ROOSTING ECOLOGY OF THE EASTERN BIG-EARED BAT, *PLECOTUS RAFINESQUII*, IN NORTH CAROLINA

by
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BIOGRAPHY

Mary Kay Clark was born in Elizabethtown, North Carolina on 2 January 1956. She graduated from East Bladen High School in 1974 and received her Bachelor of Science degree from Campbell College in 1978. In March 1979 she began employment at the North Carolina State Museum of Natural Sciences as a research technician in the mammal collection and audio-visual specialist for the education section. At present she is Curator of Mammals at the Museum. Ms. Clark married David Stephen Lee on July 10, 1982. Graduate study leading to a Master of Science degree in Ecology was begun in 1984.

ABSTRACT

CLARK, M. K. Roosting ecology of the eastern big-eared bat, *Plecotus rafinesquii*, in North Carolina (under the direction of Richard A. Lancia).

To determine roost preferences of *Plecotus rafinesquii* I measured internal variables (temperatures, light levels and disturbance rates) in buildings used, and not used, by *P. rafinesquii* in Bladen, Chowan, Pender, and Sampson counties during the nursery season of 1986. No significant differences between occupied and unoccupied sites for internal variables were observed in buildings studied.

External habitat variables; proximity to water, amount of water or wetlands near roosts, and land-use patterns that might influence roost choice were measured for 22 Bladen County sites. More closed canopy forest surrounded occupied sites than unoccupied sites. All sites studied were within 1 km of a major water body.

Physical characteristics of buildings available to *P. rafinesquii* were described as well as those of two tree roosts used by this species. Daily temperature profiles of the two tree cavities were compared to two nursery roosts in buildings. Daily temperature profiles of buildings differed considerably from tree cavities in maximum and minimum measurements. Tree cavities were more thermally stable than house sites, but buildings may make better nursery roosts than tree cavities because the higher temperatures reached in them are probably advantageous to young bats and to pregnant and lactating females.

To put observations in perspective a reproductive phenology was developed. Thermal conditions in nursery roosts were compared to those

in sites used by solitary bats. No significant differences in temperatures were observed. Light levels in solitary roosts averaged lower than those in nursery roosts.

Internal and external habitat variables from 22 sites from Bladen County were entered in discriminant function analysis to determine those that best classified sites as occupied or unoccupied. Combinations of external variables entered in discriminant function analysis (DFA) yielded more accurate classifications of occupied and unoccupied sites than did combinations of internal variables. Important external influences on _P. rafinesquii_ roost choice appear to be forest cover and water variables. Though my results are somewhat inconclusive, both qualitative and quantitative evidence gathered in my study support the contention that roost selection cannot be predicted from internal variables alone.

Social organization was not quantitatively addressed in this study, but the documented influence of environmental pressures on mating systems, combined with relevant information on _P. rafinesquii_ life history and roosting ecology influences, prompted proposition about the mating system of this bat. I suggest that high quality summer roosts may be defended by solitary males, effectively limiting access of other males to females for at least a portion of the sexually active season. The possibility that _P. rafinesquii_ has a resource-defense polygynous mating system bears further investigation.

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Paris Trail played an integral role in this study. Mr. Trail is responsible for much of the data collection and general observations in the Chowan County sites. Mr. Trail also designed and built a cage for captive *P. rafinesquii* and made meticulous notes on the behavior of two *P. rafinesquii* under his care. The full support of his wife, Dorothy, is also appreciated. The Trails often provided tick repellent, showers, food, soft beds and other field support for me and my assistants.

Partial funding for some aspects of this study was provided by three grants from the Nongame Small Grants Program of the North Carolina State Wildlife Resources Commission. These funds allowed the purchase of some equipment and supplies and also allowed me to hire field assistants when necessary during certain phases of the study.

Many people assisted in various aspects of the study and were indispensable to the completion of this research. Jeff Beane assisted, to varying degrees, in all phases of the field research and plotted sites from background studies on county and topographic maps. Locating, censusing and monitoring roosts is a labor intensive activity. Several student interns from the N.C. Institute of Government assisted with this aspect of the roosting ecology investigation, as well as in the background studies that provided the foundation for this work. One of these, Danny Ray, was my sweaty companion in the unusually hot summer of 1986, when sites were most intensively monitored. Interns that helped conduct background surveys were Kelly Smith, Todd Weaver, Dudley Aldridge, and Sherry Adcock. Danny Smith, a museum volunteer, also assisted with background studies.

The cooperation of all landowners is appreciated. I especially thank Frederick and Jeanie Inglis for taking a personal interest in the bats and allowing such uninhibited access to the nursery colony near their home. David Clark flew me over some study sites so I could take aerial photographs.

Paul Marsh was exceptionally generous with his time, providing invaluable assistance with SAS programming and statistical analysis. Marcia Gumpertz patiently guided me through discriminant function analysis. Mary Frazer prepared graphics for this paper. The illustration of the face of *P. rafinesquii* was prepared by Ruth Brunstetter. Cathy Wood typed many drafts of this paper.

I thank Richard A. Lancia for his contribution to the development of my graduate research and for his patience. I am grateful for the assistance and guidance offered by the other members of my committee as well; John B. Funderburg, Jr., Roger A. Powell, and Jeffrey R. Walters. Phil D. Doerr substituted while Dr. Powell was on sabbatical and made valuable contributions to this paper. This work was conducted through the N.C. State Museum of Natural Sciences, of which Dr. Funderburg was Director during most of this study. For his support of the project, and of my career development, I am especially grateful.

My parents, David and Miriam Clark, were supportive of my desire to pursue graduate work and I thank them for their encouragement. My husband, David S. Lee, introduced me to big-eared bats, assisted to varying degrees in all phases of the field work and read and commented on several drafts of this paper. More importantly, he was a constant source of inspiration and support.

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INTRODUCTION

My study represents the first detailed investigation of the roosting ecology of Plecotus rafinesquii, long considered one of the least-studied bats in North America (Barbour and Davis 1969, Jones 1977). This bat seems to occur naturally at low densities throughout its range and was recognized as rare as early as 1969 (Barbour and Davis 1969). The Florida Game and Freshwater Fish Commission listed P. rafinesquii as "Rare" in the State in 1978 (Brown 1978), and it was designated endangered in 1988 by the Commonwealth of Virginia (pers. comm., Karen Terwilliger, Virginia Department of Game and Inland Fisheries). Two summary reports of endangered, threatened and rare species of the United States (Morgan 1980, Berger and Nuener 1981) list P. rafinesquii as "Special Concern" in Alabama, "Endangered" in Indiana and "Rare" in Mississippi. This species was determined to be "Special Concern" in North Carolina in 1977 (Lee and Funderburg 1977) and "Vulnerable" in 1987 (Clark 1987). In 1989, P. rafinesquii was legally designated a species of "Special Concern" in North Carolina (pers. comm., Randall Wilson, Section Manager-N.C. Wildlife Resources Commission, Nongame and Endangered Species Section). The January 6, 1989 Federal Register Notice of Review (Vol. 54, No. 4) listed P. rafinesquii as Category 2 (U. S. Fish and Wildlife Service). A Category 2 species is one suspected to be in need of protection, but a status decision cannot be made because critical life history data is unknown.

Restricted to the southeastern United States (Fig. 1), P. rafinesquii occurs discontinuously west to Louisiana and Oklahoma, north in the interior to Illinois, Indiana, Ohio and West Virginia, and north big-eared bat, P. townsendii, (Jones 1977). In his revision of the genera Euderma and Plecotus Handley (1959) summarized all known information on distribution, habitat preferences, behavior, food habits, movement patterns, hibernation and reproduction of P. rafinesquii. Jones and Suttkus (1975) reported on some aspects of the ecology of P. rafinesquii, emphasizing colony structure. Jones (1977) provided a summary account of published information for this species.

Reports of P. rafinesquii are primarily from houses and other man-made structures. There is little information on natural roost sites. Handley (1959) stated that natural roosting places for the species are caves, tree cavities, crevices behind loose bark and "similar arboreal retreats." Caves and mines are used in the northern fringe of its range (Handley 1959), and mines are used in the mountain region of North Carolina (pers. obs., M. K. Clark). There are no caves in the North Carolina Coastal Plain. Published records of hollow tree roosts are few and do not include detailed descriptions of the habitat or characteristics of the trees used by these bats. The few records from natural roost sites may reflect a bias in sampling and may not be representative of true roost preferences.

Several investigators have demonstrated that the distribution and abundance of bats may largely be limited by the availability and physical capacity of roosts (Pearson et al. 1952, Humphrey 1975, and Tuttle 1976b). Temperate insectivorous bats, particularly non-migratory species, must cope with seasonally fluctuating temperatures and food supplies and do so, in part, by using a variety of roosts. Loyalty to a roost site year-after-year appears to be a general phenomenon among temperate bats (Humphrey and Cope 1976, Rice 1957, and Tuttle 1976a). Factors promoting roost fidelity include roost permanancy, morphological specialization, proximity to food resources, the stability of food resources, low risk of predation, microclimate stability and complex social organization (Kunz 1982). Roosts play a critical role in bat survival and social organization, but roost requirements are complex and poorly understood. Generalizations about roosting ecology are misleading because the selective pressures on different species, populations, sexes and age classes are diverse.

Kunz (1982) reviewed the range of bat roosting ecology and identified roost availability, roost dimensions, energetic considerations, and the risks of predation as major determinants of roost selection. Parameters that influence energetics, and thus, the selection of roosts, are: body size, physiology, foraging ecology, age and reproductive status. Studier and O'Farrell (1972) stated that, for bats, behavioral aspects of thermoregulation, such as habitat selection, together with daily and seasonal movements, may be of greater survival value than physiological thermoregulation. Bats, through clustering and the selection of roosts, may markedly alter the microclimate to which young are exposed (Tuttle 1975). The formation of nursery colonies is a way of sharing thermoregulatory costs during the period of postnatal development (Tuttle and Stevenson 1982). Colonial roosting confers physiological advantages, including thermal ones, that ensure optimum growth of embryos and young (Humphrey 1975). Energetic demands of adult female bats vary between gestation, lactation and post-weaning, and young bats are poor thermoregulators in their first few weeks (Tuttle and Stevenson 1982).

Kunz (1982) noted that even though the dominant role of roosts in bat biology is well-recognized, few studies of the roosting ecology of bats have integrated roosting habits, foraging behavior, social behavior, morphology, and energetic factors. Most roosting ecology studies have focused on roost microclimate characteristics and their influence on energetic considerations (Kunz 1982). Investigations that examined a fuller range of the parameters affecting roost selection offer compelling evidence that understanding roost microclimate requirements is not sufficient to explain roost selection in bats.

Tuttle (1976b) studied factors affecting the growth and development of gray bats, *Myotis grisescens*, and demonstrated that roosting ecology is a compromise of opposing selective pressures derived from conditions in the roost, those associated with physical characteristics of the roost structure and external factors. Tuttle and Stevenson (1982) separated factors affecting the growth and survival of young into roost and non-roost factors. Roost factors were defined as those which directly affect sucklings and females. A multi-dimensional approach was used by Raesly and Gates (1987) to study winter habitat selection of five species (*Pipistrellus subflavus*, *Myotis lucifugus*, *M. sodalis*, *M. keenii*, and *Eptesicus fuscus*) of cave and mine-dwelling bats in Maryland, Pennsylvania, and West Virginia. Observing that some sites with appropriate microclimate were not used by bats, they quantified microhabitat (within-cave) and macrohabitat (among-cave) conditions and concluded that microhabitat differences were small and could not, by themselves, predict roost selection.

The uncertain status of _P. rafinesquii_ and the lack of life history information for this bat prompted me to study its roosting ecology. Within the Coastal Plain of North Carolina I observed that many seemingly suitable buildings available to _P. rafinesquii_ were not used by them. To more clearly define roosting ecology I quantified internal and external factors that might influence roost selection. My field studies extended from 1986 to 1990, with the most intense monitoring occurring in 1986. Variables were chosen based on their apparent relevance to bats. They were derived from observations that I made in North Carolina between 1982 and 1985, from reports by other researchers on the ecology of _P. rafinesquii_ and from the literature on bat roosting ecology (reviewed by Kunz 1982).

The principal objective of my study was to define the parameters that influence roost selection of _P. rafinesquii_ by comparing sites used to those not used. Additionally, observations on two roost trees used by _P. rafinesquii_ were made and conditions in natural roosts were compared to those in buildings. I established a reproductive phenology for _P. rafinesquii_ and described behaviors possibly associated with thermoregulation.

BACKGROUND STUDIES IN NORTH CAROLINA

Background studies in North Carolina provided the foundation for this roosting ecology investigation. A summary of my field work on _P. rafinesquii_, conducted between 1982 and 1986, is provided here. Results of background studies are incorporated where appropriate in other parts of this paper.

In 1982 Lee et al. (1982) reported that only two records of P. rafinesquii were available since the 1950's from North Carolina and that the status of the species in the state was completely unknown. Only 16 distributional records for the state were compiled by the North Carolina State Museum of Natural Sciences between 1893 and 1975. There were two early reports (Brimley 1905) from the Coastal Plain, one each from Bertie County and Wayne County (Fig. 1). No reports for the Coastal Plain were on record at the Museum for the period between 1905 and 1944 (Brimley 1944). Prior to my field efforts the most recent record on file from the Coastal Plain was from the 1960s (Lee et al. 1982).

In an effort to gain more insight into the status and distribution of this species in the State, I directed a considerable amount of field effort to summer roost surveys of buildings in the Coastal Plain between 1982 and 1985. As a result, many new localities for this species were documented in its expected range and a good deal of information on the life history of P. rafinesquii was obtained. In 1984 I began a systematic attempt to survey Bladen County (Fig. 1) thoroughly for P. rafinesquii. This county was chosen because my survey efforts had generated records from the county and ones from the 1960's were also available.

To locate sites, two individuals, generally a volunteer or intern and I, attempted to drive all roads in the county, stopping at abandoned buildings to check for bats. Over 320 field-hours were devoted to this activity, and observations on 126 buildings in Bladen County were made. Three field days were also devoted to surveys in Gates County (Fig. 1). One day was spent surveying the vicinity of Camels Creek, near Aurora, in Beaufort County (Fig. 1) where a P. rafinesquii specimen (NCSM 495) was obtained in 1965. No sites surveyed in Beaufort County contained bats, and the two interns that surveyed that area reported that few sites were available for censusing.

In 1984 and 1985 68 P. rafinesquii were banded at three nursery roosts in Bladen County. A total of thirty others were banded in Gates, Pender, and Sampson counties (Fig. 1). The 98 banded P. rafinesquii included adult females, young-of-year of both sexes and solitary males. Bats were banded to help determine roost philopatry, to gather population data for status assessment, and to make possible life history observations of individuals. In some situations the traditional method of banding bats, applying a metal or plastic band to the forearm, has been detrimental, causing injury and infection. Because of concern about the possible detrimental effects of this method on P. rafinesquii, I placed bands on bead-chain necklaces which were then clasped around the necks of the bats. The necklacing method was developed by C. O. Handley, Jr. for marking tropical bats in Panama and was described by Barclay and Bell (1988).

Tropical bats are significantly larger than P. rafinesquii. Sizing the necklaces proved difficult and resulted in a minimum of 20% band loss. Some necklaces probably did not stay on the bats for long. I found 17 necklaces total on the floors of sites where bats were initially banded. Nevertheless, enough band recoveries were made, especially in 1984 and 1985, that some conclusions about life history and roost philopatry were possible.

Sites in or near mature forests and adjacent to rivers and other permanent bodies of water seemed to be preferred by *P. rafinesquii*. There are now numerous records of this bat from the Bladen Lakes area, Bladen County, but only four of them were directly associated with Carolina bay lakes (Clark et al. 1985). (Carolina bays are unique geologic features occuring between southern Florida and Maryland. They are naturally wetter at all seasons than surrounding areas. A wide spectrum of successional stages, from open lakes to bays filled with dense vegetation, can be seen among the approximately 55,000 Carolina bays.) One *P. rafinesquii* was reported by a local property owner in a hollow black gum (*Nyssa sylvatica*) cut from the edge of White Lake, another was seen by us in an abandoned hotel on this lake, and one (NCSM 4018) was from an abandoned building at Singletary Lake State Park (NCSM records).

The Dismal Swamp, where Handley (1959) reported *P. rafinesquii* collected from hollow cypress trees in Lake Drummond, is the nothernmost locality for this species on the Atlantic Coastal Plain. A specimen (NCSM 3938) from the souteastern edge of the Dismal Swamp, Gates County, and records from Dare County (Fig. 1) from the 1980s are on file in the North Carolina State Museum of Natural Sciences. Although all of Bladen County was surveyed, clusters of occupied sites were found near the South, Black and Cape Fear rivers in eastern and southeastern Bladen County. In the Coastal Plain this bat appears to be restricted to river swamps and bay lakes bordered by mature swamp forests (Clark et al. 1985).

In my surveys, no other bat species were found roosting with _P. rafinesquii_ in significant numbers. Single Eastern pipistrelles (_Pipistrellus subflavus_) and big brown bats (_Eptesicus fuscus_) were sometimes found regularly using the same roost sites as _P. rafinesquii_, but did not cluster with them and used distinct roosting areas within the shared sites.

Plecotus colonies roosted in open areas in attics near the main entrance to the attic. When roosting in rooms of abandoned buildings, _P. rafinesquii_ was generally found hanging from molding on the crevice formed at the juncture of the wall and the ceiling, most often in a corner. When not using the attic, or when attic space was not accessible to bats, the darkest area in a house, generally a closet, bathroom, or room with boarded windows, was used.

Seasonal activity patterns of _P. rafinesquii_ were found to be similar to those of other temperate bats (Kunz 1982). Females form nursery colonies in the spring and males roost alone at this time. Nursery colonies begin to form in late April in North Carolina and begin to disband in late August and September. Nursery colonies ranged in size from six to about 80 adult females.

Background surveys were conducted primarily in the summer. Winter roost sites are not well-documented in the Coastal Plain. Small numbers of _P. rafinesquii_ were found throughout the year in the Coastal Plain surveys, and it is clear that the species is not a long-distance migrant.

During these surveys I observed that many seemingly suitable buildings were not used by _P. rafinesquii_. This prompted me to initiate a roosting ecology study.

STUDY AREAS

Observations of roosting ecology were made in Bladen, Chowan, Pender and Sampson counties in North Carolina (Fig. 1). Sites in these counties were chosen because I had documented extant populations of *P. rafinesquii* in them earlier and several occupied sites in them had been monitored irregularly since 1983. Each site in my study was identified by an acronym composed of two parts, the first two letters in the county followed by a two-digit number (Table 1). In some instances a complex of buildings was given the same number with a small letter added to distinguish buildings in the complex (e.g. BL02a, BL02b, BL02c). Exact locations of study sites are on file in the N.C. State Museum of Natural Sciences.

Bladen, Pender and Sampson counties border each other and occur in the southeastern inner Coastal Plain. These three counties are large (areas in thousands of hectares, respectively: 231, 225 and 249) and are primarily agricultural. Chowan County, (60,000 ha) a small, tidewater peninsula bordered by estuaries and large sounds, is in the extreme northeast section of the State. Although Chowan County is considered on the "recreational fringe" due to its proximity to the coast (Clay et al. 1975) much of the land there remains undeveloped. All four of these counties have in common a highly rural population.

A wide variety of freshwater wetlands are found in all four counties including blackwater rivers, slow-moving streams, and extensive bottomland swamp forests. Pocosins and filled and open-water Carolina bays occur in Bladen, Pender, and Sampson counties. Part of the Great

Initially buildings occupied and unoccupied by *P. rafinesquii* were my primary focus. The discovery of two tree cavities used by *P. rafinesquii* made possible comparisons of conditions in natural roosts with those in man-made sites. A tree cavity (in a black gum, *Nyssa sylvatica*), used as a night roost by *P. rafinesquii*, was discovered during a foraging ecology study of nursery roost CH01 in 1988 (Clark, unpublished data). Paris Trail discovered an American sycamore, *Platanus occidentalis* (Fig. 2), that was used regularly by a solitary *Plecotus rafinesquii* as a day-roost in 1989 and 1990.

DEFINITIONS

Roosts may be classified in a number of ways: seasonally (winter and summer roosts), daily (day and night roosts), structurally (cave, tree or man-made), or functionally (nursery roosts). Types of roosts most frequently referred to in this paper are "nursery roost," "solitary roost" and "night roost". All three of these roost types are used in summer. Nursery roosts and solitary roosts are types of day roosts. Nursery roosts are the sites where female *P. rafinesquii* aggregate between April and August to bear and raise young. Solitary roosts are sites occupied by a single male *P. rafinesquii* during the nursery period.

In this paper, "summer" refers to late April through mid-September. The nursery period (a subset of summer) covers May, June and July when parturition, lactation and weaning of young take place. "Winter roost" refers to the sites used by *P. rafinesquii* in their less active months, October to April. In this paper "roost site" generally refers to abandoned houses. For convenience during discussions of comparisons of occupied and unoccupied buildings the term "roost site" includes any structures available to *P. rafinesquii*, regardless of whether bats were ever found in them. "Roost area" refers to the specific place used by bats within a roost site. The terms "occupied" and "unoccupied" refer to habitation by *P. rafinesquii*.

My study involves only *P. r. macrotis* and all references to *P. rafinesquii* refer to this subspecies unless otherwise stated.

METHODS

Reproductive Phenology

The phenology is a composite of all data from my field notes from 1982 to 1990 as well as information from the summer 1986 investigations. Observations made on banded *P. rafinesquii* in May 1984 provided information on late gestation and lactation. Specimens examined during foraging ecology studies (Clark, unpublished data) conducted 27-29 July 1988 at CH01 in Chowan County, provided information on post-lactating females and growth of young-of-year bats. Notes on mass, sex, age (adult and juvenile), reproductive condition, pelage color and molt were made on each bat captured for the foraging ecology study. In the winter of 1988 a large colony of *P. rafinesquii* was found in an abandoned school (CH06, Fig. 3) at White Oak, Chowan County, when crews started to demolish the building. Because there was already a great deal of disturbance in the site, bats were captured there in the winter of 1988-89 to obtain winter masses of both sexes and to acquire information on the reproductive condition of males.

On 13 February 1990 a male and female P. rafinesquii, taken from two different sites in Chowan County, were placed in captivity under the care of Paris Trail. Opportunistic observations on intraspecific interactions, feeding habits and copulation and birth in captivity were made by Mr. Trail in the winter and spring, 1990.

Physical Characteristics of Roost Sites

Physical characteristics of roost sites were not quantified. Photographs of all sites were taken and structural features of occupied and unoccupied sites in the study area were descriptively compared. Physical characteristics recorded for buildings included the exterior building material, the type of roof and the size and approximate age of the site. Photographs and measurements of the two roost trees were made. Characteristics of occupied sites described in literature and from other sources were descriptively compared to those obtained during this study.

Thermoregulatory Behaviors

The form shown in Appendix I was used to facilitate and standardize data collection inside roosts. Numbers of bats in sites were recorded by direct count on each visit as a foundation for future censuses and because increases and decreases in population size give an indication of movements between roost sites. Movements from preferred roost areas were recorded and were compared with temperature and disturbance data to try to determine whether movements were correlated with temperature or disturbance.

Upon first entering a site, investigators recorded the social spacing of nursery colonies and other behaviors that may reflect a response to thermal conditions in roosts. An individual or cluster of bats may hang either pendant or with the ventrum flush against the substrate. Roost posture of bachelors and nursery colonies was recorded as "flush" or "pendant." The position of the long ears of P. rafinesquii, folded when at rest and erect when alert and active (Fig. 4), provided an indication of metabolic state (torpid or active). Ear position was recorded when investigators entered the roost as "erect" or "curled." Clustering, posture and ear position were compared to temperatures to determine behavioral energetic strategies used and their possible correlations with the various aspects of this bat's reproductive phenology. To assess temperature differentials possibly associated with roost posture, two Taylor maximum-minimum thermometers were placed in the attic of BL38, one mounted flush against the ceiling and the other mounted pendant next to it.

Internal Influences on Roosting Ecology

Thermal characteristics of buildings and tree cavities

Taylor maximum-minimum thermometers were placed in most sites in April or early May 1986 to develop temperature profiles of occupied and unoccupied sites. The positioning of thermometers in sites where bats were present was usually determined by guano accumulations. All buildings monitored, and the locations of thermometers in them, are listed in Table 1.

Maximum, minimum and current temperatures within sites for the 1986 study period were recorded by investigators on each visit. Ambient air temperatures immediately outside of the roost were recorded for sites in Bladen, Sampson, and Pender counties. Ambient temperatures for Chowan County sites were not regularly taken. Maximum-minimum thermometers were left indefinately in some Chowan County sites, but were removed from sites in other counties in the fall, 1986.

In most sites thermometers were placed within 1 m of the preferred roost area of the bats. It was not possible to reach the roost area in one Chowan County nursery roost (CH01). This was a large, two-story barn (Fig. 5) where the bats roosted in the open on the rafters about 7 m above the second-story floor. In this site the maximum-minimum thermometer was placed approximately 2 m above the second-story floor, or about 5 m underneath the preferred roost area of the bats.

Comparisons of temperatures of different roost areas in the same roost site were made in two sites by placing maximum-minimum thermometers in two different roost areas. In BL17 temperatures in the attic and a large downstairs room were compared, and in BL20 one thermometer was placed in a closet and one in the attic. To develop daily temperature profiles seven-day, battery-operated, portable, Taylor recording thermometers were placed in one roost area in CH01, and in two roost areas in CH03, in spring and summer 1990.

Daily temperature profiles of the cavities of the black gum and the sycamore were obtained. Temperatures in the sycamore were recorded irregularly between March and October 1989. Recording thermometers were placed in both roost trees from 11 April 1990 to 3 May 1990 to compare the thermodynamic properties of the sycamore to the black gum. The daily temperature profiles of the trees were compared to those in CH01 and CH03.

Light levels

Light readings were taken in all Bladen, Pender, and Sampson county sites. A United Detector 351 photometer with a range of 20 kfc to 200 mfc was used to record light levels. At each site two light readings were taken, one at the thermometer inside the roost and one outside of the roost where ambient temperatures were recorded. Light readings were not taken in tree roosts.

Disturbance estimation

When possible, disturbance rates were compared with population numbers and movements of _P. rafinesquii_. Disturbance may be direct or indirect. I defined direct disturbance as human intrusion in the roost and included investigator disturbance as well as other human intrusion inside the roost. I calculated the average length of time of investigator disturbance using the difference between the time the site was entered and vacated by investigators. A corresponding measure for other disturbances was not possible since I did not witness these disturbances. The frequency of human disturbance between investigator visits was categorized for each roosting site based on the investigator's observations of evidence seen near or in the roosts (e.g., doors found left ajar between visits, beer cans in or around the site, vandalism). These disturbances were categorically rated as follows: 0 = no evidence of disturbance was found, 1 = evidence of disturbance was found.

Indirect disturbance was defined as evidence of disturbance outside the roost that may increase disturbance in the roost or that may be a predictor of direct disturbance. Evidence included fresh debris, signs of recent vehicular traffic, and alterations to the exterior of the structure or the immediate grounds surrounding the structure. The effect of this kind of disturbance was evaluated descriptively based on the extent of alteration and possible correlation with direct disturbance.

External Influences on Roosting Ecology

Land-use patterns

Land-use patterns in the vicinity of a site may influence roost site selection. Land-use categories were measured only for Bladen County because large-scale aerial photographs needed to measure external variables were not available for Pender and Sampson counties. Aerial photographs were available for Chowan County but land-use patterns in Chowan County were not measured because only occupied sites were monitored there.

The home range of *P. rafinesquii* was not known and could not be used to limit the geographic area for measuring external variables. Two radii, 0.5-km and 1.5-km, were selected, based on assumptions about *P. rafinesquii* movement patterns, within which land-use patterns surrounding sites were measured. Land-use patterns in the 0.5-km radius, particularly forest cover, may have a direct influence on the thermal properties of a site and influence light levels. The 1.5-km radius was suspected to encompass the foraging area. These bats were not suspected to move great distances (Handley 1959, Barbour and Davis 1969) or forage far from roosts (Clark, pers. obs.). Typically bat summer roost sites are located near foraging areas (Kunz 1982). Additionally, flight characteristics of _P. rafinesquii_ are consistent with those described by Norberg (1987) for slow-flying, non-migratory species.

Major categories of land-use measured for Bladen County sites were urban development, agriculture, and forest. I estimated the percentages of land-use types surrounding each site by the non-mapping technique described by Marcum and Loftsgaarden (1980). This method is useful when boundaries are difficult to draw due to their irregular shapes. Random points distributed over a grid are used to estimate area. Estimates of the land-use categories from both 0.5-km and 1.5-km radii surrounding 22 sites in Bladen County were made from large-scale aerial photographs used by the Bladen County tax office. I determined the number of random points falling into each predetermined land-use category for each site by centering an appropriately-sized Mylar circle, on which either 86, (0.5-km) or 100 (1.5-km), random points were distributed over the roost site on the photograph. The estimated percentage of land-use in each category was calculated by tallying the dots that fell into each category.

In the summer of 1986 mist nets were erected 15 July 1986 over a creek near a large Bladen County nursery roost (referred to as Maternity Manor) that was not monitored in 1986 (and thus, not listed in Table

1). Bats captured in mist nets were fitted with necklaces so they could be identified individually if recaptured in the net or if seen in Maternity Manor, the nearest nursery roost, the next day.

Proximity of roosts to water and amount of water surrounding sites

The contrast of the photographs used for land-use analysis was poor, and it was difficult to use these photographs to distinguish the boundaries of certain types of water or wetlands. Additionally, forest cover sometimes obscured water. To define the extent and type of water within the two radii, water variables were obtained from United States Geographical Survey 7.5-minute topographic maps.

Distance to water bodies, an estimate of the area covered by each water body and the type (lentic or lotic) of each body of water was recorded for both a 0.5-km radius and a 1.5-km radius. Estimates of area were made by measuring the length and width of the water body and multiplying the two measurements. For water bodies that varied in width, or were irregularly-shaped (such as bottomland swamps), the smallest and largest lengths and widths were averaged, and the averages were used to obtain an estimate of the area.

Multivariate Analysis

Combinations of external and internal variables for Bladen County sites were entered in discriminant function analysis (DFA) to determine which sets of variables best separated occupied and unoccupied sites. Seven internal (Table 2) and 27 external variables (Table 3) were entered in DFA. Sites in which bats were seen no more than twice during the summer period were classified as "unoccupied." Twenty-two sites in Bladen County were classified as either occupied (16) or unoccupied (6). Classifications of all sites are listed in Table 1.

Temperature and light level variables used in DFA represent a subset of all observations made in 1986 in the 22 sites. The thermodynamic properties of roost sites can influence prenatal and postnatal growth and development (Tuttle and Stevenson 1982). For P. rafinesquii gestation occurs in April and May. Sampling for these months was irregular so temperatures from them were excluded from analysis. June and July also encompass important reproductive events: parturition, lactation and the most rapid period of growth for young. Temperatures from those two months were expected to be the most critical in summer roosts, especially for females and young, so only those were used in DFA.

All variables were examined for deviations from normal distributions. Means of maximum and minimum temperatures for a 7 or 14 day period, of temperatures and light levels taken in the roost and outside of the roost, and of temperatures and light levels taken immediately outside of the roosts were transformed logarithmically to meet the assumption of normality. The square root of the log was used to transform total water variables to meet the assumption of normality. An arcsin square-root transformation yielded the best fit for the disturbance variable. Other variables did not need to be transformed.

Stepwise linear discriminant analysis (STEPDISC; SAS Institute Inc. 1982:369-380) was performed on all internal and external variables to reduce the number of variables to be used in analysis. To test the effectiveness of variables for correctly classifying occupied and unoccupied sites I created 28 other combinations of variables and entered them in DFA (PROC DISCRIM; SAS Inst. Inc. 1982:401-432). Groups contained three to five variables and tested internal and external variables alone and combinations of both types of variables.

RESULTS

Reproductive Phenology

Observations from 1986 to 1990 compiled from old White Oak School (CH06) and other Chowan County localities best illustrated the reproductive phenology of males. Males have descended testes for most of the year. Testes size decreased between January and March with the most noticeable change in size occurring in March. Testes size began to increase in late summer. A male weighing 8.25 g from CH06 had descended testes on 26 January 1990. Twelve males examined from CH06 between 01 January 1989 and 31 March 1989 had descended testes. By late March 1989 testes of males in CH06 were substantially smaller than they were in January. A bat examined from CH06 on 28 March was described as having testes "the size of wheat kernels" (Paris Trail, pers. comm.).

I found males with descended testes as early as 24 July 1984 in Bladen County, North Carolina. These results are consistent with those of others. Males with enlarged testes in August were reported by Hall (1963). England et al. (1989) reported adult males with enlarged testes and epididymides extending into the uropatagium in nursery colonies beginning in mid-August.

On 8 September 1990 Paris Trail and I captured and color-banded three solitary males at different localities in Chowan County. One of these was the male from the sycamore tree cavity. This bat weighed 11 g and had descended testes measuring 19 x 12 mm. A non-scrotal male P. rafinesquii was also captured on this date at the request of a homeowner who found the bat roosting in her garage. He weighed only 7.5 g and may have been a young-of-year bat that had recently dispersed from an unknown nursery colony.

A solitary P. rafinesquii had been seen roosting in either a barn adjacent to CH03, or in roost areas of CH03 apart from the nursery colony, since 1986. In order to determine whether the same individual was using these areas the bat was captured early in the summer of 1990, while roosting in CH03, and banded. When recaptured in the same roost area on 8 September 1990 he had descended testes which measured 20 x 11 mm. Twenty-three other bats, from a cluster of approximately 28 in another roost area in CH03, were captured and color-banded on 8 September 1990. Of these 23, 5 were non-scrotal males. The remaining 18 bats were females. Two of the males weighed 7.5 g, one weighed 8 g and two others weighed 8.5 g. Masses of females were recorded as follows: 1 at 8 grams, 9 at 8.5 g, 2 at 9 g, 5 at 9.5 g, and 1 at 10 g.

Between 28 March and through August 1989 only adult females and young of both sexes were captured in CH06. Of thirteen bats captured in this site on 26 August 1989, eight were adult females, four were young females and one was a young male.

Mating under natural conditions was not observed, but one captive mating was witnessed by Paris Trial on 13 February 1990. A male weighing 7.5 g was taken on 13 February 1990 from CH06 and placed in captivity with an adult female taken on the same date from a newly discovered site in Chowan County. Both bats were introduced into a small, metal-frame, screened cage at about 1300 hours. Live crickets were introduced into the enclosure about 2000 hours. Approximately 35 minutes later the female pursued, captured and began to eat a cricket. While she ate, the male mounted her and the two bats clung together, apparently copulating, for six minutes. At 2130 hours the male again mounted, and clung to the female until 2150 hours.

Ninety-three days later, on 17 May 1990 at 1530 hours, the captive female gave birth to a stillborn pup weighing 2.5 g. It is possible that the captive birth was due to delayed fertilization and not one resulting from the mating observed, however, Pearson et al. (1952) listed the gestation period for _P. townsendii_, a closely-related species, as 59 to 100 days.

Parturition is difficult to determine without examining the bats on each visit because neonates are obscured from view underneath their mothers. In the first few days young may be seen only when dangling from mothers' roosting pendant or when their mothers fly from roost area to roost area in the site. In North Carolina I observed females in a nursery colony in Bladen County so near term on 28 May 1984 that flight was difficult. In 1986 young bats were seen as early as 3 June in BL11 and SA03. No young were reported from Chowan sites checked on 4 June 1986, but young were reported in these sites on 12 June. In 1987 young bats were first seen on 15 June in Chowan County sites. The earliest date reported for sites in 1989 was 7 June (CH03), and young were reported for CH01 and CH03 on 12 and 13 June in 1989 and 1990, respectively. Masses of four young from CH03 recorded 17 June 1988 were 2 at 4.5 g and 2 at 5 g. Forearm length ranged from 27 to 32.5 mm (mean = 29.63).

A young bat, date of birth unknown, was observed to fly approximately 13 meters on 24 June 1988 in Bladen County, North Carolina. The bat maintained altitude but did not ascend, and the bat appeared inexperienced at flight. The flight behavior of this bat suggests that it was not capable of foraging on its own. Jones and Suttkus (1975) stated that young *P. rafinesquii* are capable of flight three weeks after birth.

Young bats apparently forage on their own by mid-July. On the night of 15 July 1986, in a net placed over a creek approximately .75 km from Maternity Manor, seven *P. rafinesquii* were captured. Six of these were young bats (five females and one male) and all six were captured in close succession. The bats were banded and released, and one banded individual was observed the next day in the adjacent nursery roost. Other banded bats may have been present, but bands may not have been visible due to the position of the bats in the cluster.

No formal studies of natality and survivorship have been conducted. Mortality of young *P. rafinesquii* is expected to be low. Dead young were found in roosts only twice between 1982 and 1990. My results are consistent with low juvenile mortatlity reported by England et al. (1989). They found only one juvenile carcass among several nursery sites in Arkansas. On two occasions I found one dead adult *P. rafinesquii*, each clinging to walls, in two different sites. One was a

P. rafinesquii necklaced in the summer of 1984 and found dead in a closet at the banding site on 16 April 1986.

Physical Characteristics of Roost Sites

The majority of the structures used by bats were old dwellings, often in an advanced state of disrepair. The exterior of nursery roost BL07 (Fig. 6) and the interior of nursery roost PE01 (Fig. 7) are typical of the architecture of most sites surveyed in the North Carolina Coastal Plain. Sites were predominantly frame, one-story homes with plaster walls and large attics. Only two sites were not frame structures. Both of these were concrete block houses (BL03 and BL13) and both were used by solitary bats.

Few openings were available in most buildings in preferred roost areas. The windows of many sites had been boarded to protect the sites from theft and vandalism. Tin roofs predominated in my sample and are common in eastern North Carolina. Attics were not insulated.

Sites occupied by *P. rafinesquii* ranged in age from a family dwelling built in the late 1800's (PE02), occupied by a small nursery colony, to two modern garages in Chowan County built in the late 1980s (not monitored in 1986). Most sites had been built prior to 1940 and had been abandoned for more than 30 years. They ranged in size from abandoned tenant houses (small, four rooms) to a large barn (CH01-Fig. 5).

The sycamore used by a solitary *P. rafinesquii* had an opening large enough for an average-size adult human to enter comfortably, and the cavity was large enough to allow upright posture (Fig. 2). The opening was 1.7 m high and was widest (.5 m) near the base of the tree. This large opening provided access to both trunks of the tree. At 1.5 meters high the circumference was 6.1 m. The width of the interior of each cavity at the widest point was .7 m. The cavity extended approximately 5 meters high in each trunk. The solitary P. rafinesquii was always found in the same trunk of the sycamore.

Circumference of the black gum (used as a night roost by members of the CH01 nursery) measured 3.8 m at the base. At 1.5 m high the circumference measured 2.6 m and at 3 m the circumference was 2.4 m. The cavity extended 26 m up from the base of the tree. The greatest width of the opening was 18 cm.

Internal Variables

Summer 1986 weather patterns

The degree to which a roost offers its occupants shelter from the elements is determined by comparing weather patterns to conditions in the site. Spring in the study area is characterized by wide ranges in temperatures as cold fronts move through. General weather patterns for the study area for May through August 1986 are summarized from the Special Weather Summaries of the Climatological Data Bulletin (Fig. 8). In 1986 the spring pattern of cold front passage every few days lasted until mid-May. Temperatures in the summer of 1986 were above normal across the State, and the State experienced one of the worst droughts ever recorded. Temperatures were above normal in May, June, and July. July was characterized as the second hottest the State had experienced in 100 years. Numerous daily maximum temperature records were broken in

From 11 June to 2 September 1986 maximum-minimum thermometers were simultaneously in the attic and in a room in BL17. The average maximum temperature was 45 C in the attic and 39 C in the room. An attic and closet were compared from 17 June to 27 August 1986 in site BL20. The mean maximum temperature for this period was 44 C in the attic and 31 C in the closet. The mean minimum temperature for both the attic and the room in BL17 was 21 C and mean minimum temperature for BL20 was also the same for both the attic and the closet, 18 C. The primary difference between roost areas in lower levels versus those in the attic was the wider range in temperatures in attics caused by the higher maximum temperatures in attics.

This trend is also illustrated in the comparison of daily temperature profiles of CH01 and CH03 (Fig. 12). Mean temperatures show little variation between roost areas (Fig. 13). Daily ranges, however, show a wide variation in daily temperatures (Fig. 12) between the roost areas. Temperature ranges in lower level roost areas have smaller ranges than those in attics. Low temperatures are similar for both the attic and the downstairs room in CH03. High temperatures are much more extreme in the attics than those recorded in lower levels. Temperatures in attics rose and fell faster than those in downstairs. The CH01 daily temperature profile was similar to that of the attic of CH03.

Light levels

Light levels outside of roosts varied considerably (Fig. 14). This was probably due to the wide variety of vegetative growth that surrounded individual sites. Some sites were in cultivated fields exposed to direct sunlight and others were obscured by forest. Conditions inside roosts were much less variable than those outside (Fig. 14).

Even though the light level was not measured in the sycamore tree cavity it appeared to be as dark and possibly darker than that in any areas in buildings used by the bats. The black gum tree used for a night roost near CH01 had only one small opening, at the base of the tree, and was in a closed canopy swamp forest. Both of these factors created an intensely dark interior in the black gum during the day.

Disturbance estimation

Total time (sum of all visits to each site) spent in roost sites in the summer of 1986 ranged from 29 minutes (site SA05, N=3) to three hours and 13 minutes (site BL20, N=10). Sixty-three percent of investigator visits were from two-to-ten minutes long. Thirty percent of the visits ranged from 11-to-20 minutes long. Disturbance rates ranged from 0 (BL04b, BL09, BL12, BL19, BL20, BL33, BL34, BL37, PE02, SA01, SA11, SA13) to 4 (BL04a, BL07, PE01) in Bladen, Pender and Sampson county sites. (This rating system was not used in the Chowan County sites.) Many sites did not experience non-investigator disturbance at all according to my rating system (12 sites) or only had one disturbance (7 sites) during summer 1986.

The magnitude of roost-switching attributable to investigator disturbance could not be determined. Because colonies were monitored every 7 to 14 days, it was difficult to relate increases and descreases in numbers of bats to investigator visits. Increases and decreases in numbers of bats in several roost sites in Chowan County indicate a considerable amount of roost-switching (Fig. 15).

No desertions or changes in occupation of roosts were observed in sites where the frequency of human disturbance between investigator disturbance was low (>2), A number of occupied sites from background studies and those studied in 1986 have undergone non-investigator internal or external disturbances that appear to have altered roost use. Two sites (BL04a, BL06 in 1986) in Bladen County and one in Chowan County (CH05 in 1988) were vandalized. Intense vandalism occurred at BL04a in the summer of 1986 where occupation of a boarded bathroom by a solitary _P. rafinesquii_ had been documented since 1983. The thermometer in the site was removed twice and smashed, boards were torn from the bathroom window and a number of derogatory phrases were spray-painted on the walls. A bat was not seen regularly in the site for the rest of the summer of 1986. In subsequent years a single _P. rafinesquii_ was again seen regularly in this same site, occupying a different room.

After my first two visits to record temperature and light levels nursery colony BL11 deserted the roost and did not return in summer 1986. This site had been long-used by bats, given the amount of guano accumulated, and it had been known prior to this investigation as a large nursery colony. A long ladder was required to reach the colony and no disturbance in the roost area other than that created by investigators is believed to have occurred. No other desertions or reductions in numbers can be directly attributed to investigator disturbance during the 1986 investigation.

The forests adjacent to, or surrounding, four sites (BL06, BL07, PE01, and CH05) were cleared between 1986 and 1989. Before logging, CH05 was surrounded by vegetation that completely obscured the site. This made CH05 barely visible from the secondary road that is only about 40 m from the site. After logging, the site was clearly visible from the road (Fig. 16), vandalism occured there and the nursery colony deserted the site. Three sites (BL02a, CH02a and CH02b-not listed in Table 1) were inhabited by humans, one site was intentionally burned (SA03), and one site (CH06) was demolished.

Three sites (BL06, BL07 and CH05) were nursery colonies previous to disturbance. Only one _P. rafinesquii_ was seen in BL06, irregularly, after boards were ripped from windows in 1987 and after the forest adjacent to the site was logged. A similar change, from a nursery roost to a solitary roost, was noted at BL07 after clearing occurred around the site in 1988. No bats have been found in CH05 since the disturbances occurred there. It is difficult to attribute the changes in occupational status of these three sites to either vandalism or external habitat alteration.

A degree of tolerance of human disturbance was found in nursery roost CH01 (Fig. 5). This large barn was actively-used for equipment storage and for other activities related to crop preparation and harvest. During the summers of 1986 and 1988 the farmer's two precocious preschoolers were observed to play frequently, and sometimes loudly, in the downstairs room underneath the area on the second floor that was used by a nursery colony. Hay was regularly put in and taken out of the loft next to the room most often used by the bats, and farm animals lived in the barn.

Tolerance of more intense disturbance was seen in CH06. Demolition of this site was slow (well over a year) because the crew was small (1-2 people) and materials from the site were being salvaged. The colony at White Oak School was reported to contain more than twice as many *P. rafinesquii* (perhaps as many as 300) when the bats were first discovered in the site as were there several months after demolition started. Although much noise and many changes occurred in the structure, bats continued to use the site as a nursery roost and a *P. rafinesquii* was occasionally seen in the site before the final stages of demolition in March 1990 (pers. comm., Paris Trail).

Bats that flew from their regular roost area when disturbed almost never exited the structure, but instead flew to other areas within the site. Leaving the roost site in response to disturbance was seen only twice and in both instances the disturbance involved my attempts to capture a bat. When disturbed, *P. rafinesquii* showed a familiarity with escape routes to other areas within the structure. Although many roosts had cracks and crevices under the eaves of attics that were large enough for the bats to use to exit the roost site, they used windows, doorways, and the main openings in the attic floor to fly to other roost areas.

Thermal characteristics of tree cavities

Thirteen visits to the sycamore (Fig. 2) were made during the day, between March and November 1989. A solitary *P. rafinesquii* was found in the sycamore on seven of these visits. The bat roosted about 3.5 m high, in an area that was visibly wet, near some fungus.

Air temperatures in the sycamore were most often several degrees lower than those of the ambient air surrounding the tree. Insulating properties of the tree were obvious on 7 March 1989. When the outside air temperature was 2 C, the inside temperature was 10 C at the bat's roosting level. On this date the bat was torpid, resting flush against the trunk. Roost posture was recorded on three other visits between March and November as pendant. On March 21, the bat was present and torpid but no temperatures were recorded. No bat was found in the tree on 28 March. The 28th was a warm day, 27 C outside temperature and 24 C in the cavity.

In April the sycamore was visited on the following dates; 3, 19, 21, 26, and 27. A bat was present on the 3rd, 21st and 26th. On the 3rd, the bat was found pendant and torpid. The temperature was 16 C at the bat and the ambient air outside the tree was recorded as 24 C. No temperature or behavior information is available for this site on the 21st. On the 26th a bat was hanging pendant, and was alert with ears erect. No bat was found in the hollow on the 27th. Temperature in the cavity on the 27th was 20 C.

One visit each was made in May and June. On 9 May no bat was found. The temperature was 14 C in the cavity at bat level. On 15 June a bat was again present in the tree, roosting pendant and torpid, he was not responsive to disturbance at a temperature of 23 C. No visits were made to the site between 15 June and 13 October. In October the site was visited only on the 13th. A bat was present but no notes were taken on the behavior of the bat. Temperatures in the tree were 19 C where the bat roosted and 27 C outside. In November the site was visited on the 5th and the 20th, but no bat was present, and no temperatures were recorded.

I do not know whether the black gum tree was used regularly as a day roost. It was not as accessible as the sycamore and was not monitored regularly. Only one observation of day-use was made in the black gum. A solitary P. rafinesquii was found in the site when we located the tree during the day on 28 July 1988, after discovering on the night of the 27th that light-tagged bats were using it as a night-roost. The site was again checked for bats when a recording thermometer was placed in the tree 11 April 1990, but no bats were seen.

External Variables

Land-use patterns

Agricultural use and forests accounted for 95% of the land-use in a 1.5-km radius around each site in Bladen County (Fig. 17). The location of the most heavily-used structures provided an indication of areas preferred for day-roosting. In a 2-km radius near the Yeopim River in Chowan County, bats used three house sites (CH02a, CH02b, CH05), one barn (CH01), one garage and at least two roost trees. This includes all of the man-made structures that were available in the 2-km area. All sites checked (N=6) in the Cape Fear River floodplain along SR 1537 and SR 1538 (combined roads approximately 4.5 km long) in Bladen County were used as either bachelor roosts (N = 4) or nursery colonies (N=2). Additionally, there was a heavy concentration of P. rafinesquii in sites along the southern half of NC 210 which is near the Black River in Bladen County.

Proximity of roosts to water and amount of water surrounding sites

Water bodies most frequently recorded (62% for all sites) were tributaries of the two major river systems in Bladen County, the Cape Fear River and the Black River. Parts of these two rivers were within 1.5-km of 5% of the sites. The percent of lotic water surrounding all sites was much greater (70%) than that of lentic water (26%). The 1.5-km radius encompassed a wide variety of water types for most sites including farm ponds, Carolina bays, creeks, swamps, irrigation ditches and portions of, or tributaries of, rivers.

There were four sites that did not contain water in the 0.5-km radius (BL03, BL04a, BL19 and BL38), but all sites were within 1 km of a major body of water or wetland (e.g., a named bay or swamp). Sites with major river systems within the 0.5-km radius were BL07 and BL08 (sites along the Black River) and BL06, BL13, BL14, BL15, and BL16 (near the Cape Fear River), all of which occur on a 4.5-km stretch of two North Carolina secondary roads, 1537 and 1538. All of these sites are known to have been actively used since at least 1984.

Several sites not used by bats were within .4km of water. Non-flowing water was not shown on maps within the either 0.5 km or 1.5 km radius for BL02c, BL07 and BL08, but there probably were unnamed and unmapped bays and sloughs in close proximity to these sites because BL07 and BL08 are in the Black River floodplain, and BL02c is near an extensive swamp, Brown Marsh.

Comparison of Unoccupied and Occupied Sites

Internal variables

There was no difference (t-tests) between any of the temperature readings of occupied and unoccupied sites taken in 1986. No significant difference was observed, at the .05 significance level, between the means of temperatures taken during the day in occupied (N = 22, mean = 26.89 sd = 4.04) and unoccupied (N = 14, mean = 28.21 sd = 4.62) sites. No significant difference was observed at the 0.5 significance level for either minimum temperatures (occupied: mean = 16.8, sd = 3.22; unoccupied: mean = 15.5, sd = 3.37) or maximum temperatures (N = 22, mean = 35.61, sd = 4.99; N = 14, mean = 38.48, sd = 5.87).

There was no significant difference in the ambient light levels of occupied (mean = 721.76, sd = 499.74) and unoccupied (mean = 558.75, sd = 401.47) sites at the .05 significance level and light levels from inside the sites were not significantly different at the .05 significance level (occupied: mean = .153, sd = .093; unoccupied: mean = .15, sd = .12).

External variables

The amount of closed canopy forest within 1.5km radius was slightly greater for occupied sites than it was for unoccupied sites (Fig. 18). Closed canopy forest around the occupied sites was 14% higher than that surrounding unoccupied sites for the 0.5-km radius. A higher percent of open canopy forest within the 0.5-km radius was observed around unoccupied sites than was found for occupied sites. This latter trend was reversed for the 1.5-km radius area. Possible external influences were more fully explored using multivariate analysis.

Multivariate analysis

A number of combinations of roost and non-roost variables were entered in discriminant function analysis. The most accurate classifications for all combinations of variables are shown in Figure 19. Three of twenty-eight variables (Tables 2 and 3) were retained by STEPDISC. No variables representing the internal roost factor group were selected by STEPDISC, all were external variables from the 1.5-km radius. These variables were: the density of roads surrounding the site, the total area covered by water in the 1.5-km radius and the amount of open canopy forest. This selection of variables yielded a high degree of accuracy in classifying both occupied and unoccupied sites. One hundred percent of the unoccupied sites and 94% of the occupied sites were correctly classified.

Combinations of internal variables yielded the most inaccurate classifications for both occupied and unoccupied sites. For five groups of internal variables (four temperature variables: maximum, minimum, daytime temperatures recorded every 7 or 14 days, and the corresponding ambient tempeature) the percent of occupied sites correctly classified ranged from 56-to-81%. The range for unoccupied sites was 50-to-100%. Of these five combinations of internal variables entered, only one (group 2 in Fig. 19) correctly classified all unoccupied sites. The most inaccurate classification was a combination of temperatures and light levels taken in the roost at the time of each visit. This combination correctly classified 56% of occupied sites and only 50% of the unoccupied sites. The best classification of occupied sites using internal influence variables was given by a combination of the maximum and minimum temperatures, a measure of disturbance rates and mean light levels in the roost. With this combination 81% of occupied sites were correctly classified, but only 67% of unoccupied sites were correctly assigned.

In general, the ten combinations of variables representing external influences provided better classifications than those representing internal influences. With external influence variables correct classifications of occupied sites ranged from 50-to-100% and those for unoccupied sites from 67-to-100%. In seven out of ten combinations, 100% of unoccupied sites were correctly classified by external influence variable groups. Seven combinations yielded correct classification rates greater than 80% for occupied sites, and three yielded rates greater than 90%. One combination of variables, consisting only of those variables describing distance to water and total area covered by water measured from the 1.5 km radius (group 3, Fig. 19), accurately placed all sites. The same variables for the 0.5-km radius yielded a much lower classification rate for occupied sites, 62%, but correctly classified all unoccupied sites. The three variables chosen by STEPDISC with a total water variable were entered and gave classification rates similar to the combination chosen by STEPDISC (see groups 1, 4 & 5 in Fig. 19). The accurate classification rate for the 1.5-km radius was slightly higher (2%) than those of the 0.5-km radius.

Of the eight groups containing both external and internal influence variables, five yielded classification rates of 75% or less for occupied and unoccupied sites. The best classifications (groups 3 and 6, Fig.

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Of the eight groups containing both external and internal influence variables, five yielded classification rates of 75% or less for occupied and unoccupied sites. The best classifications (groups 3 and 6, Fig.

19) contained temperature extremes, maximum and minimum temperatures taken at 14 day intervals, as opposed to readings taken that represented the current temperature when investigators visited.

Comparison of Nursery Roosts and Solitary Roosts

Internal variables

No significant difference (t-test) between the means of temperatures taken during the day in nursery roosts (N = 12, mean = 26.68, sd = 1.76) and in solitary roosts (N = 10, mean = 27.14, sd = 5.93) was observed at the .05 significance level. No significant difference was observed for either maximum (solitary: mean = 34.57, sd = 2.78, nursery: mean = 36.86, sd = 6.75) or minimum temperatures (solitary: mean = 17.8, sd = 1.82; nursery: mean = 15.7, sd = 4.14) at the .05 significance level.

The means of ambient light levels of bachelor (mean = 703.45, sd = 536.77) and nursery roosts (mean = 755.33, sd = 452.46) did not significantly differ from each other at the .05 significance level. The means of light levels measured inside roosts did differ significantly for nursery and bachelor roosts at the .05 significance level (nursery: mean = .16, sd = .09; bachelor: mean = .04, sd = .20).

Thermoregulatory behaviors

Although there was a variety of roost areas in most sites (at least four rooms plus an attic) certain areas of buildings were nearly always occupied by bats during the day-roosting period, and other areas were used with varying degrees of frequency, but at no time were all potential roost areas occupied. In CH06 a room was used for roosting in winter, and the attic was preferred by the nursery colony in the summer. Between January and March 1989 bats were most often found in the south room at CH06. This room was piled high with old desks and other classroom materials that may have had some insulating effect. When using the attic, the bats clustered near the center of it over the south room.

Apparent avoidance of high temperatures was noted on many visits. In several sites the bats in colonies moved from one roost area to another, usually coming down from the attic to roost in a cooler room in the house in mid-June when attic temperatures reached 36 C. This often placed the bats in brightly-lighted rooms. In BL19, when temperature highs reached 36 C or higher, the bats normally found in the attic roosted near a broken window in a large well-lighted room.

During summer 1986 surveys, solitary bats were found active 87% of the time and were torpid 13% of the time and bats in nursery colonies were active on 95% of the visits (Fig. 20). Some temperatures where bats were found torpid were also the same as those when bats were active on other visits. Solitary bats were torpid more often than nursery females. Temperatures when solitary roosting bats were torpid (N = 10, mean = 26.7, sd = 6.68) were compared to temperatures when bats in colonies were found torpid (N = 13, mean = 19.85, sd = 6.96). At a .05 significance level the temperatures when solitary bats were torpid were not significantly different from those when bats in nursery colonies were torpid. Likewise, there was no significant different between temperatures when solitary bats were active (N = 66, mean = 27.29, sd = 3.84) when they were compared to temperatures when members of colonies were active.

Clustering was seen more often in early summer in nursery colonies and females were more frequently lethargic in May before the birth of young. In nursery colonies bats were most often found clustered (87% of all observations), or having some contact with conspecifics, than spaced apart from other bats. Spacing was apparently related to high temperatures, it was more frequently observed when bats had moved from the preferred roosting area to cooler sites in the roost.

Roost posture most frequently used varied from colony to colony. Some colonies were always found roosting flush with the substrate (BL14, BL19) and others were always observed to hang pendant when roosting (CH01, CH03). A one to two degree difference was recorded for the thermometers from BL38, one mounted flush and the other hanging pendant from the attic. There was no significant difference (t-test) at the .05 level of significance, between the means of temperatures taken during the day ($N = 6$) from the thermometers mounted flush (mean = 28.5, sd = 4.7) and pendant (mean = 28, sd = 4.9). Significance tests for minimum (flush: mean = 19, sd = 3.5; pendant: mean = 17.3, sd = 3.9) and maximum temperatures (flush: mean = 41.1, sd = 3.3; pendant: mean = 40.7, sd = 3.4) were not signficantly different. Temperatures recorded from these two thermometers would probably not adequately reflect the thermoregulatory qualities of either posture because of the heat loss conducted through highly vascularized body surfaces of bats, especially those of the ears and wing and tail membranes.

Comparison of Tree Cavities and Buildings

A problem developed with the recording thermometers in tree roosts. The humidity in the trees was high causing the charts to absorb moisture. As a result, the ink spread, making a wide band on each chart that covered 2-4 degrees instead of the thin line required to read temperatures. Exact temperatures could not be determined for most days that the thermometers were in the trees. Nevertheless, the pattern of temperature fluctuations was evident in both trees, and readings from several of the first days of recording charts were precise.

Temperatures were generally lower, but much more stable, in tree roosts when compared to those recorded in buildings (Fig. 21). Variation in daily temperatures in tree roosts were not as extreme as in buildings, especially in the attics. Temperature fluctuations in CH03 were much greater than those recorded in tree cavities, ranging as much as 17 C in one 24-hour period in the attic. Extreme temperatures in buildings were higher and lower than those in tree cavities.

DISCUSSION

Factors Influencing Roost Selection of *Plecotus rafinesquii*

Selection of variables and choice of statistical procedure have a profound effect on the conclusions reached by a study (Johnson 1981). All variables used in this foraging ecology study were thought to have a significant effect on roost choice, and the importance of each as a factor influencing roost choice was qualitatively documented in my background studies or demonstrated to influence roost choice by other bat researchers (see Kunz 1982 for a summary). For discriminant analysis to be appropriate, groups must be well-defined (Williams

1983). When a species' absence is used as one of the groups, problems can arise if suitable locations are not occupied, such as when local population densities are low (Johnson 1981). Population characteristics for this species are not well known, but sites regularly-used by bats show evidence of long-term use (e.g., guano accumulations wearing on walls where individuals roost). Most sites classified as unoccupied showed no evidence of prior use.

A number of difficulties were encountered in gathering and interpreting data for my study. The wide geographic area covered in this field study made it impossible to visit all sites on the same dates, and it was not possible to devote equal effort to all locations. Logistics made it impossible to take temperatures at the same time of day in each site. Travel time to study sites was 5 hours round-trip and it took a minimum of 6 hours to gather data from all sites on a route. Primary data collection was in man-made structures. Observations may have been affected by characteristics of the site that are inherent to man-made structures or by physical characteristics of sites. Some sites were easier to enter, more spacious and well-lighted than others. The decision made by a builder or landowner regarding the location of a building is not random. Buildings are generally located on high, dry ground that has often been cleared.

Most buildings shared structural similarities, but the type or age of the structure may not be important because _P. rafinesquii_ has been shown to colonize a variety of structures (Harper 1927, Moore 1949a, Goodpaster and Hoffmeister 1952, England et al. 1989, and pers. obs. by M. Clark, M. Harvey and R. Currie in 1986 of a _P. rafinesquii_ colony roosting in a large abandoned cylindrical boiler in western North

Carolina). The lack of structural diversity among buildings appears to be an artifact of the socioeconomic characteristics of the study area rather than representing a preference for one type of building over another by the bats. Records from old wooden structures predominate in literature and museum records, but this may reflect sampling bias.

Internal variables of occupied sites did not differ significantly from those of unoccupied sites indicating that factors other than temperature and light levels are responsible for roost choice. These factors could include internal variables that were not measured, such as humidity, or may indicate that roost choice is dependent on external variables. Occupied sites occurred in clusters and were not widely dispersed among unoccupied sites. England et al. (1989) made similar observations about clustering of roosts. They attributed this to a need for _P. rafinesquii_ to have access to several suitable buildings in close proximity to each other. Clusters of occupied sites in my sample were near river systems with expanses of closed canopy bottomland forest adjacent to roosts. Based on the multivariate analysis, and my observations of many clusters of buildings that were not used by bats, I suspect that sites are chosen based on external habitat variables.

Reports from literature and museum specimens lend support to the idea that bottomland swamps are important to this species. A specimen in the U. S. National Museum was collected from a hollow cypress in the Dismal Swamp of Virginia and Harper (1927) reported finding a big-eared bat (possibly sick) under dry leaves in a cypress swamp in Georgia. A recent discovery of a solitary _P. rafinesquii_ in Virginia was from Lake Drummond in the Dismal Swamp (pers. comm., Don Scwhab, Virginia

Department of Game and Inland Fisheries). Many museum specimens are from southern plantations, including the type specimen (Handley 1959). Plantations were generally located near rivers because rivers were primary avenues of transportation.

Tree cavities like the two monitored in Chowan County are evidently traditional roosts for P. rafinesquii. The fact that a P. rafinesquii regularly used a tree cavity when other nearby man-made structues were available suggests that tree cavities are still important to them. A disadvantage of tree cavities is that they offer limited roosting spaces for colonial species and the trees eventually rot and fall, requiring the periodic relocation of inhabitants (Bradbury 1977). P. rafinesquii have been reported from bald-cypress (Taxodium distichum), a tree known for its hardness and durability. Many sites used by P. rafinesquii occur near an area along the Black River that has a nationally significant stand of old cypress. Trees in this swamp are the oldest in the eastern United States (Stahle et al. 1988), almost 2,000 years old and many are hollow (Mather 1988).

Flight characteristics of P. rafinesquii may reflect an adaptation to the physical characteristics of tree roosts. To clarify the functional basis of ecomorphological correlations in bats, Norberg and Rayner (cited in Norberg 1987) considered wing morphology in relation to flight performance and flight behavior. Wing shape, which affects optimal flight speed and flight mode, evolves as a result of different flight demands. Flight mode and optimal flight speed depend primarily on habitat structure, foraging behavior, choice of food and size of prey. Broad wings permit high lift and allow high mass-bearing potential. Wings with low aspect permit highly manueverable flight styles in, and around, cluttered environments. *Plecotus* are slow fliers but exhibit a high degree of manueverability and, unlike most North American bats, they can hover (Norberg 1987). This agility may be a result of the need to fly into narrow tree crevices and, for *P. rafinesquii*, to fly within the limited space of a tree cavity.

P. rafinesquii is not expected to use a roost site that admits too much light. Tree cavities are dark and the bat's preference for such areas in man-made structures may be a reflection of this characteristic of natural roosts. A preference for low light levels may also be a predator avoidance mechanism. Predation was not directly addressed in my study but it may be an important factor in roost choice.

Buildings probably offer greater protection from predators than do tree cavities because there are more places to escape and still remain in shelter, and there is more room to manuever. No direct evidence of predation is available for this species in North Carolina or elsewhere. Jones (1977) lists several snakes (*Elaphae guttata*, *Crotalus adamanteus*, *Agkistrodon piscivorous*) found in *P. rafinesquii* roosts in Louisiana and suggested that they may feed on bats. Other potential predators include raccoons (*Procyon lotor*), bobcats (*Felis rufus*), house cats, skunks and owls (Jones 1977). Rat snakes (*Elaphae obsoleta*) were found hanging in the rafters of CH01 near a cluster of young *P. rafinesquii* (Paris Trail, pers. comm.). On another occasion in Bladen County a rat snake (*E. obsoleta*) was seen approaching a solitary *P. rafinesquii* as the bat rested in BL16. My movements eventually startled the snake, and it retreated under a large stack of boards in the room. Although other snakes have been seen around the buildings occupied by P. rafinesquii, only rat snakes have been observed approaching the bats or have been seen near them. Rat snakes are excellent climbers, often reside in tree hollows above ground and frequently search the rafters of old farm buildings for mice and nesting birds.

Bats were not banded during the primary phase of my study so definitive statements about roost loyalty are not possible, however, sites occupied by P. rafinesquii seem to be focal points of activity year-round. The same roosts are used continuously throughout summer and also from year-to-year, probably by many of the same individuals. Winter roosts are not well-documented in the study area, but small numbers of these bats were found in Bladen and Chowan counties in winter in some roosts used as nursery and bachelor roosts. The White Oak School (CH06) site in Chowan County was used year-round, even after long-term, intense disturbance occurred in this site. Large guano accumulations were found in all of my nursery roosts and wearing on walls in the corners of darkened rooms prefered by the bats provide evidence that the sites have been used by bats for many years. Repititious occupancy by a solitary bat in the sycamore cavity, presumably the same individual, and regular use by the CH01 nursery colony, of the black gum as a night-roost (Clark, unpublished data) suggests that P. rafinesquii have a strong site attachment to both day and night roosts.

Behavior of P. rafinesquii in daytime roosts changes seasonally, particularly in regard to clustering and metabolic state, and may be a response to changes in temperature and differences in reproductive status. Female P. rafinesquii in nursery colonies cluster more often before young are born, when temperatures and food resources are less predictable in the spring, and females are more frequently torpid during this time. That solitary P. rafinesquii were torpid more often than bats in colonies is probably the result of differing energetic demands on males and females.

Pendant roosting may facilitate flight takeoff, reduce thermal disadvantages that accompany conduction to a cool substrate, or lessen accessibility to predators (Howell and Pylka 1977). Roost posture may have been more influenced by physical characteristics of the roost area than by thermoregulatory needs. Sites where bats always roosted pendant were in attics with roost surfaces that sloped, and flush-roosting nursery colonies were near the ceiling in rooms with surfaces perpendicular to the floor.

The thermal environment of P. rafinesquii is probably most affected by the entrapment of metabolic heat in a tree cavity. Clustering and colony size would be the most critical behavioral responses in tree cavities because space in a tree cavity is more limited than in a building. Attics and rooms of my study sites were large and the potential for heat dissipation from colonies to significantly alter roost temperatures, with the exception of the immediate vicinity of the cluster, was probably minimal. Higher temperatures in attics are thought to be advantageous to nursery colonies, especially during rested in BL16. My movements eventually startled the snake, and it retreated under a large stack of boards in the room. Although other snakes have been seen around the buildings occupied by _P. rafinesquii_, only rat snakes have been observed approaching the bats or have been seen near them. Rat snakes are excellent climbers, often reside in tree hollows above ground and frequently search the rafters of old farm buildings for mice and nesting birds.

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gestation and in the early growth stages of young bats (Tuttle and Stevenson 1982). Attics are probably preferred by nursery colonies during gestation and lactation because the conductive properties of the roofs, especially sites with tin roofs, are greater than those of natural roost sites causing attics to reach higher temperatures than natural cavities or lower level rooms in houses.

Many bats in the summer of 1986 appeared to be experiencing some stress on hot days when they had moved from a preferred roost area. The steadier and lower temperatures in roost trees suggest that heat stress may not be a problem in them. Movements noted in my study may be an artifact of research disturbance or they may indicate movements to satisfy microclimate requirements. Probably they reflect both, it was difficult to separate these factors in my study.

My observations indicate that *P. rafinesquii* is highly sensitive to both direct and indirect disturbance. Descriptive evidence from my study supports the view that intensity of the disturbance and seasonal timing may be more critical than duration of disturbance (Tuttle 1979). Intense vandalism in BL04a appeared to be the cause of desertion by the solitary male that occupied the site. The nursery colony at BL11 deserted the roost for the entire summer season after my first two visits. The nearest human entrance was near the preferred roost area, and these two visits coincided with the early establishment of the colony (April 1986) and either near-term pregnancy or early post-parturition (early June 1986). Bats in all sites were easily disturbed when they were in well-lighted areas, they flew to other rooms or retreated to the attic almost immediately. In general, visits every two weeks after the birth of young, of 10 minute duration of less, to census bats or to record data, did not seem to affect the bats adversely if disturbance did not include loud noise, bright lights or handling the bats.

There is probably a correlation between forest clearing and disturbances in roosts. Clearing forests around the sites makes them more visible from nea by roads. Human visitation may increase because of increased visibility or from curious members of logging crews working in the vicinity of the site. Clearing around sites exposes them to more direct solar radiation and may cause changes in temperatures and other internal factors that significantly affect the temperature profiles of roost areas in the sites.

A low tolerance of human disturbance may be inferred from the fact that the buildings used by this species are not generally inhabited by humans or other vertebrates. Handley (1959) reported that these bats will occupy both human-inhabited and non-inhabited sites, but no specific information on human habitation was included in his discussion. All sites discussed by Handley (1959) appeared to be used on a seasonal basis by humans and probably were not occupied year-round by them. For example, occupation of several schools is noted, but the time of year bats occupied the school buildings was not mentioned. In the same region, the Komareks (1938) found Plecotus in the attic of an abandoned schoolhouse and on the chimney in a cabin, but no mention of season is made for either observation and it is not known whether the cabin was a permanent residence or vacation home. Barbour (1957) located a colony in the attic and storerooms of a large log building in a recreation camp, but no description of regular human habitation of this site was provided.

Comments on Social Organization

Patterns of social organization in bats are far from fully explored, but social structure varies widely in this order, even among closely-related species, and can take many diverse forms (Hill and Smith 1984). The availability and physical capacity of roosts can influence social organization, but the extent to which the mating system is influenced by the kind and abundance of roosts remains to be determined (Kunz 1982). Bradbury (1977) stated that the two most important ecological determinants of bat social structure appear to be adequate roost sites and sufficient food supplies.

Nothing is known about the mating system of P. rafinesquii. Although social structure was not targeted in my study some of my observations suggest that the social organization of P. rafinesquii is complex and bears further investigation, particularly in the context of roost influence on mating systems. Some characteristics of the life history of P. rafinesquii are similar to those of bats having a resource-based polygynous mating system. A polygynous mating system is promoted by the defense of limited resources (Poole 1985).

Polygynous mating systems are also expected when environmental or behavioral conditions promote the formation of a compact social unit of females that may be monopolopized by single males (Emlen and Oring 1977). Males may directly control access to females by aggressively defending a harem (female defense polygyny) or they may indirectly control access to females by defending resources essential to females (resource-defense polygyny). Resource-defense polygyny is most prevalent in habitats with uneven resource distribution where the result is a mosaic of male territories of different quality (Emlen and Oring 1977). Natural roost sites for P. rafinesquii where caves do not occur are tree cavities. It is reasonable to assume that roost quality of tree cavities is highly variable. Tree cavities suitable for nursery roosts are probably limited, and since tree cavities are more prevalent in older stands, these resources may be clumped.

The operational sex ratio (OSR), the average ratio of fertilizable females to sexually active males at any given time (Emlen and Oring 1977), may be skewed in the beginning of the mating period for P. rafinesquii. Sex ratios in winter roosts and those of young bats appear to be close to 1:1 (Clark, pers. obs.), however, many more females are found in summer and fall than males. Males that are found in summer and fall are solitary and are nearly always in close proximity to female nursery colonies. A degree of mutual tolerance between a solitary male P. rafinesquii and a nursery colony was regularly observed in two nursery roosts, BL07 and CH03. In these sites solitary bats roosted in the same house, but used different roost areas away from the nursery group. England et al. (1989) stated that adult males are rarely encountered within nursery colonies when females are lactating, with those males present in nursery colonies being non-scrotal yearlings.

Mating systems that involve defense are generally associated with a long breeding season of several weeks or several months. Male P. rafinesquii with descended testes have been found in North Carolina from

August until March (Clark, pers. obs.). Males do not breed during their first year (Jones 1977). Adult males are apparently non-reproductive only while females are in gestation or raising young.

Some of my observations of male _P. rafinesquii_ roosting patterns suggest territoriality. I have not observed cohabitation of a single adult female and a single adult male or male-male cohabitation at any time in summer roosts. Single adult males, presumably the same individuals, were regularly found in close proximity to nursery colonies or in a roosting area away from, but in the same site as, a nursery colony. Prior to the 1986 roosting ecology study, a male _P. rafinesquii_ using BL04a was collected from that site and another solitary male later replaced it.

Dispersal patterns need further investigation. Jones and Suttkuss (1975) reported that females dispersed first from the natal colony. Some of my observations suggest that male _P. rafinesquii_ may disperse first from the group, other observations are somewhat conflicting. During the 1986 summer period a male young-of-year bat was found in late summer in BL21, a site not regularly-used by bats. This bat may have been a transient dispersing from a nearby natal colony. This was the only time the site had been used by bats, and the bat was not present on the next visit to this site. A small non-scrotal male, presumbaly a young-of-year, was seen alone in a garage in Chowan County in September 1990. In CH03 five non-scrotal males, with masses similar to the garage male, were found in a cluster containing at least eighteen females (cluster size estimated at 28 bats, 23 were captured and color-banded). Several female young-of-year bats, banded in 1984, were recaptured in the same site in which they were banded over the course of the summer.

Two of these (#55 and #57) were recaptured once each month in August, September, and October 1984.

Some types of polygyny occur where females in a harem are strongly bonded to each other and the female group exists as a persistent social structure in its own right (Bradbury 1977). In this type of polygyny females are closely-related, and from time to time the group is monopolized by different males. The relationship of the females in _P. rafinesquii_ nursery colonies has not been established.

Harem males of some species engage in elaborate displays and may be identified by their bahavior with respect to other bats in a social group (Racey 1988). Harem male _Saccopterryx bilineata_ displays observed by Bradbury and Emmons (1974) included vocal, visual and olfactory elements to attract and retain harems of up to eight females. The males actively defended territories (buttress cavities in trees). Harem males of _Phyllostomos hastatus_ make themselves conspicuous when they come to the edge of a cluster of females to investigate disturbance caused by human observers (McCracken and Bradbury 1981). No elaborate displays or investigatory behaviors resembling those described above were observed in _P. rafinesquii_ colonies in North Carolina, and no such behavior has been reported in the literature for this genus, however, none of my investigations or those of others have targeted this issue for _Plecotus_.

Olfactory communication is one of the more difficult to detect and analyze. Large and conspicuous glandular masses are part of the muzzle of _Plecotus rafinesquii_, giving the bat a lump-nosed appearance (Fig. 4). The primary function of these glands has never been investigated. The shape and size of these masses may help to create and funnel echolocation calls or the lumps may contain glands that may be used in olfactory communication. Displays and other evidence of male defense may be subtle or occur at times or in places where observers would not have the opportunity to witness them.

I believe the social organization of *P. rafinesquii* may be similar to the seasonally successional system of *Nyctalus noctula*, a European bat. In winter, colonies of *N. noctula* in hibernacula are sexually mixed, nursery colonies of females are formed in the spring and males roost alone (Hill and Smith 1984). In late summer, after the young have become independent, the males set up territories in hollow trees where the females join them to form transient harems (females may move among harems).

Some aspects of *P. rafinesquii* biology are similar to those of bats with selective polygynous mating systems. More directed observations are needed to assess mating strategies of this bat and the possible effect of roosting ecology on its mating system. Observations made in buildings may not reflect behaviors exhibited in natural roosts since buildings are structurally more complex and provide a number of different roost areas within the same site.

CONCLUSIONS

This investigation provides support that identification of both internal and external factors affecting roost selection is necessary to fully understand roost preferences of bats. An appropriate microclimate is critical for energetic efficiency, but microclimate limitations may be more flexible than external ones. Temperate bats have a wide repertoire of behavioral thermoregulatory responses that are effective in modifying some roost microclimate variables or that mitigate negative effects of unpredictable internal variables. The ultimate cause of roost selection may be external variables and not internal ones.

Insufficient knowledge of roosting ecology for most bat species makes it difficult to plan appropriate conservation measures. Although many recognize the importance of not disturbing the roost itself and the critical nature of a correct microclimate, conservation and management efforts for bats will not be effective without the extended knowledge of external influences. A multi-dimensional approach to roost-selection should enable resource agencies and managers to make more prudent status decisions, help to identify potential and critical habitat, and facilitate the creation of roost structures that adequately fulfill the requirements of species in need of protection. Additionally, approaches to roosting ecology studies that consider external habitat factors in combination with internal ones should result in more meaningful ecomorphological and behavioral investigations of bats.

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Table 1. Acroynyms, occupation classifications and locations of thermometers in buildings available as roost sites to *Plecotus rafinesquii* in Bladen (BL), Chowan (CH), Pender (PE) and Sampson (SA) counties.

Site	Class	Thermometer Location
BL01	bachelor	ground floor - hallway
BL02C	unoccupied*	ground floor - room
BL03	unoccupied*	ground floor - room
BL04A	unoccupied*	ground floor - bathroom
BL04B	unoccupied	ground floor - room
BL06	bachelor (+)	ground floor - room
BL07	bachelor	ground floor - room
BL08	bachelor	ground floor - hallway
BL09	unoccupied	ground floor - closet
BL11	nursery	attic
BL12	bachelor	ground floor - bathroom
BL13	bachelor	ground floor - room
BL14	nursery	ground floor - room
BL15	bachelor	ground floor - closet
BL16	bachelor	ground floor - room
BL17	unoccupied	attic and ground floor room
BL19	nursery	attic
BL20	bachelor	attic and closet
BL21	unoccupied*	attic
BL33	bachelor	ground floor - front hall
BL34	unoccupied	attic
BL37	unoccupied	ground floor - room
BL38	unoccupied	attic; 1 mounted pendant, 1 flush

Table 1 cont.

Site	Class	Thermometer Location
PE01	nursery	attic
PE02	nursery	ground floor - hallway
PE03	unoccupied	attic
SA01	unoccupied*	ground floor
SA03	nursery	attic
SA06	unoccupied	attic
SA10	unoccupied	attic
SA11	bachelor	attic
SA13	unoccupied	attic
CH01	nursery	second floor
CH02	nursery	attic
CH03	nursery	attic and ground floor-room
CH04	bachelor	ground floor-room
CH05	nursery	ground floor-room
CH06	nursery	ground floor and attic

* = one _Plecotus_ _rafinesquii_ was seen in the site 1 or 2 times
\+ = prior to 1986 this was a _P._ _rafinesquii_ nursery colony

Table 2. Descriptions of seven internal influence variables that were measured in summer roost sites of *Plecotus rafinesquii* and used in discriminant function analysis. Temperature variables cover 1 June-31 July 1986. Light levels were averaged over all visits made between 15 May-15 September.

Variable Mnemonic	Description
1. ROTEMP	1. mean air temperature (C) recorded inside the roost
2. AMTEMP	2. mean air temperature (C) recorded outside the roost as in 1.
3. MMAXTEMP	3. mean maximum temperature (C) within the roost
4. MMINTEMP	4. mean minimum temperature (C) within the roost
5. ROLITE	5. mean light level (fc) inside the roost
6. AMLITE	6. mean light level (fc) outside the roost
7. SDISTURB	7. the number of times disturbances were noted in the roost (categorized as "0" for no disturbance evidence, "1" for disturbance noted)

Table 3. Descriptions of 21 external habitat variables measured for twenty-two buildings occupied or unoccupied by *Plecotus rafinesquii* in Bladen County, North Carolina. Variables were measured for both 0.5-km (identified by a "1") and a 1.5-km (identified by a "2") radius surrounding each site.

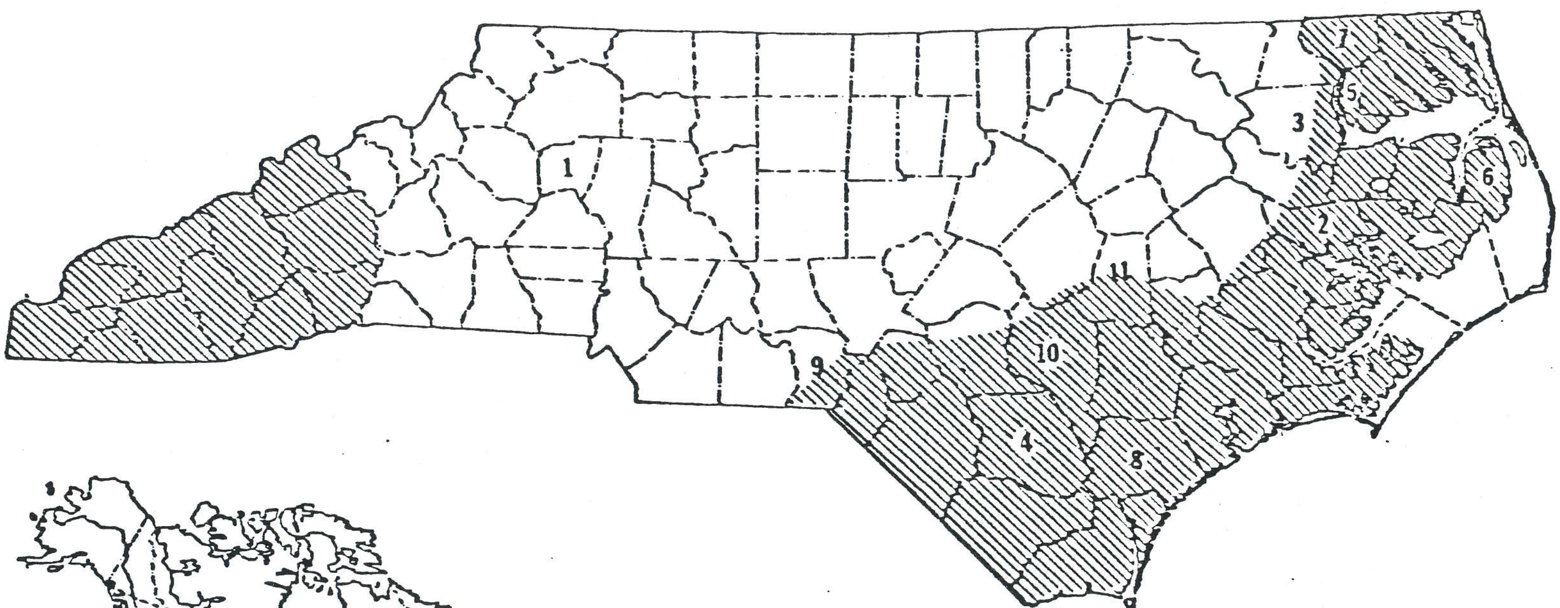
Variable Mnemonic	Description
1. CANOPY1 & 2	1. estimate of the total forest surrounding site = CANO + CANC
2. CANO1 & 2	2. estimate of open canopy forest in either radius
3. CANC1 & 2	3. estimate of closed canopy forest in either radius
4. DEVELOP1 & 2	4. estimate of developed land surrounding the site
5. ALLROADS1 & 2	5. estimate of the density of roads surrounding site
6. DAG1 & 2	6. estimate of agricultural land surrounding site
7. TWAT1 & 2	7. total area water covered within either radius
8. TWATNF1 & 2	8. total area of nonflowing water within either radius
9. MDIST1 & 2	9. minimum distance to a permanent water body from the roost site
10. MDISTNF1 & 2	10. minimum distance from the roost to a permanent nonflowing water body
11. RN2	11. estimate of the density of roads within a 1.5-km radius surrounding a site

Table 4. Percent of temperatures (C), in 10 degree increments, recorded in roost sites of Plecotus rafinesquii in Bladen, Chowan, Pender, and Sampson counties. Percentages are given for the means of the maximum (MAX), minimum (MIN) and current temperatures (DAYTEMP) recorded in the summer of 1986.

C	MAX(n=388)	MIN(n=388)[a]	DAYTEMP(n=380)[b]
0 - 9	0%	14%	1%
10 - 19	0%	45%	6%
20 - 29	11%	40%	60%
30 - 39	52%	0%	29%
40 - 49	22%	0%	3%
50 - 54	1%	0%	0%
Total	100%	99%	99%

(a) One percent of the observations for the minimum temperatures were under -5 degrees. (b) Rounding error accounts for missing percent.

Figure 1. The shaded areas represent the known and expected distribution of *Plecotus rafinesquii* in North Carolina. Two subspecies occur in North Carolina: *rafinesquii* in the Mountain region and *macrotis* in the Coastal Plain. The range in North America is indicated by the blackened area on the inset map (from Lee et al. 1982). A hiatus is evident throughout the Piedmont of the southeastern United States. Counties monitored for the roosting ecology study, and others discussed in the text, are indicated by number.



1. Alexander County
2. Beaufort County
3. Bertie County
4. Bladen County
5. Chowan County
6. Dare County
7. Gates County
8. Pender County
9. Richmond County
10. Sampson County
11. Wayne County

Figure 2. The large cavity in this double-trunked American sycamore (*Plantanus occidentalis*), found in Chowan County, North Carolina, was used regularly as a day-roost by a solitary *Plecotus rafinesquii* in the summers of 1989 and 1990.

Figure 3. This old schoolhouse (CH06), in White Oak, Chowan County, North Carolina, was used year-round by *Plecotus rafinesquii* until it was demolished in 1990.

Figure 4. When *Plecotus rafinesquii* are active the large ears are erect, but when the bat is torpid the ears are curled about the head and neck (illustrations by Ruth Brunstetter). The function of the lumps on the muzzle of *P. rafinesquii* has not been determined. (Illustration approximately 1.5x natural size.)

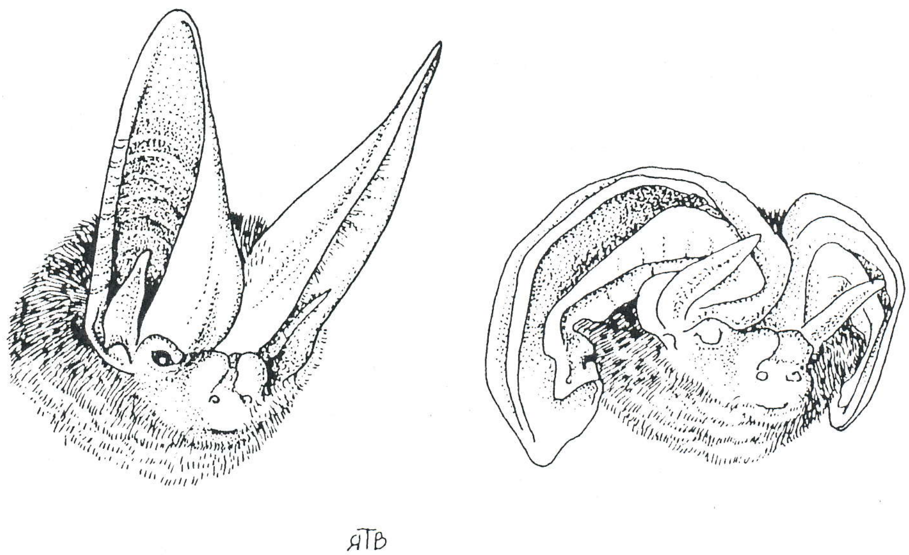

RTB

Figure 5. This large two-story barn in Chowan County, North Carolina was used as a nursery roost by *Plecotus rafinesquii* from 1986 to 1990.

Figure 6. This abandoned house (BL07), near Black River in Bladen County, North Carolina, was used by a nursery colony of *Plecotus rafinesquii*, and is typical of most sites occupied by this bat in the Coastal Plain of the State.

Figure 7. The interior of PE01 (in Pender County, North Carolina), a nursery roost for Plecotus rafinesquii, is typical of most sites occupied by this bat in the Coastal Plain of the State. As in this site, most study sites had plaster walls and often had boarded windows. The colony most frequently roosted in the attic. The attic opening can be seen in the upper left-hand corner of the photograph. Wearing and staining of the wall where bats alternately roosted can be seen to the left of the opening.

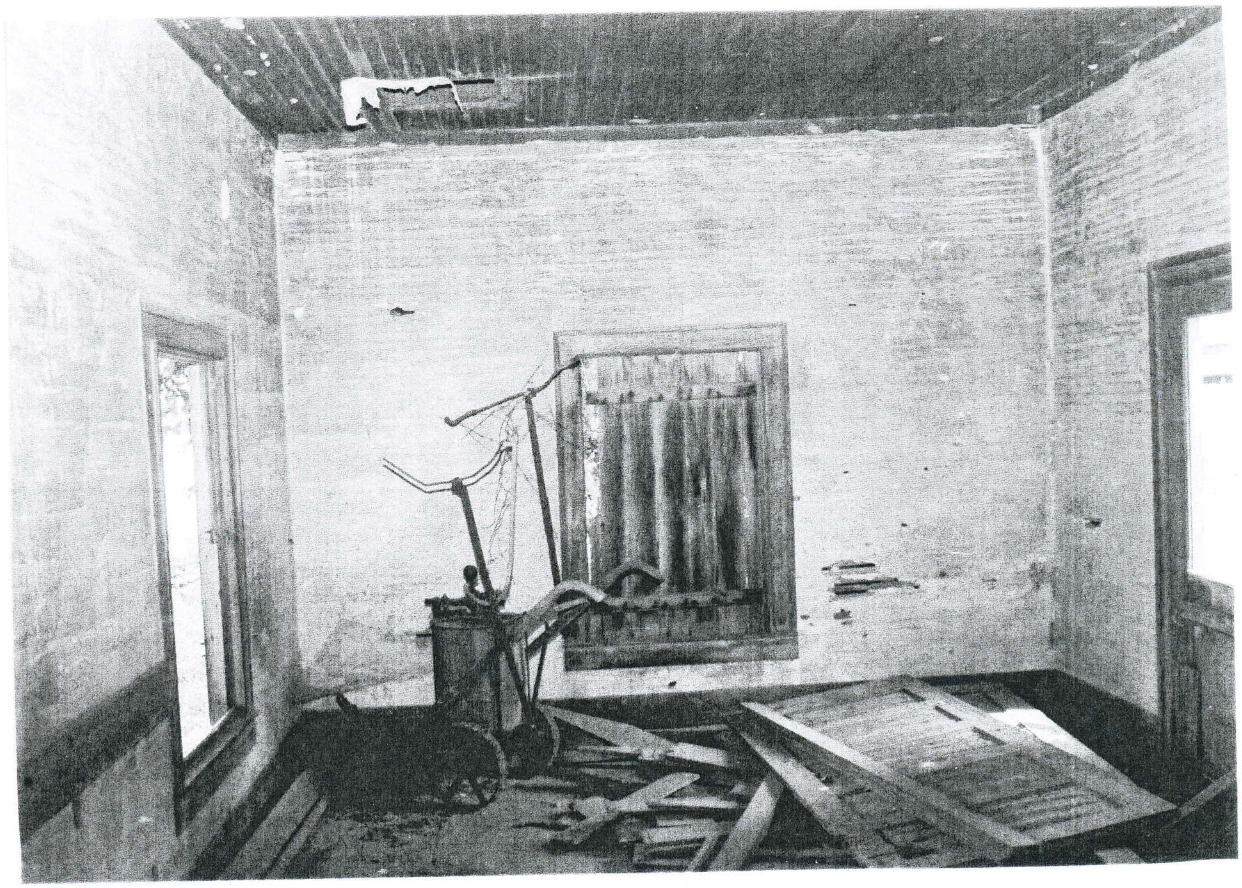


Figure 8. Maximum and minimum temperatures recorded per day, in the summer of 1986, by the Edenton station in Chowan County, North Carolina for the National Weather Service.

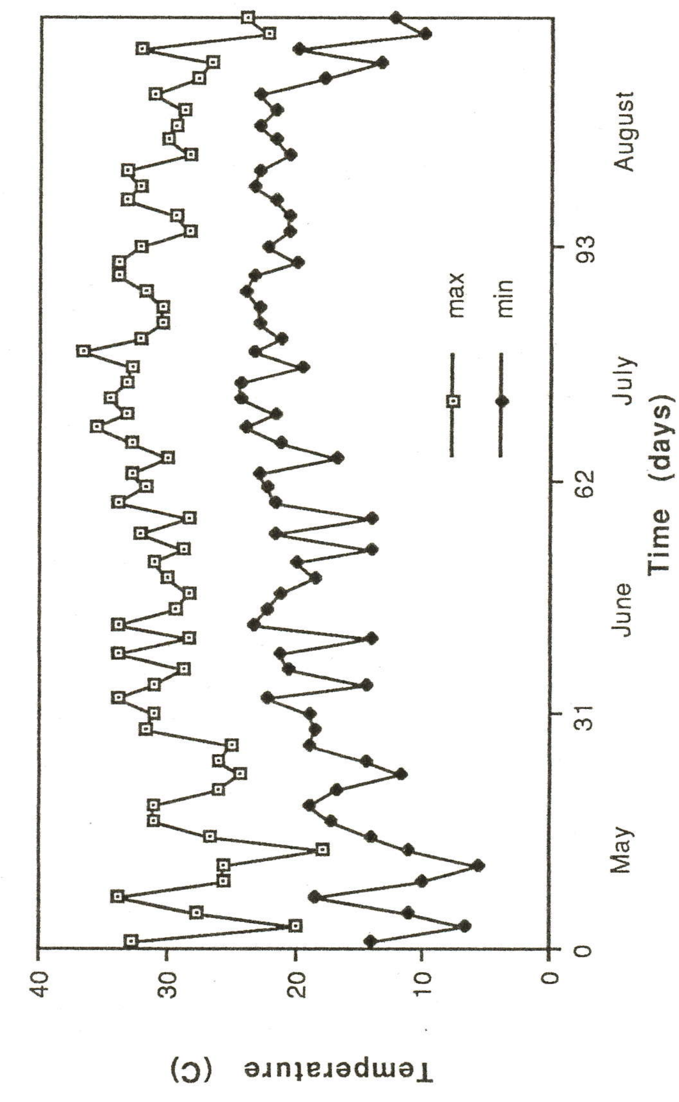
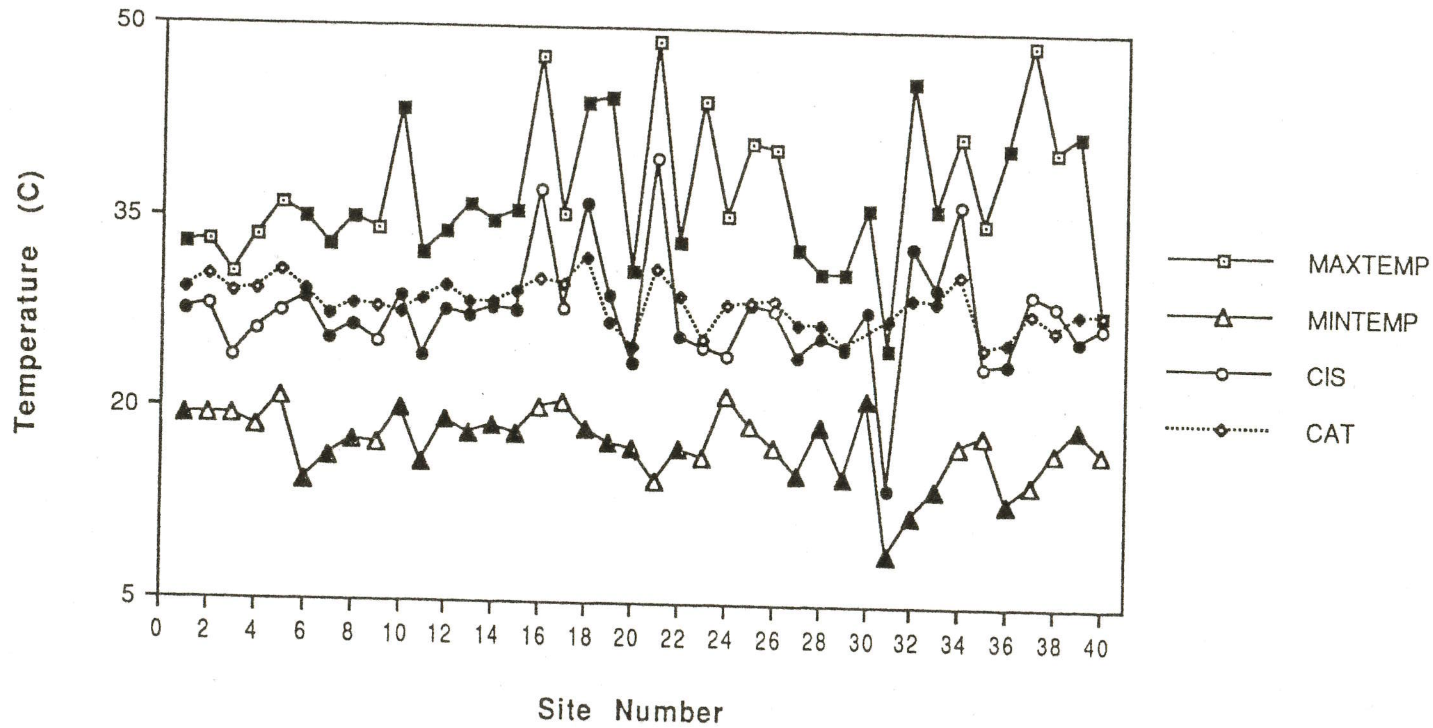

Temperature (C)
40
30
20
10
0
0
31
62
93
May
June
July
August
Time (days)
max
min

Figure 9. Comparison of all mean temperatures recorded at 7-14 day intervals in buildings, in the North Carolina Coastal Plain used (blackened symbols), and not used (open symbols), by *Plecotus rafinesquii* in summer 1986. MAXTEMP = maximum temperature in building, MINTEMP = minimum temperature in building, CIS = current temperature recorded when investigators visited, CAT = current ambient temperature. Site numbers correspond to those on the x-axis as follows:

1.	BL01	11.	BL12	21.	BL21	31.	CH05
2	BL02c	12.	BL13	22.	BL33	32.	PE01
3.	BL03	13.	BL14	23.	BL34	33.	PE02
4.	BL04a	14.	BL15	24.	BL37	34.	PE03
5.	BL04b	15.	BL16	25.	BL38F	35.	SA01
6.	BL06	16.	BL17A	26.	BL38P	36.	SA03
7.	BL07	17.	BL17D	27.	CH01	37.	SA06
8.	BL08	18.	BL19	28.	CH02	38.	SA10
9.	BL09	19.	BL20A	29.	CH03	39.	SA11
10.	BL11	20.	BL20C	30.	CH04	40.	SA13

*Site numbers followed by a capitol letter indicate a thermometer position as follows: A = attic, C = closet, D = lower level room, F = flush, P = pendant.

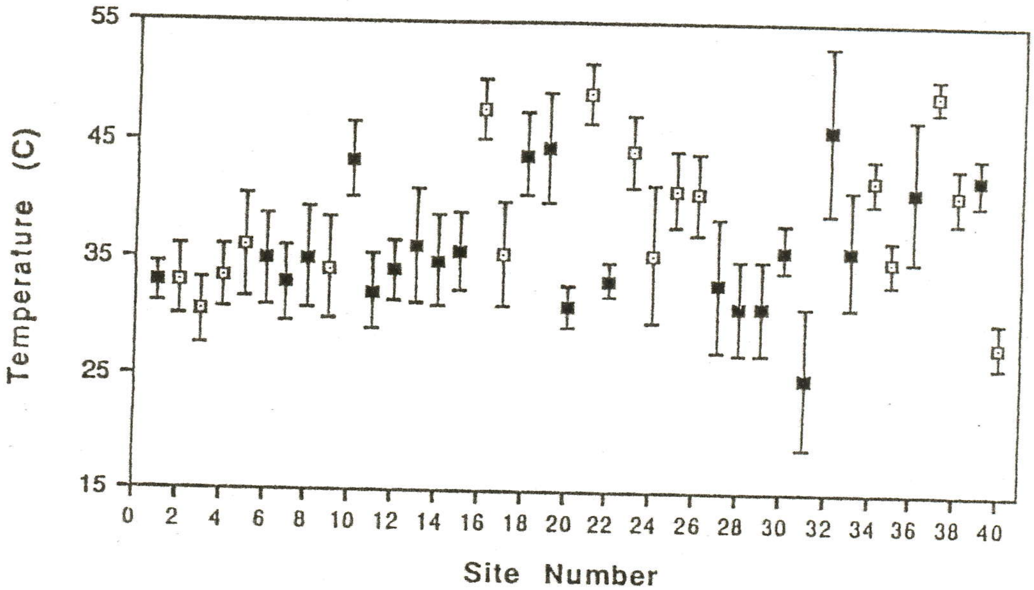


50
35
20
5
Temperature (C)
0 2 4 6 8 10 12 14 16 18 20 22 24 26 28 30 32 34 36 38 40
Site Number
MAXTEMP
MINTEMP
CIS
CAT

Figure 10. Means and standard deviations of maximum temperatures (top) and minimum temperatures (bottom), recorded at 7 or 14 day intervals, inside buildings used (blackened symbols) and not used (open symbols) by *Plecotus rafinesquii* in the North Carolina Coastal Plain in summer 1986. Site numbers* correspond to those on the x-axis as follows:

1.	BL01	11.	BL12	21.	BL21	31.	CH05
2	BL02c	12.	BL13	22.	BL33	32.	PE01
3.	BL03	13.	BL14	23.	BL34	33.	PE02
4.	BL04a	14.	BL15	24.	BL37	34.	PE03
5.	BL04b	15.	BL16	25.	BL38F	35.	SA01
6.	BL06	16.	BL17A	26.	BL38P	36.	SA03
7.	BL07	17.	BL17D	27.	CH01	37.	SA06
8.	BL08	18.	BL19	28.	CH02	38.	SA10
9.	BL09	19.	BL20A	29.	CH03	39.	SA11
10.	BL11	20.	BL20C	30.	CH04	40.	SA13

*Site numbers followed by a capitol letter indicate a thermometer position as follows: A = attic, C = closet, D = lower level room, F = flush, P = pendant.


55
45
35
25
15
Temperature (C)
0 2 4 6 8 10 12 14 16 18 20 22 24 26 28 30 32 34 36 38 40
Site Number

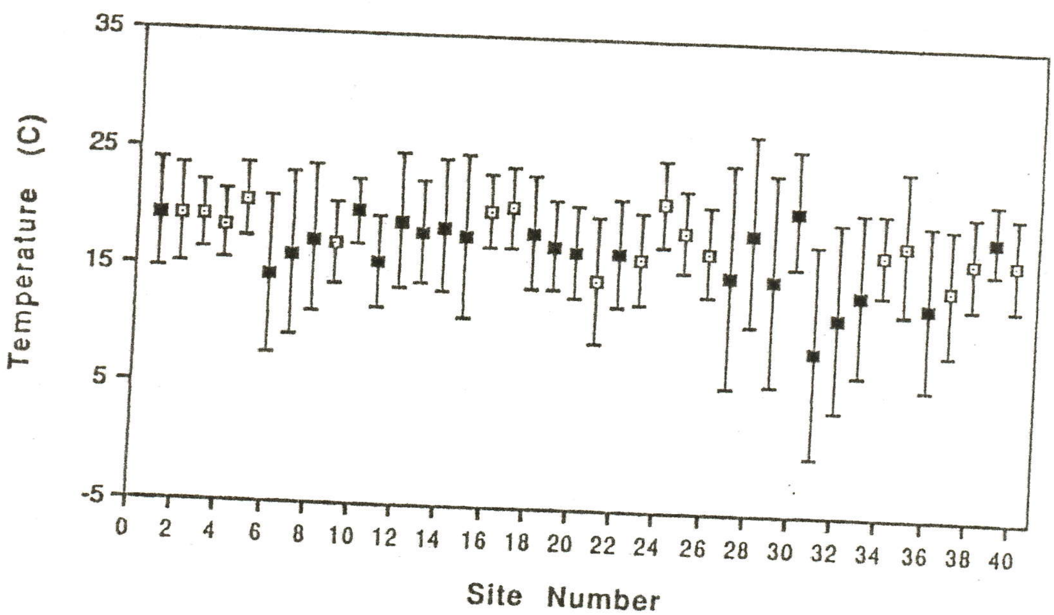
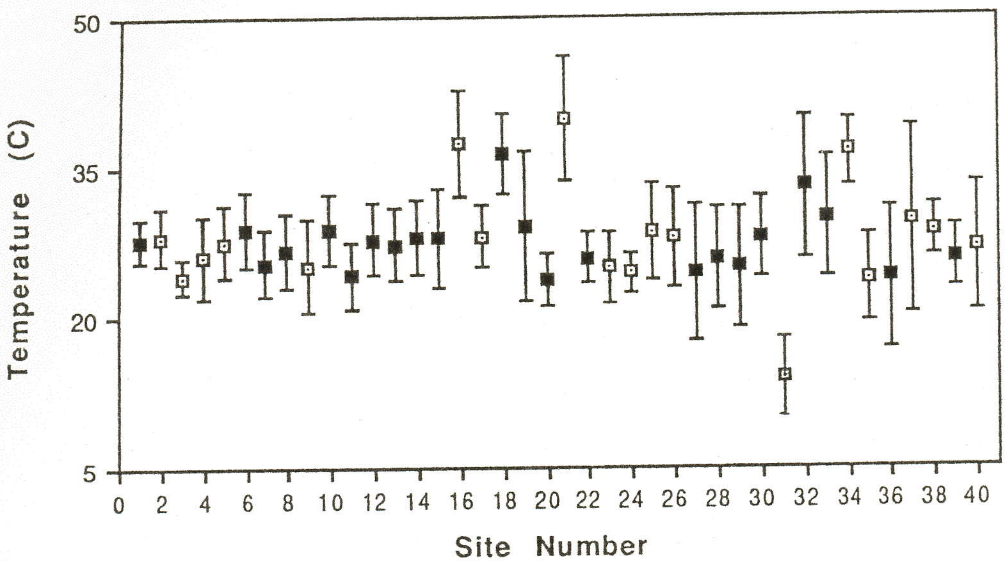

35
25
15
5
-5
Temperature (C)
0 2 4 6 8 10 12 14 16 18 20 22 24 26 28 30 32 34 36 38 40
Site Number

Figure 11. Means and standard deviations of temperatures recorded during the day, at 7-14 day intervals, inside (top) and outside of (bottom) buildings used (blackened symbols) and not used (open symbols) by *Plecotus rafinesquii* in the North Carolina Coastal Plain in summer 1986. Site numbers* correspond to those on the x-axis as follows:

1.	BL01	11.	BL12	21.	BL21	31.	CH05
2	BL02c	12.	BL13	22.	BL33	32.	PE01
3.	BL03	13.	BL14	23	BL34	33.	PE02
4.	BL04a	14.	BL15	24.	BL37	34.	PE03
5.	BL04b	15.	BL16	25.	BL38F	35.	SA01
6.	BL06	16.	BL17A	26.	BL38P	36.	SA03
7.	BL07	17.	BL17D	27.	CH01	37.	SA06
8.	BL08	18.	BL19	28.	CH02	38.	SA10
9.	BL09	19.	BL20A	29.	CH03	39.	SA11
10.	BL11	20.	BL20C	30.	CH04	40.	SA13

*Site numbers followed by a capitol letter indicate a thermometer position as follows: A = attic, C = closet, D = lower level room, F = flush, P = pendant.


50
35
20
5
Temperature (C)
0 2 4 6 8 10 12 14 16 18 20 22 24 26 28 30 32 34 36 38 40
Site Number

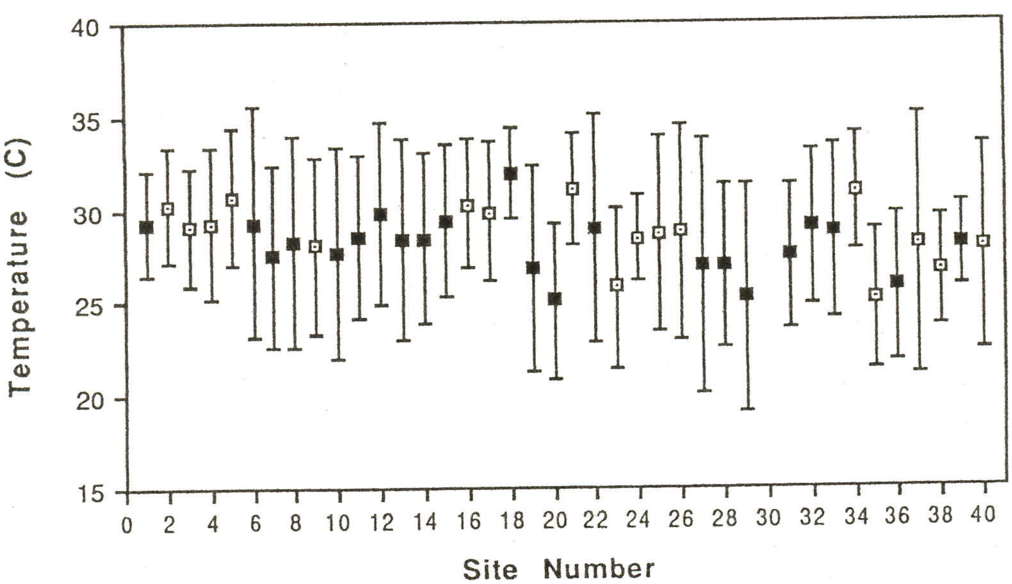
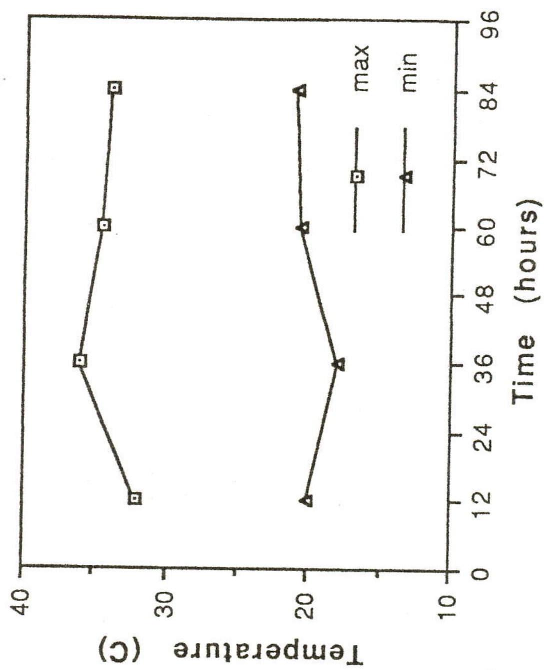

40
35
30
25
20
15
Temperature (C)
0 2 4 6 8 10 12 14 16 18 20 22 24 26 28 30 32 34 36 38 40
Site Number

Figure 12. Comparison of the daily temperature profile of CH01 with that of two roost areas in CH03 (a = attic, d = downstairs). Temperatures in CH01 are from the second story of this large barn. Daily temperature fluctuations are similar for the second story of CH01 and the attic of CH03. Both sites are *Plecotus rafinesquii* nursery roosts. The graph on the right shows the ambient maximum and minimum temperatures recorded for the National Weather Service by the Edenton station in Chowan County, North Carolina.


Temperature (C)
Time (hours)
max
min

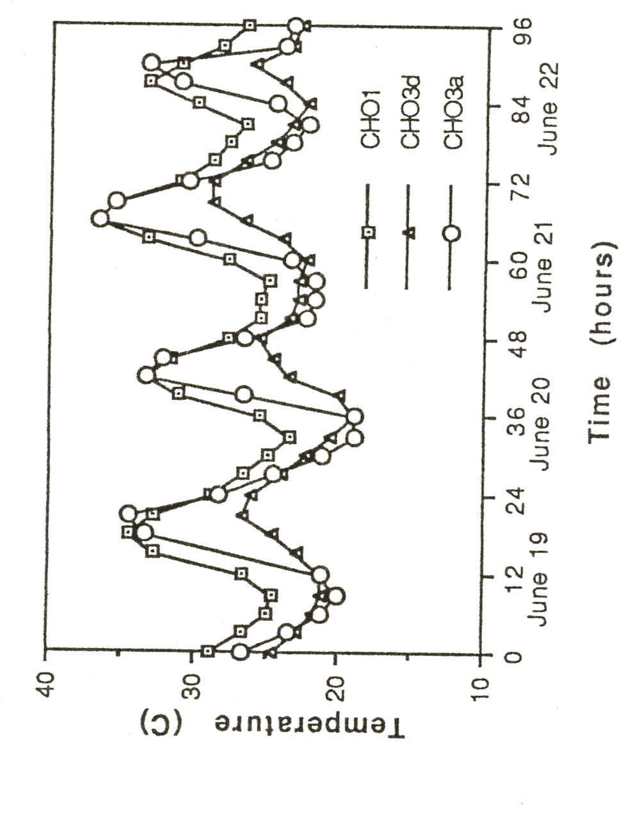

Temperature (C)
Time (hours)
June 19
June 20
June 21
June 22
CHO1
CHO3d
CHO3a

Figure 13. Mean weekly temperatures recorded from seven day recording thermometers in the attic and a downstairs room in nursery site CH03 for 5 weeks in April and May 1990.

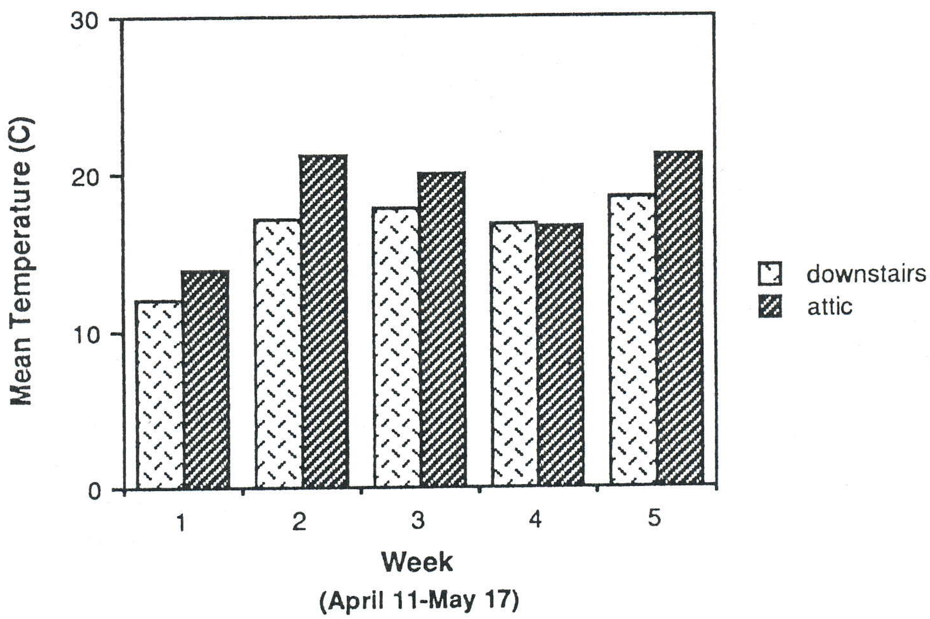
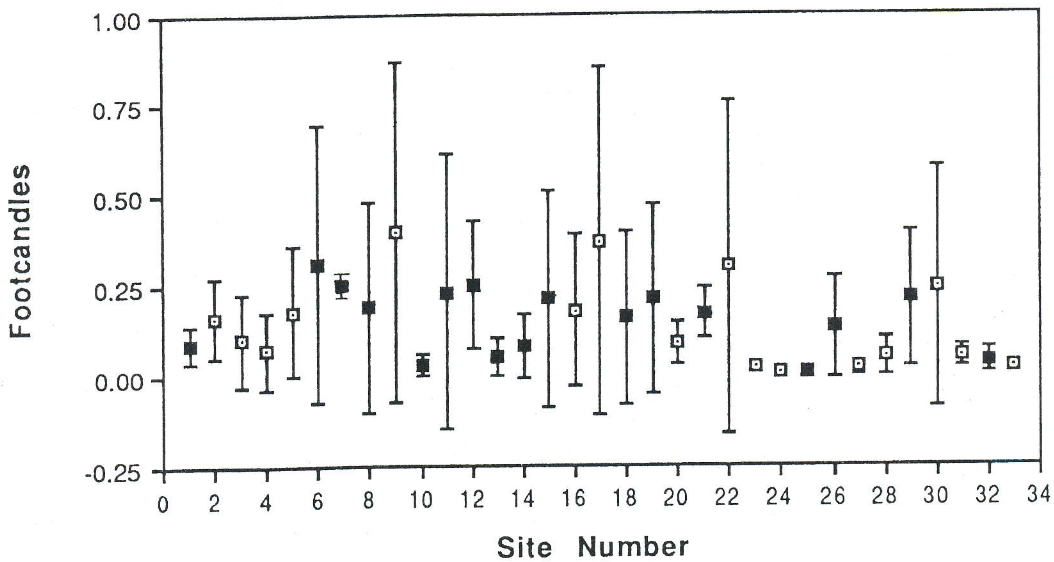

30
20
10
0
Mean Temperature (C)
1
2
3
4
5
Week
(April 11-May 17)
downstairs
attic

Figure 14. Means and standard deviations of ambient light levels (top) and light levels inside buildings (bottom) used (blackened symbols) and not used (open symbols) by <u>Plecotus</u> <u>rafinesquii</u> as summer roosts in the North Carolina Coastal Plain in 1986. Site numbers correspond to those on the x-axis as follows:

1.	BL01	11.	BL12	21.	BL33	30.	SA06
2	BL02c	12.	BL13	22.	BL34	31.	SA10
3.	BL03	13.	BL14	23.	BL37	32.	SA11
4.	BL04a	14.	BL15	24.	BL38	33.	SA13
5.	BL04b	15.	BL16	24.	BL38		
6.	BL06	16.	BL17A*	25.	PE01		
7.	BL07	17.	BL17D*	26.	PE02		
8.	BL08	18.	BL19	27.	PE03		
9.	BL09	19.	BL20	28.	SA01		
10.	BL11	20.	BL21	29.	SA03		

*In this site readings were taken in both the attic (A) and a lower level roost area (D).


Footcandles
1.00
0.75
0.50
0.25
0.00
-0.25
0 2 4 6 8 10 12 14 16 18 20 22 24 26 28 30 32 34
Site Number

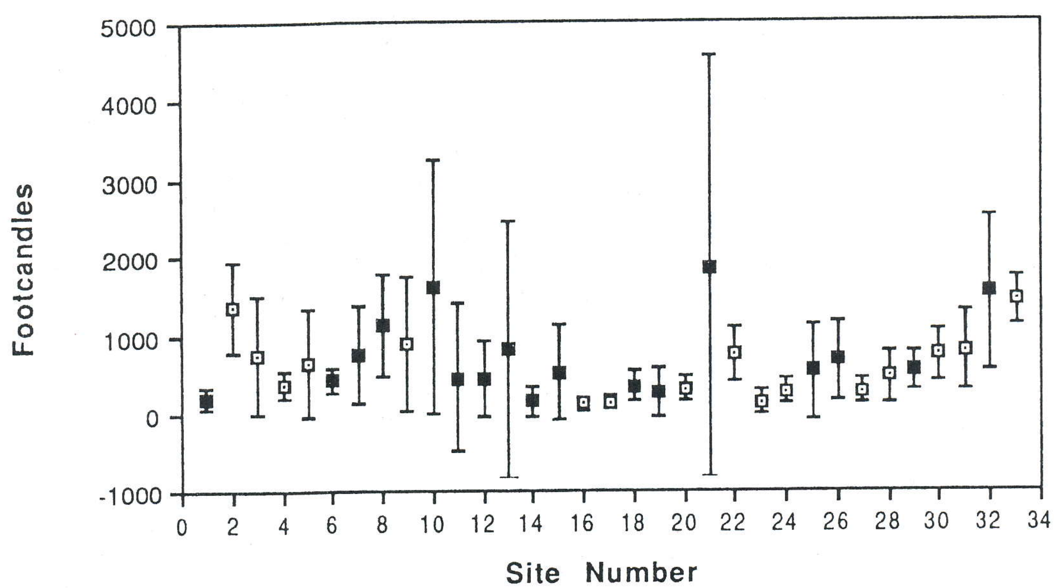
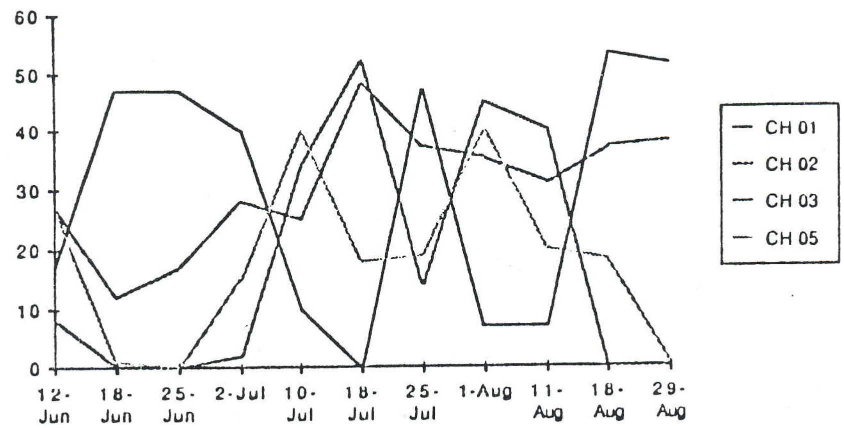

Footcandles
5000
4000
3000
2000
1000
0
-1000
0 2 4 6 8 10 12 14 16 18 20 22 24 26 28 30 32 34
Site Number

Figure 15. Significant increases and decreases in numbers of bats occurred in four Chowan County nursery colonies (CH01, CH02, CH03, CH05) during the summer of 1986. In 1986 the colony at CH01 apparently used CH02 as an alternate roost (top). In 1987 when site CH02 was no longer available the colony from CH01 apparently used CH05 as an alternate roost (bottom).


60
50
40
30
20
10
0
12-Jun
18-Jun
25-Jun
2-Jul
10-Jul
18-Jul
25-Jul
1-Aug
11-Aug
18-Aug
29-Aug
CH 01
CH 02
CH 03
CH 05

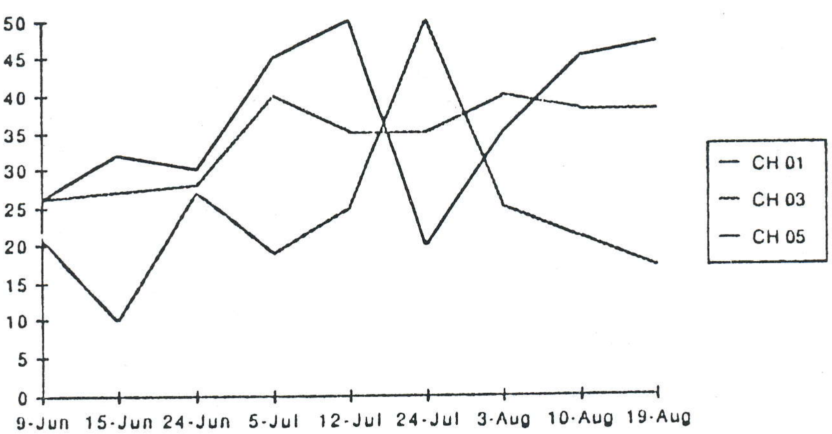

50
45
40
35
30
25
20
15
10
5
0
9-Jun
15-Jun
24-Jun
5-Jul
12-Jul
24-Jul
3-Aug
10-Aug
19-Aug
CH 01
CH 03
CH 05

Figure 16. This house in Chowan County (CH05) was used as a nursery roost by *Plecotus rafinesquii* until the nearby forest was logged in 1988. The photograph was taken in the summer of 1990 from the road that passes near the site. Although close to the road the house was not visible before logging because it was obscured by vegetation.

Figure 17. Mean percentages of agriculture, forest and developed land in a 1.5-km radius that surrounded occupied (N = 16) and unoccupied (N = 6) sites available to *Plecotus rafinesquii* in Bladen County, North Carolina.

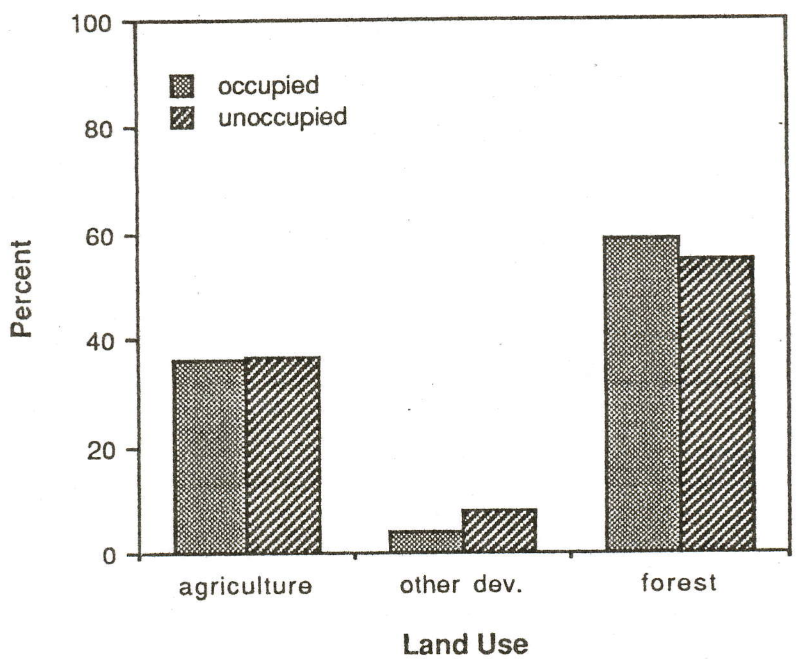
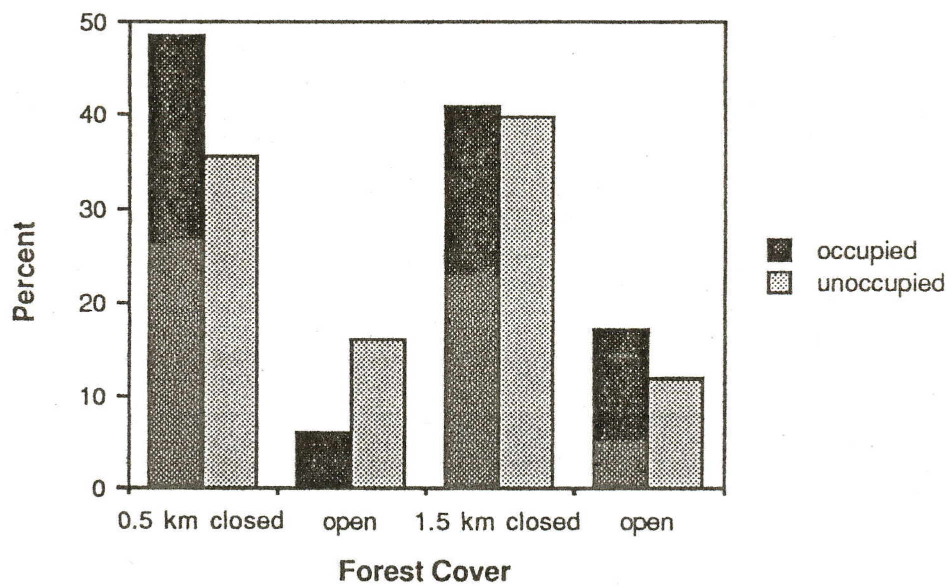

100
80
60
40
20
0
Percent
occupied
unoccupied
agriculture
other dev.
forest
Land Use

Figure 18. Mean percentage of open and closed canopy forest cover that surrounded 22 buildings (within either a 0.5-km or a 1.5-km radius) available to *Plecotus rafinesquii* as roost sites in Bladen County, North Carolina.



50
40
30
20
10
0
Percent
0.5 km closed
open
1.5 km closed
open
Forest Cover
occupied
unoccupied

Figure 19. Percentage of occupied sites correctly classified from seven combinations of variables that measured external and internal influences on roosting ecology. Group 1 represents the variables selected by STEPDISC (SAS Institute Inc. 1982:369-380), group 2 contained only internal variables, group 3 contained only water variables, groups 1, 4, and 5 are combinations of external variables and groups 6 and 7 contain both internal and external variables. Variable groups are (1) RN2, TWAT2, CANO2 (2) MMAXTEMP, MMINTEMP, ROLITE (3) MDIST2, MDISTNF2, TWAT2, TWATNF2 (4) CANC1, RN1, DAG1, TWAT1 (5) CANC2, RN2, DAG2, TWAT2 (6) CANOPY2, RN2, TWAT2, MMAXTEMP, MMINTEMP (7) CANO2, SDISTURB, MMAXTEMP, MMINTEMP. Variable mnemonics and descriptions are in Tables 2 and 3.

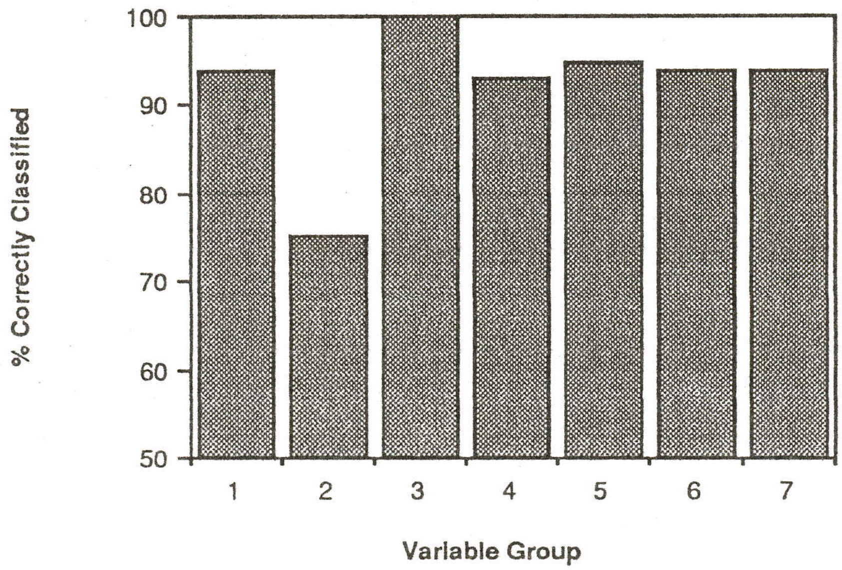
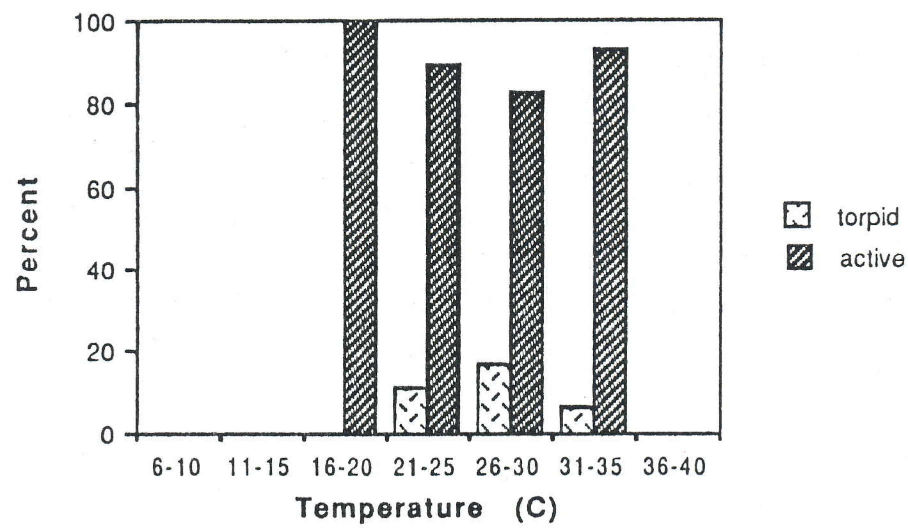
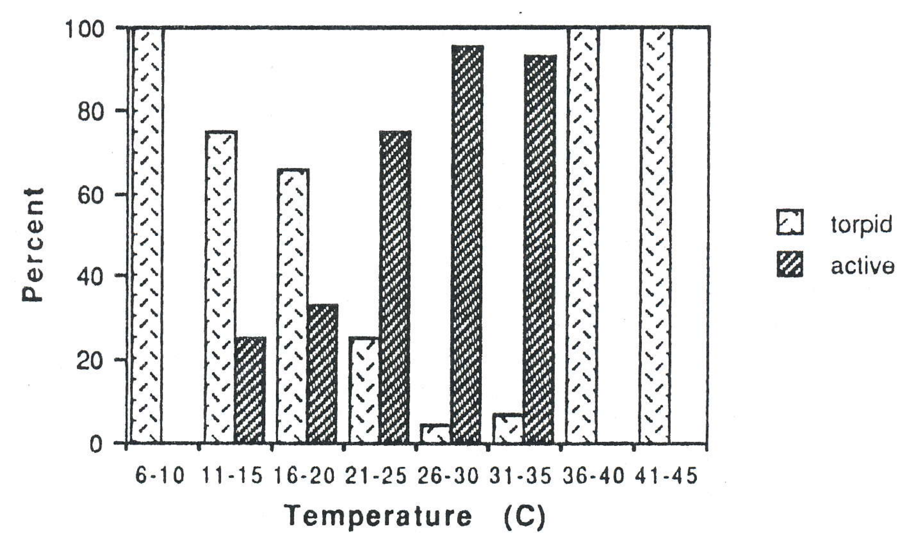

100
90
80
70
60
50
% Correctly Classified
1
2
3
4
5
6
7
Variable Group

Figure 20. Percent of observations when solitary bats (top) were active or torpid in relation to temperature (N = 77 temperature readings) and when bats in nursery colonies were active or torpid (N = 83 temperature readings). Data were obtained in Bladen, Chowan, Pender, and Sampson counties in summer 1986.

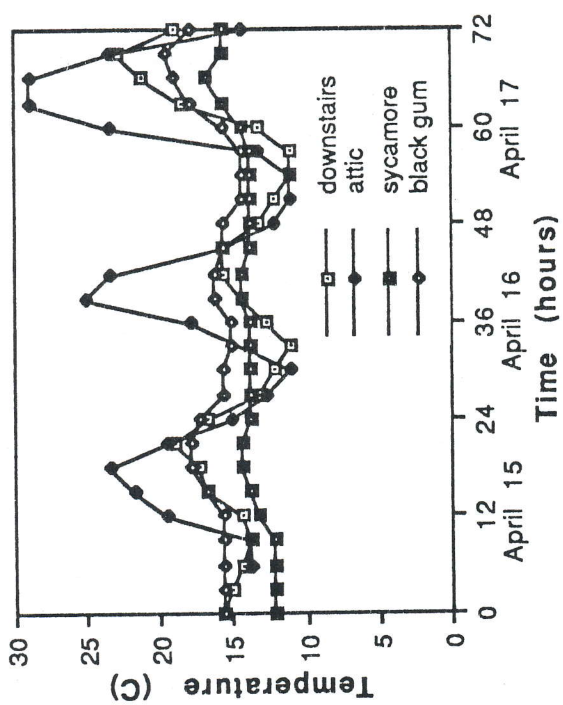


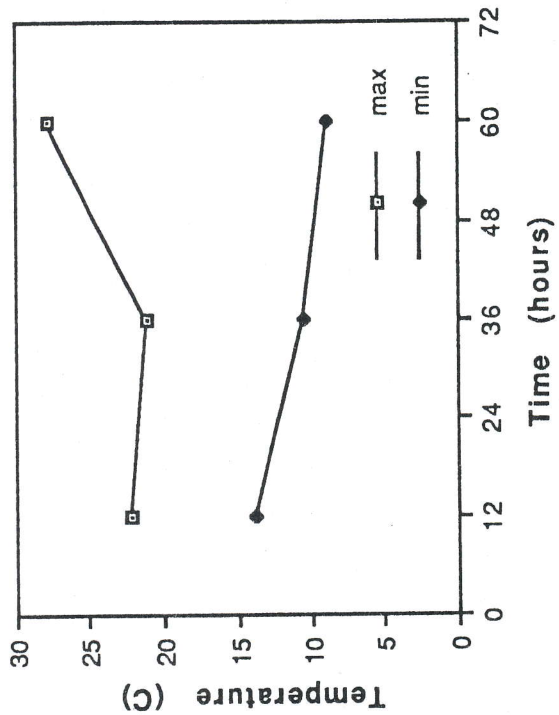
100
80
60
40
20
0
Percent
6-10 11-15 16-20 21-25 26-30 31-35 36-40
Temperature (C)
torpid
active



100
80
60
40
20
0
Percent
6-10 11-15 16-20 21-25 26-30 31-35 36-40 41-45
Temperature (C)
torpid
active

Figure 21. Comparison of the daily temperature profiles of tree cavities with those of two roost areas in CH03 (attic and downstairs). The graph on the right shows the ambient maximum and minimum temperatures recorded for the National Weather Service by the Edenton station in Chowan County, North Carolina. The black gum was used as a night roost by *Plecotus rafinesquii* in summer 1988. A solitary *P. rafinesquii* roosted in the hollow sycamore in the summers of 1989 and 1990. Site CH03 was used from 1986 to 1990 as a nursery roost.


Temperature (C)
30
25
20
15
10
5
0
0
12
April 15
24
36
April 16
48
60
April 17
72
Time (hours)
downstairs
attic
sycamore
black gum


Temperature (C)
30
25
20
15
10
5
0
0
12
24
36
48
60
72
Time (hours)
max
min