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Roosting Ecology of Rafinesque's Big-Eared Bat, *Corynorhinus rafinesquii*, in Southeastern Mississippi

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The University of Southern Mississippi

ROOSTING ECOLOGY OF RAFINESQUE'S BIG-EARED BAT, *CORYNORHINUS RAFINESQUII*, IN SOUTHEASTERN MISSISSIPPI

by

Austin Webb Trousdale, III

A Dissertation
Submitted to the Graduate Studies Office
of The University of Southern Mississippi
in Partial Fulfillment of the Requirements
for the Degree of Doctor of Philosophy

Approved:

[redacted]

May 2008

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ABSTRACT

ROOSTING ECOLOGY OF RAFINESQUE'S BIG-EARED BAT, *CORYNORHINUS RAFINESQUII*, IN SOUTHEASTERN MISSISSIPPI

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May 2008

Rafinesque's big-eared bat, *Corynorhinus rafinesquii*, is considered rare and/or declining throughout its range. Concrete bridges are potentially important roosts for *C. rafinesquii*, especially in the Gulf Coastal Plain where the species' natural roosts (caves and large hollow trees) are inherently scarce. Successful efforts to monitor and conserve this species must account for its movements among multiple roosts and determine the duration of its roost use (including bridges) at different temporal scales. Therefore, I investigated roosting ecology of *C. rafinesquii* from 2000-2005 within a mixed hardwood-pine (*Pinus* spp.) system in southeastern Mississippi. I conducted surveys of concrete bridges to determine phenological pattern of use and found that maternity colonies began to arrive at bridges as early as 9 March (in 2000), increased in size and abundance as spring progressed (with pups being born in mid-to late May), and persisted through August (with pups nursing as late as 25 July [2001]). Solitary *C. rafinesquii* roosted under bridges throughout the year, but general scarcity of bats found under bridges during cooler months implied use of alternate roosts. To locate such structures, I captured and radiotagged 25 *C. rafinesquii* at bridge roosts and subsequently attempted to find these individuals. Radiotagged bats used 14 hollow trees (*Nyssa* spp. and *Magnolia grandiflora*) and 11 human-made structures (e.g., bridges, abandoned houses) as roosts. Radiotagged bats switched roosts every 2.1 days, switched roosts 2.6 ± 2.0 (mean ± *SD*) times and used 2.5 ± 1.2 roosts per tracking period (9.1 ± 2.6 days). Bats showed low daily fidelity to tree roosts, which were relatively common in some areas (but not exceptionally stable), and maintained higher fidelity to human-made roosts that were rare but of higher structural integrity. To examine roost fidelity of *C. rafinesquii* over longer time periods, I relied on recoveries of banded bats at bridges. Of 144 bats captured and banded, I recaptured 55; age-class (juvenile vs. adult) affected probability of recapture. In most instances (91 percent) recaptured bats were found at their original roost. Distance that a marked bat had moved from its initial roost (0-4 km) did not correlate with the length of time from its banding to its first (or only) recapture, indicating that *C. rafinesquii* maintained long-term fidelity to bridges, up to 4 years by some individuals. Results of this investigation corroborate that *C. rafinesquii* possesses low vagility and likely perceives its environment at a fine-grain scale. Thus, loss of its habitat on even a local level could have deleterious effects.

DEDICATION

To my family, for their love and patience through the years

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CHAPTER I

SEASONAL USE OF BRIDGES AS ROOSTS

Introduction

Rafinesque's big-eared bat, *Corynorhinus rafinesquii* (Lesson), is an insectivorous bat native to the southeastern and south-central United States (Barbour and Davis 1969). Apparent rarity of *C. rafinesquii* led to its listing under the Endangered Species Act as a Category 2 species, meaning that it was possibly threatened or endangered, though conclusive information was lacking, when the designation was recognized (Lance and Garrett 1997). At present, *C. rafinesquii* is a species of concern throughout its range (Harvey et al. 1999), and vulnerability of its roosts to disturbance is hypothesized to have contributed to its apparent decline (Whitaker and Hamilton 1998). *Corynorhinus rafinesquii* seeks open, relatively well-lit conditions for roosts (Barbour and Davis 1969), using the twilight section of caves (Hurst and Lacki 1999), abandoned buildings (Jones and Suttkus 1975, England et al. 1990), cisterns (Hoffmeister and Goodpaster 1963), and cavities of large trees (Clark 1990).

Lance and Garrett (1997) first reported that *C. rafinesquii* uses bridges as day-roosts and further documented that maternity or nursery colonies occupied the undersides of concrete bridges in Louisiana. Lance et al. (2001) found that percentage of mature deciduous forests surrounding a bridge was a significant factor in predicting occupancy by *C. rafinesquii*. Considering that the species of trees in which *C. rafinesquii* has been found to roost (e.g., *Nyssa* spp.; Clark 1990, Lance et al. 2001) are typical of such forest, *C. rafinesquii* may prefer bridges in close proximity to natural roosting sites. Use of bridges could also be a consequence of the species' tendency to switch roosts frequently

(Lance et al. 2001, Trousdale et al. in press) with bridges, abandoned buildings (England et al. 1990, Jones and Suttkus 1975) and hollow trees serving as alternate roosts (Lance et al. 2001). Concrete bridges may provide important shelter for *C. rafinesquii*, particularly in areas where natural roosts have been reduced or are scarce.

Bridges, particularly concrete ones, have long been recognized as providing shelter for a diversity of insectivorous bats. For example, Davis and Cockrum (1963) found that maternity colonies of *Eptesicus fuscus*, *Tadarida brasiliensis*, *Antrozous pallidus*, and *Myotis* spp. used bridges in Arizona. Adam and Hayes (2000) recorded *E. fuscus*, *Corynorhinus townsendii*, and several species of *Myotis* using bridges as night-roosts in Oregon. Potential advantages of bridges as roosts include their abundance in some areas, their relative permanence, and their capacity to house large numbers of individuals.

In a prior survey of the undersides of 99 bridges in central and southern Mississippi, Trousdale and Beckett (2002) located six bridges in DeSoto National Forest (NF) that were used as daytime roosts by *C. rafinesquii*. In 2001 many bridges in DeSoto NF were slated for replacement due to decay of their wooden pilings. The USDA Forest Service planned to retain the "cast-in-place" (Adam and Hayes 2000) style of construction used previously (D. Berens [Chickasawhay Ranger District, DeSoto NF, Laurel, MS], pers. comm.) to facilitate use of these structures as roosts by *C. rafinesquii* (Lance et al. 2001). However, data are lacking on duration and seasonal use of bridges by *C. rafinesquii*. Timing of events that relate to reproduction in this species (e.g., formation and duration of maternity colonies) should influence decisions regarding removal and subsequent replacement of concrete bridges. The objective of the present study was to describe the phenological progression of use of bridges by *C. rafinesquii*, "one of the least known of all bats in the eastern United States" (Harvey et al. 1999).

Materials and Methods

Study area

My study was primarily conducted within the Chickasawhay and DeSoto Ranger Districts of the DeSoto NF in southern Mississippi, USA (Fig. 1). These two districts were disjunct from one another with their approximate geographical centers 70 km apart and nearest boundaries are approximately 27 km apart. The Chickasawhay was the more northerly of the two districts and encompassed portions of Jones, Wayne, and Greene counties, while portions of the DeSoto were located in Forrest, Perry, Stone, Pearl River, Greene, George, Harrison, and Jackson counties. Much of this area historically supported longleaf pine (*Pinus palustris*) savanna maintained by periodic fires in uplands. Lowland and mesic sites supported a diverse forest community inhabited by a variety of oaks (*Quercus* spp.), beech (*Fagus grandifolia*), magnolias (*Magnolia* spp.), and loblolly pine (*Pinus taeda*) (Frost et al. 1986). Baldcypress (*Taxodium distichum*) and tupelos (*Nyssa* spp.) occurred along streams and associated swampy areas. Suppression of natural fire regimes, along with intense harvest of trees during the early 20th century, greatly altered structure and composition of forests in southern Mississippi. For example, most stands of longleaf pine were replaced by faster-growing loblolly pine and slash pine (*Pinus elliottii*) (Frost et al. 1986). Restoration of the original longleaf pine community is underway within some areas of the NF, with riparian areas dominated by native hardwoods.

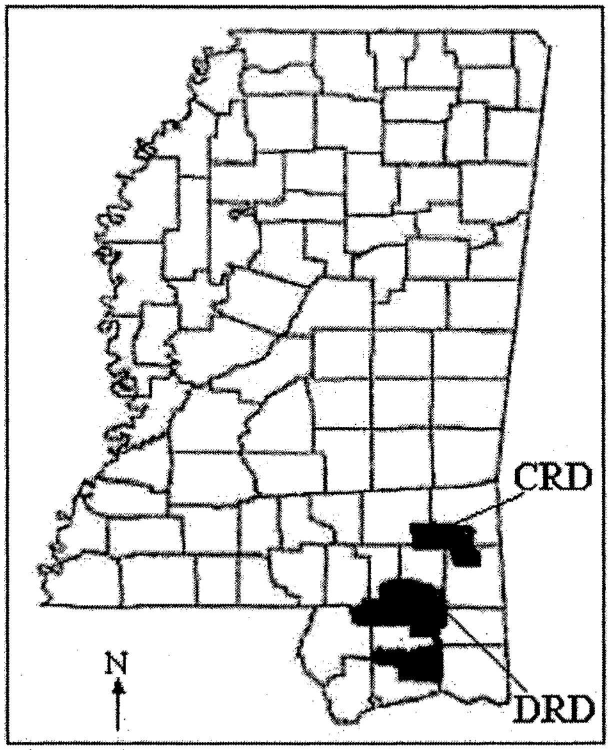


Figure 1. State of Mississippi with DeSoto National Forest in bold and the Chickasawhay Ranger District (CRD) and the DeSoto Ranger District (DRD) both indicated.

Roost monitoring

To locate bridge-roosting *C. rafinesquii*, I surveyed 90 bridges from March through June 2000. If I found at least one *C. rafinesquii* on our initial visit to a bridge, I subsequently visited that site once per two weeks through September 2000 and once per month from October 2000 through January 2001. I did not count presence of guano under a bridge as proof of its use by *C. rafinesquii* because I could not verify that the scat had been left by this species. I routinely checked 14 bridges in the Chickasawhay District and 14 bridges in the DeSoto District during the aforementioned interval. In February 2001 the USDA Forest Service identified 22 bridges (including most of the 14 that we were checking) to be replaced within the Chickasawhay District, eight of which had not previously been surveyed for bats. Consequently, I checked 22 bridges in the Chickasawhay District once per month during February-April, while continuing to check bridges in the DeSoto District. I conducted biweekly surveys of bridges in both districts from May 2001 through July 2001. After a seven-month break, I resumed bridge surveys in the Chickasawhay District from late March through September 2002. In 2002 I visited bridges biweekly during May through July, but conducted monthly surveys outside of this interval.

Surveys of bridges always occurred during daylight hours and consisted of one or more investigators visually scanning the underside of the bridge for bats. Upon finding *C. rafinesquii*, I counted them and noted whether pups were present (a maternity colony). To minimize disturbance to colonies I assessed development of pups by observing them (from a distance $\geq$ 3 m) with close-focus binoculars. I identified bats as juveniles or adults based on color of pelage, with juveniles being dark gray during the first 2-3 months of life (Jones 1977) and adults having a rich brown coat on their dorsal side (Jones and Suttkus 1975). I attempted to capture solitary *C. rafinesquii* throughout the survey but did not disturb colonies if there were females nursing young. To catch bats I used a "butterfly" net attached to an aluminum handle of adjustable length. I determined sex, age-class (juvenile or adult), mass (g), and length of forearm (mm) for captured individuals and placed an individually numbered, split-plastic ring (A.C. Hughes Ltd., Hampton Hill, Middlesex, UK) on each bat's right or left forearm (depending on the sex of the bat). These methods followed University of Southern Mississippi IACUC protocol # 204-004.

Results

Thirty-six bridges in DeSoto NF were used by *C. rafinesquii* at least once during the survey. Number of bats present under an occupied bridge ranged from 1 to 25. Combining both districts, mean number of individuals per occupied bridge was 4.6 (*SD* = 5.8) in 2000 and 3.9 (*SD* = 5.0) in 2001. This value was 3.0 (*SD* = 4.4) in the Chickasawhay District in 2002. Mean number of adult females per maternity colony over the duration of the study was 5.6 (*SD* = 3.1). I identified 20 bridges as maternity roosts.

Development of maternity colonies

I first observed a maternity colony on 9 March 2000 and found small numbers (1-5) of females at a few bridges during that month. Upon capturing a few individuals at several bridges, I palpated their noticeably swollen abdomens and determined them to be pregnant. Mean and maximum numbers of bats slowly increased through early May (Fig.'s 2-3). I first observed pups in mid-May. I saw a female nursing a naked pup on 12 May 2000 under a bridge in the Chickasawhay District (three adults without pups also were present in this colony). In the DeSoto District, I discovered pups at four sites on 18 May 2000; all of these pups (both naked individuals and those covered in hair) were nursing. In both districts, I found the largest colonies in June 2000 (Fig.'s 2-3). In the Chickasawhay District mean number of individuals per bridge occupied by *C. rafinesquii* peaked in July 2000 with 5.4 (*SD* = 5.7). In the DeSoto District the highest mean number of bats was 11.1 (*SD* = 8.9) per bridge in June 2000. By early June, pups had attained flight, but I continued to catch females with exposed nipples through 14 July.

Occupancy of bridges by bats peaked in late spring/early summer 2000 in both districts (Fig.'s 2-3). In the Chickasawhay District, *C. rafinesquii* used the highest proportion of bridges (59%; 10 of 17 checked) during June 2000. In the DeSoto District, bats were most frequently encountered in May 2000 (65%; 17 of 26). Percentage of bridges used in the Chickasawhay District declined sharply as summer progressed, stabilized in early fall, then declined to zero from November through January, before rising slowly toward a second (albeit much smaller) late-spring peak in 2001 (Fig. 2). A more gradual decline in use of bridges by *C. rafinesquii* occurred in the DeSoto District during summer and fall 2000 (Fig. 3).

In 2001 I did not observe maternity colonies until 20 April in the Chickasawhay District and 5 May in the DeSoto District. We saw the first pups of the year on 15 May and 17 May in the Chickasawhay and DeSoto Districts, respectively; the pups were naked in both cases. In 2001, the largest colonies in the Chickasawhay District were found in May, during which mean number of individuals per occupied bridge was 5.0 (*SD* = 6.7) and maximum number of individuals was 20. In the DeSoto District, the highest mean for 2001 was found in July (6.8; *SD* = 6.4). Although proportion of bridges used by bats fluctuated during the early months of 2001, 50% (13 of 26) of all bridges surveyed in the DeSoto District during July 2001 were used as roosts. In 2001, I last observed juvenile *C. rafinesquii* in the company of lactating adult females on 25 July.

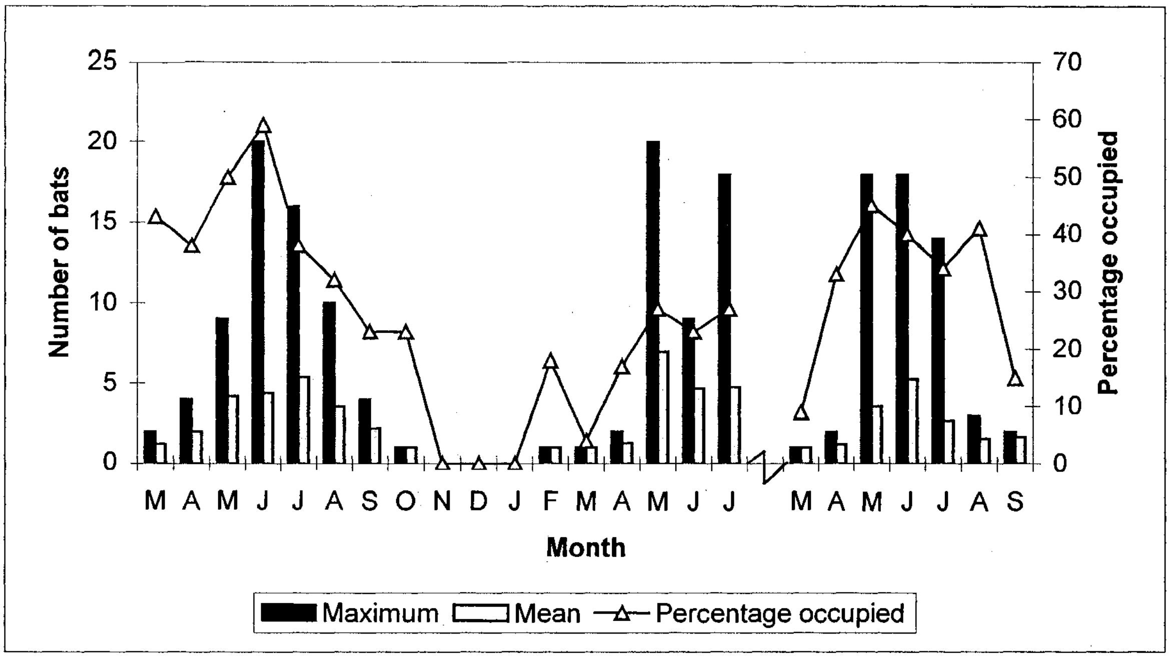


Figure 2. Relative abundance of *Corynorhinus rafinesquii* in the Chickasawhay District, DeSoto National Forest, based on maximum and mean number of bats roosting under occupied bridges and percentage of bridges surveyed that were used by bats. (Data are grouped by month.) Surveys conducted from March 2000 through July 2001 (no bats were found during November, December, or January) and March 2002 through September 2002.

In 2002, I found the first maternity colonies at two bridges on 15 May; visits to these sites over the next two weeks revealed that the pups were born between 23 and 27 May. The largest colonies were comprised of 18 individuals (adult females and pups) in both May and June. Bats were most commonly found under bridges in May, and highest mean number of bats per bridge (5.3; *SD* = 6.6) was found in June (Fig. 2). I captured lactating adult females as late as 16 July. The last example of maternal behavior that I observed consisted of an adult female roosting with a juvenile male on 17 August 2002.

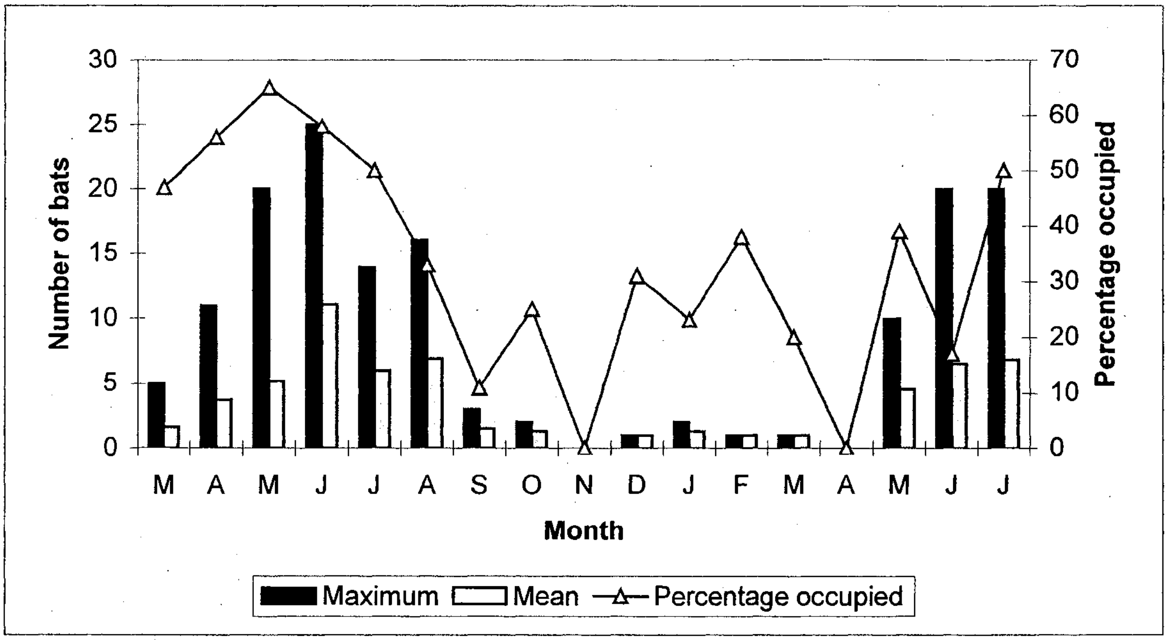


Figure 3. Relative abundance of *Corynorhinus rafinesquii* in the DeSoto District, DeSoto National Forest, based on maximum and mean number of bats roosting under occupied bridges and percentage of bridges surveyed that were used by bats. (Data grouped by month.) Surveys conducted from March 2000 through July 2001 (no bats were found during November 2000 and April 2001).

Occurrences of solitary roosting

Colonies were absent from bridges that I checked between 26 September 2000 and 8 April 2001, and from 29 March 2002 through 2 May 2002. However, solitary *C. rafinesquii* were present under bridges throughout most of the study period. We sometimes found solitary bats in torpor on days following nights where temperatures dropped to ≤ 16° C. This phenomenon was especially common in the DeSoto District, where solitary bats occupied approximately one-third of all bridges in December 2000 and nearly 40% of all bridges in February 2001 (Fig. 3).

Solitary *C. rafinesquii* were typically adult males. A male found under a bridge on 9 March 2000 had enlarged testes and epididymides descended fully into the uropatagium. Enlargement of testes coincides with periods of mating in *Corynorhinus* (Whitaker and Hamilton 1998), which, according to Barbour and Davis (1969), extend from fall through winter in *C. rafinesquii.* I did not capture any more males displaying this condition until mid-October 2000, but four of five males captured during that month had enlarged testes and epididymides. I located adult males roosting beside females only twice, on 28 August 2000 (one male and two females) and on 12 October 2000 (one male and one female). The few males that we found in colonies during the late spring and early to mid-summer were juveniles.

Discussion

Phenological development of maternity colonies was similar among the three years of observation. I found the first colonies of the year as early as mid-March and as late as mid-May. In southern Arkansas, maternity colonies formed during March inside abandoned buildings (England et al. 1990). I consistently noted a trend toward greater abundance of *C. rafinesquii* and increased use of bridges as spring progressed. In the present study, the timing of parturition was more precise than the onset of colony formation. I found naked (newborn) pups on 12 May and 18 May in 2000, on 15 May and 17 May in 2001, and on 27 May 2002. These data are consistent with dates of parturition reported for *C. rafinesquii* by Jones and Suttkus (1975) in southwestern Mississippi and in southeastern Louisiana, but are somewhat earlier than what Clark (1990) observed in the Coastal Plain of North Carolina (early to mid-June). In mid- to late summer, I noted a decline in colony size and concomitant decrease in proportion of bridges used in both districts in 2000 and in the Chickasawhay District in 2002 (I did not conduct surveys after July in 2001). Considering that these colonies consisted almost exclusively of adult females and their offspring, and that solitary individuals encountered during cooler months were mostly males, lack of females bats found under bridges outside of the maternity season was likely due to roost switching by females. Jones and Suttkus (1975) reported that male *C. rafinesquii* were more common at roosts from fall through winter and females were more common during spring and summer. Hurst and Lacki (1999) found that population size in *C. rafinesquii* over time was stable despite low juvenile mortality, suggesting that emigration (particularly by females) offset any expected gain from recruitment. Data from recaptures of *C. rafinesquii* that were banded at bridges (see Chapter 4) corroborate Jones and Suttkus' (1975) opinion that long-term residents of roost sites tend to be males.

Relative scarcity of *C. rafinesquii* under bridges in fall and winter suggested that most of the population used other types of roosts during these seasons. England et al. (1990) reported a decline in abundance of *C. rafinesquii* roosting in abandoned houses during fall and a concomitant increase in bats found in cisterns. A colony numbering in excess of 100 individuals was observed at an abandoned school in southern Arkansas during autumn (D. Saugey [Jessieville-Winona-Fourche Ranger District, Ouachita NF, Jessieville, AR] and R. Sikes [University of Arkansas at Little Rock], pers. comm.). Although I located several abandoned buildings within the study area, use of these structures by colonies of *C. rafinesquii* was limited. On 24 September 2001 I located a colony roosting inside a dilapidated house; in subsequent visits to this site over the next two weeks, I found that the colony was comprised of both sexes and fluctuated in number between two and approximately 25 individuals. Regardless, no colony used this building after fall 2001. Hurst and Lacki (1999) documented *C. rafinesquii* using a cave in

Kentucky as a winter hibernaculum, but Best et al. (1992) recorded only a single specimen of *C. rafinesquii* during their surveys of caves in the Coastal Plain of Alabama. Although no caves are known from DeSoto NF, several limestone caves are found along the Vicksburg Group in Wayne County (Cliburn and Middleton 1983), located approximately 25 km from the northernmost boundary of the Chickasawhay District. However, no *C. rafinesquii* were found in any of these caves during warm or cool months (A. Trousdale and D. Beckett, unpublished observations).

Sizes of colonies of *C. rafinesquii* that I observed were generally smaller than those reported by other investigators. I never found more than 25 bats in a single colony, but Lance et al. (2001) observed a maximum of approximately 50 individuals under a single bridge. A maternity colony using a cave in Kentucky numbered over 100 individuals (Hurst and Lacki 1999), while Hoffmeister and Goodpaster (1963) recorded up to 64 bats from a cistern in Tennessee. Mean number of adult females per maternity colony in DeSoto NF (5.6; *SD* = 3.1) was considerably smaller than that reported by England et al. (1990) from abandoned houses (30; *SD* not reported). Difference in size of colonies among roosts may reflect intensity of intraspecific competition, with smaller colonies occurring where quality or availability of foraging habitat are low (Entwistle et al. 2000). Another factor influencing colony size in this study might have been the high density of potential roosts, which allowed bats to use multiple roosts over short-term periods instead of returning to the same site each day (see Chapters 2-3).

Finally, I concur with Jones and Suttkus (1975) and Belwood (1992) that *C. rafinesquii*'s tendency to roost at sites susceptible to human disturbance and their fidelity to these roosts could easily imperil populations. Managers and engineers should consider the “window” of time in which maternity colonies of *C. rafinesquii* depend on concrete bridges as nursery roosts, so that repairs or replacement of bridges not coincide with their presence. Based on these data, this time interval extends from March through August in southern Mississippi.

CHAPTER II

CHARACTERISTICS OF TREE ROOSTS

Introduction

Roosts are critically important to bats because of the amount of time spent within them and the roles that these shelters serve in metabolic regulation and social interaction (Altringham 1996). Forests offer a diversity of potential roosting sites to bats (Kunz and Lumsden 2003), but cavities in trees offer advantages of a relatively stable microclimate and protection from predators (Kunz 1982), as well as greater permanence than other organic structures such as foliage and loose bark (Lewis 1995). Even so, tree cavities, especially those found in snags, have a finite "lifespan" as optimal roosts (Vonhof and Barclay 1996). Although trees of variable species, size and age may contain defects that can be exploited as roosts by bats (see Barclay and Brigham 1996), some species are highly selective in their choice of cavities (Sedgeley and O'Donnell 1999a). Furthermore, the low fidelity that bats often display toward these sites (e.g., O'Donnell and Sedgeley 1999, Willis and Brigham 2004) suggests that cavity-roosting bats require patches of habitat containing a sufficient supply of potential roosts. Such stands of forest are characterized by mature and/or senescent timber (Sedgeley and O'Donnell 1999b). In the southeastern United States, native forests were extensively cleared during the past century or modified by silvicultural practices in recent decades (Allen et al. 1996). Increased knowledge of the status of roosting opportunities for forest-dwelling bats within this altered landscape will improve strategies to manage these species.

Rafinesque's big-eared bat, *Corynorhinus rafinesquii*, is a small (< 14 g), insectivorous bat native to the southeastern and south-central United States (Jones 1977).

Most ecological studies of *C. rafinesquii* have focused on populations that principally used caves (Hurst and Lacki 1999) or manmade structures (Hoffmeister and Goodpaster 1963; Jones and Suttkus 1975) as roosts. A scarcity of information exists regarding use of tree roosts by *C. rafinesquii*, which Harvey et al. (1999) described as "one of the least known of all bats in the United States." Day roosts of this species have been found in American beech (*Fagus grandifolia*) (Hurst and Lacki 1999, Mirowsky et al. 2004) and sycamore (*Platanus occidentalis*) (Clark 1990), but *C. rafinesquii* is best known for roosting within "tupelo gum" trees, *Nyssa* spp. (Clark 2000). In northeastern Louisiana Gooding and Langford (2004) located roosts in a bottomland hardwood ecosystem primarily by searching cavities of *Nyssa aquatica*. Lance et al. (2001), working in south-central Louisiana, reported that *C. rafinesquii* captured under concrete bridges (and subsequently radiotagged) also roosted within hollow *Nyssa sylvatica*. Prior to the present study, no natural roosts of *C. rafinesquii* were documented from southeastern Mississippi. I attempted to document the use of tree roosts by *C. rafinesquii* in an upland pine/bottomland hardwood forest by locating and identifying tree roosts of *C. rafinesquii* in southeastern Mississippi and describing and measuring characteristics of tree roosts and their surrounding habitat. I also provide information regarding both roost fidelity and the distances among roosts used by individual bats.

Materials and Methods

Study area

I conducted this study primarily within the Chickasawhay Ranger District of the DeSoto National Forest (NF) in southeastern Mississippi (31° 30'N, 88° 53'W). The Chickasawhay District encompasses portions of Jones, Wayne and Greene counties. I also worked within the DeSoto District (in southern Perry County) of DeSoto NF; this Perry County site was located approximately 50 km south of the Chickasawhay District. The lands now covered by DeSoto NF historically supported longleaf pine (*Pinus palustris*) savanna in uplands (that were sustained by periodic fires) and a mixed hardwood and pine forest (e.g., *Pinus taeda*, *Pinus glabra*) in lowlands. Due to intense harvesting of trees during the early 20th century, their replacement by faster-growing loblolly pine (*P. taeda*), and suppression of natural fires by private landowners, structure and composition of these forests have been greatly altered (Frost et al. 1986). At present most of the NF is composed of restored *P. palustris* woodland with occasional hardwoods such as dogwood (*Cornus florida*) and white oak (*Quercus alba*) and former plantations of *P. taeda* or slash pine (*Pinus elliottii*). Forest in mesic sites currently approximates original conditions of diversity, if not size and age. A variety of oaks (*Quercus* spp.), *F. grandifolia*, magnolias (*Magnolia* spp.), *Nyssa* spp., and baldcypress (*Taxodium distichum*) inhabit riparian areas.

Capture, radiotracking, and location of roosting bats

I captured and radiotracked bats from August 2001 until August 2004 during late spring to early fall. Due to low success in trapping *C. rafinesquii* using mist nets (Lance and Garrett 1997, Trousdale and Beckett 2002), I used daytime surveys of concrete bridges to locate bats (see Chapter 1 for description of surveys). I captured bats that roosted underneath bridges using a handheld, "butterfly" style net. To minimize disturbance to colonies, I attempted to time captures of bats so as not to coincide with parturition nor the period (ca. 3 weeks) afterward until pups were capable of flight (Chapter 1). I determined sex and age-class (juvenile or adult, based on ossification of epiphyseal joints of the phalanges; Anthony 1988) and mass (g) for all captured bats. To identify individuals, I placed a distinctly numbered or colored band (A.C. Hughes Ltd., Hampton Hill, Middlesex, UK) on the right forearm for male bats, and left forearm for females. After clipping a small amount of hair from between the scapulae, I attached a radiotransmitter (Model LB-2, Holohil Inc., Carp, Canada) to the dorsum of each bat by using surgical adhesive (Skin-Bond, Smith and Nephew Inc., Largo, FL). Because weight of each transmitter was ca. 0.46 g and the mean weight of captured bats was 8.9 g (*SD* = 1.1, min. = 7.5, max. = 11.5), the bats' ability to fly should not have been impaired by wearing the tags (Aldridge and Brigham 1988). After holding bats for ca. 15 min to allow the glue to dry, I released each one underneath the bridge at which it was captured. These methods followed USM IACUC protocol # 204-004.

I began radiotracking bats to day roosts on the day following their capture. I returned to the capture site and listened for the transmitter's signal using a radio receiver (Model TRX1000S, Wildlife Materials, Inc., Carbondale, IL) with a 3-element yagi antenna (Advanced Telemetry Systems, Inc., Isanti, MI) attached. If I detected the signal, I determined its direction and used homing to locate the roost. If I were unable to detect a signal, I drove to the nearest bridge and continued searching. Due to logistical considerations, I did not conduct emergence or "flyout" counts to verify most roosts. Reliability of homing was corroborated by my observation that the suspected roost was usually the only tree in the immediate vicinity to possess an obvious cavity. I tracked bats in this manner daily until the transmitter's battery failed (after ca. two weeks) or the transmitter fell off the bat and was recovered. I defined reuse of tree roosts as both revisits to a tree by an individual bat and use of an individual tree by ≥ 2 bats.

Upon finding a tree roost, I identified its species and measured its diameter (cm) at breast height (DBH) using a DBH tape. I visually assessed condition of the tree and assigned it a value (1-8) on a scale of increasing decay with 1 representing a live tree with no visible defects and 8 representing a hollow, dead tree no longer standing. I classified cavity type according to Sedgeley and O'Donnell (1999a) and measured entrance aspect of its opening using a compass. I estimated both height (m) of the tree and height (m) of the center of the cavity's opening using a clinometer. Using a spherical densiometer, I measured canopy closure for the tree at the base of its trunk and within an 18-m radius (ca. 0.1 ha), circular plot centered on the tree. I obtained latitude and longitude of the tree using a global positioning system (GPS) handheld receiver (GPS III Plus, Garmin International Inc., Olathe, KS). I also used the GPS unit to obtain coordinates of the bridge at which each bat was captured, to measure the distance (km) from each tree to the nearest stream and to calculate distances (km) between roosts.

To categorize the habitat in which tree roosts were located, their GPS coordinates were uploaded to a vegetation map (provided by the USDA Forest Service) using a geographic information system (ArcView Version 3.2, Environmental Systems Research Institute, Redlands, California). Forest types were broadly categorized on the basis of percentage dominant and co-dominant basal areas being softwoods, i.e., *Pinus* spp (≥ 70%), hardwoods (≥ 70%), pine-hardwood (51-69% *Pinus* spp.) or hardwood-pine (51-69% hardwoods). Stands within these types were classified according to dominant tree species. Pine stands were identified as loblolly pine, longleaf pine, and slash pine. Pine-hardwood stands present on the study area were identified as loblolly-pine hardwood and shortleaf pine-oak. Hardwood-pine stands included bottomland hardwood-yellow pine and southern red oak-yellow pine. Hardwood stands were identified as laurel oak-willow oak, sweet bay-swamp tupelo-red maple, and white oak-red oak.

Results

I captured and radiotagged 25 *C. rafinesquii* (15 females, 10 males) at seven bridges located in the Chickasawhay District and at one bridge located in the DeSoto District. I captured and radiotracked eight individuals during August-October 2001, eight individuals during May-November 2002, six individuals during July-August 2003, and four individuals during July-August 2004 (one of these individuals [an adult female] had been previously radiotagged and tracked]). Up to four bats were monitored at any time. Instead of randomly selecting individuals to radiotag, I preferentially tagged some bats and passed over others to ensure that both sexes were well represented and that individuals from different bridges were monitored. I successfully located bats on 144 out of 235 total days (d) of tracking (overall detection rate = 0.61). On average, bats were tracked 9.0 d per individual (*SD* = 2.5). Mean number of locations obtained per bat was 5.5 (*SD* = 3.7). Twelve bats (9 females, 3 males) led me to at least one tree roost during the period that they were tracked via radiotelemetry. Earliest use (within a year) of a tree as a day roost by a radiotagged bat occurred on 28 May (2002); latest use of a tree roost was on 20 November (2002). I captured, radiotagged, and tracked the same individual bat (an adult female) on two separate occasions, in early July 2003 and late July through early August 2004.

I radiotracked bats to 14 tree roosts (Table 1) and 11 human-made structures (8 bridges, two abandoned houses, and an empty oil storage tank). All tree roosts were located in the Chickasawhay District and were either *Nyssa* spp. (*n* = 10) or *Magnolia* spp. ($n = 4$). Three *Nyssa* spp. trees were snags, and the remaining seven were live *Nyssa aquatica.* Likewise, one *Magnolia* sp. was a snag, and the remaining three were live *Magnolia grandiflora.* of which were *Nyssa aquatica.* The remaining three *Nyssa* sp. were snags. Three tree roosts were live *Magnolia grandiflora*; one *Magnolia* sp. was a snag. Decay class ranged from 3 (a live tree possessing a large opening to cavity) to 7 (a hollow snag in an advanced stage of decay); the mode was 3. All trees were hollow, and all but one tree contained a single entrance hole; this tree had two openings and an apparently continuous cavity between them. Twelve trees possessed an opening located along the trunk but not at the base. In most cases, the opening had been apparently formed by bifurcation of the trunk followed by loss of one of the main branches. One tree possessed one such opening along with a basal entrance; another tree possessed only a basal opening. Mean height of the opening to the cavity was 5.2 m ($SD = 2.8$). Mean DBH of tree roosts was 79.4 cm ($SD = 18.9$) and mean height of the tree was 18.5 m ($SD = 10.7$). Mean canopy closure for plots centered on tree roosts was 91 percent ($SD = 5.8$) and mean canopy closure at the tree was 92 percent ($SD = 2.5$).

Table 1

Measurements of characteristics of tree roosts used by Corynorhinus rafinesquii *in the Chickasawhay District of DeSoto National Forest from August 2001- August 2004.*

Tree roost characteristic	Mean ± *SD*	Minimum	Maximum
Diameter at breast height (cm)	79.4 ± 18.9	44.4	111
Height of tree (m)	18.5 ± 10.7	4.6	44
Height of opening to cavity (m)	5.2 ± 2.8	0.7[a]	11
Percent canopy closure at tree	92.0 ± 2.5	88	96
Percent canopy closure in 0.1-ha plot	91.0 ± 5.8	78	99
Distance to nearest bridge at which bat was captured (m)	462.5 ± 328.8	91	940
Distance to nearest stream (m)	28.4 ± 41.1	0.1	140

[a] Measurement taken from midpoint of basal opening

Tree roosts were located in stands classified as bottomland hardwood-yellow pine ($n = 10$ trees), loblolly pine ($n = 3$), or laurel oak-willow oak ($n = 1$). Mean distance from a roost to the nearest stream was 28.4 m (*SD* = 41.1). Roosts in *Nyssa* sp. (n = 11) were typically located beside permanent sources of water (mean distance to stream = 25.1 m; *SD* = 43.6). Four such trees were located within stream channels, two tree roosts were located atop the bank of the nearest stream, and five trees were located beside depressions within the floodplain where water seasonally pooled. *Magnolia* trees ($n = 3$)

were located within relatively dry areas (mean distance to stream = 36.7 m; *SD* = 38.5). Mean distance between the bridge at which bats were captured and all of their determined tree roosts was 462.5 m (*SD* = 328.8). Mean horizontal distance between sequential tree roosts used by individual bats was 356.7 m (*SD* = 238.5); mean distance between sequential roosts of all types was 572.8 m (*SD* = 640.3).

Corynorhinus rafinesquii captured from certain bridges were loyal to habitat patches containing multiple roosts. Six trees were used by multiple individuals; five of these roosts were occupied simultaneously by ≥ 2 radiotagged *C. rafinesquii* (Table 2a). Bats that I knew had roosted together under bridges sometimes reunited within cavities of trees. During July 2003, two lactating females and one juvenile female (bats #9, #10 and #11[03], see Table 2) that had been captured together at a bridge subsequently all shared the same tree roost on four of 11 d that they were tracked. One of these adults and the juvenile also reunited in two additional trees. These two bats roosted together on nine of 11 d monitored. In summer 2004 the adult bat of the pair (bat #11[04]) reused a tree in which it had roosted during the previous year along with a tree roost that had not been previously identified. Two live *N. aquatica* trees were used (by different bats) for three consecutive years, one during 2001-2003 and another from 2002-2004.

Within their radiotracking sessions, radiotagged bats typically showed low daily fidelity to any particular tree roost (Table 2b). In areas where tree roosts could be located by homing, bats detected for ≥ 5 d generally apportioned their stays among multiple trees, or trees and 1-2 bridges. (Bat #4 used one bridge and [at minimum] one tree.) Seven individuals spent consecutive d (maximum = 5) at the same tree roost. Maximum number of determined tree roosts used by a radiotagged bat was four, by an adult female.

Table 2a

Locations of Corynorhinus rafinesquii *monitored via radiotelemetry in DeSoto National Forest from August 2001-August 2004. Age class of bats denoted by "a" (adult) or "j" (juvenile) and sex denoted by "f" (female) or "m" (male). Day (d) of a bat's capture at a bridge and attachment of its transmitter is designated as 0. Abbreviations of bridges are: ETC = East Tiger Creek, PWC = Piney Woods Creek, GC = Gunstock Creek, TC = Tiger Creek, ThC = Thompson Creek. Types of tree roosts used are Nyaq =* Nyssa aquatica, *Nysg =* Nyssa *snag, Magr =* Magnolia grandiflora, *Masg =* Magnolia *snag. An unknown location is denoted by "?," n/a indicates a day that bats were not tracked and (...) denotes that a bat was not located during the remainder of the tracking period. For bat #11, data from tracking period in 2003 is indicated by 03 and from 2004 by 04.*

	d tracked						
Bat #	0	1	2	3	4	5	6
1 (af)	ETC	Nyaq #1	Nyaq #1	?	…		
2 (af)	PC	n/a	Magr #1	?	…		
3 (af)	GC	?	Magr #1	GC	Magr #1	?	…
4 (am)	GC	GC	?	GC	Magr #1	GC	Magr #1
5 (af)	GC	Nyaq #6	Nyaq #6	Nyaq #6	GC	GC	n/a
6 (af)	GC	Nyaq #2	Nyaq #2	?	…		
7 (af)	TC	Nysg #1	?	…			
8 (am)	TC	?	?	?	?	?	?
9 (af)	TC	?	Nyaq #3	Nyaq #3	ETC	ETC	n/a
10 (jf)	TC	ETC	Nyaq #3	Nyaq #3	Magr #3	Masg #1	n/a
11 (af) 03	TC	ETC	Nyaq #3	Nyaq #3	Magr #3	Masg #1	n/a
11 (af) 04	TC	Nyaq #7	Nyaq #7	Nyaq #3	Nyaq #3	Nyaq #3	n/a
12 (jm)	ThC	Nyaq #4	?	?	ThC	n/a	n/a

Table 2a continued

	d tracked					
Bat #	7	8	9	10	11	12
1 (af)						
2 (af)						
3 (af)						
4 (am)	GC	GC	?	n/a	?	GC
5 (af)	GC	GC	GC	Nyaq #2	?	n/a
6 (af)						
7 (af)						
8 (am)	Nysg #2	Nyaq #3	n/a	n/a	n/a	?
9 (af)	Nysg #3	Nyaq #1	Nyaq #3	Nyaq #3	Tag	
10 (jf)	?	Nyaq #3	Nyaq #3	Nyaq #3	Nyaq #3	Nyaq #3
11 (af) 03	Nyaq #1	Nyaq #1	Nyaq #3	Nyaq #3	Nyaq #3	Nyaq #3
11 (af) 04	Nyaq #3	Nyaq #3	Nyaq #3	Nyaq #3	Nyaq #3	n/a
12 (jm)	Nyaq #5	?	…			

Table 2b

Summary of Table 2a, use of tree roosts by Corynorhinus rafinesquii *as determined by radiotelemetry in DeSoto National Forest from August 2001- August 2004. "Total # d located" refers to the number of days that a bat was detected at a tree or bridge roost subsequent to its capture and radiotagging. For bat #11, data from tracking period in 2003 is indicated by (03) and from 2004 by (04).*

Bat #	# trees confirmed used	Total # d detected at trees	Total # d located	# d used a single tree
1	1	2	2	2
2	1	1	1	1
3	1	2	3	2
4	1	2	8	2
5	2	4	9	3, 1
6	1	2	2	2
7	1	1	1	1
8	2	1	2	1, 1
9	3	6	9	4, 1, 1
10	3	9	10	7, 1, 1
11 (03)	4	10	11	6, 2, 1, 1
11 (04)	2	10	10	8, 2
12	2	2	3	1, 1

Discussion

This study is the first to document natural roosts of *C. rafinesquii* in the upland pine/bottomland hardwood forest community that characterizes much of southeastern Mississippi. *Corynorhinus rafinesquii* roosted primarily inside live *Nyssa* in the Chickasawhay District of DeSoto NF, as has been reported in Louisiana (Lance et al. 2001; Gooding and Langford 2004), North and South Carolina (Clark 2003) and Texas (Mirowsky et al. 2004). In the absence of caves, *C. rafinesquii* is noted for roosting in spacious, relatively well-lit structures (Lowery 1974); close association of this species with *Nyssa* in the Gulf Coastal Plain may be due to the apparent tendency of these trees to develop large cavities. I also located roosts in live *M. grandiflora* and in snags of this genus and of *Nyssa*. This investigation is also the first to report the use of *M. grandiflora* as a day-roost by *C. rafinesquii*; in my study, this tree species occurred within drier portions of bottomland hardwood forest. Tree roosts of *C. rafinesquii*, particularly in *Nyssa*, have typically been reported to contain extensive basal hollows (e.g., Clark 2003, Gooding and Langford 2004, Mirowsky et al. 2004). However, the *C. rafinesquii* that I monitored roosted within trees that contained mostly "trunk hollows" (Sedgeley and O'Donnell 1999a) rather than basal openings. Although these roosts were typically located within dense forest, their accessibility to bats might have been enhanced by their proximity to stream corridors, which opened the canopy somewhat.

Corynorhinus rafinesquii showed fidelity to a particular group of tree roosts (more so than to any individual tree) and did so within and between years. This tendency is well documented in *Eptesicus fuscus*, another cavity-roosting species (Kalcounis and Brigham 1998, Willis et al. 2003). Fidelity to well-defined areas of forest containing day-roosts has also been reported for bats that shelter within crevices and under bark (e.g., *Myotis sodalis*; Kurta et al. 2002) and for some foliage-roosting species (e.g., *Pipistrellus subflavus*; Veilleux and Veilleux 2004). Lewis (1995) concluded that bats that roosted within tree cavities reused larger trees more often than smaller ones. In this study, trees that were used by multiple individuals (either concurrently or among discrete tracking sessions) were among the largest roost trees that we found; five of these trees possessed a DBH ≥ 80 cm. Distances among tree roosts that *C. rafinesquii* sequentially used were relatively low, consistent with saltatory movements between day-roosts reported for many other cavity-roosting species (Kunz and Lumsden 2003). On several occasions, groups of bats that had been captured together at bridges subsequently roosted together within tree roosts. Lance et al. (2001) also noted this phenomenon in *C. rafinesquii* in Louisiana, albeit rarely. Further study to determine whether populations of tree-roosting *C. rafinesquii* maintain such cohesion within colonies over longer periods of time (as does *E. fuscus*; Willis and Brigham 2004) is warranted.

Considering the size of my study area, tree roosts of *C. rafinesquii* (as determined via radiotelemetry) were not widespread in DeSoto NF. Only two of six creek drainages (five located in the Chickasawhay District, one located in the DeSoto District) from which I radiotagged bats contained ≥ 3 tree roosts. The extent to which *C. rafinesquii* reused tree roosts further suggested their novelty within the landscape. Availability of roosts influences their reuse by bats in that fidelity is generally low where roosts are common and high where roosts are rare (Lewis 1995). In a landscape where roosts were abundant, < 20% of tree cavities were used more than once by radiotagged *Chalinolobus tuberculatus* (O'Donnell and Sedgeley 1999). Stochastic events reduced the pool of available tree roosts in my study area. Two trees used in July 2003 had fallen or been snapped by wind by the following summer. Measurement of the distribution and abundance of large, cavity-bearing trees in landscapes, recently undertaken in other areas of the Gulf Coastal Plain (D. Richardson [U.S. Fish and Wildlife Service, Noxubee National Wildlife Refuge, MS], pers. comm.), will help ascertain the extent to which this habitat limits *C. rafinesquii* and other cavity-roosting bats. Concrete bridges of appropriate configuration (see Lance et al. 2001) can provide important seasonal roosts for *C. rafinesquii* in this region (Trousdale and Beckett 2004). However, forest managers should also attempt to conserve natural roosts of this declining bat; e.g., retaining and encouraging recruitment of bottomland hardwood timber (especially *Nyssa* spp.) via streamside management zones.

CHAPTER III

SHORT-TERM ROOST FIDELITY

Introduction

Frequent movement among diurnal shelters is known for a variety of mammalian species, e.g., red foxes (*Vulpes vulpes*—Marks and Bloomfield 2006), spotted-tailed quolls (*Dasyurus maculatus*—Glen and Dickman 2006), striped and western spotted skunks (*Mephitis mephitis* and *Spilogale gracilis*—Doty and Dowler 2006) and many bats (Lewis 1995). Bats spend a considerable amount of time within their shelters or roosts, and the roost is the primary site at which some important behaviors occur (Altringham 1996). Therefore, increased knowledge of bats' patterns of temporal roost use should enhance conservation of their populations. Roosting ecology of bats is influenced by characteristics inherent to the structure used (e.g., availability, physical structure and integrity, proximity to other resources), physiological needs of the individual bat and sometimes sociality (Kunz and Lumsden 2003). When phylogeny is controlled for, roost fidelity of bats is generally positively correlated with permanence of the structure and negatively correlated with abundance of the type of structure used (Lewis 1995). Consequently, bats in eastern North America that shelter within crevices and cavities of trees would be expected to switch roosts more frequently than bats inhabiting caves. Bats that use tree cavities, in turn, are typically less labile in their movements among roosts than are foliage-roosting species (Kunz and Lumsden 2003). Crevice- and cavity-roosting bats often show loyalty to patches of habitat where dead or senescent trees are concentrated, especially where such structures are located ≤ 1 km apart (e.g., Kurta et al. 2002, Sasse and Pekins 1996, Vonhof and Barclay 1996, Weller and Zabel 2001). Fitness benefits to bats of using different roosts should exceed fitness costs of moving among them (Lewis 1995). Short-term benefits of switching roosts could include avoiding parasites and predators (Lewis 1995), increasing proximity to feeding sites (Rydell 1989) and finding a more favorable roost microclimate (Cryan et al. 2001). Long-term advantages may include increased familiarity with locations of roosts (Kurta et al. 2002) and enhanced opportunities for social interactions (O'Donnell 2000, Willis and Brigham 2004).

Roost selection and fidelity of forest-dwelling bats are relevant to their conservation because conditions at the roost affect survival and reproductive success (Kunz and Lumsden 2003). Unfortunately, land-use practices that prohibit persistence and/or development of older stands of forest may remove snags and other high quality roosting sites (Campbell et al. 1996, Sedgeley and O'Donnell 1999b). Under natural conditions, roosts in tree cavities can already be a limiting resource for populations because their availability to wildlife varies over time and depends on a continuing supply of suitable trees (Bonar 2000). Colonies of bats are more likely to be social units than simple aggregations of conspecifics that co-occupy a roost at a given time (Fenton 2003), and one cavity within a particular tree might not be sufficiently large to accommodate all members (Willis et al. 2006). Given these factors, the life histories and social behavior of cavity-roosting bats might require their frequent movement among roosts (O'Donnell 2000). For example, maternity colonies of *Eptesicus fuscus* probably require multiple tree roosts due to individuals' shifting requirements for improved thermoregulation (Willis and Brigham 2004).

Rafinesque's big-eared bat, *Corynorhinus rafinesquii*, is native to the south central and southeastern United States and roosts in human-made structures, caves, and trees (Jones 1977). *Corynorhinus rafinesquii* is a species of concern over most of its range (Harvey et al. 1999). Its rarity in the Gulf Coastal Plain (where caves are scarce) is due in part to the decline of bottomland hardwood forest, its historic roosting habitat in this region (Clark 2003). After Lance and Garrett (1997) documented *C. rafinesquii* roosting under concrete bridges, investigators began using surveys of bridges to refine its distribution and population status in the southeastern United States. *Corynorhinus rafinesquii* are sometimes loyal to particular bridges in the Gulf Coastal Plain over a period of months and even years (Ferrara and Leberg 2005a; see also Chapter 4). However, long-term fidelity by bats to specific roosts does not necessarily reflect a similar pattern of behavior during shorter time intervals (Sherwin et al. 2005). Furthermore, populations of *C. rafinesquii* that occur within remnant or altered habitat and depend on artificial structures may demonstrate considerable differences in their roosting ecology from populations living under more natural conditions (Clark 2003; Menzel et al. 2001). Efforts to assess populations of bats that show plasticity in type of roosts used are hampered without basic knowledge of their patterns of roost switching (Bogan et al. 2003).

Roost fidelity may differ among members of a population based on their reproductive condition (Vonhof and Barclay 1996); thus, I tested the null hypothesis that a difference in roost fidelity existed between sexes or age-classes. Because my study area was an upland pine, mixed hardwood-pine system that offered a variety of potential roosts (natural and human-made), I also tested the null hypothesis that no difference existed by habitat (location of capture). I thereby tested Lewis' (1995) prediction that bats that roosted primarily within artificial structures would exhibit higher roost fidelity than individuals that roosted primarily in tree cavities. Using radiotelemetry, I identified roosts of *C. rafinesquii* and quantified individual roost switching behavior using both traditional metrics (e.g., mean number of roosts per bat, number of times that an individual switched roosts) and an index of roost fidelity that I calculated and compared among tagged bats.

Materials and Methods

Study area

I conducted this study primarily within the Chickasawhay Ranger District of the DeSoto National Forest (NF) in southern Mississippi (31°30′N, 88°53′W). The Chickasawhay District encompasses portions of Jones, Wayne and Greene counties. I also worked at a site within the DeSoto Ranger District (in southern Perry County) of DeSoto NF located approximately 50 km south of the Chickasawhay District. The region historically supported longleaf pine (*Pinus palustris*) savanna in upland areas and mixed hardwood and pine (e.g., *Pinus taeda*, *Pinus glabra*) forest in lowlands. The structure and composition of this ecosystem have been substantially altered by intense tree harvesting (especially during the early 20th century), replacement of native forest by monocultures of loblolly pine (*P. taeda*), and suppression of natural fires (Frost et al. 1986). At present most of the forest is a mosaic of restored *P. palustris* forest with occasional hardwoods such as dogwood (*Cornus florida*) and various oaks (*Quercus* spp.) and plantations of *P. taeda* or slash pine (*Pinus elliottii*). Extant mesic forest is inhabited by oaks (e.g., *Quercus nigra*), sweetgum (*Liquidambar styraciflua*), beech (*Fagus* *grandifolia*), and magnolias (*Magnolia* spp.). Tupelo gums (*Nyssa* spp.) and baldcypress (*Taxodium distichum*) occur in wetter sites. Private land within the National Forest includes parcels managed for agriculture (e.g., timber or cattle) or oil extraction, as well as single-family residences.

Capture and radiotelemetry

Due to low success in trapping *C. rafinesquii* using mist nets (Lance and Garrett 1997, Trousdale and Beckett 2002), I surveyed concrete bridges in the daytime to locate bats (see Chapter 1). To reduce disturbance to maternity colonies, I timed capture attempts to not coincide with parturition or the ca. 3 weeks after this event before pups could fly (Trousdale and Beckett 2004). From August 2001 to August 2004 I captured bats using a handheld, "butterfly" net. On several occasions I preferentially radiotagged some individuals over others to ensure that both sexes were represented in my sample and that individuals captured at different bridges were monitored. For all bats that I captured, I measured mass (g) and forearm length (mm) and determined their sex, reproductive condition if female (pregnant, lactating, nonreproductive), and age-class (juvenile or adult, based on ossification of epiphyseal joints of the phalanges [Anthony 1988]). I placed distinctly-numbered or -colored bands (A.C. Hughes Ltd., Hampton Hill, Middlesex, UK) on the forearm of bats (right forearm for males, left for females) for future identification of individuals. After clipping a small amount of hair from between the scapulae, I attached a radiotransmitter (Model LB-2, Holohil Inc., Carp, Ontario, Canada) to each bat by using surgical adhesive (Skin-Bond, Smith and Nephew Inc., Largo, Florida). Mean mass (± *SD*) of captured bats was 8.9 ± 1.1 g. Mass of each transmitter was ca. 0.46 g; maximum load carried by radiotagged individuals just exceeded 6% of body mass for the smallest individuals (which weighed 7.5 g) but was ≤ 5% for 22 of 25 bats in my sample (see Aldridge and Brigham 1988). After holding for ca. 15 min to allow the glue to dry, each bat was released underneath the bridge where it was captured. These methods followed USM IACUC protocol # 204-004 and recommendations of the American Society of Mammalogists (1998).

I began radiotracking bats to day-roosts on the day following their capture. I returned to the bridge at which the bat was found and listened for the bat's signal using a Model TRX1000S radioreceiver (Wildlife Materials, Inc.) and a 3-element yagi antenna. If I detected the signal, I determined its direction and used homing to locate the roost. If I were unable to detect a signal, I drove to the nearest bridge and continued searching. Due to logistical considerations, I did not conduct emergence or "flyout" counts to verify most roosts. Reliability of homing was corroborated by my observation that the suspected roost was usually the only tree in the immediate vicinity to possess an obvious cavity. I tracked bats in this manner daily until the transmitter's battery failed (after ca. two weeks) or the transmitter fell off the bat and was recovered. If I located a signal at a bridge, we walked underneath that structure to verify the bat's presence. Similarly, if I detected a bat within an abandoned building or other human-made structure, I attempted to obtain visual confirmation of the bat's presence by peering inside a window or entering the structure. I tracked bats in this manner daily until the transmitter's battery failed (after ca. 14 days) or the transmitter fell off the bat. In most cases I obtained exact locations (accuracy ± 15 m) for all roosts using a Global Positioning System (GPS) receiver (GPS III Plus, Garmin International, Olathe, Kansas) and used this unit to determine distances (km) among roosts used by individual bats.

Data analysis

I calculated minimum frequency of roost switching by bats by dividing total number of days that all radiotagged bats were located by total number of roost changes made by these individuals (Kurta et al. 2002). Given the frequent movements among roosts and their reuse by bats in my sample, I supplemented traditional measures of roost fidelity (e.g., residence time by an individual at a specific roost, number of times that a bat switched roosts) with a metric which incorporated both number of roosts used by an individual (richness) and relative "contribution" made by each of these structures during the period of monitoring (evenness). Therefore, I used the Shannon diversity index,

$$H' = -\Sigma p_i \log p_i, \tag{1}$$

where p_i = proportion of the total number of individuals from a collection/community that belong to species i (Brower et al. 1998). In my calculations $p_i = n_i/N$ where n_i = number of days spent by a bat at a particular roost and N = total number of days that the bat was found at any roost during the radiotracking period. I also selected this approach to reduce potential biases in sampling effort (length of time that an individual was radiotracked) or sampling success (i.e., how many of its roosts that I located). I therefore calculated roost diversity (H') of each individual for which I had located roosts via radiotelemetry on ≥ 4 days ($n = 13$). On days that I searched for a bat but did not detect its signal, I assumed that the bat spent them at one unknown roost that counted toward its index (conditional upon having later located the bat at a previously used roost). Days on which I did not search for a bat were not used in the calculations. For bats captured and radiotracked more than once, I included only data from their first session of monitoring. A bat with a high H' score would be an individual that used a relatively large number of roosts and apportioned its stays evenly among them, and a bat with a low value would be one that used few roosts and stayed predominantly at a single roost.

To test whether roost fidelity (*H'*) differed by sex, age-class, or locality of capture, I used a 2-tailed *t*-test for each comparison (JMP IN Version 5.1, SAS Institute, Inc., Cary, North Carolina) with a sequential Bonferroni correction to conserve power (Rice 1989). I compared mean indices of all males ($n = 6$) to females ($n = 7$) and juveniles ($n = 5$) to adults ($n = 8$) regardless of where they were captured. I also compared indices of bats captured in 2 different localities in the Chickasawhay District (heretofore designated as West and North) that were located ca. 11 km apart. Based on previous radiotracking studies of *C. rafinesquii* (e.g., Hurst and Lacki 1999, Menzel et al. 2001), I assumed that these areas were sufficiently distant from one another that likelihood of overlap by individual bats was low. Furthermore, I never recovered banded *C. rafinesquii* > ca. 4 km from their site of capture during a mark-recapture effort on DeSoto NF concurrent with the present study (see Chapter 4). Eight of 13 bats for which I calculated an index of roost fidelity were captured at one of these two localities. The West group ($n = 4$) consisted of two adult females, a juvenile female and a juvenile male and the North group ($n = 4$) included two adult females, one adult male and one juvenile female.

Establishment and description of localities

To characterize the habitat within each locality, I used data on area, tree species composition, and condition of forest stands provided by the USDA Forest Service and imported them into a geographic information system (GIS) (ArcView Version 3.2, Environmental Systems Research Institute, Redlands, California). I used a GPS receiver

(Pathfinder Pro XR, Trimble Navigation Limited, Sunnyvale, California) to obtain coordinates of bridge roosts at West and North. I used the GIS to calculate the straight-line distances between a pair of bridge roosts situated along a road at each locality and to designate the midpoint of each segment. I delineated boundaries of each locality by creating a circular, 800 ha buffer (1.6 km radius) centered on the midpoint (XTools ArcView Extension, M. DeLaune, Oregon Dept. Forestry). I then identified stands contained entirely or partially within each buffer and calculated area covered by various types of forest (Microsoft Excel 97). I generated 20 random points within Forest Service holdings in the area of each locality (Random Point Generator 1.3 Extension, Jenness Enterprises, Flagstaff, Arizona) then visited them to confirm the vegetation type present. Nineteen of 20 points (95%) within the West area were correctly classified, and 18 of 20 points (90%) in the North locality matched descriptions provided by the Forest Service. When data for composition and condition of forest stands were not available (i.e., private property), I instead characterized land cover by interpreting aerial photos in combination with ground truthing where access was granted or property was visible from a road. I ground truthed ca. 60% (71 ha) of private land in the West locality and ca. 23% (49 ha) of private property in the North area.

Two adjoining streams, Tiger Creek and East Tiger Creek, drained the West locality. Three concrete bridges (constructed in 1969, 1978 and 1993) were located within a 1.6 km span of gravel road in this area; I used the midpoint between the two furthest bridges as a reference to place the buffer (Fig. 4). Longleaf pine forest was the most abundant vegetation type, covering ca. 294 ha (36% of the buffer), over 90% of which was classified as sawtimber (mean DBH $\geq$ 27 cm). Approximately 128 ha (16%)

were covered by bottomland hardwood forest in sawtimber stage. Private property covered 121 ha (15%) and was comprised mostly of loblolly-mixed hardwood forest at various successional stages (sapling to mature timber).

The North locality included two concrete bridges (both built in 1967) situated 1.6 km apart on a gravel road and two streams, Big Branch Creek and an unnamed branch of Thompson's Creek (Fig. 4). Approximately 216 ha (27%) were held in private ownership and mostly managed as either dense pine plantation or nonforest (e.g., oil extraction, pasture). Bottomland hardwood forest in sawtimber stage was the fourth most abundant type of land cover (after private land, longleaf, and slash pine) and covered ca. 57 ha (7%). Laurel-willow oak forest in sawtimber stage covered ca. 56 ha (7%).

Day roost surveys

I visually assessed presence of *C. rafinesquii* at day roosts located in the West and North areas from 15 May through 10 September in 2002 and from 16 May through 23 August in 2003. During a survey, I visited all of the bridges and other human-made structures that were known at the time to be roosts at both localities and counted the number of roosting bats per structure. I conducted 35 surveys over 112 days (every 3.2 days) in 2002 and 12 surveys over 98 days in 2003 (every 8.2 days). My 2002 effort included daily visits to both localities during a "pre-parturition" session from 15-20 May and two "post parturition" periods, 27 May-2 June and 23-30 June and 2-3 July.

Results

I affixed radiotransmitters to 25 *C. rafinesquii* captured at seven different bridges located in the Chickasawhay District and at one bridge located in the DeSoto District. Sixteen of these bats were females (14 adults, including 3 that were lactating at the time of capture, and 2 juveniles) and 9 of these bats were males (4 adults and 5 juveniles). Up to four bats carried active radiotransmitters at any time. (See Chapter 2 for temporal distribution of capture and radiotracking sessions.) Number of days for which an individual was searched was 9.1 ± 2.6 per bat (numbers reported as decimals = mean ± *SD* unless otherwise stated). I successfully located bats on 140 out of 227 total days of tracking (overall detection rate = 62 percent); I located bats on 5.6 ± 3.9 occasions per individual. I located all but one radiotagged bat at least once (based on detection of the signal leading me to a roost) following its capture.

I located 25 different roost structures; of these, 14 sites were hollow trees: *Nyssa aquatica*, *Nyssa* sp., and *Magnolia grandiflora* (see Chapter 2 for further description). The remaining 11 structures were human-made and included 8 bridges, 2 abandoned houses, and an empty oil storage tank. I located 14 maternity roosts (7 trees, 5 bridges, 1 house, and the oil tank). Radiotagged bats typically switched roosts during the period that they were monitored and used 2.5 ± 1.2 roosts per individual. Bats switched roosts 2.6 ± 2.0 times per radiotracking session every 2.1 days (140 days located ÷ 66 roost changes). Bats changed roosts from zero (two bats, both juvenile males) to 8 times (an adult male that used a bridge, a tree and at least one undiscovered roost). Maximum number of consecutive days (within an individual's session of tracking) spent in a roost was 4.5 ± 3.0 per bat ($n = 18$; seven of the 25 tagged individuals did not spend more than one day at any roost). Maximum number of consecutive days spent at human-made structures and trees was 4.9 ± 3.3 per bat ($n = 14$), and 3.2 ± 1.5 per bat ($n = 4$), respectively. Females and males used 2.6 ± 1.4 and 2.0 ± 0.7 roosts, respectively. Mean distance that bats moved between sequential roosts was 572.8 ± 640.3 m; values ranged from ca. 120 m to 4 km.

I calculated indices of roost diversity (*H'*) for 13 individuals (Table 3). Roost diversity differed by capture locality but not by sex or age-class. Following Rice (1989), I established statistical significance for the first test by dividing α (0.05) by the number of tests, *k* (3), then compared this value (0.017) to the smallest *P*-value (0.006, obtained for North vs. West) and determined that this result was significant. The second lowest *P*-value (0.19, obtained for males vs. females) exceeded 0.025 (as calculated by $\alpha \div [k\text{-}1]$). I thus determined that this test and the third test (juveniles vs. adults, $P = 0.32$) were nonsignificant at the table-wide α level (Rice 1989). Individuals from the North area ($n = 4$) therefore displayed higher fidelity (lower diversity) to their roosts (mean $H' = 0.20$) than did bats from West ($n = 4$; mean $H' = 0.53$; $t = 4.08$, *d.f.* = 6, $P = 0.006$). Indices for females ($n = 7$; mean $H' = 0.40$) did not differ from those of males ($n = 6$; mean $H' = 0.24$; $t = 1.41$, *d.f.* = 11, $P = 0.19$), nor did roost fidelity of juveniles ($n = 5$; mean $H' = 0.25$) differ from that of adults ($n = 8$; mean $H' = 0.37$; $t = 1.03$, *d.f.* = 11, $P = 0.32$).

Individuals from the West locality used 3.6 ± 1.7 roosts each, while North bats used 2.0 ± 0.0 roosts. I located 8 tree roosts in the West area (Fig. 4) but detected no radiotagged bats in tree roosts in the North locality. Aside from the two bridges, bats captured in the North were also found in an abandoned house and an oil tank (Fig. 4), the interior of which was accessible through a rectangular opening at its base. I discovered the house and oil tank during a June 2002 tracking session, although a different radiotagged individual used each structure. (A juvenile male from North radiotagged in

2004 was not used in the comparison of fidelity by locality due to removal of the oil tank and collapse of the abandoned house between 2003 and 2004.)

Bats that were captured together sometimes reunited at different roosts. Five hollow trees were occupied simultaneously by ≥ 2 radiotagged bats, and four of these roosts were found at the West locality. I radio-tagged multiple bats from the same bridge on six occasions and subsequently located these individuals (up to 3 at a time) sharing another roost during three such periods of tracking (see Chapter 2).

Number of bats present at human-made roosts (where I could readily count them with minimal disturbance) in both localities was quite variable during the maternity season (March – August; see Trousdale and Beckett 2004), with bats often absent from these structures during surveys. During my 2002 monitoring period (see Day roost surveys – Materials and Methods), mean number of bats was 5.3 ± 6.2 in the North locality and 3.9 ± 5.3 in the West locality. I observed maximum numbers of 20 and 18 bats at a single roost on a single date in the North and West localities, respectively. In 2003, mean number of bats at human-made structures was 4.4 ± 6.7 in the North locality, with a maximum of 21 bats per single roost per date. In the West locality, mean number of bats was 1.8 ± 3.7 (maximum = 17). Bats were most abundant from late May through early July when multiple mothers and their pups were clustered together at maternity roosts (Trousdale and Beckett 2004).

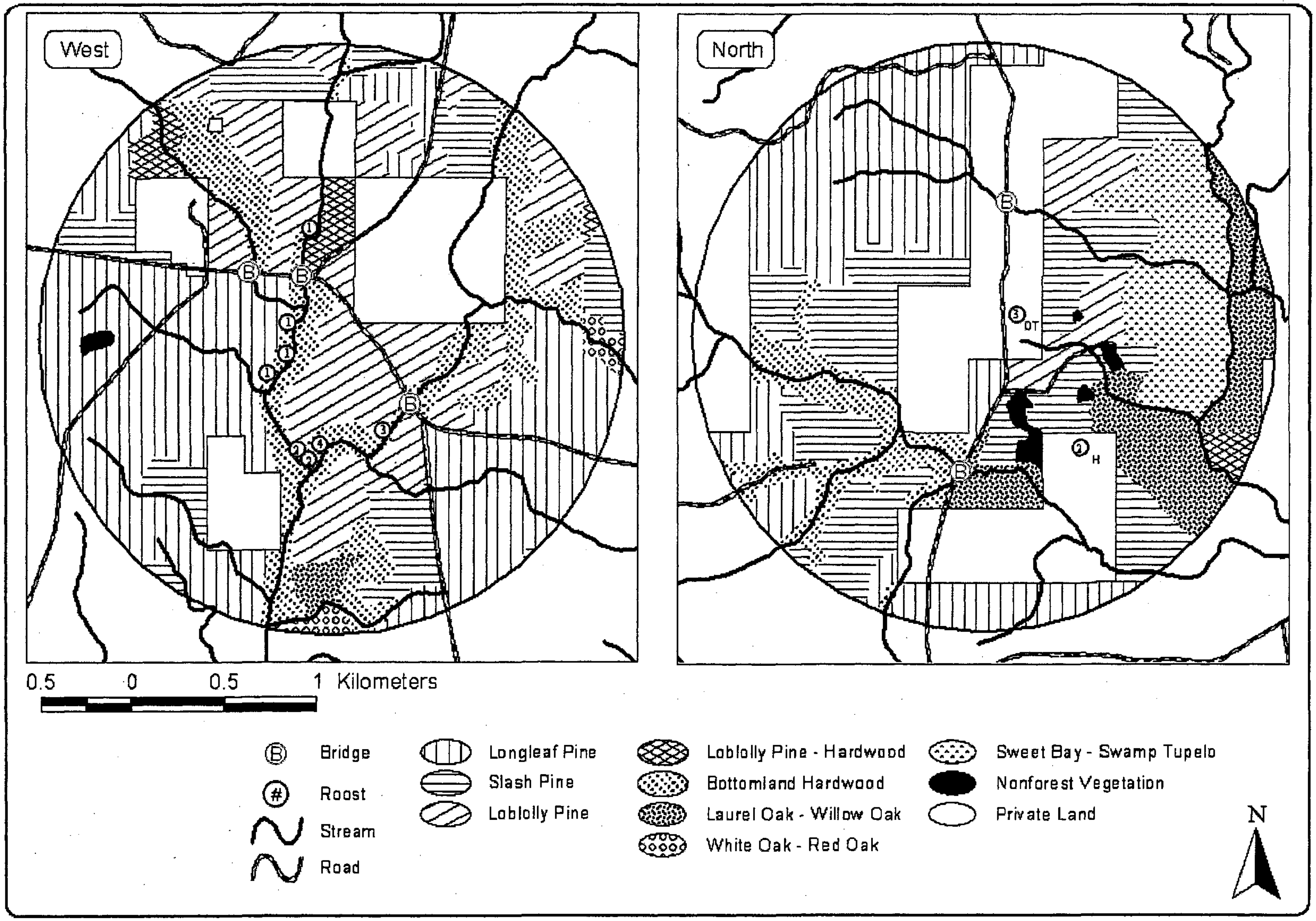
Table 3

Corynorhinus rafinesquii *from DeSoto National Forest for which indices of roost diversity (H') were calculated based on monitoring via radiotelemetry from August 2001-August 2004. Age-class denoted by "a" (adult) or "j" (juvenile), sex denoted by "f" (female) or "m" (male), and lactating females indicated by "l." Capture location defined by either the name of the locality (see text for descriptions) or the name of the creek spanned by the bridge at which the bat was captured. Number of times switched indicates the number of instances that an individual changed roosts as ascertained by radiotelemetry.*

Bat	Age-class, Sex	Location of Capture	# days tracked	# days located	# roosts located	# times switched	H′
1	afl	North	8	8	2	2	0.28
2	am	North	9	8	2	3	0.28
3	jf	North	4	11[a]	2	1	0.12
4	af	North	11	11	2	1	0.12
5	jm	North	10	10	1	0	0.00
6	jm	West	9	7	2	3	0.35
7	afl	West	9	8	5	5	0.62
8	jf	West	10	10	5	5	0.50
9	afl	West	11	11	6	6	0.64
10	am	Gunstock	12	8	3	8	0.43
11	jm	Gunstock	4	4	2	1	0.29
12	af	Gunstock	10	9	3	4	0.49
13	am	Tiger	11	11	2	1	0.12

[a] Radiotransmitter fell off the bat after the fourth day of monitoring; bat's presence at roost confirmed visually and its identity verified by band on forearm.

Figure 4. Map of habitat and locations of bridges and other roosts used by *Corynorhinus rafinesquii* in the localities of West and North, Chickasawhay District, DeSoto National Forest, from August 2001-August 2004. (See text for descriptions of localities.) Numbers within circles indicate the number of bats radiotracked to each non-bridge roost (tree or otherwise) during the study period. Abandoned house and oil tank in North denoted by "H" and "OT," respectively.


West
North
B
1
2
3
4
3 DT
2 H
0.5 0 0.5 1 Kilometers
Bridge
Roost
Stream
Road
Longleaf Pine
Slash Pine
Loblolly Pine
Loblolly Pine - Hardwood
Bottomland Hardwood
Laurel Oak - Willow Oak
White Oak - Red Oak
Sweet Bay - Swamp Tupelo
Nonforest Vegetation
Private Land
N

Discussion

The roosting strategy of *C. rafinesquii* was flexible depending both on availability of roosts and on type of structure used. Tree roosts were located in stands classified by the Forest Service as bottomland hardwood (n = 10 trees), loblolly pine (n = 3), or laurel oak-willow oak (n = 1). The West locality contained roosts in 8 hollow trees, and several of them were located in close proximity to one another within bottomland hardwood forest along two streams (Fig. 4). Despite comparable effort in both captures and radiotracking, I did not find any tree roosts in the North locality. Where land-use patterns have resulted in a scarcity of tree hollows, cavity-denning or cavity–roosting mammals must seek alternative structures for shelter (Birks et al. 2005). Adjustment in roost fidelity is a predictable consequence of such a shift by bats. I conclude that the apparent scarcity of natural roosts in the North area (possibly a consequence of its forest's age and composition), coupled with the fact that the structures used by bats were human-made, explained the higher roost fidelity at this locality. Gooding and Langford (2004) reported that colonies of *C. rafinesquii* switched tree roosts "every few days" at a Louisiana site rich in hollow trees (65.5/ha). Similarly, in habitat where roosts (cavity-bearing trees) were not likely a limiting factor, *Chalinolobus tuberculatus* had one of the lowest residence times reported for a bat (O'Donnell and Sedgeley 1999). In contrast, most radiotagged *C. rafinesquii* monitored by Hurst and Lacki (1999) maintained fidelity to their maternal cave roost in Kentucky. Trees are at the opposite end of the spectrum from caves both in terms of their abundance within most landscapes and their longevity as roosts to bats (Kunz 1982). Within our study area, an upland pine, mixed hardwood-pine system, *C. rafinesquii* followed Lewis' (1995) generalization: low day-to-day roost fidelity in a habitat containing tree roosts that were locally common (West) but not exceptionally stable and higher fidelity in a habitat where comparatively permanent, human-made structures were found (North).

Variable roost fidelity among habitats that afford different opportunities for roosting has been noted for other species of bats. *Plecotus auritus*, a former congener of *C. rafinesquii*, exhibited high daily fidelity to buildings in Scotland (Entwistle et al. 2000) but frequently switched roosts (located in bat boxes) within a defined area in Germany (Entwistle et al. 2000, citing Heise and Schmidt [1988]). Brigham (1991) argued that populations of *E. fuscus* were "tenaciously loyal" to human-made structures and also showed high fidelity to roosts in rock crevices but readily moved among tree cavities. Bachelor and maternity colonies of *Corynorhinus townsendii* were each more faithful to roosts in caves than in mines, the former occurring at lower densities in the landscape than the latter (Sherwin et al. 2005).

The type of shelter selected by an individual animal may affect its fitness, especially if use imposes a compromise between critical factors such as expenditure of energy via thermoregulation and risk of predation (Birks et al. 2005). Ferrara and Leberg (2005b) found that in the Gulf Coastal Plain, *C. rafinesquii* selects bridges that are dark and located close to both the ground and the abutment but are far from the bridge's sides (although larger maternity colonies may be exceptions to some of these generalizations). These factors affect the microclimate in that roosts are warmer than non-roost locations under bridges (during April-October) but cooler than ambient temperatures recorded alongside bridges (Ferrara and Leberg 2005b). Furthermore, likelihood of a bridge's use by *C. rafinesquii* increased with proportion of nearby deciduous or hardwood forest in

Louisiana (Lance et al. 2001), habitat that may contain cavity-bearing trees such as *Nyssa* spp. (Trousdale and Beckett 2005). However, *C. rafinesquii* are absent or rare at bridges during cooler months (Trousdale and Beckett 2004). These factors suggest that roosts in trees seasonally offer some component lacking in bridge roosts. Considering that bats can enter deep torpor more safely where risk of predation is low (Lausen and Barclay 2006), perhaps roosts in trees are less accessible to predators than those under bridges. During summer, roosting under bridges may enhance thermoregulation by granting bats (whether solitary or in groups) relief from high daytime temperatures (Ferrara and Leberg 2005b). Use by maternity colonies of the expansive spaces that bridges offer may also benefit juvenile bats that would otherwise need to leave the roost to make "practice flights" (Lausen and Barclay 2006). Occasional use of tree roosts by these colonies during summer could enhance fitness of their members by familiarizing them with locations of alternate roosts (Kurta et al. 2002).

Roost fidelity of *C. rafinesquii* (as measured by number of roosts used, residence time or frequency of roost switching) was comparable to observations made for other populations of this species (e.g., Clark 2003; Lance et al. 2001) and also of cavity-roosting, forest dwelling bats such as *Chalinolobus tuberculatus* (O'Donnell and Sedgeley 1999), *E. fuscus* (Brigham 1991), *Lasionycteris noctivagans* (Crampton and Barclay 1998), *Myotis evotis* (Waldien et al. 2000), and *Myotis lucifugus* (Crampton and Barclay 1998). Although my captures of *C. rafinesquii* might have prompted radiotagged individuals to initially switch roosts, counts made during my less intrusive visits to bridges (and other artificial structures) indicated that number of roosting individuals fluctuated. Moreover, insectivorous bats often move between day roosts in absence of apparent disturbance (Ferrara and Leberg 2005a; Rydell 1989; Sherwin et al. 2005; Veilleux et al. 2003; Whitaker 1998).

Neither sex nor age-class influenced fidelity of *C. rafinesquii* to roosts in this study. Overlap in variance of H′ between males and females and between adults and juveniles was high, perhaps a consequence of pooling across age-classes when comparing sexes and vice versa, and contributed (along with small sample size) to very low power (≤ 0.16) of tests used in these comparisons. However, Brigham (1991) similarly documented no variation in roost fidelity (percent of time that an individual returned to the same roost) among *E. fuscus* due to differences in age or reproductive condition of individual bats, though type of roost used seemed to affect this behavior. Vonhof and Barclay (1996) found that residence time (in days) of radiotagged *L. noctivagans* was longer in tree cavities than in roosts located under bark (the latter type of roost being more common) and that lactating females with young used tree cavities exclusively. In contrast, lactating female bats that I radiotagged ($n = 4$) changed roosts (bridge to tree or bridge to building) following capture then moved again at least once during their monitoring sessions. When I captured these individuals, pups that were present were volant and presumably no longer in need of moving, an added energetic cost of roost switching to lactating females (Vonhof and Barclay 1996).

Social factors might have influenced my findings. Nonrandom associations may occur among individuals within aggregations of bats (Kerth and Konig 1999), and these relationships may contribute to their selection of roosts (O'Donnell 2000, Willis and Brigham 2004). Consequently, a network of roosts in close proximity to one another may develop, with some communal sites or hubs reused more frequently than others (Rhodes et al. 2006). This phenomenon might explain use of 2 trees by ≥ 3 radiotagged bats over the duration of this study and the tendency of bats (especially groups) to roost under certain bridges in the study area. Radiotagged bats that I captured together subsequently roosted together among several sites but sometimes roosted apart, especially in the West locality. These observations were similar to ones made for *Myotis sodalis* (Kurta et al. 2002), *Myotis thysanodes* (Cryan et al. 2001), *C. tuberculatus* (O'Donnell 2000) and *E. fuscus* (Kalcounis and Brigham 1998; Willis and Brigham 2004). Further study is warranted to determine whether *C. rafinesquii* conforms to the fission-fusion model of sociality, as do tree-roosting *E. fuscus* (Willis and Brigham 2004) and *Myotis bechsteinii* (Kerth and Konig 1999).

Protection of roosts remains an important emphasis in promoting conservation of bats, but managers sometimes operate under the flawed assumption of near-constant fidelity to roosts (Sherwin et al. 2005). Successful strategies to conserve *C. rafinesquii* must therefore take into account the species' plasticity in this regard and its potential for movement among a variety of structures within relatively short periods of time. Such advice seems especially pertinent in areas where natural and human-made roosts both exist, but the local abundance of structures of either type is likely insufficient for resident populations to use either kind exclusively.

CHAPTER IV

LONG-TERM ROOST FIDELITY

Introduction

Adaptive values of the opposing tendencies of dispersal (permanent movement of an individual away from its site of origin to a new area [Shields 1983]) and philopatry (relatively localized dispersal or its absence altogether [Shields 1983]) are determined by intensity of crowding or competition during an organism's life history and a balance between deleterious effects of inbreeding and outbreeding (Horn 1983). Ability of bats to disperse may be constrained by their morphology (Entwistle et al. 1996), which reflects each species' ecological specialization (Norberg and Rayner 1987), and in turn has implications for its conservation (Racey and Entwistle 2003). For instance, bats that possess low wing area relative to body size and consequently high wing loading (Altringham 1996) are capable of rapid, sustained flight (Norberg and Rayner 1987). In contrast, species that possess broad wings with relatively large area (and thus low wing loading) have sacrificed speed for maneuverability (Norberg and Rayner 1987). Bats with the latter type of wing would therefore be ill-suited for commuting efficiently among potential roosts or patches of habitat that were widely separated, either naturally or by anthropogenic fragmentation (Jones et al. 2003).

Roosting ecology of bats is influenced by local diversity and abundance of roosts, availability of food and water, an individual's need to balance energy gain with expenditure, and sometimes sociality (Kunz and Lumsden 2003). One aspect of roosting ecology is roost fidelity (Kunz 1982), a strategy that potentially benefits the individual because it may increase familiarity with foraging habitat and enhance both thermoregulation and the opportunity for social interactions in colonial species (Lewis 1995, Kerth and Konig 1999, Willis and Brigham 2004). Fidelity to roosts over periods of days to weeks may be assessed via radiotelemetry (e.g., Brigham 1991, Cryan et al. 2001, Hutchinson and Lacki 2000, Trousdale et al. in press, Veilleux and Veilleux 2004). In contrast, banding or ringing is used to assess roost fidelity of individuals and colonies during longer periods (e.g., Entwistle et al. 2000, Ferrara and Leberg 2005a, Jones and Suttkus 1975, Petit and Mayer 1999, Rivers et al. 2006, Rydell 1989), especially to structures that are easily located and are readily accessible to investigators (Kurta and Murray 2002). Banding by investigators also affords them the opportunity to assess population structure and turnover via mark-recapture methods (Entwistle et al. 2000, Hoffmeister and Goodpaster 1963, Jones and Suttkus 1975, Sandel et al. 2001, Thomas and LaVal 1988, Whitaker and Gummer 2000).

When controlling for phylogeny, bats show more fidelity to structures that are relatively permanent and/or rare in the landscape than to roosts that are more ephemeral and/or common (Lewis 1995). Bridges, which represent the former roost type, have long been known to shelter both day- and night- roosting insectivorous bats in North America (e.g., Adam and Hayes 2000, Davis and Cockrum 1963, Felts and Webster 2003). Concrete bridges in particular have high structural integrity, may provide open spaces (along their undersides) varying in size and configuration that attract roosting bats, and have been added by humans to many landscapes (Keeley and Tuttle 1999).

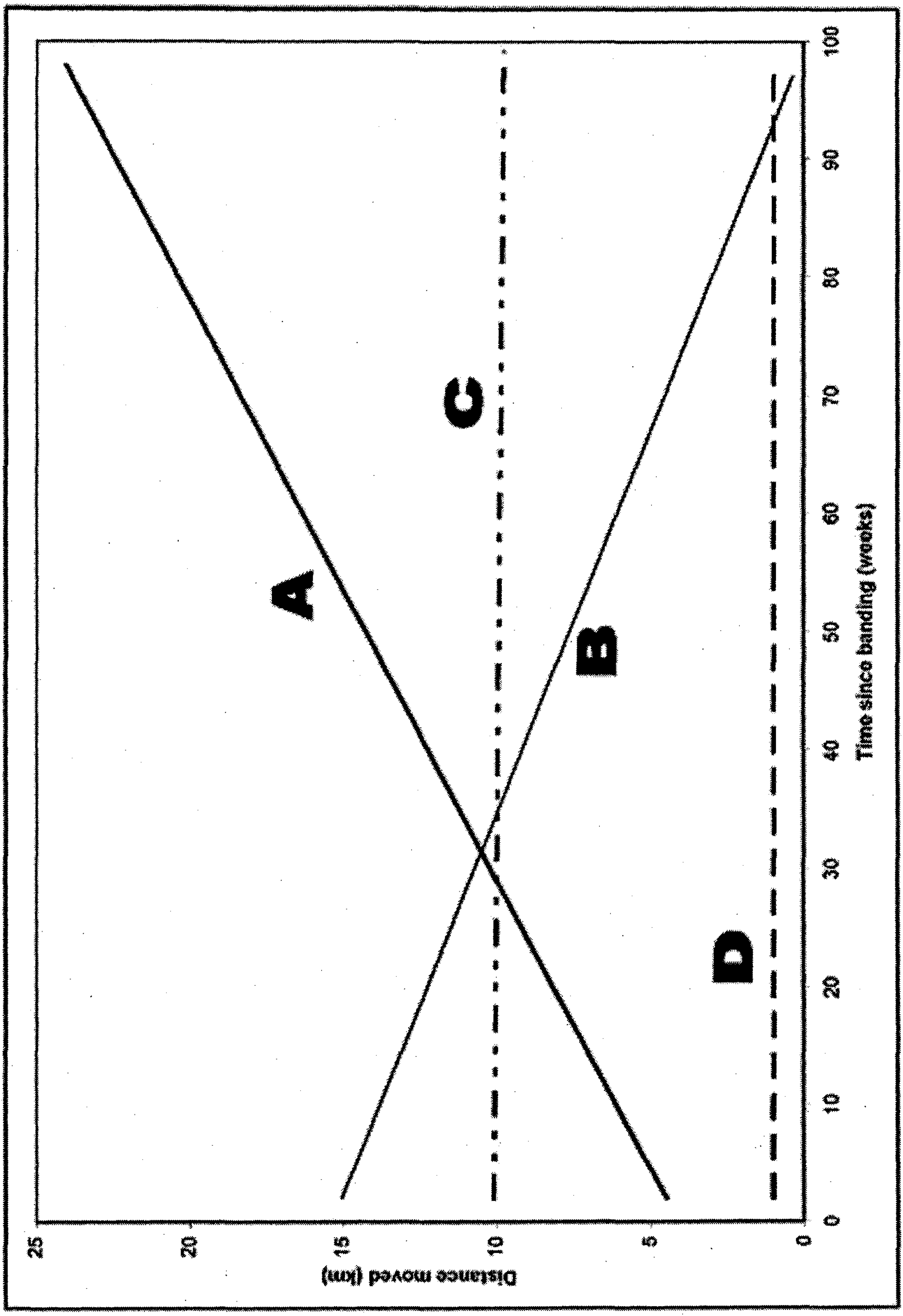
Rafinesque's big-eared bat, *Corynorhinus rafinesquii*, roosts by day within spacious, enclosed areas (Barbour and Davis 1969), including caves (Hurst and Lacki 1999), abandoned houses (Clark 1990, England et al. 1990, Jones and Suttkus 1975) cisterns (Hoffmeister and Goodpaster 1963) and large cavities of hollow trees (Clark 2003, Gooding and Langford 2004, Mirowsky et al. 2004, Trousdale and Beckett 2005). Reproductive females (and their offspring) form maternity colonies in spring that persist at day roosts through summer (Jones and Suttkus 1975) while males tend to roost singly during this time (Trousdale and Beckett 2004). Lance and Garrett (1997) reported that *C. rafinesquii* roosted underneath concrete bridges in Louisiana, subsequently observed elsewhere in the Gulf Coastal Plain (Trousdale and Beckett 2002). *Corynorhinus rafinesquii* in Louisiana used only bridges that contained either girders or compartments along their underside, and the amount of bottomland hardwood forest surrounding a bridge improved its likelihood of being occupied (Lance et al. 2001). This finding might be explained by the species' behavior; *C. rafinesquii* may frequently move relatively short distances (≤ 1 km) among roosts (bridges and trees) within short-term periods, i.e., days to weeks (Trousdale and Beckett 2005, Trousdale et al. in press). *Corynorhinus rafinesquii* are faithful to bridge roosts over months to years (Ferrara and Leberg 2005a). However, these bridges are occasionally replaced (Lance et al. 2001), and abandoned buildings in which *C. rafinesquii* may also roost deteriorate quickly and are subject to vandalism (Clark 1990).

Like other plecotine bats, *C. rafinesquii* possesses wings with low loading (Jones and Suttkus 1971) and low aspect ratio (Altringham 1996). Thus, *C. rafinesquii* would be expected to forage by hovering and gleaning (Norberg and Rayner 1987) and travel conservative distances while foraging (e.g., maximum distance of 2.5 km from roost as reported by Hurst and Lacki 1999) or commuting between roosts due to the high energetic expense of its flight (Entwistle et al. 1996). Therefore, *C. rafinesquii* may be particularly vulnerable to widespread fragmentation or other modifications of its forest habitat in the Gulf Coastal Plain (Piaggio and Perkins 2005). Knowledge of the extent of philopatry and dispersal by this bat, designated a species of special conservation concern throughout its range (Harvey et al. 1999), should better enable managers to make informed decisions regarding conservation planning or predictions about its responses to alteration of habitat.

My objective was to determine the extent to which *C. rafinesquii* showed long-term fidelity to roosts where these structures were both durable and relatively widespread in the landscape. I predicted that if *C. rafinesquii* showed fidelity to particular bridges, then marked individuals would be recaptured on a subsequent visit to these same locations. Conversely, if *C. rafinesquii* did not show fidelity to particular bridges, then these individuals would either not be recaptured or would be recaptured elsewhere. Philopatry may vary within a single species of bat (Kurta and Murray 2002, Petit and Mayer 1999), so I first tested whether differences existed among sex and age classes of bats in likelihood of recapture. I then measured extent of roost fidelity within the sample by examining the relationship between length of time from an individual's capture (and banding) to its recapture and distance between the roosts where these events occurred.

Concordant with a null hypothesis of no roost fidelity, I predicted three possible, mutually exclusive scenarios: the "dispersal hypothesis," the "disturbance hypothesis" or the "random movement hypothesis." Conversely, if recaptured bats demonstrated fidelity to their roosts, then bats would be recaptured at their original bridges regardless of length of time since their banding. If distance from the original capture site were positively correlated with time, this finding would suggest that bats had gradually dispersed or moved away from their original site of capture; I termed this assumption the "dispersal hypothesis" (Fig. 5, Line A). Its converse was the "disturbance hypothesis," a scenario under which individuals that were recaptured sooner would have moved further than individuals that were recaptured later. Thus, distance would be negatively correlated with time (Fig. 5, Line B). Such a trend would be consistent with the notion that capture and banding prompted bats to initially flee their original roost but gradually return. A third option under the hypothesis of no roost fidelity, the "random movement hypothesis" predicted that no discernible trend would exist in terms of when and where bats were recaptured. Therefore, no correlation would exist between distance moved and length of time since recapture (Fig. 5, Line C). Lack of a linear association between distance and time would also be expected if recaptured bats demonstrated fidelity to their roosts. In this case, however, data points (recaptures) would be concentrated along the x-axis due to the high number of "0" values for the dependent variable or y-coordinate, distance moved (Fig. 5, Line D).

Figure 5. Potential long-term trends in occupancy of human-made roosts by *Corynorhinus rafinesquii* (based on recaptures of individuals) using linear regression to determine whether length of time between an individual's capture and initial recapture predicts distance that it moved between these events. If distance and time are positively correlated (Line A), bats have gradually moved away from their original site of capture ("dispersal"). If distance and time are negatively correlated (Line B), individuals recaptured sooner have moved further than individuals that were recaptured later ("disturbance"). Line C indicates lack of correlation between distance and time with no discernible trend existing in timing and location of recaptures ("random movement"). Line D indicates lack of correlation between distance and time with data points (recaptures) concentrated along the x-axis ("fidelity").


Distance moved (km)
25
20
15
10
5
0
Time since banding (weeks)
0
10
20
30
40
50
60
70
80
90
100
A
B
C
D

Materials and Methods

Study area

This study was conducted in the Chickasawhay Ranger District (CRD) and the DeSoto Ranger District (DRD) of DeSoto National Forest (NF) in southeastern Mississippi. The vegetative communities native to this region were predominantly longleaf pine (*Pinus palustris*) savanna in uplands and beech-magnolia (*Fagus grandifolia* and *Magnolia* spp., respectively) forest in lowlands with tupelo gums (*Nyssa* spp.) and various oaks (*Quercus* spp.) found in poorly drained soils. Over much of the Gulf Coastal Plain these communities have largely been replaced by plantations of loblolly pine (*Pinus taeda*) or slash pine (*Pinus elliottii*) (Frost et al. 1986) or eliminated entirely by other development.

In 1999 Trousdale and Beckett (2002) surveyed 84 bridges in south-central and southeastern Mississippi to refine knowledge of the distribution of *C. rafinesquii* in this area. In most cases, they selected bridges without previous knowledge of their style of construction or of surrounding landscape features that might have affected their suitability as potential roosts (Lance et al. 2001). Because all six bridges at which bats were found were located in DeSoto NF, I restricted further surveys to sites contained within the NF boundary. I eventually selected 26 bridges in the CRD and 14 bridges in the DRD for monitoring (see below) based on the presence of *C. rafinesquii* on my initial visit or their proximity to known bridge roosts. Using a geographic information system (GIS) (ArcMap Version 9 [ESRI, Redlands, CA] with XTools extension), I determined extent of the area (including private land) that was contained within an imaginary polygon that encompassed these bridges in each district. Pairs of bridges that were located furthest apart (north and south, east and west) in each district served as points to delineate its polygon's boundaries. Using the GIS, I calculated size of the CRD polygon to be ca. 39,316 hectares (ha) and area of the DRD polygon as ca. 15,820 ha.

Capture and banding of bats

I banded bats from July 2000-July 2004, using a handheld, "butterfly" net to capture them. To minimize disturbance to maternity colonies I generally avoided capturing bats that roosted together in groups during mid- to late May, when I expected parturition to occur (Jones and Suttkus 1975, Trousdale and Beckett 2004) but resumed capturing and banding in maternity colonies once juveniles were volant at ca. 3 weeks of age. I also captured solitary bats, which tended to be adult males (Trousdale and Beckett 2004), throughout the study period. I marked each bat by placing an individually numbered, split plastic ring (A.C. Hughes Ltd., Hampton Hill, Middlesex, UK) on its forearm (right for males, left for females) then released all bats at their site of capture. All bats marked in 2000 received orange bands but from 2001 through 2004 (the year when banding ceased), bats were frequently assigned different-colored bands based on capture location.

After commencing banding of bats at bridges in both districts, I revisited these roosts to locate marked bats. I surveyed bridges in the CRD at least once per 2 weeks during summers and about once per month during the other three seasons from 2000 through 2004. I also checked bridges in the CRD on 27 May 2005 and an intern with the Forest Service (S. L. Hammond) surveyed selected bridges in the CRD from May through July 2005. In the DRD, I checked bridges once per 2 weeks during summers of 2000 and 2001, and about once per month during spring 2000, fall 2000, and spring 2001.

I revisited bridges in the DRD (previous locations of maternity colonies only) sporadically during 2002 and once each in the summers of 2003 and 2004. I also occasionally searched for bats in abandoned buildings in both districts, following a similar protocol for captures.

Data analysis

To determine whether a bat's sex or age-class affected its probability of being recaptured or resighted (when positively identified), I constructed a multifactor model using nominal logistic regression with maximum likelihood ratio tests (Fit Model, JMP IN Version 5.1, SAS Institute, Inc., Cary, NC). This method enabled me to test for an interaction between the independent variables (sex × age-class) and to consider each factor separately without requiring further tests for non-independence. To reduce bias in recapture effort, which was uneven between districts because the CRD was much more frequently visited, especially after 2001, I excluded from this analysis individuals that were banded at bridges (or other roosts) that were seldom or never re-checked or were banded in 2004 or thereafter (regardless of district).

When I recaptured a bat, I recorded both length of time (in weeks) that had passed since its initial capture and banding and distance (km) that it had moved between roosts. Distance was 0 if I recaptured the individual at the same roost where I banded it. I measured distance (± 15 m) between roosts in the field using a handheld Global Positioning System (GPS) receiver (GPS III Plus, Garmin International, Olathe, KS). I compared distances moved between male and female bats using a Wilcoxon rank sum test (Oneway Analysis, JMP IN Version 5.1) under the null hypothesis of no difference between sexes in distance moved. Finally, I used linear regression to determine whether length of time between an individual's capture and recapture predicted distance that it moved between these events (Bivariate Fit, JMP IN Version 5.1).

Results

I captured and banded 144 *C. rafinesquii* from 2000 through 2004, 79 females (54.9 percent) and 65 males (45.1 percent). I recaptured or re-sighted 55 individuals. Of these, 32 bats were females, representing 39.2 percent of all female bats that were captured, and the remaining 23 bats were males, a recovery rate of 35.4 percent for this sex (Table 4). I encountered a previously banded bat in 310 instances that I visited a bridge roost or abandoned structure. On 162 of these occasions (0.52), I identified a marked bat either from its band number or transmitter frequency (if the individual had been radiotagged; see Chapter 3). In 73 cases (0.24), I identified a marked bat by visual recognition (no handling necessary) on the basis of its band's color (if novel to the forest district at which it had been banded). On 75 occasions (0.24), I sighted a marked bat but could not identify the individual due to my not capturing the bat, either because it escaped or because I did not attempt to capture it (due to reproductive phenology).

Table 4

Number of Corynorhinus rafinesquii *captured and banded from bridges and other human-made roosts in DeSoto National Forest from 2000-2004. Age-class of bats denoted by "A" (adult) or "J" (juvenile) and sex denoted by "F" (female) or "M" (male).*

Sex	Age-class when banded	Number banded
F	J	16
F	A	63
F	Total	79
M	J	27
M	A	38
M	Total	65

I found a difference among bats ($n = 125$) in probability of being recaptured ($\chi^2 = 9.26$, DF = 3, $P = 0.026$). The combination of sex × age-class did not affect probability of recapture ($P = 0.11$), nor did sex of individual ($P = 0.76$). Age-class influenced probability of recapture ($P = 0.015$). I recaptured a significantly higher proportion of bats that had been banded as adults (44 of 90, 49%) than I did individuals that were banded as juveniles (9 of 35, 26%; Table 5). To avoid confounding the comparison of distance moved by recaptured males and females, I excluded juveniles from that analysis.

Table 5

Number of Corynorhinus rafinesquii *captured and banded at bridges and other human-made roosts in DeSoto National Forest and entered into a nominal logistic regression model to identify differences among individuals in probability of recapture. Age- class of bats denoted by "A" (adult) or "J" (juvenile) and sex denoted by "F" (female) or "M" (male).*

Age-class when banded	Sex	Number banded	Number (%) recaptured	Number never recaptured (%)
J	F	14	5 (36%)	9 (64%)
J	M	21	4 (19%)	17 (81%)
J	Total	35	9 (26%)	26 (74%)
A	F	58	25 (43%)	33 (57%)
A	M	32	19 (59%)	13 (41%)
A	Total	90	44 (49%)	46 (51%)

No linear association existed between the length of time from a bat's capture/banding to its recapture and the distance that the bat had moved, distance (km) = 0.00049(time [weeks]) + 0.28 ($r = 0.029$, $DF = 54$, $F = 0.046$, $P = 0.83$). The inability of time to predict distance from this regression, because mean distance moved by recaptured bats was low (0.30 ± 0.71 km), supported the roost fidelity hypothesis (Fig. 6). Beginning in the summer of 2000 (the first season in which bats were "available" for recapture), distribution of recaptures was largely concentrated at approximately 50-week intervals. In most cases, an individual's first or only recapture occurred either during the same season (within ca. 12 weeks) that it had been banded or during a subsequent summer.

Most recaptured bats (42 out of 55, 76 percent) were found on their first or only recapture at the same site at which they were banded. Marked individuals that I could either positively identify (via recapture) or otherwise ascertain to have been banded at a particular roost location (based on their band's color) were subsequently found at their site of initial capture 91 percent of the time (281 of 310 encounters with previously-banded bats [initial and all subsequent recaptures or re-sightings]). When bats had switched roosts between captures, they had usually moved to the bridge closest to the original roost (Fig.'s 7-8). Mean distance moved by female bats (0.36 ± 0.85 km) did not differ from that of males (0.23 ± 0.62 km; S = 371.5, $Z = -1.78$, $P = 0.07$). Maximum number of bridges that were used by a single marked bat (an adult female) was three; all these bridges were located within a 1.2-km stretch of Forest Road (FR) 202 in the CRD. The maximum verified distance that a recaptured bat moved between any two bridges was 4.1 km by an adult female. On 5 May 2001, I encountered a colony of *C. rafinesquii*, including one marked female, while visiting a bridge in the DRD that had not previously been surveyed. This site (Snider Road at Cypress Creek) was located 4.4 km from the nearest bridge at which any *C. rafinesquii* had been captured and banded (Benndale Road at Beaver Creek). I was unable to recapture the marked individual and thus could not determine exactly how far it had dispersed. Bats were also conservative in terms of intercolonial movement by individuals; I documented only one such instance. An adult male found on 14 July 2000 shared a roost (Calf Branch) with 9 other individuals on Benndale Road but on 11 August 2000 roosted with 15 other *C.*

rafinesquii at another bridge (Beaver Creek) located ca. 2.5 km away on this same road. This individual's age and sex might have made its "membership" in either colony questionable (see below). However, based on recapture data, females that were banded at either bridge did not likewise mix.

Most of the recaptured *C. rafinesquii* were recovered only once and relatively soon after their banding. Most recaptures (41% of females, 65% of males) occurred within 1 year that a bat had been marked (Table 6). Female bats were recaptured up to 4 years after having been banded, males up to 2 years. Fourteen bats were recaptured < 1 year after having been banding, 23 individuals were recaptured one year (usually the following summer) after their initial capture, and I recaptured 18 individuals > 1 year after they were banded. The longest period of time between the initial capture and banding of an individual and its recapture spanned nearly 4 years (14 July 2000 to 27 March 2004). Among bats that were recaptured, median number of recaptures was 1, and the mean number of recaptures was 2.4 times (*SD* = 4.0). One male bat (Orange #32) was recaptured or resighted at the same bridge (FR 202 at East Tiger Creek) 29 times from 2000-2002. When I recalculated these values, excluding that individual, mean number of recaptures per recaptured bat was 2.0 times (*SD* = 1.8). I observed philopatry, operationally defined here as adult bats being recaptured at the same bridge where they had been banded as juveniles (≥ 1 year previously), by 5 females at 4 sites and by two male bats at different bridges. In several instances, bats that had been captured together were again found roosting colonially at the same bridge in subsequent months or years. Most maternity and non-maternity roosts alike were used by *C. rafinesquii* throughout the study period.

Although both solitary individuals and maternity colonies roosted at several locations (Appendix 1), 10 bridges and two houses were never documented as maternity roosts (Appendix 2). Previously-marked individuals typically comprised a low proportion (mean ± *SD* = 28.2 ± 29.8%) of *C. rafinesquii* annually seen at maternity roosts (Fig.'s 9-10). In contrast, most non-maternity roosts were consistently occupied by the same solitary individuals (Fig. 11), usually adult males. At non-maternity roosts (both districts combined), previously-banded individuals comprised 61.5 ± 40.0% of *C. rafinesquii* annually seen per roost.

Figure 6. Scatter plot (including trendline, regression equation, and coefficient of determination) of recaptures of *Corynorhinus rafinesquii* in DeSoto National Forest. Length of time from an individual's capture to its first (or only) recapture is the independent variable; distance that the individual moved between these events is the dependent variable. Each data point represents a single bat.

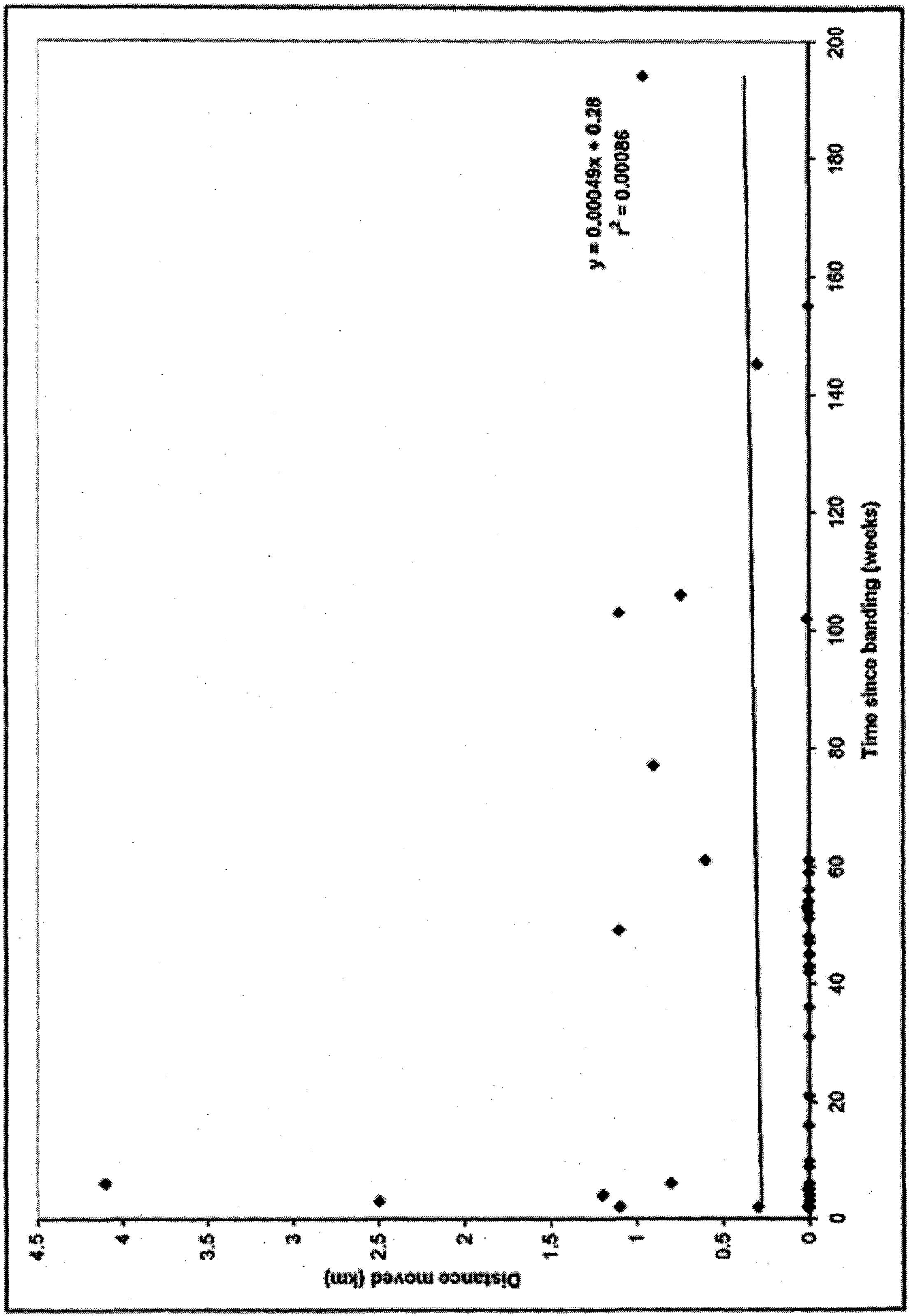

Distance moved (km)
0
0.5
1
1.5
2
2.5
3
3.5
4
4.5
Time since banding (weeks)
0
20
40
60
80
100
120
140
160
180
200
y = 0.00049x + 0.28
r^2 = 0.00086

Figure 7. Locations of human-made roosts with recaptures of *Corynorhinus rafinesquii* in the Chickasawhay Ranger District of DeSoto National Forest from 2000-2005. Roosts are bridges (denoted as short line segments across roads), abandoned houses (rectangles) or an abandoned oil tank (cylinder). Triangles represent male bats and circles represent female bats. The number immediately beside the triangle or circle is the individual's band number according to the band's color. The year in which the recapture event occurred is denoted by the last two digits of that year (e.g., 00 = year 2000). Number of recaptures per individual at a particular roost within a particular year is contained within parentheses. Ovals with dotted boundaries contain adjacent roosts both used by ≥ 1 bat, and ovals with entire boundaries denote overlap in use of nonadjacent roosts by ≥ 1 bat.

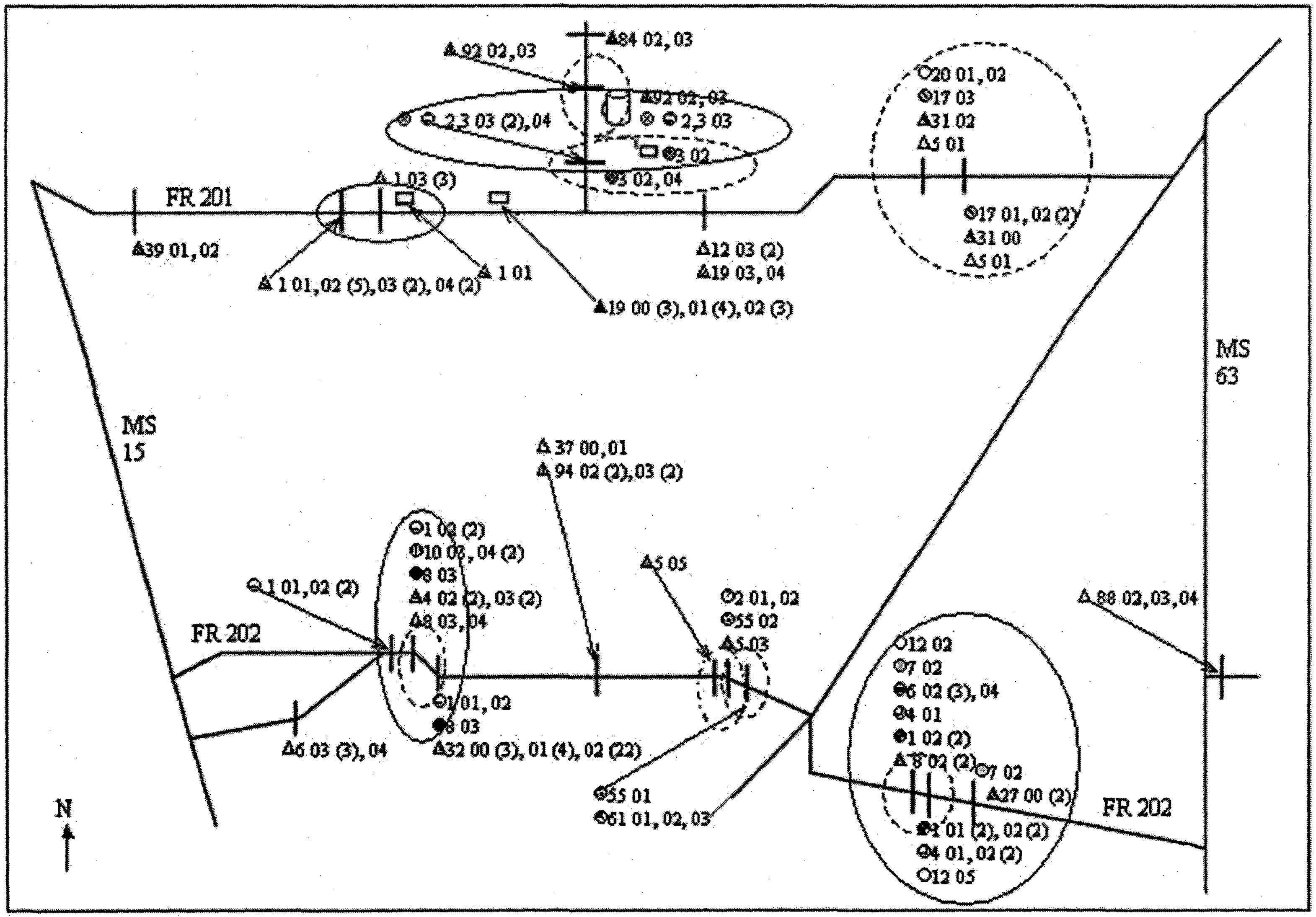

▲92 02, 03
▲84 02, 03
▲92 02, 03
⊗ ⊖ 2,3 03 (2), 04
⊗ ⊖ 2,3 03
●3 02
●3 02, 04
▲1 03 (3)
FR 201
▲39 01, 02
▲1 01, 02 (5), 03 (2), 04 (2)
▲1 01
▲19 00 (3), 01 (4), 02 (3)
▲12 03 (2)
▲19 03, 04
○20 01, 02
⊖17 03
▲31 02
Δ5 01
⊖17 01, 02 (2)
▲31 00
Δ5 01
MS 63
MS 15
Δ 37 00, 01
Δ 94 02 (2), 03 (2)
⊖1 02 (2)
⊖10 02, 04 (2)
●8 03
▲4 02 (2), 03 (2)
▲8 03, 04
⊖1 01, 02 (2)
FR 202
⊖1 01, 02
●8 03
Δ6 03 (3), 04
▲32 00 (3), 01 (4), 02 (22)
Δ5 05
⊖2 01, 02
⊖55 02
▲5 03
⊖55 01
⊖61 01, 02, 03
Δ 88 02, 03, 04
○12 02
⊖7 02
●6 02 (3), 04
⊖4 01
●1 02 (2)
Δ 8 02 (2)
⊖7 02
▲27 00 (2)
●1 01 (2), 02 (2)
⊖4 01, 02 (2)
○12 05
FR 202
N

Figure 8. Locations of human-made roosts with recaptures of *Corynorhinus rafinesquii* in the DeSoto Ranger District of DeSoto National Forest from 2000-2004. Roosts are bridges (denoted as short line segments across roads) or an abandoned house (rectangle). Triangles represent male bats and circles represent female bats. The number immediately beside the triangle or circle is the individual's band number according to the band's color. ID? is substituted for number when a previously-banded but unidentified individual was observed at a bridge at which no bats had been captured (see text for further details). The year in which the recapture event occurred is denoted by the last two digits of that year (e.g., 00 = year 2000). Number of recaptures per individual at a roost within a particular year is contained with parentheses.

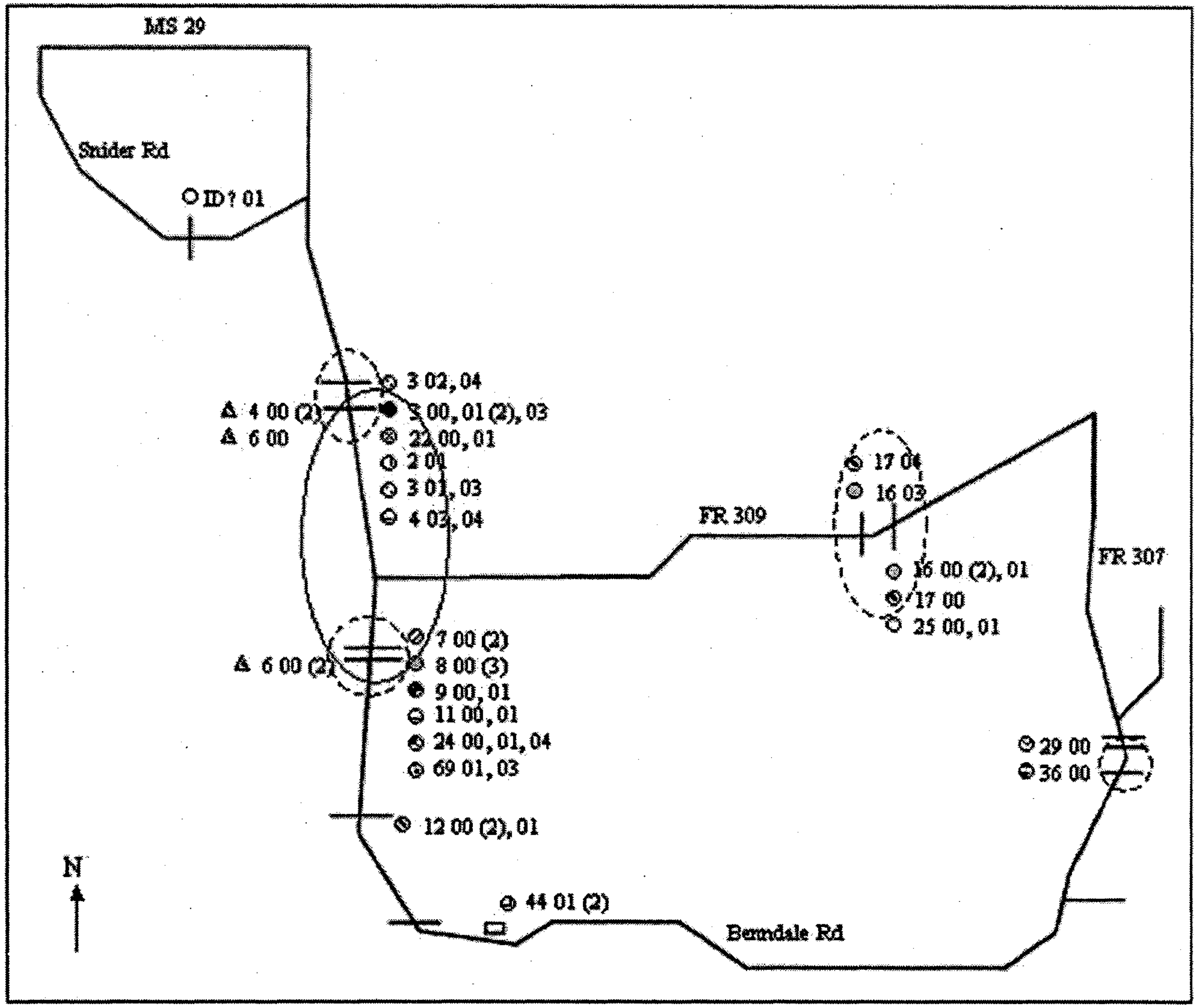

MS 29
Snider Rd
ID? 01
Δ 4 00 (2)
Δ 6 00
3 02, 04
3 00, 01 (2), 03
22 00, 01
2 01
3 01, 03
4 03, 04
Δ 6 00 (2)
7 00 (2)
8 00 (3)
9 00, 01
11 00, 01
24 00, 01, 04
69 01, 03
12 00 (2), 01
44 01 (2)
Berndale Rd
FR 309
17 04
16 03
16 00 (2), 01
17 00
25 00, 01
FR 307
29 00
36 00
N

Table 6

Number of Corynorhinus rafinesquii *recaptured in DeSoto National Forest after different intervals of time with percentage of total recaptures of each sex given in parentheses. Data represent an individual's first or only recapture and span July 2000-May 2005.*

Years between captures	Females	Males
< 1	13 (41%)	15 (65%)
1	14 (44%)	6 (26%)
2	2 (6%)	2 (9%)
3	2 (6%)	0 (-)
4	1 (3%)	0 (-)

Figure 9. Number of marked (banded) and unmarked *Corynorhinus rafinesquii* counted annually at maternity roosts in the Chickasawhay Ranger District, DeSoto National Forest from 2001-2005. Localities comprised of > 1 structure represent areas where banded bats used > 1 roost based on recapture data (see Fig's. 7-8). The locality "East" refers to a pair of bridges located at Gunstock and Piney Woods Creeks along Forest Road (FR) 202 (eastern end). The locality "Hollis" refers to a pair of bridges located at Holiis Creek and Whetstone Branch, respectively, along FR 201. The locality "N Thompson" refers to a bridge along FR 201 located at Thompson Creek (upstream site). The locality "North" refers to one bridge (creek unnamed) along FR 206, an abandoned house, and an empty oil tank (the last two roosts being found at different locations east of FR 206). The locality "S Thompson" refers to a pair of bridges along FR 202 that cross Thompson Creek (downstream site) and a nearby swampy area. The locality "West" refers to 3 bridges located at Little Tiger, Tiger, and East Tiger Creeks along FR 202 (western end). Number of visits made annually to each roost is given in parentheses following locality and year surveyed. The locality "Spring" (see Appendix 1) not depicted due to rarity of bats (< 5 individuals per year) recorded during 2001-2004.

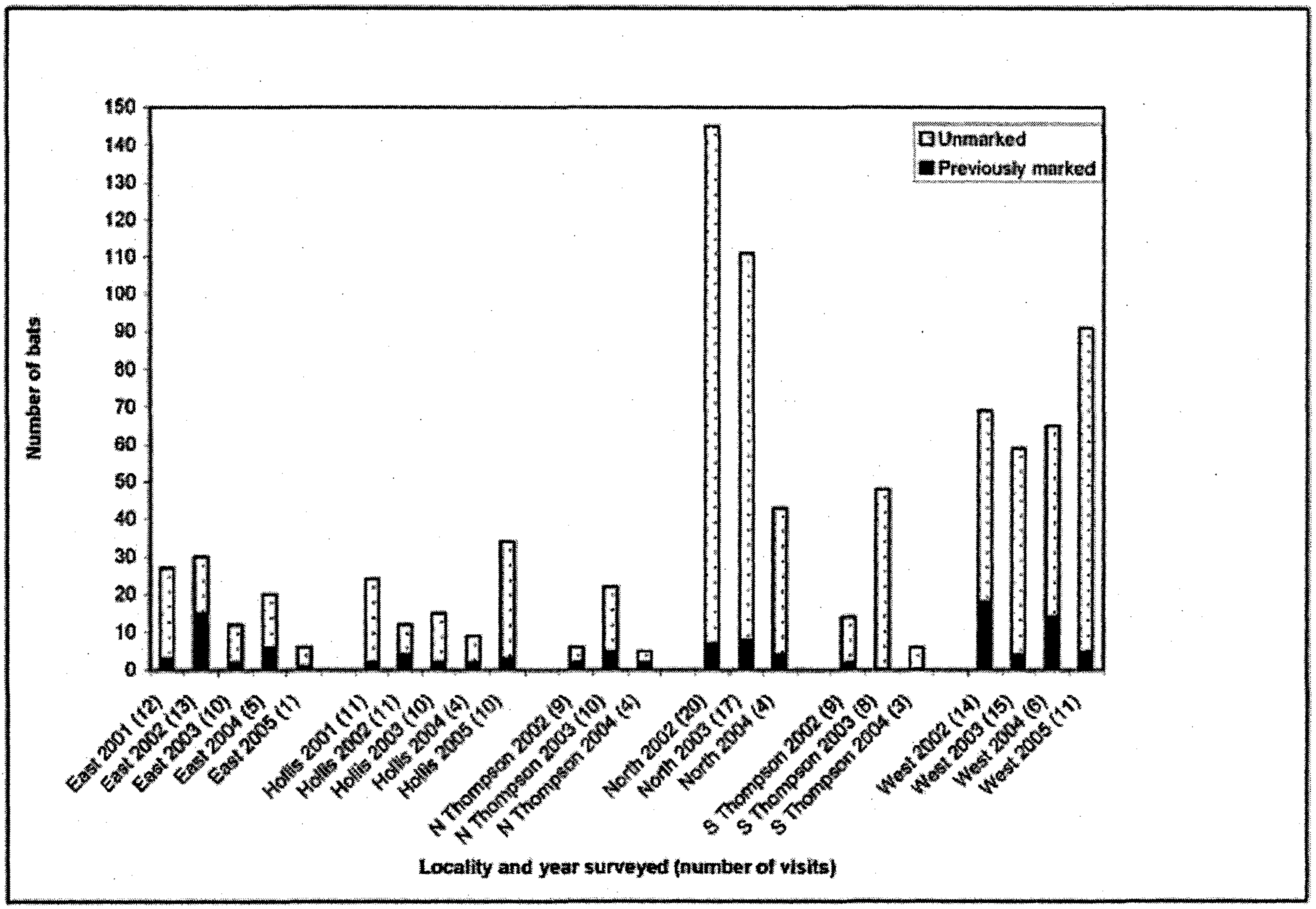

Unmarked
Previously marked
Number of bats
150
140
130
120
110
100
90
80
70
60
50
40
30
20
10
0
East 2001 (12)
East 2002 (13)
East 2003 (10)
East 2004 (5)
East 2005 (1)
Hollis 2001 (11)
Hollis 2002 (11)
Hollis 2003 (10)
Hollis 2004 (4)
Hollis 2005 (10)
N Thompson 2002 (9)
N Thompson 2003 (10)
N Thompson 2004 (4)
North 2002 (20)
North 2003 (17)
North 2004 (4)
S Thompson 2002 (9)
S Thompson 2003 (8)
S Thompson 2004 (3)
West 2002 (14)
West 2003 (15)
West 2004 (6)
West 2005 (11)
Locality and year surveyed (number of visits)

Figure 10. Number of marked (banded) and unmarked *Corynorhinus rafinesquii* seen annually at localities used as maternity roosts in the DeSoto Ranger District, DeSoto National Forest from 2001-2004. Localities comprised of > 1 structure represent areas where banded bats used > 1 roost based on recapture data (see Fig's. 7-8). The locality "Beaver-Hickory" refers to a pair of bridges that cross Benndale Road at these respective creeks. "Benndale" refers to a bridge that crosses an unnamed creek on Benndale Road. "Calf" refers to a pair of bridges that span Calf Branch and a nearby (< 50 m away) ditch along Benndale Road. "Whiskey North" refers to a pair of bridges located along Forest Road (FR) 309 that cross Water Prong and Whiskey Creeks (upstream site). "Whiskey South" refers to three bridges located along FR 307 that cross Whiskey Creek (downstream site), a swampy area adjacent this stream, and its tributary, Flat Branch, respectively. Number of visits made annually to each roost is given in parentheses following locality and year surveyed.

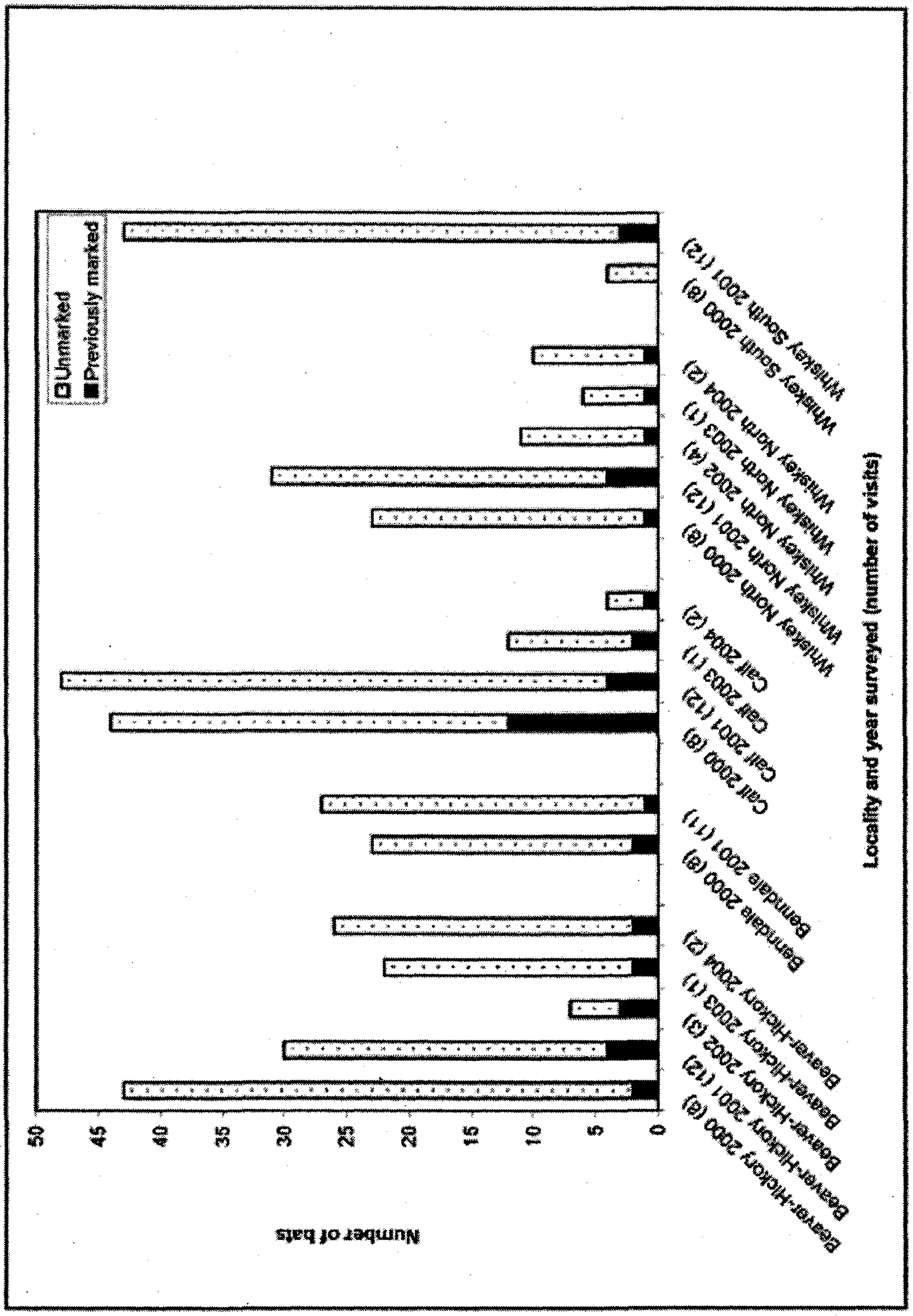
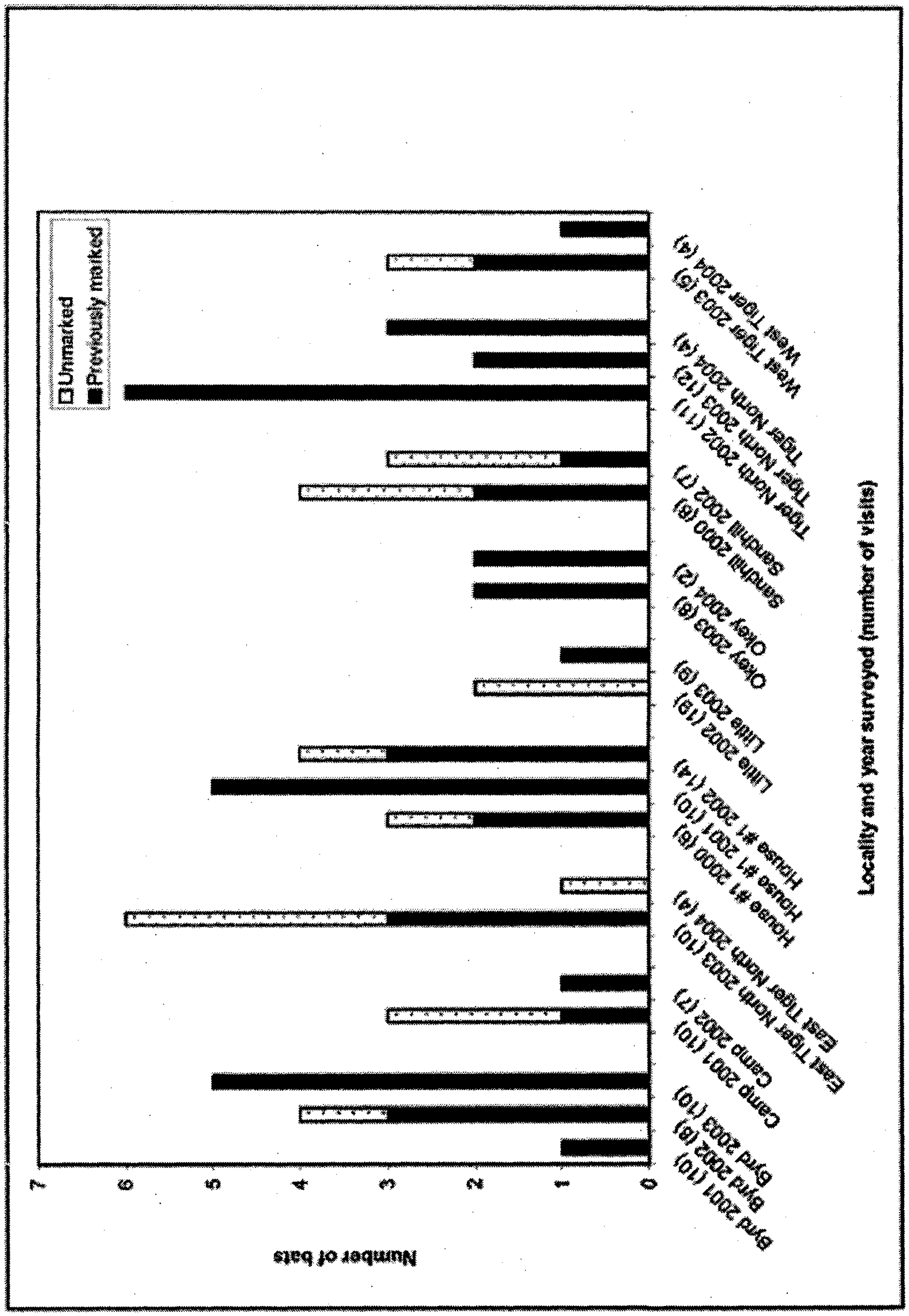

Number of bats
0
5
10
15
20
25
30
35
40
45
50
☐ Unmarked
■ Previously marked
Beaver-Hickory 2000 (8)
Beaver-Hickory 2001 (12)
Beaver-Hickory 2002 (3)
Beaver-Hickory 2003 (1)
Beaver-Hickory 2004 (2)
Berndale 2000 (8)
Berndale 2001 (11)
Calf 2000 (8)
Calf 2001 (12)
Calf 2003 (1)
Calf 2004 (2)
Whiskey North 2000 (8)
Whiskey North 2001 (12)
Whiskey North 2002 (4)
Whiskey North 2003 (1)
Whiskey North 2004 (2)
Whiskey South 2000 (8)
Whiskey South 2001 (12)
Locality and year surveyed (number of visits)

Figure 11. Number of marked (banded) and unmarked *Corynorhinus rafinesquii* seen annually at non-maternity roosts in the Chickasawhay Ranger District, DeSoto National Forest from 2001-2004. Locality names represent particular bridges (named for the creek at which they were located) or an abandoned house located adjacent Forest Road (FR) 201. Number of visits made annually to each roost is given in parentheses following locality and year surveyed.


Unmarked
Previously marked
Number of bats
0
1
2
3
4
5
6
7
Byrd 2001 (10)
Byrd 2002 (8)
Byrd 2003 (10)
Camp 2001 (10)
Camp 2002 (7)
East Tiger North 2003 (10)
East Tiger North 2004 (4)
House #1 2000 (6)
House #1 2001 (10)
House #1 2002 (14)
Little 2002 (13)
Little 2003 (9)
Okey 2003 (8)
Okey 2004 (2)
Sandhill 2000 (8)
Sandhill 2002 (7)
Tiger North 2002 (11)
Tiger North 2003 (12)
Tiger North 2004 (4)
West Tiger 2003 (5)
West Tiger 2004 (4)
Locality and year surveyed (number of visits)

Discussion

Where multiple roosts are available within a defined area, *C. rafinesquii* and other forest-dwelling bats will commonly traverse a "circuit" of these sites within a short-term period of days to weeks (Brigham 1991, Crampton and Barclay 1998, Cryan et al. 2001, Trousdale et al. in press) so that fidelity to any particular roost is low during this interval. At a longer temporal scale (months to years), however, *C. rafinesquii* recaptured in this study displayed a high degree of roost fidelity to their roosts or roosting areas. Lack of dependence of distance moved between roosts on length of time since their banding (and indeed, the lack of observed movement by most individuals) agreed with the prediction of the roost fidelity hypothesis. Both reproductive female and adult male *C. rafinesquii* primarily expressed long-term roost fidelity, and several juveniles of both sexes (especially females) displayed philopatry, suggesting that long-term roost fidelity occurs within all segments of the population to some extent. Although I recovered < 40% of banded bats, and the species was rare or absent from bridges (at a population level) during winter months (Trousdale and Beckett 2004), some individual *C. rafinesquii* returned to these structures over periods of months and even years. The incidence of multiple recaptures of some individuals over the study period and persistence of colonies at certain locations corroborates the notion (see below) that *C. rafinesquii* uses the same bridges or other human-made roosts over long-term periods of time in the Gulf Coastal Plain.

Recaptures of *C. rafinesquii* in abandoned buildings by Jones and Suttkus (1975) were biased toward females due to persistence of maternity colonies. In my study, the clumped distribution of female bats at maternity roosts during summer enabled me to capture and band more females than males. However, neither sex nor this variable in combination with age explained variation within the sample of recaptured bats. Instead, a higher probability of recapture existed for adult *C. rafinesquii* than juveniles. Four potential scenarios may explain the disproportionately low number of juvenile bats that were recaptured: 1. abandonment of the roost due to disturbance from capture/banding; 2. mortality due to injuries resulting from banding; 3. mortality due to other factors; 4. dispersal. The disturbance hypothesis was refuted (for the sample in general) by the regression analysis. Furthermore, I consistently observed bats remaining under the bridge upon their release (instead of fleeing into the adjacent forest), often flying to the other end of the bridge before they resumed roosting. There was no observational evidence that juvenile bats were more adversely affected by their capture and handling than were adults. The remaining three hypotheses are considered in depth below.

Banded bats occasionally show wounds (having been inflicted by the bat itself or by the band) that could potentially become infected (Barclay and Bell 1988). In two instances, I removed bands from bats that had been recaptured > 3 months following their banding. Both bats showed slight damage to their skin (evidently by the band's pinching) of the wing membrane just below their forearm, but in neither case did the wound prevent the bat from apparently normal flight. I applied 1-2 drops of topical antiseptic to each bat's wound and did not re-band these animals. After the first instance of removal in February 2001 (the second one was performed on a bat that had been banded prior to February 2001), I subsequently modified all bands that I would place on bats by trimming the sharp edges or corners of the plastic ring (where it split) and slightly increasing width of the gap, thus allowing the band to slide more easily along the forearm. Altering the bands in this way likely did not hamper their persistence on the bats' forearms (and thus potentially affect assessment of roost fidelity) considering that some individuals that wore trimmed bands were recaptured months or years after being marked (either as juveniles or as adults) and showed no apparent damage at the site of contact with the band. Thus, banding was unlikely to have contributed to mortality.

Higher mortality of juvenile bats due to factors other than banding would be conceivable if this segment of the population behaved in such a way that more often exposed them to risk factors. For instance, if juvenile bats were relegated to foraging in less productive habitat than that used by adults (Bradbury and Vehrencamp 1977), these individuals would more likely suffer mortality. Similarly, dispersing juveniles might select unfamiliar roosts that were suboptimal, i.e., thermally unfavorable or accessible to predators. This prediction would seem especially applicable to juvenile males considering the relatively (though not significantly) low number of individuals from this demographic that I recaptured.

I found no interaction between sex and age-class, possibly due to capture sizes (especially for juvenile females [n = 14]) insufficient to detect a difference between age groups within each sex. If juvenile male *C. rafinesquii* dispersed from their natal roosts, as would have been consistent with other bat species (e.g., *Eptesicus nilssoni*, Rydell 1989), where these individuals went remains unanswered. I recaptured only two adult male bats that had been banded as juveniles and located both individuals at the same bridges where I had first captured them. Regarding juvenile female bats, I suspect that lack of recaptures of individuals that were banded as such was not due primarily to dispersal. Considering that abundance of adult females (marked and otherwise) at bridges peaked just after parturition (Trousdale and Beckett 2004), and that I avoided recapturing reproductive females before their pups were volant, I conceivably underestimated incidence of philopatry in female bats. Relative abundance of *C. rafinesquii* at bridges declines as summer progresses (Trousdale and Beckett 2004), and once pups became volant, short-term fidelity of colonies to particular maternity roosts became more dynamic (A. Trousdale, personal observations). Under these conditions, opportunities for locating marked individuals likely became scarcer. During warm weather, juvenile bats might also have habitually roosted in structures different from those used by adults (i.e., bridges) already resident in the area. For example, hollow trees were known to occur in the vicinity of some bridge roosts (Trousdale and Beckett 2005).

The low percentage of recoveries, coupled with lack of evidence for intersite exchange of individuals in the present study, begs the question of the fate of most banded bats. Such a trend is comparable to that recorded for *Pipistrellus subflavus* that seasonally roosted in box culverts (Sandel et al. 2001). *Plecotus auritus* showed low rates of return (39% females, 48% males) to roosts in buildings and low recruitment based on number of marked young-of-year returning as adults to the natal roost, indicating either dispersal or high juvenile mortality (Entwistle et al. 2000). Hurst and Lacki (1999), having observed that summer emergence counts of *C. rafinesquii* from a cave were consistent among years, suggested that dispersal occurred from a mixed colony (adults of both sexes present) in Kentucky. A colony or deme of *C. rafinesquii* that roosted in a cistern fluctuated in composition as evident by replacement of banded bats by new (unmarked) individuals over a two-year period (Hoffmeister and Goodpaster 1963). Rates of recapture for *Myotis nattereri* banded at a cave system ranged from ca.

3% to 21% per cave with individuals rarely switching among them (Rivers et al. 2006). Although Jones and Suttkus (1975) recaptured ca. 75 percent of *C. rafinesquii* at roosts that were used throughout the year and in settings where these structures were either isolated (a single house) or clumped (multiple buildings concentrated in a single area), they also detected circumstantial evidence for emigration by females in that number of young-of-year males recaptured repeatedly exceeded that of females. *Corynorhinus rafinesquii*'s low annual reproductive output and capacity for longevity (> 10 years [Jones 1977]) are life history characteristics evolved by temperate mammalian species for which expected risk of extrinsic mortality should be low (Barclay and Harder 2003). Juvenile mortality at maternity roosts is likely rare (England et al. 1990, Hurst and Lacki 1999), but further investigation is warranted to assess survival of these individuals once nursery colonies disband.

A high rate of turnover within aggregations of bats observed at roosts does not necessarily preclude a pronounced degree of fidelity by some individuals to these structures (Whitaker and Gummer 2000). Other studies of *C. rafinesquii* in the Gulf Coastal Plain and elsewhere corroborate my findings that this species shows long-term fidelity to human-made roosts. Ferrara and Leberg (2005a) recaptured individuals at bridges in Louisiana up to 4 years following their banding by Lance (unpubl. Master's thesis). Philopatry by females that returned to abandoned houses has been noted in eastern North Carolina (Clark 1990) and in southern Arkansas (D. Saugey, [Jessieville-Winona-Fourche Ranger District, Ouachita NF, Jessieville, AR] pers. comm.). Jones and Suttkus (1975) recaptured individuals up to 7 years after their banding in Louisiana in

Mississippi, although a maximum of 3 years was the norm. Individuals reused a cistern for consecutive winters in northwestern Tennessee (Hoffmeister and Goodpaster 1963).

Philopatry by a low-fecundity species such as *C. rafinesquii* promotes spatial subdivision of its population into demes in which their constituents' eventual high degree of relatedness can be considered familial (Shields 1983). Infrequent interchange of individuals among different demes, as is also the case for other bats with similar wing morphology (e.g., *Corynorhinus townsendii* [Fellers and Pierson 2002], *Plecotus auritus* [Entwistle et al. 2000]) would facilitate this outcome (but see Piaggio and Perkins 2005). Having noted the segregation of adult male *C. rafinesquii* from nearby maternity colonies over long periods (observations corroborated by the present investigation), Clark (1990) categorized the social system of this species as polygyny, whereby territorial males defend a specific day roost, or (more likely), access to the female bats that occasionally co-habit the structure or roost within its vicinity, as is known in other bats, e.g., *Artibeus jamaicensis* (Morrison 1979). If within-colony copulations were discouraged (by adult males already resident in a roost area and/or by avoidance mechanisms, i.e., kin recognition), then dispersal by juvenile males, which do not typically breed their first year (England et al. 1990, Jones and Suttkus 1975), might improve their fitness under such circumstances. In species where high site fidelity is the norm, sex-biased dispersal (but still within the constraints of philopatry) may buffer deleterious effects of extreme inbreeding (Shields 1983). Alternatively, populations may depend on "extra-colony copulations" that occur outside the maternity season between females from these social units and nonaffiliated males, as is the case in *P. auritus* (Burland et al. 1999).

The tendency of some individuals to roost at > 1 bridge within a particular area (usually defined by the drainage of a particular stream), and because some individuals returned to sites at which replacement of the bridge had occurred, suggests that *C. rafinesquii* showed interannual fidelity to a particular locality or "roost area" rather than merely to a specific structure. This notion is consistent with the habits of other nonmigratory, forest-dwelling species of bats, e.g., *Chalinolobus tuberculatus* (O'Donnell 2000), *Eptesicus fuscus* (Willis and Brigham 2004), *Myotis bechsteinii* (Kerth et al. 2001), and *P. subflavus* (Veilleux and Veilleux 2004) as well as *Myotis sodalis*, a short distance migrant (Kurta and Murray 2002). Furthermore, certain localities were occupied each year by both maternity colonies and solitary individuals; e.g., in the CRD, the East (Gunstock-Piney Woods Creeks) and West localities (Tiger and East Tiger Creeks) along FR 202 and in the DRD, Whiskey-Water Prong Creeks and Hickory-Beaver Creeks along Benndale Road.

Rather than inhabiting large areas of forest in which they could have been found at any number of bridges or other manmade roosts, recaptured bats typically showed fidelity to single roosts or to pairs of bridges or other structures that were located near (ca. 1 km) one another. In contrast, I consistently observed absence or scarcity of bats at other bridges, even when they were monitored regularly. These data imply that *C. rafinesquii*'s distribution in the study area approximated that of a metapopulation – a spatially subdivided population with concentrations of individuals amid a matrix of presumably unsuitable habitat (Wiens 1996). Considering that the study area was a mosaic of forest cover and that *C. rafinesquii* forage in a variety of forested conditions, e.g., oak-hickory forest (Hurst and Lacki 1999) or pine stands in the sapling stage

(Menzel et al. 2001), lack of foraging habitat was unlikely limiting. On the other hand, presence of bridges reflected particular habitat conditions (streams and associated riparian forest) that were neither uniformly nor randomly distributed across the landscape; indeed, with their potential to serve as roosts, bridges represented novel and potentially valuable habitat components for *C. rafinesquii*. A similar situation exists in the Western U. S., where *C. townsendii* apparently exists in metapopulations based on the distribution of suitable roosts (mines or caves) and the geological conditions that make such features possible (Sherwin et al. 2005). Proper classification of a metapopulation requires knowledge of the dynamics within such a population's subunits as well as their degree of connectivity (Stith et al. 1996). Therefore, further investigation of demographic processes in the studied population of *C. rafinesquii* is necessary.

In *C. rafinesquii* each sex may benefit from long-term roost fidelity for different reasons. Roost fidelity by reproductive female bats increases their familiarity with areas containing roosts that enhance their fitness (Kunz and Lumsden 2003), an outcome further promoted by natal philopatry (Veilleux and Veilleux 2004). Beneficial aspects of a roost to female bats might include its close proximity to patches where food is plentiful (Rydell 1989), safety from predators (Lausen and Barclay 2006), a microclimate that promotes growth of young (Lausen and Barclay 2006), and/or likelihood of use by fellow members of a social unit (Willis and Brigham 2004). For male *C. rafinesquii,* in addition to the first two factors, defense of resources (i.e., females) would facilitate their fidelity to a particular site (and its constituent roosts) where such resources were also present (Rydell 1989).

Widespread loss of bottomland hardwood forests that contained its natural roosts (large hollow trees) in the Gulf Coastal Plain has made *C. rafinesquii* increasingly dependent on bridges and other human-made structures (Clark 2003). Securing these roosts is obviously a priority for conservation of this species, but retaining diverse vegetation communities within the landscape ensures that the full suite of its life history requirements may be met. Maintaining connectivity of these habitats is critical for bats such as *C. rafinesquii* whose morphology, specialization in habitat, and philopatric nature make them particularly susceptible to fragmentation (Safi and Kerth 2004). This study contributes further evidence to the paradigm that *C. rafinesquii* perceives its environment at a relatively fine scale. Thus, disturbances or actions that reduce its roosts in number or otherwise diminish quality of its forest habitat at even a local scale could potentially damage the species' populations.

Appendix A

BANDINGS AT MATERNITY ROOSTS

Locations of maternity colonies of Corynorhinus rafinesquii *in DeSoto National Forest from 2000-2004. "East" refers to a pair of bridges located at Gunstock and Piney Woods Creeks along Forest Road (FR) 202 at its at the eastern end. "Hollis" refers to a pair of bridges located at Hollis Creek and Whetstone Branch, respectively, along FR 201 (eastern end). "North" refers to one bridge (creek unnamed) along FR 206, an abandoned house, and an empty oil storage tank (the last two roosts being found at different locations east of FR 206). "North Thompson" refers to a bridge along FR 201 that crosses Thompson Creek (upstream site). "South Thompson" refers to a pair of bridges along FR 202 that cross Thompson Creek (downstream site) and a nearby swampy area. "Spring" is a single roost named for the creek spanned by this bridge along FR 202. "West" refers to 3 bridges located at Little Tiger, Tiger, and East Tiger Creeks along FR 202 (western end). Chickasawhay Ranger District is indicated by "CRD," and DeSoto Ranger District is abbreviated "DRD." "Beaver-Hickory" refers to a pair of creeks that cross Benndale Road and are each spanned by a different bridge. "Benndale" refers to an unnamed creek crossed by Benndale Road at a bridge. "Calf" refers to a pair of bridges that span Calf Branch and a nearby (< 50 m away) ditch along Benndale Road. "Whiskey North" refers to a pair of bridges that cross Water Prong and Whiskey Creeks (upstream site) along FR 309. "Whiskey South" refers to three bridges located along FR 307 that cross Whiskey Creek (downstream site), a swampy area adjacent this stream, and its tributary, Flat Branch, respectively. Dates when bats were captured and number of individuals banded per month are provided.*

Locality (# bridges)	District	Dates of banding (number of bats banded)
East (2)	CRD	September 2000 (1), June 2001 (1), July 2001 (2), May 2002 (2), July 2002 (1), August 2002 (2), July 2004 (2)
Hollis (2)	CRD	August 2000 (1), July 2001 (11), August 2001 (1), June 2003 (1)
North (3[a])	CRD	June 2001 (1), June 2002 (2), August 2002 (1), November 2002 (1), June 2003 (2), June 2004 (1), July 2004 (1)
North Thompson (1)	CRD	September 2000 (1), July 2001 (1), May 2003 (2), June 2003 (2), July 2003 (1), August 2003 (1)
South Thompson (2)	CRD	July 2001 (3), May 2002 (1), July 2002 (1), September 2002 (1), March 2003 (1), July 2003 (3)
Spring (1)	CRD	July 2001 (2)
West (3)	CRD	August 2000 (1), July 2001 (1), July 2002 (2), November 2002 (1), June 2003 (5), July 2003 (4)
Beaver-Hickory (2)	DRD	July 2000 (4), August 2000 (1), June 2001 (1), July 2001 (3), July 2003 (1)
Benndale (1)	DRD	July 2000 (4), June 2001 (1)

Appendix A continued

Calf (2)	DRD	July 2000 (6), August 2000 (3), June 2001 (2), July 2001 (6)
Whiskey North (2)	DRD	July 2000 (2), August 2000 (3)
Whiskey South (3)	DRD	22 August 2000 (1), 12 October 2000 (1), 25 July 2001 (4)

[a] Includes one bridge, an abandoned house, and an empty oil tank

Appendix B

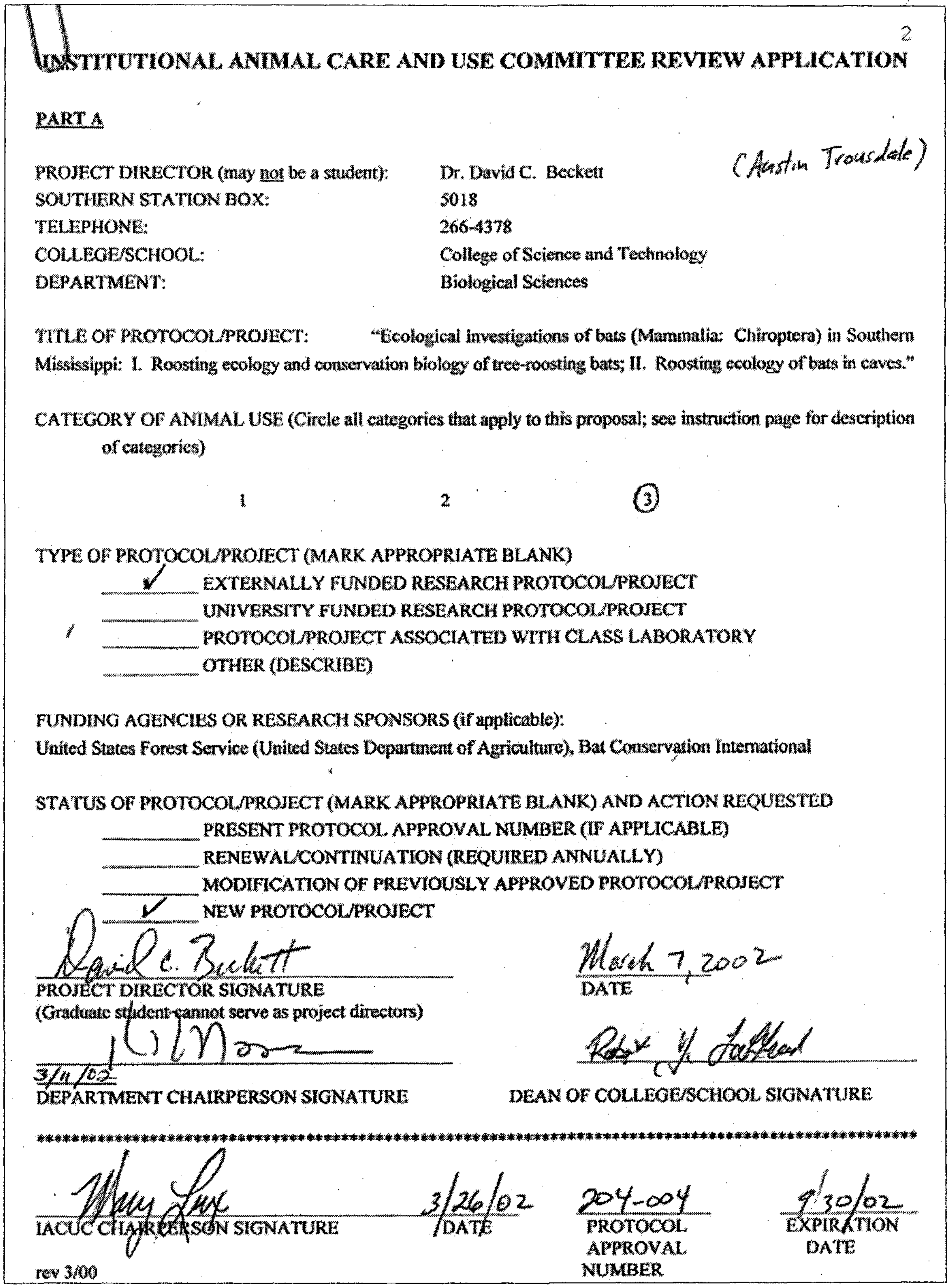
BANDINGS AT NON-MATERNITY ROOSTS

Locations of non-maternity roosts of Corynorhinus rafinesquii *in DeSoto National Forest with number and sex of bats captured and banded at each site from 2000-2004. Locality names represent particular bridges (named for the creek at which they were located) or abandoned houses. Chickasawhay Ranger District indicated by "CRD," and DeSoto Ranger District is abbreviated "DRD."*

Locality	District	Date(s) of banding (sex of bat)
Byrd	CRD	October 2000 (♂), June 2002 (♂)
Camp	CRD	May 2001 (♂)
East Tiger (North)	CRD	May 2002 (♂)
House #1	CRD	July 2000 (♂)
Little	CRD	May 2002 (♂)
Okey	CRD	July 2002 (♂)
Sandhill	CRD	August 2000 (♂)
Tiger	CRD	September 2001 (♂)
West Tiger	CRD	April 2003 (♂)
Cypress	DRD	July 2001 (3 ♂'s)
Deep	DRD	October 2000 (♀)
House #2	DRD	June 2001 (♀)

Appendix C

COPY, INSTITUTIONAL ANIMAL CARE AND USE COMMITTEE APPROVAL



2

INSTITUTIONAL ANIMAL CARE AND USE COMMITTEE REVIEW APPLICATION

PART A

PROJECT DIRECTOR (may not be a student): Dr. David C. Beckett (Austin Trousdale)
SOUTHERN STATION BOX: 5018
TELEPHONE: 266-4378
COLLEGE/SCHOOL: College of Science and Technology
DEPARTMENT: Biological Sciences

TITLE OF PROTOCOL/PROJECT: "Ecological investigations of bats (Mammalia: Chiroptera) in Southern Mississippi: I. Roosting ecology and conservation biology of tree-roosting bats; II. Roosting ecology of bats in caves."

CATEGORY OF ANIMAL USE (Circle all categories that apply to this proposal; see instruction page for description of categories)

1 2 [✓ 3]

TYPE OF PROTOCOL/PROJECT (MARK APPROPRIATE BLANK)
__✓__ EXTERNALLY FUNDED RESEARCH PROTOCOL/PROJECT
_____ UNIVERSITY FUNDED RESEARCH PROTOCOL/PROJECT
_____ PROTOCOL/PROJECT ASSOCIATED WITH CLASS LABORATORY
_____ OTHER (DESCRIBE)

FUNDING AGENCIES OR RESEARCH SPONSORS (if applicable):
United States Forest Service (United States Department of Agriculture), Bat Conservation International

STATUS OF PROTOCOL/PROJECT (MARK APPROPRIATE BLANK) AND ACTION REQUESTED
_____ PRESENT PROTOCOL APPROVAL NUMBER (IF APPLICABLE)
_____ RENEWAL/CONTINUATION (REQUIRED ANNUALLY)
_____ MODIFICATION OF PREVIOUSLY APPROVED PROTOCOL/PROJECT
__✓__ NEW PROTOCOL/PROJECT

David C. Beckett
PROJECT DIRECTOR SIGNATURE
(Graduate student cannot serve as project directors)

March 7, 2002
DATE

3/11/02
DEPARTMENT CHAIRPERSON SIGNATURE

DEAN OF COLLEGE/SCHOOL SIGNATURE

****

Mary Lux
IACUC CHAIRPERSON SIGNATURE

3/26/02
DATE

204-004
PROTOCOL APPROVAL NUMBER

9/30/02
EXPIRATION DATE

rev 3/00

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