtee (1906) reported *E. lucifuga* as usually occurring on walls; they found only three individuals on the floor. My combined data agree with those findings in that 68% of all salamanders recorded were on walls (Table 11.) But because Banta and McAtee did not state total number observed, a direct comparison of percentages is impossible. In Great Onyx Cave salamanders selected the floor and walls almost equally. This agrees with data reported by Hutchison (1958) who stated that within the twilight zones of caves *E. lucifuga* were found on the floor almost as often as on the wall. Microhabitat selection in terms of wall or floor may have been influenced by surface moisture, or by some other factor not measured.

Banta and McAtee (1906) reported only two or three *E. lucifuga* in shallow water, and concluded that this salamander is not very aquatic. Later studies by Hutchison (1958), who never observed *E. lucifuga* in pools or streams, and Green et al. (1967), who found only one gravid female in water

(presumably to deposit eggs), also indicate this species is essentially terrestrial. But Williams (1980), reported 16% of the *E. lucifuga* he observed from a cave stream, most beneath rocks. He suggested that previous investigators failed to document *E. lucifuga* in water because they didn't sample aquatic habitats sufficiently. I frequently recorded salamanders near pools in Barnett Cave, and often found them submerged in a shallow pool or "puddle" in Great Onyx Cave. Perhaps previous investigators did not find *E. lucifuga* in cave pools or streams because of the lack of those habitats in the caves studied. Further research is necessary to determine what factors influence *E. lucifuga*'s selection of this cave microhabitat.

Orientation

Salamanders detected on exposed walls (N=146) were scored according to their orientation. If found in a horizontal position, they were scored facing either toward or away from the cave entrance, if vertical, as either head up or head down. Results are shown in Figure 18. Horizontal individuals (100) significantly outnumbered (chi square 19.9, 1 df) vertical ones (46). Of the horizontal animals, those headed in (54) outnumbered slightly, but not significantly (chi square 0.64, 1 df), those headed out (46). Vertical orientation was predominantly upward (39), significantly (chi square 22.26, 1 df) outnumbering downward (7). These results suggest that cave salamanders prefer to orient horizontally rather than vertically and that no preference exists for orientation into or out of the cave. Vertical individuals seem to opt for head up versus head down.

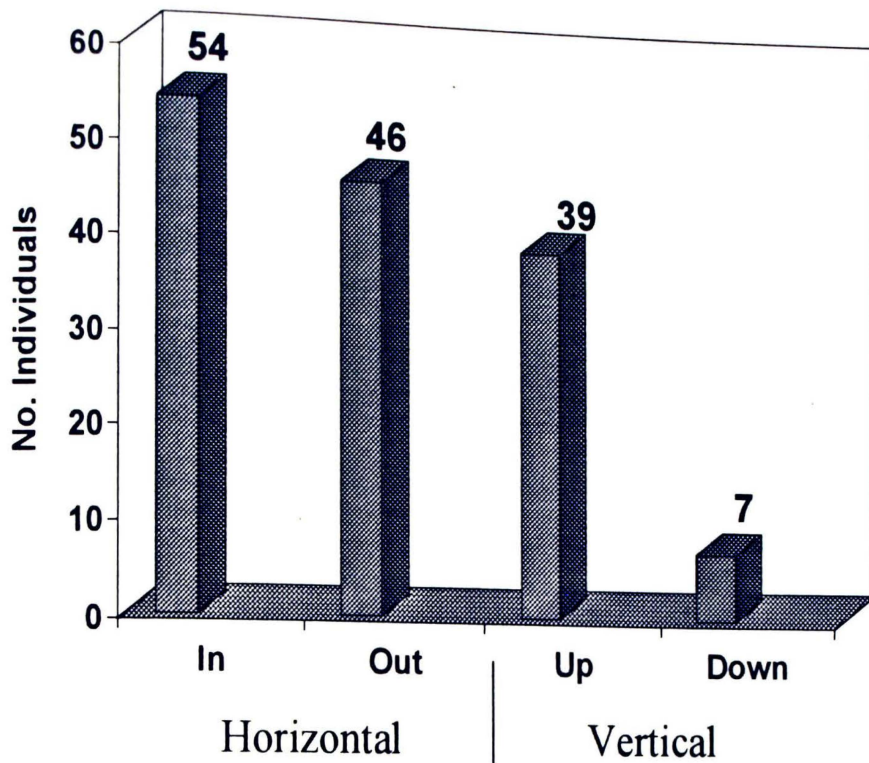


Figure 18. Orientation of individual *Eurycea lucifuga* observed in this study, relative to cave entrance and gravitational field.

Twenty-four-Hour Surveys

Diel Activity

Data from the quarterly 24-hour counts of the numbers of *E. lucifuga* detected every 2-hours at Dunbar and Great Onyx caves are graphed in Figure 19. Except for the February survey at Dunbar Cave, salamanders were present throughout each survey in both caves. Although more salamanders were consistently detected at Great Onyx Cave than at Dunbar Cave, the temporal activity in the two caves were similar. In each an initial peak occurred between 0400 and 0800, and a secondary peak between 1600 and 2000.

Data from the February, May, and November surveys clearly indicate a dual-peak pattern; early morning and early evening. The August surveys for both caves show these two peaks, but a third peak in population size was recorded at 1200 in both caves. In Great Onyx Cave this increase followed a decline

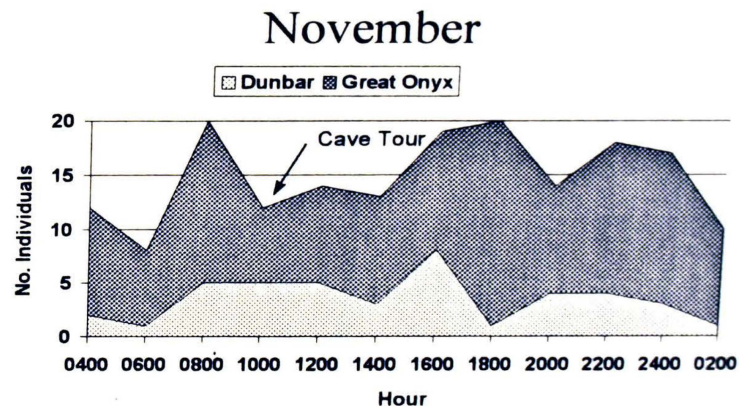
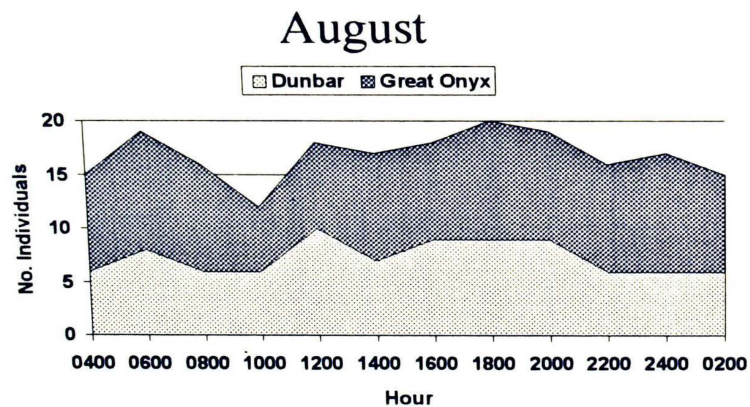
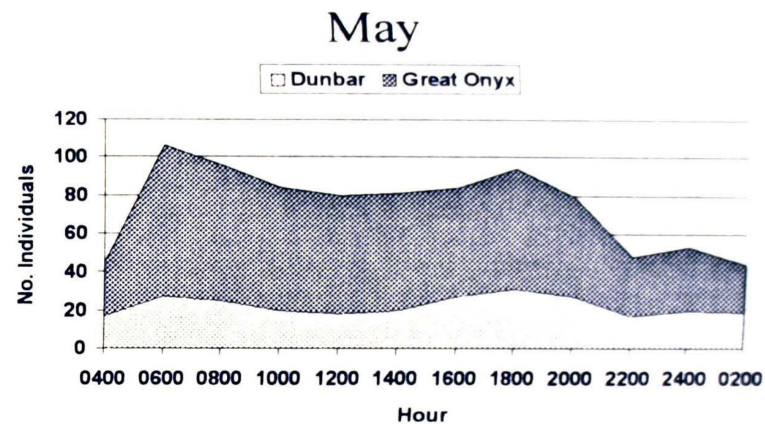
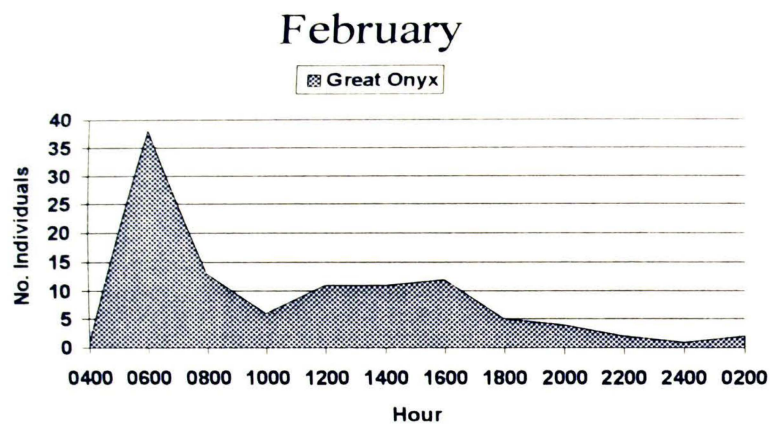


Figure 19. Numbers of *Eurycea lucifuga* individuals detected during each quarterly 24-hour census at Dunbar and Great Onyx caves.

in numbers between 0800 and 1000 hours. This may have resulted from the cave door being left open for some time (unscheduled tour group), flooding the area with light and causing relative humidity within the twilight zone to approach epigeal conditions. The increase in population size observed between 1000 and 1200 hours may have resulted from the restoration of "normal" conditions. No similar fluctuations in relative humidity occurred at Dunbar Cave during this time, leaving unexplained the mid-day peak observed there.

Sinclair (1950) reported seeing *E. lucifuga* during both day and night in and around Tennessee caves and suggested that they were not subjected to the same crepuscular limitations as are other salamanders species that primarily occupy epigeal habitats. Laboratory and field studies by Hutchison (1958) suggest arrhythmic activity in cave populations of *E. lucifuga*. But Green et al. (1967) stated that cave populations of *E. lucifuga* are nocturnal, emerging from cover after dark to crawl around the floors, walls, and ceilings of caves, and Besharse and Brandon (1974) considered them to be crepuscular. My data indicate that *E. lucifuga* inhabiting caves are not arrhythmic, although whether or not they are nocturnal or crepuscular is unclear.

Abiotic Factors and Their Relationships

Air Temperature and Relative Humidity. The raw data collected on air temperature and relative humidity during each of the quarterly 24-hour surveys at Dunbar and Great Onyx caves are presented in Appendix C (Tables C-1 and C-2). A summary and discussion of these data are given here.

The differences in mean outside air temperatures at the two caves during the February, May, and August surveys (Table 13) were small. During the November survey, however, the mean outside air temperature at Dunbar Cave (14°C) was much warmer than at Great Onyx Cave (8°C).

The mean cave air temperatures for each cave during each survey are shown in Table 14. There was less than a 1°C difference between the two study caves during surveys conducted in November, May, and August. During surveys conducted in February, however, the difference was 8°C, with Great Onyx Cave being much warmer (8.7°C) than Dunbar Cave (0.3°C). Outside air temperatures varied as much as

Table 13 Means of outside air temperatures and relative humidities recorded during each 24-hour survey at Dunbar and Great Onyx caves. Standard deviations are shown in parentheses.

Survey	Temperature (°C)		Relative Humidity	
	Dunbar	Great Onyx	Dunbar	Great Onyx
NOV 1994	14.08 (3.18)	8.05 (4.19)	89.08 (9.35)	81.60 (6.79)
FEB 1995	-1.67 (2.60)	1.83 (2.25)	52.08 (5.09)	96.67 (2.23)
MAY 1995	23.30 (5.77)	21.09 (1.68)	76.33 (19.50)	91.67 (4.81)
AUG 1995	27.75 (13.84)	27.63 (3.91)	82.83 (14.40)	82.33 (14.80)
Overall Mean	14.15 (12.45)	14.94 (10.89)	74.80 (18.99)	88.35 (10.53)

Table 14. Means of cave air temperatures and relative humidities recorded during each 24-hour survey at Dunbar and Great Onyx caves. Standard deviations are shown in parentheses.

Survey	Temperature (°C)		Relative Humidity	
	Dunbar	Great Onyx	Dunbar	Great Onyx
NOV 1994	12.98 (0.40)	12.43 (0.69)	97.21 (1.79)	94.64 (1.24)
FEB 1995	0.31 (1.38)	8.70 (3.45)	43.67 (3.75)	96.54 (2.52)
MAY 1995	12.28 (0.56)	12.88 (1.87)	98.00 (0.00)	94.75 (5.80)
AUG 1995	13.53 (0.77)	14.40 (2.31)	98.00 (0.00)	92.12 (11.20)
Overall Mean	9.78 (6.33)	12.10 (2.42)	84.22 (27.04)	64.51 (5.24)

10°C during the 24-hour surveys, but cave air temperatures remained relatively constant at both abiotic sampling stations: a maximum fluctuation of 3.0°C was recorded at Station 1 during the February surveys at both caves (Tables C-1 and C-2). Unlike the data recorded at caves in Hutchison's (1958) study, no distinct daily temperature lag was evident. This may have been due in part to differences in both the microclimate at given cave on given day (fluctuations in outside air temperature correlated with fluctuations found within caves) and in the caves themselves. As mentioned previously, air temperatures in caves are commonly influenced by airflow into and out of the caves and that airflow results from changes in outside barometric pressure and temperature (Hutchison, 1958). The velocity of such currents depends on the number of entrances to the surface, the size and type of entrance, and the size and structure of the cave.

Mean outside relative humidities were similar at both caves during November and August (Table

13). But at Great Onyx Cave they were 15% higher during May and 45% higher in February.

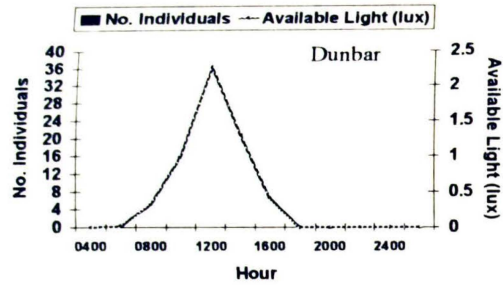
Mean cave relative humidities for each survey followed a trend similar to that of mean cave air temperature (Table 14). During November, May, and August the differences were small. During February, however, readings differed greatly (Great Onyx at 96.5%, Dunbar Cave at 43.7%).

Although air temperature and relative humidity varied slightly at each abiotic sampling station, within any 24-hour period the means for these factors remained relatively constant at both caves (Tables C-1 and C-2). Thus it is not surprising that no correlation was found between the changes in observed population size and fluctuations in mean air temperature or relative humidity within any 24-hour period. During the February survey, when no salamanders were detected at Dunbar Cave, conditions inside the caves differed dramatically. This may have been due to more outside air moving into Dunbar Cave via its large entrance, than at Great Onyx Cave. Although the mean outside air temperature at the two caves differed by only 3.3 °C (Table 13), the mean cave air temperature at Great Onyx Cave (with its solid steel door) was 8.4 °C higher than at Dunbar Cave (Table 14). The differences in cave relative humidities were even greater with Great Onyx Cave at 96.54% compared to Dunbar Cave at 43.67% (Table 14). Although cave air temperature and relative humidity do not appear to influence diel activity, they may be important in determining where and when populations can exist.

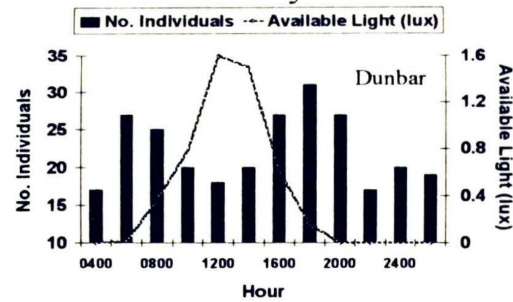
Light Intensity. Within any cave a twilight zone exists. The length of this zone is dependent on the size and configuration of the entrance and the contour of the cave (Hutchison, 1958). It also varies with the time of day, the season, and such other external factors as nearby obstructions and their influences on the amount or angle of entering light, vegetation, and local climatic conditions (Hobbs, 1992). In my study, the amount of light outside the entrance differed dramatically between the two caves, because of differences in entrance types (solid door at Great Onyx Cave, and a large unobstructed entrance at Dunbar Cave). Since the instrument I used to measure light intensity was incapable of registering very low light levels, readings in Great Onyx Cave were made at the bottom of the door, the only place where light entered directly. This was adequate in determining relative changes in light intensity within Great Onyx Cave, but the data were not comparable with data taken at Dunbar Cave, which had no such door.

Light was first detected shortly after sunrise and generally continued to increase in intensity until mid-day, then decreased until disappearing shortly after sunset. Except for November, when light intensity was not recorded, the early morning peaks recorded in numbers of salamanders in both caves occurred when light intensity was still zero but just prior to the check when light was first detected (Figure 19). The early evening peaks occurred just prior to the check when light intensity was again zero. Because numbers of visible individuals increased and decreased between these peaks independent of increases and decreases in light intensity, no overall significant correlation was detected between the two factors. But clearly the number of *E. lucifuga* occupying the twilight zone of caves increases shortly before dawn and just after sunset. The data suggest that rather than photo cueing, the salamanders are responding to an internal "diurnal clock." A flaw in my study design was that I began my surveys at a standardized hour (0400), rather than at sunrise with subsequent checks every two hours thereafter. For example, the May data indicate that the early morning peaks occurred at 0600 (Fig. 20), when in all likelihood they occurred sometime between 0500 and 0600, just prior to sunrise. As my checks were made every two hours, the true fluctuations may have been missed. Future studies concerned with diel activity should proceed according to specified intervals from actual sunrise, not in intervals based on standard time. Despite design flaws in both the timing and instrument used to measure light intensity, the relationship between available light and visible population size is evident. Further studies are needed to determine whether or not salamanders are responding to photo cues or an internal clock. More research is needed to determine if the salamanders are actually leaving the cave at these peak periods. If they are, do they remain active outside the cave throughout the night? Based on observations made during each survey, I believe that the salamanders are nocturnal, leaving the cave after the sun sets and returning before daybreak. Throughout the survey period salamanders would remain motionless for several hours at a time. But when their numbers peaked salamanders were changing positions, many actually moving toward the door or under it and out of the cave. Green et al. (1967) state that during the day *E. lucifuga* are found in caves under rocks, wood slabs, and other debris, emerging after dark.

February



May



August

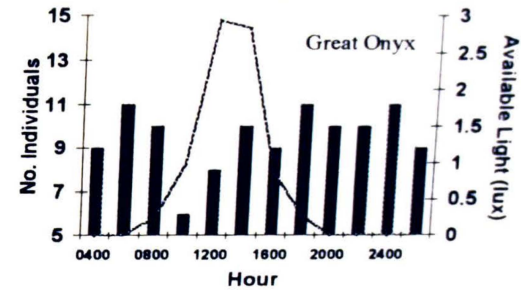
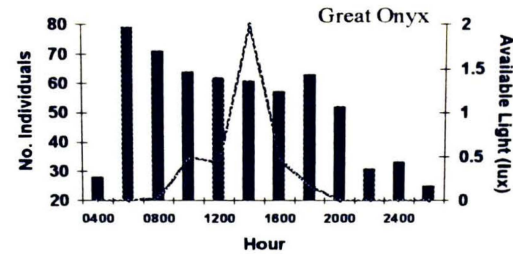
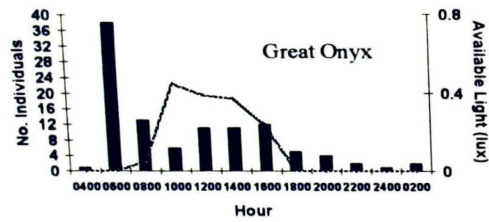
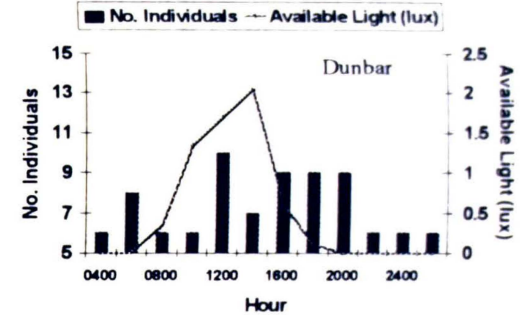


Figure 20. Numbers of *Eurycea lucifuga* individuals and light intensity readings during each quarterly survey at Great Onyx and Dunbar caves. No salamanders were observed at Dunbar Cave during the February survey.

Mohr (1944) reported that *Eurycea longicauda* in caves may remain motionless for hours, and that they were taken just outside caves only in the early evening hours.

Additional Observation

Reaction to Light

Although Banta and McAtee (1906) state that *E. lucifuga* is not easily induced to move, and will remain in place when a light is shown on them, observations by Green et al. (1967) indicate that light causes them to retreat. In my study they would remain motionless while a light was shown on them, and even while a ruler was placed as close to their bodies as possible. Their failure to move even with a moving object nearby was reported also by Banta and McAtee (1906). The salamanders moved only when touched: that reaction is described below.

Reaction to Touch

Eurycea lucifuga is surprisingly quick and agile. When touched they moved quickly to escape, either deeper into a wall crevice or along the floor. This behavior has been noted previously by Banta and McAtee (1906), Hutchison (1958), and Green et al. (1967). All investigators described the salamander's escape reaction as an almost violent motion, beginning with an initial leap, followed by a series of leaps and wriggles.

Feeding Behavior

Eurycea lucifuga's diet within caves has been determined in some detail. Hutchison (1958) showed the primary food items of the species in his study area were dipterans, mites, ticks, lepidopterans, and pseudoscorpians. Brandt (1946) reported *E. lucifuga* as eating soft bodied roaches. Both Smith (1948) and Peck (1974) listed helomyzid flies as the most abundant food source found in cave populations of *E. lucifuga*. Although a recent study by Helf and Poulson (1996) did not show *E. lucifuga* to be a predator of the cave cricket (*Hadenoeus subterraneus*), these crickets have been reported as prey items of

E. lucifuga by Peck (1974). I observed two individuals eating this cricket during my 24-hour survey of Great Onyx Cave during February. Other larger prey items reported by Peck (1974) included millipedes (*Pseudotremia*) and crickets of the genus *Ceuthophilus*.

Although patterns in salamander population density observed in both my year-long and 24-hour studies correlated significantly with various abiotic factors, one must not assume a cause-effect relationship. It is possible that these patterns were due to the availability of food. In a study of seasonal fluctuations in cave populations of *Typhlotriton spelaeus* (Brandon, 1971), salamanders were most abundant when the walls were wettest, with relative abundance correlated with rainfall. However, highest numbers also occurred when insects were most abundant and feeding success in this salamander was greatest. *Hadenocoecus subterraneus*, a known prey item of *E. lucifuga*, is a key species in cave ecology in the Mammoth Cave National Park region. It is found in high densities in many cave entrances (Poulson et al., 1995) and has been observed as a prey item of *E. lucifuga* in Great Onyx Cave. This cricket forages at night, only comes out of the cave after a rain during hot dry summers, and is limited in winter by temperature extremes, coming out to forage only when temperatures are above 15°C and relative humidity is high. It is possible that the patterns I observed, both in the year-long study and the 24-hour study of *E. lucifuga*, were in fact related to some unmonitored factor (e.g. food availability) also related to the abiotic conditions studied.

Courtship Behavior

Courtship behavior of *E. lucifuga* in a controlled laboratory environment has been described in detail by Organ (1968). Courtship behavior of the species in caves has not. During my study, no obvious courtship behavior was noted.

Eggs and Larvae

According to Banta and McAtee (1906) and Myers, (1958), *E. lucifuga* lays eggs deep within the cave where the larvae hatch and remain until metamorphosis is complete. I made several trips during different times of the year beyond the survey zones of my study caves, but found no eggs or larvae.

Prehensile Tail

I agree with previous investigators that *E. lucifuga* is an excellent climber (Green et al., 1967) and that it uses its tail to assist in climbing (Banta and McAtee, 1906; Hutchison, 1958). But I never observed any individual hanging by its tail alone, as reported by those authors.

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APPENDIXES

APPENDIX A
Data Sheets Used

FIELD DATA SHEET
LONG TERM MONITORING OF CAVE-DWELLING SALAMANDER POPULATIONS
(Eurycea lucifuga, Plethodon glutinosus, Plethodon dorsalis)
IN MAMMOTH CAVE NATIONAL PARK
 Page 1 of _____

RESEARCHERS: _____ ASSISTANTS: _____

CAVE CODE: _____ DATE: _____ TIME: _____ to _____

CURRENT OUTSIDE WEATHER:

GENERAL CONDITIONS: _____

AIR TEMP. (C): START _____ FINISH _____

RELATIVE HUMIDITY: START _____ FINISH _____

PRECIPITATION: NONE; RAIN, SNOW: LIGHT, MODERATE, HEAVY

PREVIOUS OUTSIDE WEATHER (GENERAL CONDITIONS): _____

CAVE CHEMISTRY:

STATION	TEMP (°C)	RH (%)	pH	MOIST	REMARKS
1					
2					
3					
SUM					
AVG					

OTHER HERPTILE SPECIES PRESENT: _____

GENERAL COMMENTS: _____

Figure A-1. Page 1 of data sheet used on monthly visits to the study caves.

Cave Salamanders Census, Field Data Sheet, Continued

Date:

Cave :

Page _____ of _____

[illegible]

Figure A-2. Page 2 of monthly survey data sheets.

Field Data Sheet
Diurnal Activity of *Eurycea Lucifuga*

RESEARCHERS: _____ ASSISTANTS: _____
 CAVE CODE: _____ DATE: _____ TIME: _____ TO _____
 CURRENT OUTSIDE WEATHER: _____
 GENERAL CONDITIONS: _____
 AIR TEMP. (C): START _____ FINISH _____
 RELATIVE HUMIDITY: START _____ FINISH _____
 PRECIPITATION: NONE, RAIN, SNOW: LIGHT, MODERATE, HEAVY
 PREVIOUS OUTSIDE WEATHER (GENERAL CONDITIONS): _____

No.	Time Begin	Time End	Out RH	Out °C	St1 RH	St1 °F	St3 RH	St3 °F	# EL	Remarks
1										
2										
3										
4										
5										
6										
7										
8										
9										
10										
11										
12										

Figure A-3. Data sheet used during quarterly 24-hour surveys of Dunbar and Great Onyx caves.

APPENDIX B

Raw Data for Abiotic Factors Sampled on

Monthly Visits to Each Cave

Table B-1. Raw Data for abiotic factors sampled during each monthly survey of Barnett Cave.

Month	Air Temperature (°C)					Relative Humidity					Surface Moisture		
	Outside		Inside			Outside		Inside					
	Before	After	ST.1	ST.2	ST.3	Before	After	ST.1	ST.2	ST.3	ST.1	ST.2	ST.3
JAN	4	*	5.20	5.30	7.00	45	*	39	68	88	0.0	3.0	4.0
FEB	-1	-1	0.94	3.67	6.55	55	78	51	87	97	2.0	3.0	4.0
MAR	5	5	3.10	5.10	6.70	40	42	40	79	93	0.0	3.0	4.0
APR	15	28	12.00	8.20	9.20	46	26	49	85	98	0.0	4.0	4.0
MAY	21	25	21.50	11.40	11.20	46	50	58	85	98	0.0	4.0	4.0
JUN	28	33	16.50	14.60	13.50	71	50	85	90	95	4.0	3.0	4.0
JUL	26	27	19.20	16.80	14.70	71	67	78	82	98	4.0	3.0	2.0
AUG	35	*	21.40	16.70	14.70	50	*	70	94	98	2.0	4.0	4.0
SEP	22	18	18.06	16.17	15.67	73	89	83	91	92	2.0	4.0	4.0
OCT	19	21	15.00	14.55	14.39	65	68	81	88	92	0.0	4.0	4.0
NOV	13	12	12.56	13.00	13.11	37	39	66	78	91	0.0	4.0	4.0
DEC	12	12	12.50	12.00	12.00	81	86	80	91	94	2.0	4.0	4.0
Mean	16.58	18.00	13.16	11.46	11.56	56.67	59.50	65	84.8	93.7	1.33	3.58	3.83

Table B-2. Raw Data for abiotic factors sampled during each monthly survey of Dunbar Cave.

Month	Air Temperature (°C)					Relative Humidity					Surface Moisture		
	Outside		Inside			Outside		Inside					
	Before	After	ST.1	ST.2	ST.3	Before	After	ST.1	ST.2	ST.3	ST.1	ST.2	ST.3
JAN	*	1	3.10	3.70	4.20	*	84	59	63	61	0.00	0.00	0.00
FEB	0	0	1.61	2.28	3.06	68	70	60	59	72	2.00	2.00	2.00
MAR	5	6	5.60	4.10	5.30	44	42	37	43	63	2.00	3.00	0.00
APR	25	28	15.90	9.80	9.70	20	16	36	74	75	0.00	3.00	2.00
MAY	13	14	10.00	10.00	10.40	73	71	92	89	90	2.00	3.00	3.00
JUN	30	33	13.50	12.90	12.70	65	57	97	98	98	4.00	4.00	2.00
JUL	28	27	15.80	13.80	13.10	64	62	80	92	93	3.00	3.00	3.00
AUG	28	28	14.20	13.50	12.80	65	60	98	98	98	4.00	3.00	2.00
SEP	25	23	14.44	14.28	14.28	77	81	93	93	94	0.00	2.00	2.00
OCT	*	28	14.56	13.33	14.11	*	27	82	93	96	0.00	3.00	3.00
NOV	11	*	13.83	12.56	12.61	43	*	54	66	70	0.00	0.00	1.00
DEC	12	12	13.00	12.50	12.00	76	82	83	90	91	0.00	4.00	1.00
Mean	17.70	18.18	11.30	10.23	10.36	59.5	59.27	72.6	79.8	83.4	1.67	2.50	1.75

Table B-3. Raw Data for abiotic factors sampled during each monthly survey of Woodson Cave.

Table B-3. Raw Data for abiotic factors sampled during 1997													
Month	Air Temperature (°C)					Relative Humidity					Surface Moisture		
	Outside		Inside			Outside		Inside			ST 1	ST 2	ST 3
	Before	After	ST.1	ST.2	ST.3	Before	After	ST.1	ST.2	ST.3			
JAN	4	1	4.50	6.00	6.00	70	90	58	61	68	4	4	0
FEB	0	0	3.00	3.10	4.20	67	72	56	61	65	4	4	0
MAR	6	5	6.50	6.20	6.80	42	46	46	63	84	4	4	4
APR	25	28	17.60	11.50	10.30	23	22	47	62	74	0	4	0
MAY	25	22	15.10	12.50	13.40	68	70	75	81	89	4	4	1
JUN	32	32	22.70	18.20	15.80	58	58	83	73	82	3	2	1
JUL	28	31	23.70	17.50	15.80	66	64	71	78	91	4	4	3
AUG	35	24	22.50	18.20	16.70	55	95	82	86	90	2	4	0
SEP	*	23	19.78	17.23	16.06	*	79	89	87	89	0	4	0
OCT	*	23	21.06	15.50	16.06	*	49	62	81	84	0	4	0
NOV	10	9	13.05	12.61	14.11	44	45	58	61	69	4	4	1
DEC	*	11	15.00	13.00	13.00	*	78	82	82	89	2.75	3.83	1.17
Mean	18.33	17.42	15.37	12.63	12.35	54.78	64.00	67.4	73	81.1			

*Indicates missing data.

Table B-4. Raw Data for abiotic factors sampled during each monthly survey of Austin Cave.

Month	Air Temperature (°C)					Relative Humidity					Surface Moisture		
	Outside		Inside			Outside		Inside					
	Before	After	ST.1	ST.2	ST.3	Before	After	ST.1	ST.2	ST.3	ST.1	ST.2	ST.3
JAN	-12	-9	-6.70	-0.80	-2.03	67	58	43	74	60	0	0	0
FEB	6	5	4.90	5.40	5.43	51	71	48	75	80	0	0	0
MAR	2	2	3.30	5.30	4.90	51	77	63	89	98	0	0	0
APR	5	5	4.40	3.50	4.20	41	43	31	62	62	0	0	0
MAY	15	15	10.30	9.40	9.73	100	100	84	95	98	0	0	0
JUN	26	27	12.50	11.50	11.90	73	71	90	92	94	3	2	1
JUL	26	25	15.20	13.20	13.73	61	60	72	76	84	2	2	2
AUG	28	28	16.70	11.70	13.33	70	72	65	94	98	2	1	2
SEP	20	18	14.55	12.33	13.26	90	89	83	89	91	0	2	3
OCT	17	19	12.11	11.83	12.11	55	54	84	92	94	1	1	1
NOV	19	19	13.72	11.39	12.26	49	52	68	92	94	0	0	0
DEC	7	5	7.00	8.00	8.33	65	77	78	83	90	0	0	1
Mean	13.25	13.25	9.00	8.56	8.93	64.42	69.5	67.4	84.4	87.2	0.83	0.73	0.88

Table B-5. Raw Data for abiotic factors sampled during each monthly survey of Great Onyx Cave.

Month	Air Temperature (°C)					Relative Humidity					Surface Moisture		
	Outside		Inside			Outside		Inside					
	Before	After	ST.1	ST.2	ST.3	Before	After	ST.1	ST.2	ST.3	ST.1	ST.2	ST.3
JAN	-4	-3	1.30	4.50	6.10	50	48	64	84	93	4	0	3
FEB	9	8	8.20	7.60	8.40	60	58	66	85	94	4	3	4
MAR	5	4	7.70	8.10	8.80	65	67	47	92	98	4	2	3
APR	9	9	9.20	9.60	9.90	37	38	38	80	91	4	0	3
MAY	15	*	11.70	11.40	14.80	100	*	98	98	98	4	3	3
JUN	24	28	16.06	13.86	13.17	72	53	80	85	87	4	2	3
JUL	22	22	18.80	14.60	13.80	87	87	74	74	80	4	0	2
AUG	32	32	18.80	15.30	13.80	57	54	58	70	78	0	0	2
SEP	25	25	16.72	15.56	12.94	50	47	77	79	95	4	0	1
OCT	22	22	15.89	15.78	14.55	48	49	80	80	83	4	0	1
NOV	21	*	12.05	14.28	13.00	55	*	84	86	92	4	0	0
DEC	7	7	10.00	12.00	12.00	73	72	87	94	95	4	0	3
Mean	15.58	15.40	12.20	11.88	11.77	62.83	57.3	71.1	83.9	90.3	3.67	0.83	2.33

Table B-6. Raw Data for abiotic factors sampled during each monthly survey of Crystal Cave.

Month	Air Temperature (°C)					Relative Humidity					Surface Moisture		
	Outside		Inside			Outside		Inside					
	Before	After	ST.1	ST.2	ST.3	Before	After	ST.1	ST.2	ST.3	ST.1	ST.2	ST.3
JAN	-6	-1	-3.50	0.90	3.00	54	51	41	73	81	0	0	0
FEB	8	9	5.40	6.00	7.80	61	53	58	87	93	0	0	0
MAR	2	2	5.00	7.20	7.70	76	73	56	91	93	3	0	0
APR	7	8	6.60	8.00	8.60	42	39	45	84	92	1	0	0
MAY	15	15	11.20	10.80	10.50	100	100	85	96	98	3	1	1
JUN	28	28	14.10	12.40	12.10	68	70	74	82	90	3	1	0
JUL	38	38	17.40	14.10	12.50	70	66	56	69	80	2	1	1
AUG	31	31	16.60	13.30	12.60	66	62	65	72	80	3	2	2
SEP	22	23	15.83	12.33	12.50	59	59	82	90	90	3	2	2
OCT	20	20	13.10	12.78	12.22	52	52	80	83	89	0	1	1
NOV	20	21	13.83	11.72	11.73	51	52	70	82	87	0	0	1
DEC	5	5	12.00	9.00	10.00	79	73	81	91	95	2	0	0
Mean	15.83	16.58	10.63	9.88	10.10	64.83	62.5	65.8	83.3	89	1.67	0.67	0.67

* Indicates missing data.

APPENDIX C

Abiotic Data Collected

During Quarterly 24-hour Surveys

Table C-1. Abiotic data collected during quarterly surveys of Dunbar Cave.

Hour	Relative Humidity			Air Temperature (°C)			Light (lux)
	Out	ST 1	ST 3	Out	ST 1	ST 3	
February							
0600	40	40	51				
0800	55	42	51	-7.0	-3.0	-0.7	0.02
1000	53	42	43	-5.0	-2.5	-0.5	0.32
1200	49	41	41	-4.0	-1.9	-0.3	0.99
1400	48	39	41	1.0	-0.9	0.7	2.27
1600	48	40	44	2.0	0.3	1.4	1.30
1800	52	39	40	1.0	0.4	1.6	0.41
2000	54	41	42	-1.0	0.5	1.6	0.00
2200	55	43	49	-1.0	0.3	1.9	0.00
2400	56	44	48	-1.0	0.4	1.9	0.00
0200	57	45	47	-1.0	0.3	1.9	0.00
0400	58	46	49	-2.0	0.2	1.9	0.00
May							
0600	90	98	98	20	13.6	11.9	0.02
0800	85	98	98	20	12.7	11.9	0.36
1000	*	98	98	*	12.7	11.9	0.78
1200	*	98	98	*	12.7	11.7	1.60
1400	*	98	98	*	12.6	11.7	1.50
1600	54	98	98	30	12.5	11.7	0.61
1800	*	98	98	*	12.7	11.7	0.16
2000	*	98	98	*	12.9	11.8	0.00
2200	*	98	98	*	12.6	11.7	0.00
2400	*	98	98	*	12.7	11.7	0.00
0200	*	98	98	*	12.7	11.7	0.00
0400	*	98	98	*	13.0	11.9	0.00
August							
0600	93	98	98	23	14.4	13.2	0.01
0800	92	98	98	25	14.2	12.8	0.34
1000	76	98	98	26	14.1	12.8	1.34
1200	58	98	98	33	13.7	12.8	1.69
1400	57	98	98	35	14.2	12.9	2.04
1600	68	98	98	33	15.7	12.8	0.62
1800	84	98	98	29	14.1	13.0	0.12
2000	92	98	98	26	14.0	12.9	0.00
2200	93	98	98	26	14.0	12.8	0.00
2400	93	98	98	26	14.0	12.8	0.00
0200	94	98	98	26	14.1	12.8	0.00
0400	94	98	98	25	13.9	12.8	0.00
November							
0600	93	98	93	14	13.4	13.2	*
0800	88	98	98	16	13.3	12.7	*
1000	82	98	98	17	13.3	12.6	*
1200	77	98	98	18	13.4	12.8	*
1400	69	98	98	20	13.3	12.8	*
1600	85	98	98	15	13.4	12.6	*
1800	93	98	98	12	13.7	12.6	*
2000	93	97	96	13	13.5	13.3	*
2200	94	98	98	12	13.3	12.7	*
2400	95	98	98	12	13.1	12.6	*
0200	100	95	98	10	12.8	12.6	*
0400	100	91	97	10	12.2	12.3	*

* Indicates Missing data.

Table C-2. Abiotic data collected during quarterly surveys of Great Onyx Cave.

Hour	Relative Humidity			Air Temperature (°C)			Light (lux)
	Out	ST 1	ST 3	Out	ST 1	ST 3	
February							
0600	100	89	98				
0800	94	91	98	6.0	6.1	11.8	0.00
1000	95	92	98	2.0	3.0	12.0	0.05
1200	93	98	98	3.0	7.0	12.0	0.45
1400	95	98	98	3.0	6.0	12.0	0.39
1600	95	97	98	3.0	6.0	12.0	0.37
1800	97	97	98	3.0	6.0	12.0	0.24
2000	97	97	98	2.0	6.0	12.0	0.00
2200	99	94	98	1.0	6.0	12.0	0.00
2400	99	96	98	-1.0	5.0	12.0	0.00
0200	98	96	98	-1.0	4.0	12.0	0.00
0400	98	96	98	-2.0	4.0	12.0	0.00
May							
0600	90	90	89	21.7	15.0	12.0	0.00
0800	96	90	98	18.9	15.0	11.0	0.03
1000	93	90	100	19.5	15.0	11.0	0.50
1200	90	90	100	20.0	14.0	11.0	0.43
1400	89	95	100	20.0	14.0	11.0	2.00
1600	78	78	100	24.0	14.0	11.0	0.48
1800	93	92	100	22.0	15.0	11.0	0.17
2000	94	94	100	21.0	14.0	11.0	0.00
2200	94	94	100	20.0	15.0	11.0	0.00
2400	94	94	100	20.0	15.0	11.0	0.00
0200	94	95	100	22.0	15.0	11.0	0.00
0400	95	95	100	24.0	15.0	11.0	0.00
August							
0600	95	97	98	23.0	16.2	12.0	0.01
0800	91	82	98	24.5	18.0	12.0	0.24
1000	71	70	75	30.5	16.9	14.2	0.98
1200	59	82	98	32.5	17.3	12.5	2.94
1400	63	81	98	33.0	15.9	12.1	2.84
1600	61	98	98	33.0	16.0	12.0	0.87
1800	79	98	98	30.0	16.1	12.0	0.30
2000	92	98	98	27.0	15.8	12.0	0.00
2200	94	98	98	25.5	17.6	12.0	0.00
2400	94	98	98	25.0	16.2	12.0	0.00
0200	94	98	98	24.0	16.5	12.0	0.00
0400	95	98	98	23.5	16.4	12.0	0.00
November							
0600	89	*	*	*	*	*	*
0800	*	92	95	*	*	*	*
1000	79	91	95	12.0	12.5	13.0	*
1200	76	95	95	12.5	12.5	12.5	*
1400	73	95	95	14.0	13.5	12.5	*
1600	83	96	95	12.0	13.0	12.5	*
1800	90	95	95	8.0	13.0	12.5	*
2000	90	96	95	5.0	12.5	12.5	*
2200	74	92	95	6.0	12.0	13.0	*
2400	76	92	95	4.0	11.0	13.0	*
0200	87	95	95	4.0	11.0	12.5	*
0400	88	95	96	3.0	11.0	12.5	*

* Indicates missing data.