

MORRIS, ADAM D., M.S. Use of Forest Edges by Bats in a Managed Pine Forest Landscape in Coastal North Carolina. (2008)  
Directed by Dr. Matina Kalcounis-Rüppell. 43 pp.

Forest edges represent the interface of two vegetation types and often have increased species richness and abundance (edge effects). Edges can affect spatial distribution of species and dynamics of species interactions. Landscapes of intensively managed pine stands are characterized by mosaic-patterning of forest patches and linear forest edges. Managed pine forests are a major landscape feature of the Southeastern U.S., and the effects of intensive pine management on bat communities are poorly understood. Therefore, I examined bat foraging behavior in four structurally distinct stand types (young open-canopy pine, pre-thinned pine, thinned pine, and unmanaged forest) and along forest edges within a managed pine forest landscape in the coastal plain of North Carolina during the summers of 2006 and 2007. At each sampling site, from dusk until dawn, I recorded echolocation calls of bats using Pettersson D240X bat detectors with digital recorders. At each site, I indexed the insect community using malaise insect traps. I captured bats with mist nets to obtain reference echolocation calls. I used negative binomial count regression models to describe bat foraging behavior relative to stand types, forest edges, and availability of insect prey. For all species detected, bat foraging behavior was strongly related to forest edges. Edges were used extensively by six aerial-foraging bat species, but avoided by clutter-tolerant *Myotis* species. My results emphasize that forest edges are important landscape features in fragmented landscapes.

**USE OF FOREST EDGES BY BATS IN A MANAGED PINE FOREST  
LANDSCAPE IN COASTAL NORTH CAROLINA**

by

Adam D. Morris

A Thesis Submitted to  
the Faculty of The Graduate School at  
The University of North Carolina at Greensboro  
in Partial Fulfillment  
of the Requirements for the  
Master of Science

Greensboro  
2008

Approved by

---

Committee Chair

**APPROVAL PAGE**

This thesis has been approved by the following committee of the Faculty of The Graduate School at The University of North Carolina at Greensboro.

Committee Chair \_\_\_\_\_

Committee \_\_\_\_\_

\_\_\_\_\_

\_\_\_\_\_

\_\_\_\_\_

\_\_\_\_\_  
Date of Acceptance by Committee

\_\_\_\_\_  
Date of Final Oral Examination

## **ACKNOWLEDGEMENTS**

Thanks to my graduate advisor Dr. Matina Kalcounis-Rüppell, and thesis committee members Dr. Darren A. Miller, Dr. Anne Hershey, and Dr. Elizabeth Lacey. Weyerhaeuser Company provided funding for the project. Thanks to Darren Miller, Bill Barber, and Brian Hulka for facilitating this project and providing logistical support in the field. Students in the UNCG Bat lab Melissa Vindingi, David Allgood, and John Hart-Smith helped in the field and in the lab. Lindsey Shiflet, Jessica McDonough, Megan Fitzgerald, and Justin Stowens also helped in the laboratory. Thanks to Jackie Metheny and John Bowles for their support throughout. Thanks to Dr. Kirsten Doehler for statistical advice.

## TABLE OF CONTENTS

	Page
LIST OF TABLES.....	v
LIST OF FIGURES.....	vi
CHAPTER	
I. INTRODUCTION.....	1
II. METHODS.....	6
Study Area.....	6
Sampling Design .....	7
Acoustic Sampling .....	8
Mist Netting.....	9
Insect Trapping .....	10
Regression Analysis .....	10
III. RESULTS.....	12
Model Selection.....	13
Overall Bat Activity .....	13
Bat Species Activity.....	14
IV. DISCUSSION.....	15
Management Implications.....	18
REFERENCES.....	34

## LIST OF TABLES

	Page
<b>Table 1.</b> Summary of Time-expanded Echolocation Calls Recorded in Stands and Along Forest Edges.....	20
<b>Table 2.</b> Model Selection Criteria for Overall Bat Activity Models.....	21
<b>Table 3.</b> Model Selection Criteria for Bat Species Activity Models .....	22
<b>Table 4.</b> Parameter Estimates for Overall Bat Activity and Feeding Activity Count Regression Models .....	23
<b>Table 5.</b> Parameter Estimates for Negative Binomial Models of Bat Species Activity.....	24

## LIST OF FIGURES

	Page
<b>Figure 1.</b> Location of Weyerhaeuser Parker Tract in Eastern North Carolina.....	25
<b>Figure 2.</b> Mosaic Pattern Landscape of the Weyerhaeuser Parker Tract.....	26
<b>Figure 3.</b> Forest Edges of the Weyerhaeuser Parker Tract.....	27
<b>Figure 4.</b> Weyerhaeuser Parker Tract Sampling Sites.....	28
<b>Figure 5.</b> Comparison of Model Fit for Overall Bat Activity Models.....	29
<b>Figure 6.</b> Comparison of Model Fit for Bat Species Activity Models .....	30
<b>Figure 7.</b> Overall Bat Activity and Feeding Activity in Stands and Along Forest Edges.....	31
<b>Figure 8.</b> Relative Bat Activity in Forest Stand Interiors .....	32
<b>Figure 9.</b> Relative Bat Activity along Forest Edges.....	33

## CHAPTER I

### INTRODUCTION

The coastal plain of North Carolina is largely composed of forested wetlands that have been converted into agricultural areas and managed timberlands (Guldin and Wigley 1998; Schultz 1999; NCSSF 2005). Managed pine (*Pinus* spp.) forests are economically important to the southeastern United States, accounting for 60% of timber products made in the United States (NCSSF 2005). Active forest management in eastern North Carolina involves draining of standing water and the creation of a mosaic pattern of forest patches in different seral stages (Watts and Wilson 2005; Kuusipalo and Kangas 1994). Mosaic-pattern fragmentation of landscapes leads to a large increase in amount of forest edge (Guldin and Wigley 1998).

Edges provide a unique set of microhabitats because they encompass the interface of two vegetation types (Forman and Godron 1981; Matlack 1994). Forest edges filter sunlight, wind, heat, humidity, and moisture entering the forest interior (Yahner 1988; Forman and Godron 1981; Matlack 1994). Effects of abiotic influences within forest stands typically decrease with further distance from an edge (Schlaepfer and Gavin 2001). Spatial configuration of edges in a landscape can have varying effects on species assemblages and interactions between species (Ewers and Didham 2006; Yahner 1988; Fagan et al. 1999; Herlin 2001; Cadenasso and Pickett 2000, 2001; Schlaepfer and Gavin



2001; Donovan et al. 1997). Plant community composition along edges may be enhanced by fast-growing, shade intolerant “gap specialists,” causing edges to have high species abundance and diversity (Yahner 1988; Ewers and Didham 2006; Fagan et al. 1999). Increase in plant diversity along edges may be accompanied by an increase in herbivory and predator-prey interactions (Cadenasso and Pickett 2000; Donovan et al. 1997). This increased species richness and species abundance along edges is termed the ‘edge effect’ (Ewers and Didham 2006). Edges can affect spatial distribution of species by limiting or preventing dispersal of a species across a boundary (Yahner 1988; Fagan et al. 1999; Herlin 2001). The resulting accumulation of species along edges may affect frequencies of interactions among species. Edges may contribute toward instability of species interactions (*hyperdynamism*) (Ewers and Didham 2006). Although many species are abundant along edges, other species are restricted to undisturbed interior habitat and avoid edges (Ewers and Didham 2006; Fraver 1994; Yahner 1988). Because species respond to edges in different ways (Yahner 1988; Fagan et al. 1999; Herlin 2001; Cadenasso and Pickett 2000, 2001; Schlaepfer and Gavin 2001; Donovan et al. 1997), it is important to examine species-level effects of generating numerous forest edges across a landscape.

Insectivorous bats are important nocturnal predators in pine forest landscapes of the southeastern U. S. However, effects of intensive pine management on bat communities are not well understood (Miller et al. 2003; *but see* Miller 2003; Miles et al. 2006; Menzel et al. 2005; Elmore et al. 2005). Forest edges associated with intensive pine management may have important effects on bat foraging behavior. Bats have been

observed using forest edges for commuting and foraging (Hogberg et al. 2002; Grindal et al. 1999; Clark et al. 1993; Tibbels and Kurta 2003; Walsh and Harris 1996) and are known to use canopy gaps created by natural or anthropogenic disturbances (Fenton et al. 1998; Crome and Richards 1988). Edges may support different insect communities than forest interiors, which could affect bat foraging patterns. Some bats are thought to use edges and gaps to avoid navigating through structurally complex habitat (Kusch et al. 2004, Clark et al. 1993). Therefore, forest edges may provide valuable commuting and foraging opportunities.

Bat species are constrained to certain foraging habitats by their body and echolocation morphology (Norberg and Rayner 1987; Aldridge and Rautenbach 1987; Fenton 1990; Fenton et al. 1998). Bats species are often sorted into guilds based on their hunting strategies, morphologies, and habitat use (Fenton 1990; Schnitzler and Kalko 2001; Schnitzler et al. 2003). These guilds or groups are largely based upon bats' ability to fly and hunt within varying levels of clutter, which is defined as any structural objects within a habitat that interfere with bats' ability to navigate and hunt using echolocation (Sleep and Brigham 2003). Some species are more maneuverable in flight and forage effectively in structurally complex forest habitat, whereas other species are less agile and hunt in open areas (Menzel et al. 2005; Kusch et al. 2004; Norberg and Rayner 1987; Crome and Richards 1988; Aldridge and Rautenbach 1987). Maneuverability of insectivorous bats has commonly been described using two morphological indices: 'wing-loading' (ratio of weight to wing surface area) and 'aspect ratio' (ratio of weight to wingspan) (Norberg and Rayner 1987; Crome and Richards 1988; Kalcounis and

Brigham 1995; Aldridge and Rautenbach 1987). In general, large bats have high wing loadings and aspect ratios, fly fast, and aren't very maneuverable in complex habitat (Aldridge and Rautenbach 1987). Bats with smaller wing loadings and aspect ratios are much more maneuverable and can hunt within complex forest interiors (Aldridge and Rautenbach 1987). In addition to limitations on bats' flight abilities, insectivorous bats are restricted to areas in which they can effectively use echolocation to locate and capture insects (Fenton 1990). Bats use echolocation calls that correspond with the spatial environment in which they are hunting (Schnitzler and Kalko 2001). Bats that forage in open areas often use long, loud, constant-frequency (CF) echolocation calls, whereas bats that forage within the forest canopy use shorter frequency-modulated (FM) calls (Schnitzler and Kalko 2001). Bat species that use a combination of CF and FM calls are flexible in their foraging behavior and may use multiple habitat types.

Bats' choice of foraging habitat may also be based on diversity and/or abundance of insect prey available (Kusch et al. 2004, Meyer et al. 2004; Tibbels and Kurta 2003; Verboom and Spoelstra 1999). Many insectivorous bat species are thought to be dietary generalists while others appear to be more specialized (Kalcounis-Rüppell et al. 2007). It remains unclear whether bats select foraging areas based largely on concentrations of available prey, or if prey selection is secondary to choosing habitats based on structural characteristics. There have been correlations recorded between bat size and the size of insect prey taken (Hickey et al. 1996; Carter et al. 2003). However, this trend may be a result of habitat partitioning (Barclay and Brigham 1994) or due to limitations in what

prey are detected by echolocation (Barclay and Brigham 1991), rather than the result of active prey discrimination.

Given the number of acres under intensive pine management in the southeastern U.S. and the general lack of information on bat ecology within these systems, it is important to better understand response of bat communities to intensive silviculture. Additionally, understanding potential prey occurrence relative to forest management is relatively unknown within intensively managed pine landscapes. My results may provide information useful to managers to allow better integration of forestry and wildlife objectives. Therefore, the purpose of my study was to examine foraging behavior of bats within intensively managed pine landscape with an emphasis on use of edges. Using acoustic monitoring data, I developed a series of regression models that describe bat activity in relation to landscape structure and prey availability. I tested the null hypotheses that overall bat activity, bat feeding activity, and species-specific bat activity were unrelated to stand structure, forest edges, and the distribution of insect orders.

## CHAPTER II

### METHODS

#### Study Area

This study was conducted on Weyerhaeuser Company's Parker Tract, an intensively managed pine landscape in the coastal plain in Washington County, North Carolina, near Plymouth, NC (Figure 1). The 4,000 ha Parker Tract was composed primarily (76.1%) of managed loblolly pine (*Pinus taeda*) stands with a mosaic pattern of even-aged forest patches of different ages. In addition, some stands in the Parker Tract were natural hardwood stands as part of a conservation easement between Weyerhaeuser and the Environmental Defense Fund (1997). Typical silviculture of intensively managed stands included clearcut harvest at 27-35 years old following by site preparation, planting of loblolly pine seedlings on a wide (6.1 m) row spacing, vegetation control, fertilization, thinning, and final harvest. I classified stands into four classes based on structural appearance: young *open*-canopy pine plantation, *pre-thinned* pine plantation, *thinned* pine plantations, and *unmanaged* forest. *Open* plantations had been clearcut and replanted recently, averaging 7.8 years old (range 0-15 years old). *Pre-thinned* plantations contained mid-age pines (average=19.6, range 14-24 years old) with canopies densely cluttered with branches, and lacking groundstory structure. *Thinned* pine plantations, averaging 28.2 years old (range 25-33 years old), had open canopy structure, with variable understory and midstory development between wide rows of mature pines.

*Unmanaged* stands were dominated by red maple (*Acer rubrum*) and red bay (*Persea borbonia*) and have been referred to as coastal hardwood swamp (Wilson et al. 2000).

These four forest stand types were well distributed across the Parker Tract (Figure 2) with forest edges common due to the mosaic patterning of these seral patches. Forest edges were defined as 100 meter wide buffer areas along the boundaries between heterogeneous stands (Figure 3). The relative area of edge depends on the size and shape of patches and ranged from 22% to 100% of total patch area. I focused on the hard forest edges occurring between forested stands (*pre-thinned*, *thinned*, or *unmanaged*) and *open* stands. Hard forest edges accounted for 28.1% of all edges, and occupied 45.7% of the area of *open* stands.

### **Sampling Design**

I used Pettersson D240X full spectrum bat detectors (Pettersson Elektronik AB, Sweden) coupled with digital recorders (*see below*) to record echolocation calls of bats during June and July of 2006 and from May to June 2007 (Figure 4). I sampled selected stands randomly to avoid temporal effects. I concurrently sampled sites in two non-bordering stands each night, selecting representative sites within the constraint of travel distance between sites. I sampled novel sites each night, instead of repeatedly sampling the same sites. This approach allowed measurement of within-stand variability (Link et al. 1994), while providing replication at the stand level. I chose stand interior sites that were at least 100 meters from any edges or roads. Along edges, I set detectors in open stands within 100 meters from bordering forested stands. At each sampling site, I set two

bat detectors to record from dusk until dawn: one Pettersson D240X in heterodyne mode and one Pettersson D240X in time-expansion mode. Detectors were housed in plastic boxes with small holes cut around their microphones. I stacked the plastic boxes within a large wooden box for weather protection. I positioned the wooden boxes 1-2 meters above ground level, tied around trees or metal poles using elastic cords. I oriented the detectors at 45 degrees above horizontal and pointed them toward canopy openings to limit effects of vegetation on sound propagation (Patriquin et al. 2003) and to record maximum number of bats (Weller and Zabel 2002).

## **Acoustic Sampling**

### **I. Heterodyne Mode Recording**

At each sampling site I used a D240X bat detector in heterodyne-mode to record echolocation calls of bats continuously through the night to a Sony digital recorder (Sony Memory Stick Voice Recorder; Sony Electronics Inc.). Heterodyne mode recording uses frequency subtraction to lower frequency of ultrasonic echolocation calls of bats, allowing them to be recorded (Parsons et al. 2000). I tuned my heterodyne detectors to 40 kHz, and therefore sampled the window of frequencies ranging from 35 kHz to 45 kHz, a range commonly used by bat species in the Southeastern U.S. Heterodyne recordings cannot be used to identify individual bats, but can provide a useful index of bat activity (counts of bat echolocation sequences). Heterodyne bat recordings also allow identification of echolocation sequences used for feeding due to presence or absence of a ‘feeding buzz’, a distinct sound that bats make as they approach and capture an insect

prey item (Griffin 1960). From heterodyne recordings, I obtained counts of bat echolocation sequences and counts of feeding echolocation sequences.

## **II. Time Expansion Recording**

At each sampling site I used a D240X bat detector in time-expanded mode to record full-spectrum echolocation calls of bats to an iRiver digital recorder (iRiver ifp, Reigncom Ltd., Korea). Time-expansion recording involves a recording delay in which recorded sounds are played back and recorded at a tenth of actual speed to capture a high-resolution sonogram of each bat vocalization (Parsons et al. 2000). I recorded 1.7 second segments of sound, which takes 17 seconds to process and record. This spectral resolution allows identification of bat species from sonograms, but does not allow continuous sampling due to the recording delay. Recorded sound files were uploaded to a computer and analyzed using Sonobat 2.5 sound analysis software (Sonobat, 315 Park Ave, Arcata, CA 95521). I qualitatively identified echolocation sequences to species groups using a reference echolocation call library as described by Kalcounis-Rüppell et al. (2007). Passes that did not contain search-phase echolocation pulses were discarded.

## **Mist Netting**

I captured bats using mist nets (Avinet Inc., Dryden, New York, USA) of various sizes (2m, 6m, 9m, or 12m wide; 2.6m or 5.2m high) over water sources and across corridors within the managed forest landscape. I captured bats for species verification and to obtain reference echolocation calls. Upon capture, I took standard measurements (species, sex, weight (g), age class (juvenile or adult), reproductive condition). I fitted



captured bats with light tags or followed them with a spotlight as they were released to record reference echolocation calls. All animal handling followed the guidelines of the American Society of Mammologists, the UNCG Institutional Animal Care and Use Committee Protocol #06-11, and the Wildlife Resources Committee of the state of North Carolina.

### **Insect Trapping**

I used passive malaise traps to capture flying and terrestrial insects overnight at sites I sampled with bat detectors. I preserved insects in 95% ethanol solution upon capture. I identified insects to order using an Olympus SZ30 dissecting microscopes (Olympus America, Inc. Center Valley, PA) at 9X-40X using taxonomic keys (Arnett 2000). Only insect orders with total counts of 50 or more individuals were included in the regression analyses.

### **Regression Analysis**

I used a series of count regression models to address the null hypotheses that overall bat activity (counts of bat echolocation sequences), bat feeding activity (counts of echolocation sequences containing a feeding buzz), and bat species activity (counts of echolocation sequences identified to a given species) were not related to stand types, forest edges, and the availability of insects. I used count regression models because response variables in the form of counts (non-negative integers) often violate the distributional assumptions of parametric modeling techniques (Vincent and Haworth

1983; White and Bennetts 1996) and may be skewed due to a high frequency of zero-counts (Cunningham and Lindenmayer 2005, Martin et al. 2005). I modeled counts of bat echolocation sequences using Poisson (Vincent and Haworth 1983), negative binomial (Bliss and Fisher 1953; White and Bennetts 1996), zero-inflated Poisson (ZIP), and zero-inflated negative binomial (ZINB) regression models (Lambert 1992; Cunningham and Lindenmayer 2005). I evaluated the fit of these four distributions for each response variable using probability-count plots and AIC and BIC scores (Akiake 1973) as described by Sileshi (2006). After selecting a model distribution, I evaluated hierarchical candidate models based on the significance ( $\alpha=0.05$ ) of their parameter estimates and their AIC and BIC scores.

In count regression models, forest stand types (*open, prethinned, thinned, unmanaged*) and forest edges (*edge, interior*) were introduced as categorical (indicator) variables, and counts of insects (by order) as continuous model predictors. This approach allowed simultaneous testing of the effects of landscape and prey availability on bat foraging behavior. I also tested significance of the covariates daily mean temperature ( $^{\circ}\text{C}$ ) and daily mean precipitation (cm) to attempt to resolve some temporal variation in bat activity. I created parsimonious final models by retaining only the most useful predictors. All regression models were fit and analyzed using PROC COUNTREG and PROC GENMOD procedures in SAS 9.1 (SAS, Cary, NC).

## CHAPTER III

### RESULTS

I acoustically sampled 156 sites over 78 nights between May and July of 2006 and 2007 (Figure 4). Sampling sites were within *open* (n=27), *pre-thinned* (n=26), *thinned* (n=28), and *unmanaged* (n=27) stands and along hard forest *edges* (between open and forested stands) (n=46). At these sites I captured 15,153 total insects representing 18 Orders (Diptera n=12,456; Homoptera n=797; Lepidoptera n=564; Hymenoptera n=254; Coleoptera n=179; Collembola n=169; Hemiptera n=55; Orthoptera n=40; Thysanoptera n=36; Tricoptera n=24; Neuroptera n=16; Pscoptera n=14; Blattaria n=4; Megaloptera n=2; Dermoptera n=1; Diplura n=1; Mantidae n=1; and Isoptera n=1). In addition, I captured 142 bats of 5 species (*Lasiurus borealis* n=79, *Eptesicus fuscus* n=20, *Nycticeius humeralis* n=40, *Perimyotis subflavus* n=2, *Corynorhinus rafinesquii* n=1) using mist nets. I analyzed approximately 950 hours of heterodyne recordings which were found to contain 19,986 total bat echolocation sequences, including 1,909 feeding echolocation sequences. I analyzed over 100,000 time-expanded sound files containing 6,236 identifiable search-phase bat echolocation calls. The time-expanded bat echolocation sequences were qualitatively identified to seven species or species groups (*Lasiurus borealis* n=3,489; *Eptesicus fuscus* n=1,525; *Nycticeius humeralis* n=175, *Tadarida brasiliensis* n=526; *Lasiurus cinereus* n=270; *Perimyotis subflavus* n=159; and *Myotis spp.* n=92) (Table 1). Echolocation sequences from bats of the genus *Myotis* were

grouped because of their similar call structure. The *Myotis* spp. group could contain *Myotis septentrionalis* and/or *Myotis austroriparius*.

## **Model Selection**

Negative binomial regression models for overall bat activity (Table 2) and activity of seven species groups (Table 3) consistently gave lower AIC and BIC scores than Poisson or zero-inflated models. Negative binomial models also fit the distribution of counts better than Poisson models, due partially to the high observed frequency of zero-counts (Figures 5, 6). Significance tests for *alpha* (the over-dispersion parameter), supported negative binomial models over Poisson models. Therefore candidate models were fit using negative binomial regression. I selected parsimonious models for overall bat activity (Table 4) and the activity of seven species groups (Table 5) by retaining only variables significant at  $\alpha = 0.05$ .

## **Overall Bat Activity**

Overall bat activity was high along *edges* ( $p < 0.0001$ ), within *thinned* ( $p < 0.0001$ ) and *unmanaged* ( $p = 0.0002$ ) stands (Figure 7), and was positively correlated with counts of *Lepidoptera* ( $p = 0.01$ ). Counts of echolocation sequences containing a feeding buzz were high along *edges* ( $p = 0.001$ ), and within *thinned* stands ( $p = 0.017$ ), and were positively related to captures of *Lepidoptera* ( $p = 0.037$ ). The proportion of recorded echolocation sequences containing a feeding buzz was similar across all stand types and along edges (mean=0.102; 95% confidence interval=0.079, 0.125).

### **Bat Species Activity**

Activity of *Lasiurus borealis* was positively related with forest *edges* ( $p=0.043$ ), *unmanaged* stands ( $p=0.046$ ), and counts of *Lepidoptera* ( $p=0.008$ ). Activity of *Eptesicus fuscus* was high along *edges* ( $p<0.0001$ ), and in *thinned* ( $p<0.0001$ ) and *open* ( $p=0.041$ ) stands. Activity of *Tadarida brasiliensis* was high along *edges* ( $p=0.017$ ), but low in *unmanaged* ( $p=0.033$ ) stands. Activity of *Lasiurus cinereus* was high along *edges* ( $p<0.0001$ ) and in *open* stands ( $p<0.0001$ ), and was positively correlated with counts of *Lepidoptera* ( $p<0.0001$ ). Activity of *Perimyotis subflavus* was high along *edges* ( $p=0.001$ ), and was positively related to abundance of *Diptera* ( $p=0.016$ ). Activity of *Nycticeius humeralis* was high along *edges* ( $p=0.017$ ), and in *thinned* ( $p=0.0453$ ) and *unmanaged* ( $p=0.0284$ ) stands. Activity of *Myotis spp.* was negatively related with *edges* ( $p<0.0001$ ), *open* stands ( $p=0.0003$ ), and *thinned* stands ( $p=0.025$ ).

## CHAPTER IV

### DISCUSSION

Overall heterodyne-recorded bat activity and foraging activity were high along *edges*, and within *thinned* and *unmanaged* stands. Overall activity was also correlated with counts of *Lepidoptera*. These trends were likely driven by the most common species I recorded, *Lasiurus borealis* and *Eptesicus fuscus*. Species models show that patterns observed from heterodyne recordings were not universal across species, *i.e.* species-specific trends were obscured by treating a bat community as a single entity (Patriquin and Barclay 2003). Models for bat activity and foraging activity yielded very similar results because the proportion of echolocation sequences containing a feeding buzz was relatively constant (Figure 7). Kalcounis-Rüppell et al. (2007) found similar foraging rates for the bat community in the piedmont of North Carolina. Bats in the managed pine forest may be constantly feeding at a maximum rate while in flight, independent of habitat type. Additionally, to maximize foraging efficiency, bats may spend more time in preferred foraging areas.

Stand type and distribution of insect prey had species-specific effects on bat foraging behavior. Our results support studies that categorize bats based upon their ability to navigate and hunt within various levels of clutter. However, species also exhibited flexibility in their foraging behavior (Fenton 1990). *Lasiurus cinereus* and *Eptesicus fuscus* were active within *open* stands. *Lasiurus cinereus* is known to avoid

clutter, and is limited to foraging in open habitats (Fenton 1979). *Eptesicus fuscus* is known to be flexible in habitat use (Kalcounis-Ruppell et al. 2007), and was detected in moderate clutter and open areas. *Tadarida brasiliensis* is sometimes considered an open-area forager (Fenton 1979) and was detected frequently in *open* stands (Figure 8). Several bat species foraged within moderate amounts of clutter in *unmanaged* and *thinned* stands. *Unmanaged* forest patches had high activity of *Lasiurus borealis* and *Nycticeius humeralis*. *Unmanaged* forest patches may provide undisturbed roosting areas for tree-roosting bat species (Miles et al. 2006). *Thinned* stands were associated with high activity of *Eptesicus fuscus* and *Nycticeius humeralis* (Figure 8). Thinning removes structural clutter from stands, making them accessible to bat species like *Eptesicus fuscus*. Bats of the genus *Myotis* consistently foraged within stand interiors and avoided edges. Furthermore, *Myotis spp.* activity was negatively related with *open* and *thinned* stands. *Myotis septentrionalis* likely makes up a proportion of our *Myotis* detections (Morris et al. *in prep*), and is known to glean prey from substrates (Faure et al. 1993; Ratcliffe and Dawson 2003). This foraging strategy is not useful in open areas, and *Myotis septentrionalis* is known to avoid gaps and open areas (Owen et al. 2003; Patriquin and Barclay 2003).

Distribution of insect prey also played a role in our results. Insect order variables retained in models were useful in the presence of other explanatory variables; that is, they explained significant variation in the dependent variable after accounting for the effects of other model predictors. After accounting for site effects, counts of total echolocation sequences and echolocation sequences containing feeding buzzes were positively

correlated with counts of *Lepidoptera*. This trend was strongest in *Lasiurus borealis* and *Lasiurus cinereus*, which are known to specialize on *Lepidoptera* (Kalcounis-Rüppell et al. 2007). In addition, *Perimyotis subflavus* was most active in sites where *Diptera* were abundant. *Perimyotis* spp. is known to consume *Diptera*, and may be limited to small prey due to their own small size (Barclay and Brigham 1994).

My models suggest stand-level structural characteristics are more important across bat species than distribution of insects. Foraging behavior in bats likely involves a two-step process by which bats (1) choose an appropriate hunting habitat, based on mechanical (flight) constraints, and then (2) hunt certain prey within that habitat, based on functional constraints (echolocation). Stand-level characteristics like clutter conditions are of primary importance and insect availability may play a secondary role in shaping bat foraging behavior. Bat species may also partition habitat based on other resources (Arlettaz 1999; Saunders and Barclay 1992), such as proximity to roosts (Crampton and Barclay 1998) and water sources (Walsh and Harris 1996; Kusch et al. 2004; Vaughan et al. 1997).

In addition to showing stand-type preferences in foraging activity, bat species showed strong associations with forest edges. Six bat species (*Lasiurus borealis*, *Eptesicus fuscus*, *Nycticeius humeralis*, *Tadarida brasiliensis*, *Lasiurus cinereus*, *Perimyotis subflavus*) had substantially higher activity along forest edges than in forest interiors (Figure 9). This result is consistent with studies that show high species richness and abundance along edges (edge effects). These six bat species are aerial-hawking hunters with varying levels of clutter tolerance. For the bat species that were active in



forested stands (*Lasiurus borealis*, *Nycticeius humeralis*, *Perimyotis subflavus*), forest edges may provide valuable foraging opportunities because they are free of structural clutter. However, bat species that were most active in open areas (*Tadarida brasiliensis*, *Lasiurus cinereus*, *Eptesicus fuscus*), also had higher activity along edges than in stand interiors. For bats that forage efficiently in absence of clutter, forest edges may create a semi-permeable barrier to movements of bats into the forest, causing an accumulation of bat activity along edges. Furthermore, forest edges may redirect flow of foraging bats parallel to edges. Bats have been observed foraging along edges within the managed pine forest landscape (personal observation) and in other forested landscapes (Hogberg et al. 2002; Grindal et. al 1999; Clark et al. 1993; Tibbels and Kurta 2003; Walsh and Harris 1996). In addition to providing foraging habitat, linear forest edges may function as landmarks by which bats could orient themselves. Bats are known to use linear landscape features like roads and riparian corridors as flight paths (Law and Chidel 2002), and it is possible that linear forest edges may improve connectivity between foraging areas. This function of forest edges operates at a broader spatial scale and would require use of alternative methods (*e.g.* radiotelemetry) to examine effectively.

### **Management Implications**

I have shown that bats in intensively managed pine forest respond to landscape structure in species-specific ways. Thus, management for bats should attempt to accommodate different foraging strategies. Stand types appeared to be partitioned based on clutter conditions. The maintenance of a variety of cluttered and uncluttered stands,

ranging from open cutovers to closed canopy pine stands, may adequately provide foraging areas for bats with various tolerances for clutter. Linear forest edges affected activity patterns of all seven bat species groups detected. Edges were exploited by six common aerial hunting bat species. My results emphasize the importance of edges to bats within fragmented landscapes as foraging areas and possibly for aiding in navigation. Forest management that increases the amount of linear forest edges across the landscape likely benefits several bat species. However, interior forest patches are important to other species (*Myotis*), and should be retained. The relative areas of patch interiors and patch edges are determined by the size and shape of forest patches. Therefore, to best provide a variety of interiors and edge areas, stand patches should be heterogeneous in size and shape.

**Table 1.** Summary of Time-expanded Echolocation Calls Recorded in Stands and Along Forest Edges. Time-expanded echolocation sequences were identified to seven bat species groups. Means and standard errors of echolocation sequences per site per night are shown for each site type. Data are from acoustic monitoring within an intensively managed pine forest (Weyerhaeuser Parker Tract, Washington Co, North Carolina), during summers of 2006 and 2007. (*Myotis spp.* contains *Myotis septentrionalis* and/or *Myotis austroriparius*).

Bat species	Forest Edges (n=44)		Open Pine (n=26)		Pre-thinned Pine (n=21)		Thinned Pine (n=24)		Unmanaged (n=27)	
	mean	±se	mean	±se	mean	±se	mean	±se	mean	±se
<i>Lasiurus borealis</i>	31.48	±6.58	8.19	±3.06	26.05	±15.03	16.04	±7.38	35.52	±13.35
<i>Eptesicus fuscus</i>	23.98	±5.21	2.50	±0.81	1	±0.74	15.54	±11.89	0.41	±0.18
<i>Tadarida brasiliensis</i>	8.27	±5.70	3.46	±2.35	0.95	±0.76	1.67	±0.69	0.44	±0.14
<i>Lasiurus cinereus</i>	4.80	±2.96	1.88	±1.13	0.19	±0.11	0.25	±0.15	0	0
<i>Perimyotis subflavus</i>	2.91	±1.93	0.31	±0.14	0	0	0.17	±0.10	0.70	±0.53
<i>Nycticeius humeralis</i>	1.66	±0.51	0.27	±0.16	0.38	±0.33	1.63	±1.10	1.78	±1.16
<i>Myotis spp.</i>	0.10	±0.06	0.08	±0.05	1.14	±0.53	0.46	±0.34	1.89	±0.43

**Table 2.** Model Selection Criteria for Overall Bat Activity Models. Count regression models for total bat activity and feeding activity were compared based on Akaike information criterion (AIC), and Bayesian information criterion (BIC). Data are from acoustic monitoring within an intensively managed pine forest (Weyerhaeuser Parker Tract, Washington Co, North Carolina), during summers of 2006 and 2007. (*Myotis spp.* contains *Myotis septentrionalis* and/or *Myotis austroriparius*).

<b>Dependent variable</b>	<b>Model distribution</b>	<b>AIC</b>	<b>BIC</b>
total echolocation sequences	Poisson	21861	21876
	Negative Binomial	1571	1589
	ZIP	21412	21430
	ZINB	1573	1594
total feeding sequences	Poisson	3779	3791
	Negative Binomial	884	899
	ZIP	2658	2673
	ZINB	886	903

**Table 3.** Model Selection Criteria for Bat Species Activity Models. Count regression models for activity indices for seven bat species groups were compared based on Akaike information criterion (AIC) and Bayesian information criterion (BIC). Data are from acoustic monitoring within an intensively managed pine forest (Weyerhaeuser Parker Tract, Washington Co, North Carolina), during summers of 2006 and 2007. (*Myotis spp.* contains *Myotis septentrionalis* and/or *Myotis austroriparius*).

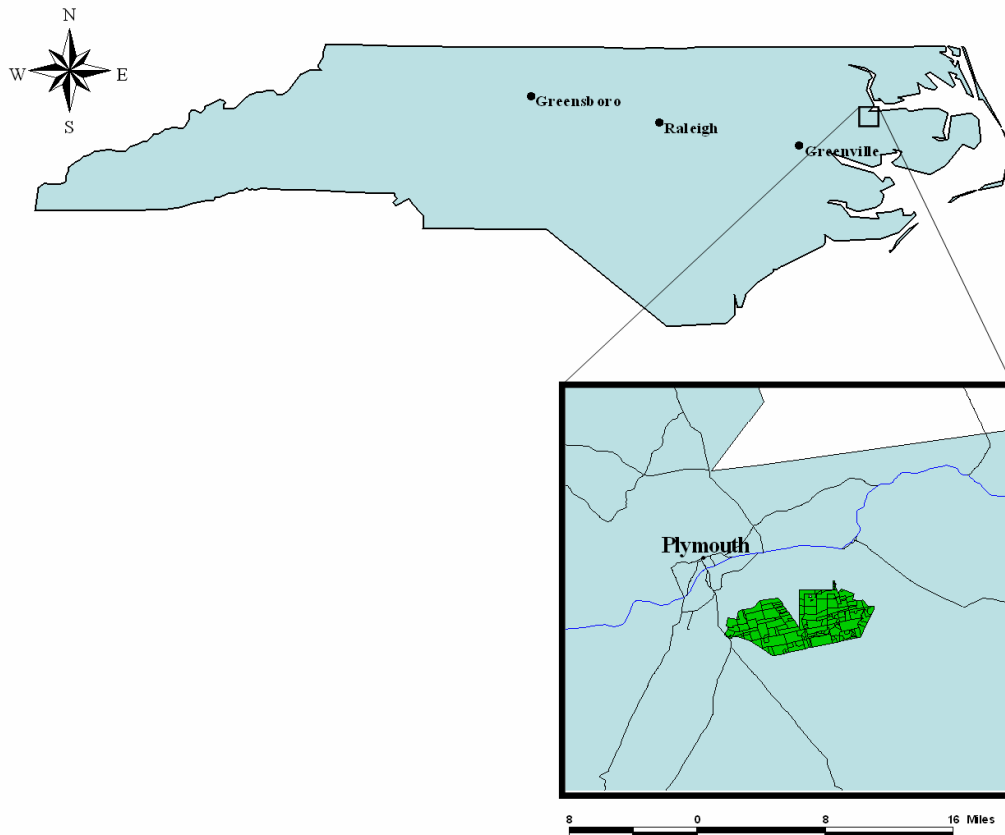
<b>Bat Species Activity</b>	<b>Model distribution</b>	<b>AIC</b>	<b>BIC</b>
<i>Lasiurus borealis</i>	Poisson	7759	7771
	Negative Binomial	985	999
	ZIP	5586	5601
	ZINB	986	1004
<i>Eptesicus fuscus</i>	Poisson	3802	3817
	Negative Binomial	684	702
	ZIP	3195	3213
	ZINB	686	707
<i>Tadarida brasiliensis</i>	Poisson	2563	2571
	Negative Binomial	429	441
	ZIP	1647	1659
	ZINB	431	446
<i>Lasiurus cinereus</i>	Poisson	850	862
	Negative Binomial	288	303
	ZIP	666	681
	ZINB	290	307
<i>Perimyotis subflavus</i>	Poisson	532	541
	Negative Binomial	217	229
	ZIP	248	260
	ZINB	219	234
<i>Nycticeius humeralis</i>	Poisson	776	788
	Negative Binomial	311	326
	ZIP	433	448
	ZINB	313	331
<i>Myotis spp.</i>	Poisson	326	338
	Negative Binomial	248	262
	ZIP	263	277
	ZINB	250	267

**Table 4.** Parameter Estimates for Overall Bat Activity and Feeding Activity Count Regression Models. Models describe total bat activity (count of echolocation sequences), and bat foraging activity (count of feeding echolocation sequences) in relation to stand types, forest edges, and insect community. Stand types and forest edges were represented with indicator variables. Significance of the over-dispersion parameter ‘\_Alpha’ implies that the negative binomial model fits better than the Poisson model. Data were collected using acoustic monitoring with bat detectors and insect trapping in four stand types and along forest edges in an intensively managed pine forest (Weyerhaeuser Parker Tract, Washington Co, North Carolina), during summers of 2006 and 2007.

Variable	Parameter	Estimate	Standard Error	t Value	Approx Pr >  t
total echolocation sequences	Intercept	3.477713	0.227495	15.29	<.0001
	edge	1.480178	0.268169	5.52	<.0001
	thinned	1.241288	0.317521	3.91	<.0001
	unmanaged	1.245035	0.336677	3.70	0.0002
	Lepidoptera	0.089388	0.034707	2.58	0.0100
	_Alpha	1.652393	0.176377	9.37	<.0001
total feeding sequences	Intercept	1.459155	0.304847	4.79	<.0001
	edge	1.132257	0.349674	3.24	0.0012
	thinned	1.016240	0.424547	2.39	0.0167
	Lepidoptera	0.111760	0.053434	2.09	0.0365
	_Alpha	3.207634	0.429831	7.46	<.0001

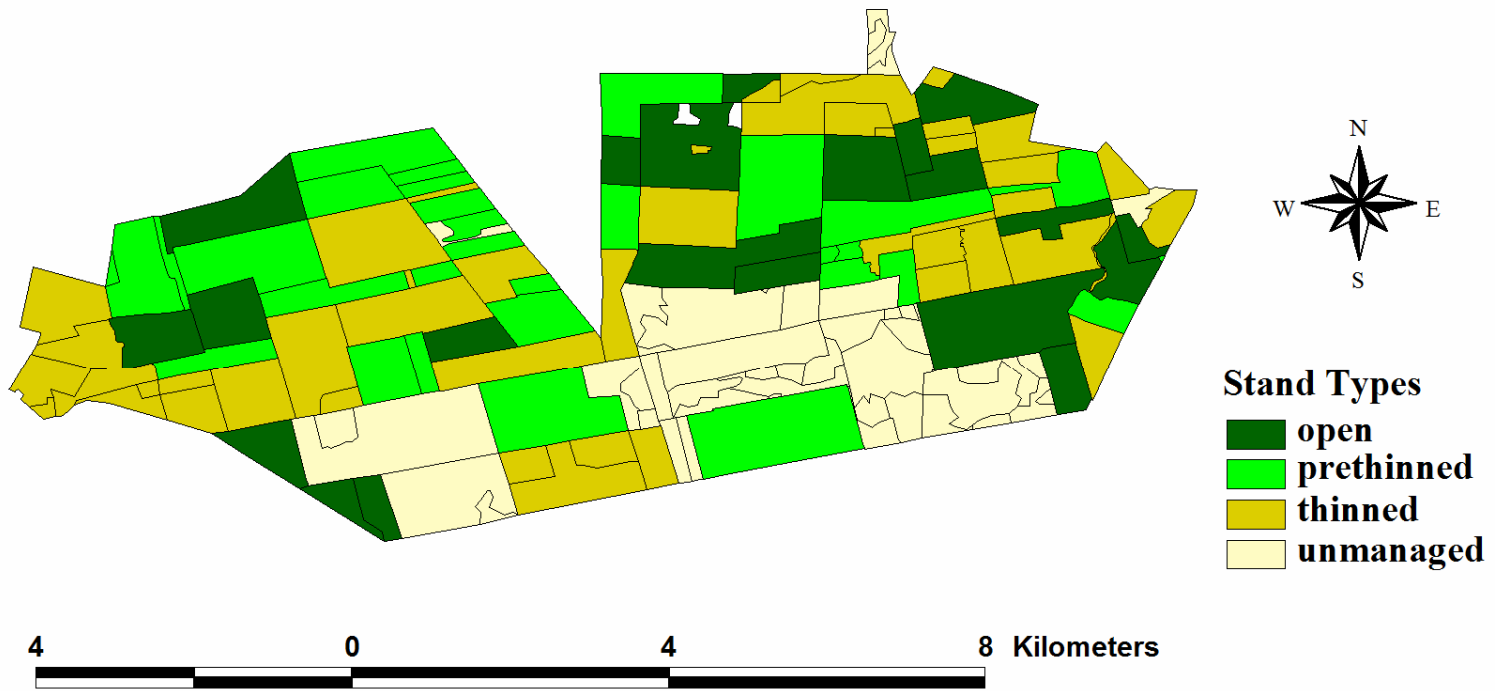
**Table 5.** Parameter Estimates for Negative Binomial Models of Bat Species Activity. Models describe bat species activity (count of time-expanded echolocation sequences) for (a) *Lasiurus borealis*, (b) *Eptesicus fuscus*, (c) *Tadarida brasiliensis* (d) *Lasiurus cinereus*, (e) *Perimyotis subflavus*, (f) *Nycticeius humeralis*, and (g) *Myotis spp.* in relation to stand types, forest edges, and insect community. Stand types and forest edges were represented with indicator variables. Significance of the over-dispersion parameter ‘\_Alpha’ implies that the negative binomial model fits better than the Poisson model. Data were collected using acoustic monitoring with bat detectors and insect trapping in four stand types and along forest edges in an intensively managed pine forest (Weyerhaeuser Parker Tract, Washington Co, North Carolina), during summers of 2006 and 2007.

Species	Parameter	Estimate	Standard Error	t Value	Approx Pr >  t
(a) <i>Lasiurus borealis</i>	Intercept	2.118129	0.314570	6.73	<.0001
	edge	0.765270	0.377208	2.03	0.0425
	unmanaged	0.917182	0.460501	1.99	0.0464
	Lepidoptera	0.139188	0.052053	2.67	0.0075
	_Alpha	3.731955	0.473351	7.88	<.0001
(b) <i>Eptesicus fuscus</i>	Intercept	-7.941085	2.787512	-2.85	0.0044
	temperature	0.102806	0.037924	2.71	0.0067
	edge	3.444103	0.428090	8.05	<.0001
	open	1.042912	0.510485	2.04	0.0411
	thinned	2.864776	0.508245	5.64	<.0001
	_Alpha	3.357229	0.513284	6.54	<.0001
(c) <i>Tadarida brasiliensis</i>	Intercept	0.747955	0.358310	2.09	0.0368
	edge	1.365009	0.572315	2.39	0.0171
	unmanaged	-1.558886	0.729243	-2.14	0.0325
	_Alpha	8.642072	1.626962	5.31	<.0001
(d) <i>Lasiurus cinereus</i>	Intercept	-3.432133	0.587489	-5.84	<.0001
	open	3.424406	0.682931	5.01	<.0001
	edge	2.825405	0.578806	4.88	<.0001
	Lepidoptera	0.272789	0.062642	4.35	<.0001
	_Alpha	4.437628	1.090073	4.07	<.0001
(e) <i>Perimyotis subflavus</i>	Intercept	-2.029891	0.372209	-5.45	<.0001
	edge	1.887338	0.546753	3.45	0.0006
	Diptera	0.004263	0.001763	2.42	0.0156
	_Alpha	5.794666	1.802269	3.22	0.0013
(f) <i>Nycticeius humeralis</i>	Intercept	-1.142097	0.508792	-2.24	0.0248
	edge	1.648367	0.691286	2.38	0.0171
	thinned	1.627605	0.812962	2.00	0.0453
	unmanaged	1.717462	0.783759	2.19	0.0284
	_Alpha	9.033535	2.098570	4.30	<.0001
(g) <i>Myotis spp</i>	Intercept	0.446287	0.280546	1.59	0.1117
	thinned	-1.226446	0.548051	-2.24	0.0252
	open	-3.011236	0.836297	-3.60	0.0003
	edge	-2.821193	0.633782	-4.45	<.0001
	_Alpha	3.137878	0.966676	3.25	0.0012

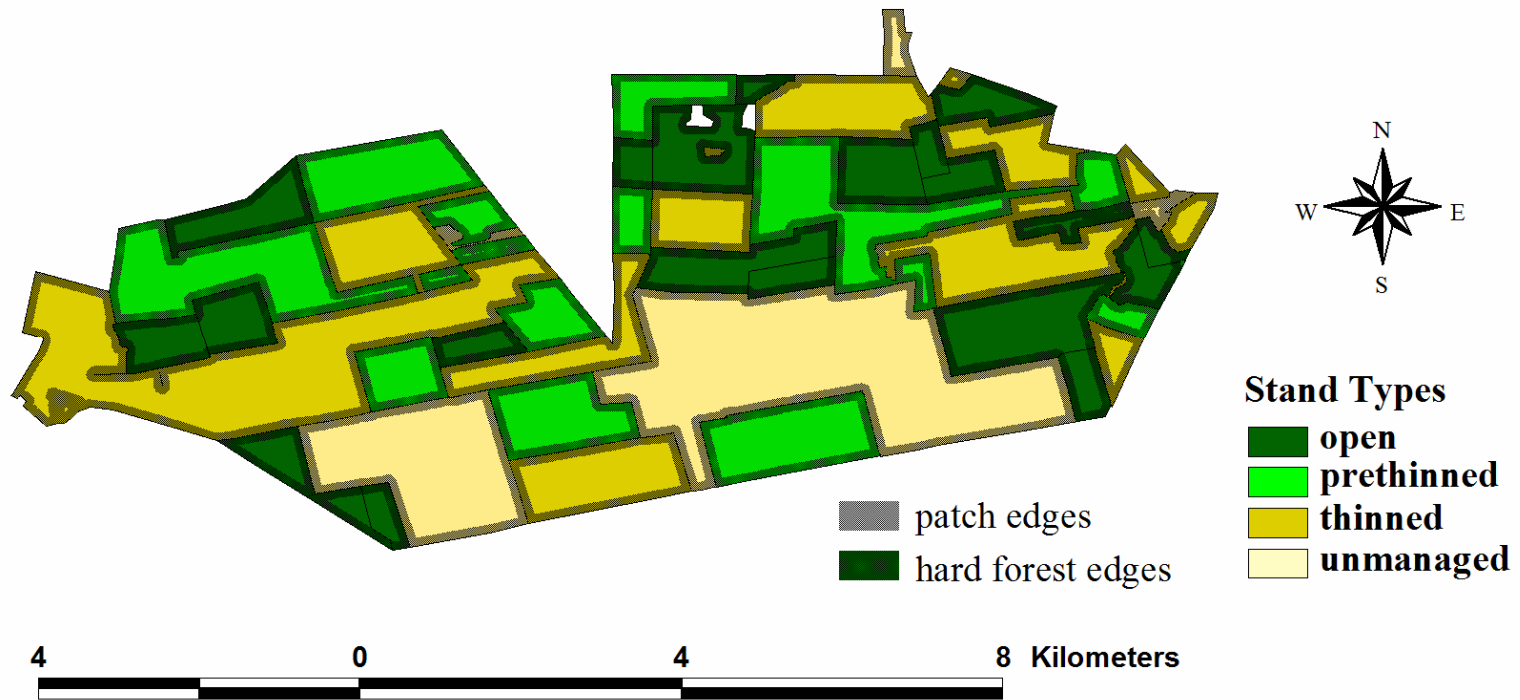


**Figure 1.** Location of Weyerhaeuser Parker Tract in Eastern North Carolina. Washington County, near Plymouth, NC. Map author: Adam Morris

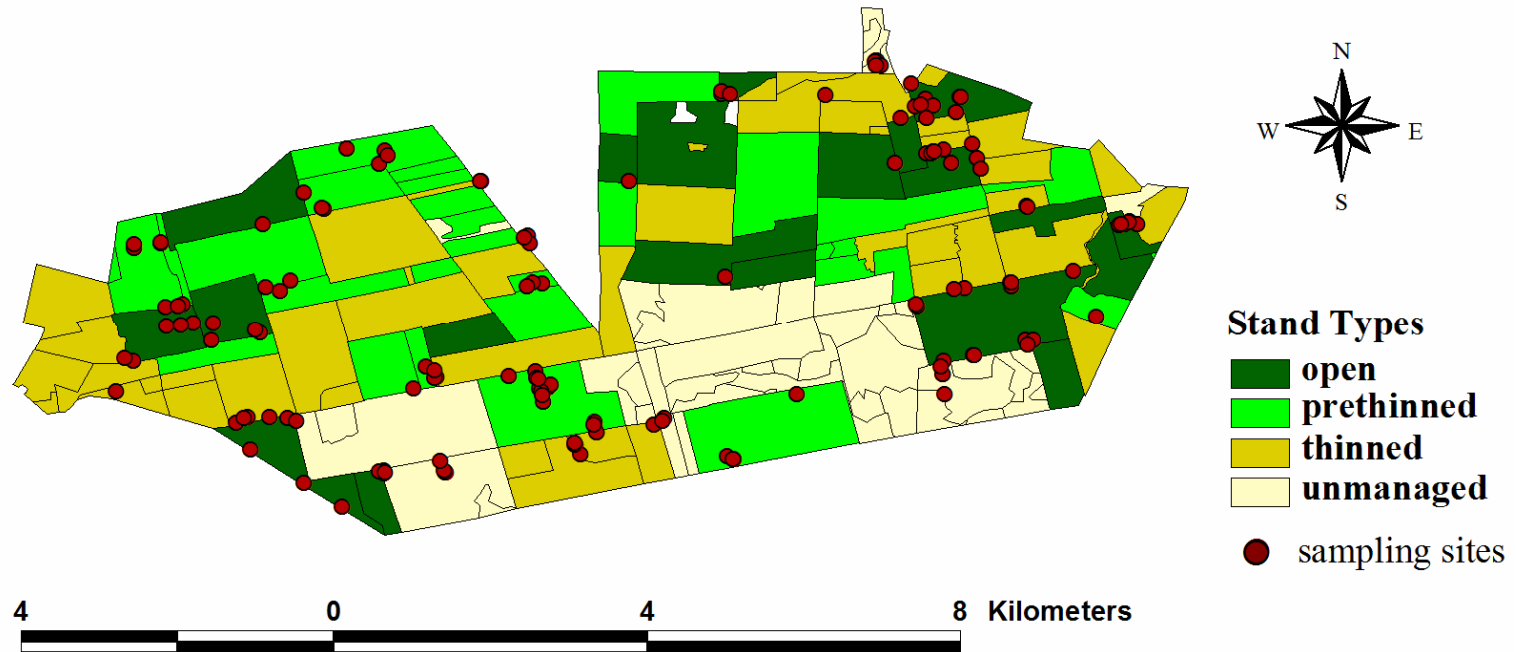




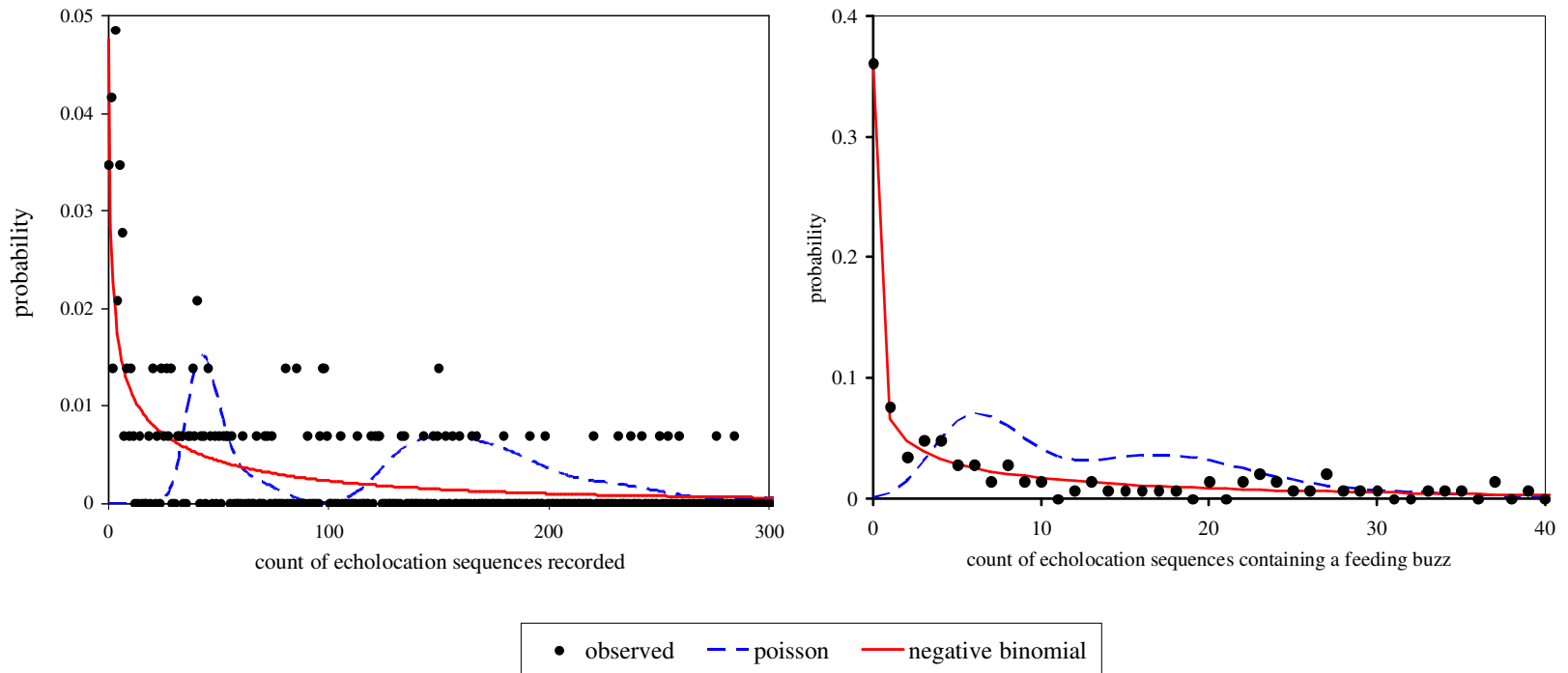
**Figure 2.** Mosaic Pattern Landscape of the Weyerhaeuser Parker Tract. Washington County, North Carolina.  
Map author: Adam Morris



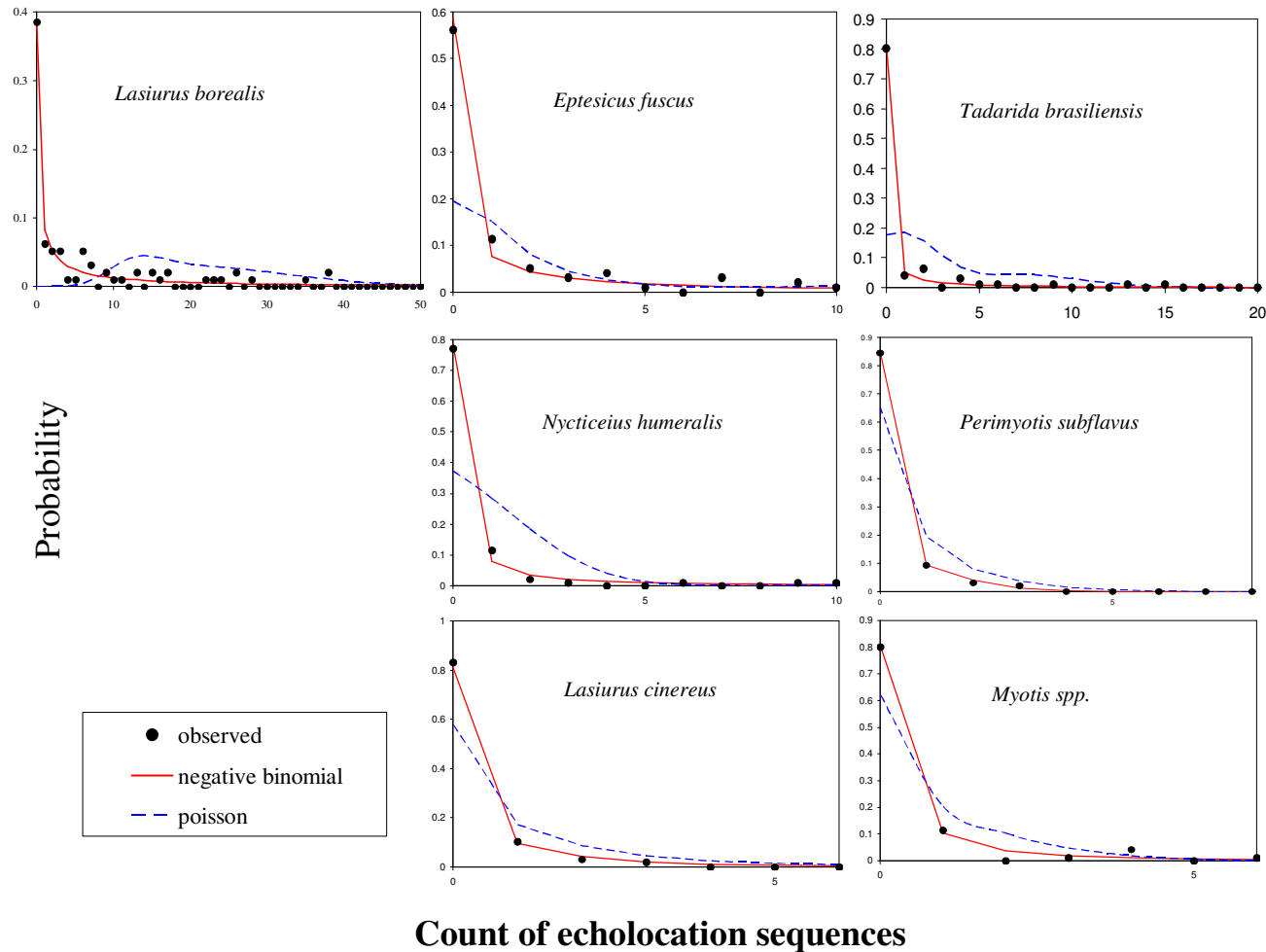
**Figure 3.** Forest Edges of the Weyerhaeuser Parker Tract. Edges occur at borders between heterogeneous stands, and extend 100 meters into stands. Edges accounted for 39.5 % of the managed landscape. Of those edges, 28.1% were hard forest edges (occurring at the boundary between forested and open stands) which accounted for 45.7% of the total area of open stands.



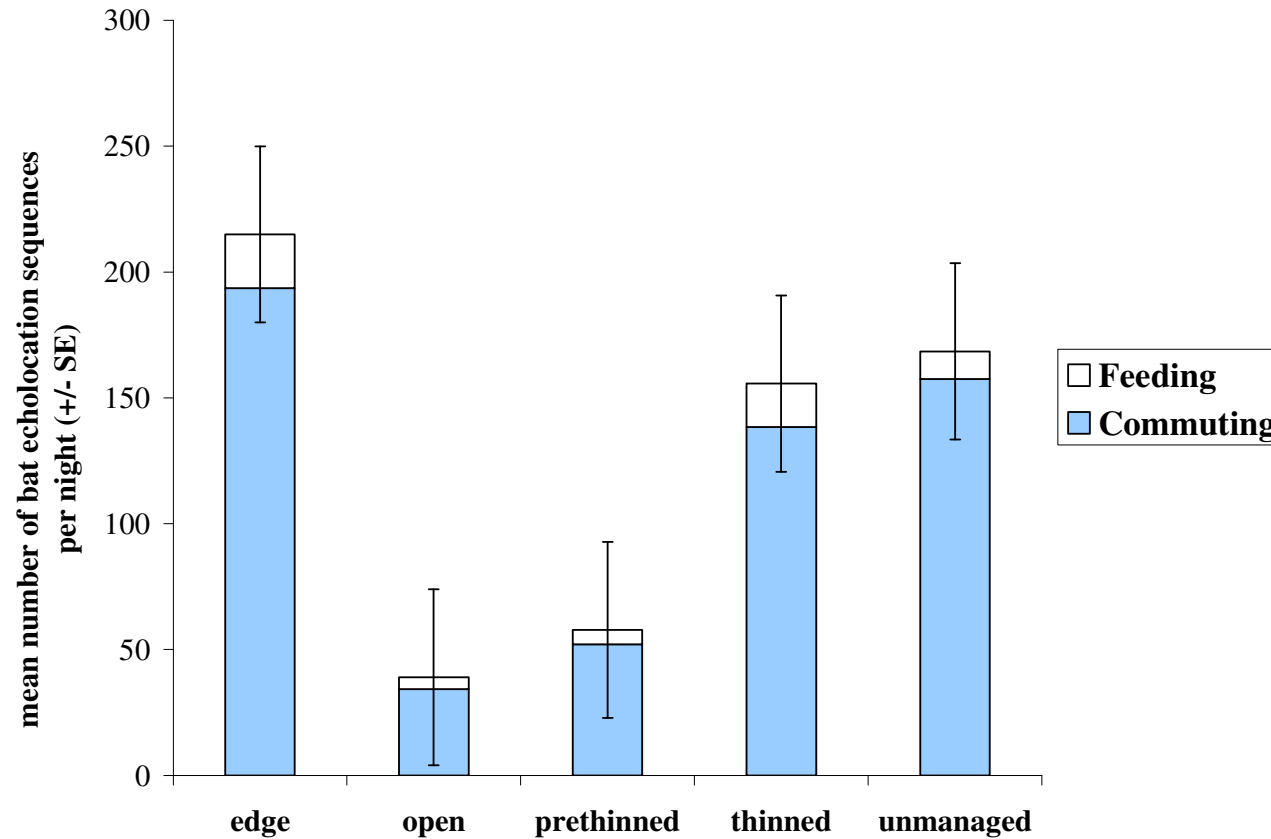
**Figure 4.** Weyerhaeuser Parker Tract Sampling Sites. Sites where acoustic data and insect trap data were collected during the summers of 2006 and 2007 (Washington County, North Carolina). Map author: Adam Morris



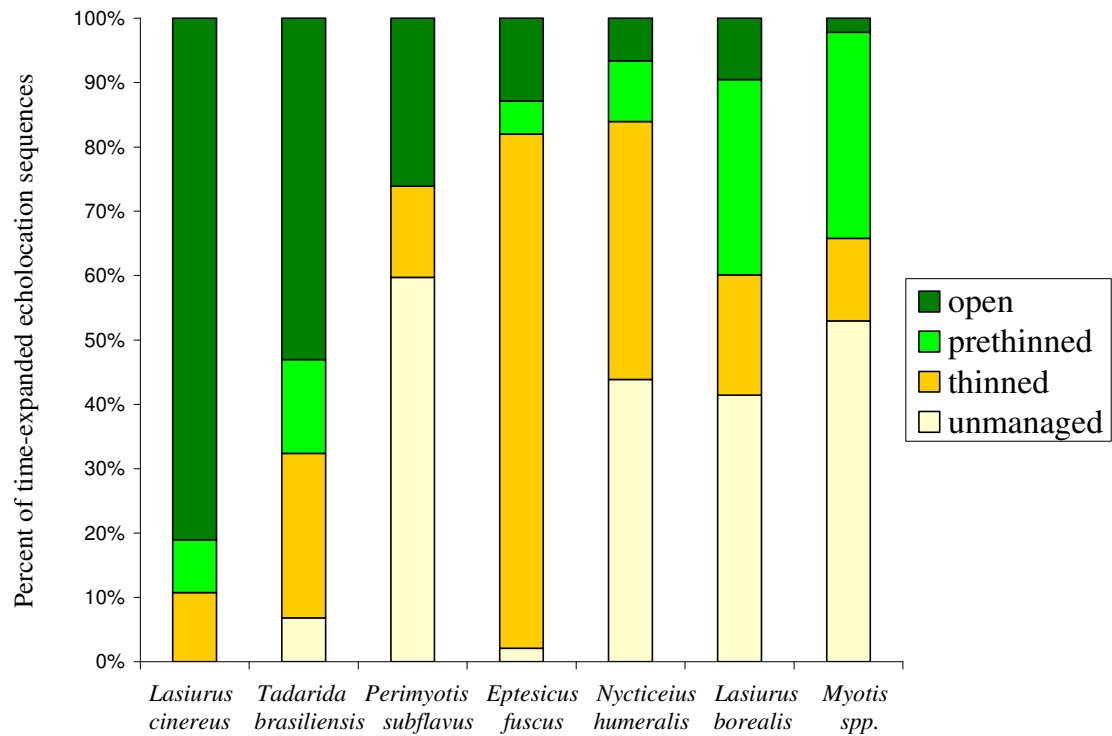
**Figure 5.** Comparison of Model Fit for Overall Bat Activity Models. Poisson and negative binomial regression models were compared using probability-count plots. Negative binomial models fit well due to the large proportion of zero-counts and the highly skewed distribution. Acoustic data were collected within an intensively managed pine forest (Weyerhaeuser Parker Tract, Washington Co, North Carolina), during the summers of 2006 and 2007.



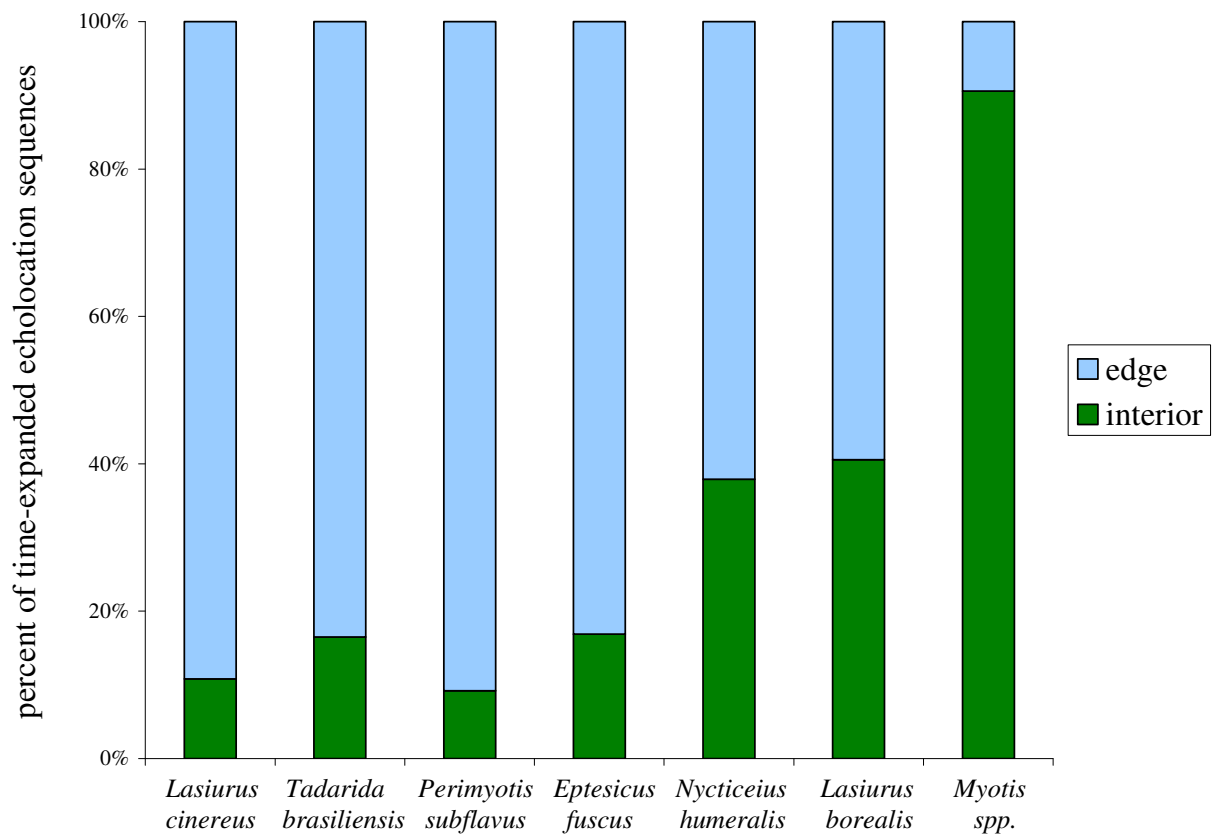
**Figure 6.** Comparison of Model Fit for Bat Species Activity Models. Probability-count plots compare Poisson and negative binomial regression models. Models predict the activity of seven bat species groups. Data were collected within an intensively managed pine forest (Weyerhaeuser Parker Tract, Washington Co, North Carolina), during the summers of 2006 and 2007.



**Figure 7.** Overall Bat Activity and Feeding Activity in Stands and Along Forest Edges. Mean number of bat echolocation sequences recorded per night ( $\pm$  SE) across four stand types and along forest edges. Echolocation sequences were classified as *feeding* if they contained a feeding buzz, and *commuting* if they did not. Acoustic data were collected within an intensively managed pine forest (Weyerhaeuser Parker Tract, Washington Co, North Carolina), during the summers of 2006 and 2007.



**Figure 8.** Relative Bat Activity in Forest Stand Interiors. Percent of time-expanded bat echolocation sequences recorded within four stand types. Acoustic data were collected within an intensively managed pine forest (Weyerhaeuser Parker Tract, Washington Co, North Carolina), during the summers of 2006 and 2007.



**Figure 9.** Relative Bat Activity along Forest Edges. Percent of time-expanded bat echolocation sequences recorded along hard forest edges versus within stand interiors. Acoustic data were collected within an intensively managed pine forest (Weyerhaeuser Parker Tract, Washington Co, North Carolina), during the summers of 2006 and 2007.



## REFERENCES

- Agosta, S. J. 2002. Habitat use, diet and roost selection by the big brown bat (*Eptesicus fuscus*) in North America: a case for conserving an abundant species. *Mammal Review* 32:179-198.
- Akaike, H. 1973. Information theory and an extension of the maximum likelihood principle. *International Symposium on Information Theory*, 2<sup>nd</sup>. 267-281.
- Aldridge, H. D. J. N., and I. L. Rautenbach. 1987. Morphology, echolocation and resource partitioning in insectivorous bats. *The Journal of Animal Ecology* 56:763-778.
- Arlettaz, R. 1999. Habitat selection as a major resource partitioning mechanism between the two sympatric sibling bat species *Myotis myotis* and *Myotis blythii*. *Journal of Animal Ecology* 68:460-471.
- Arlettaz, R., N. Perrin, and J. Hausser. 1997. Trophic resource partitioning and competition between the two sibling bat species *Myotis myotis* and *Myotis blythii*. *Journal of Animal Ecology* 66:897-911.
- Arnett, R. H., Jr. American insects. A handbook of the insects of America north of Mexico. Second Edition. 2000. CRC Press, Boca Raton, FL.
- Baldwin, V.C., Jr. and Feduccia, D.P. 1987. Loblolly pine growth and yield prediction for managed west gulf plantations. Res. Pap. SO-236. New Orleans, LA: U.S. Department of Agriculture, Forest Service, Southern Forest Experiment Station. 27 p.
- Barclay, R. M. R., and R. M. Brigham. 1991. Prey detection, dietary niche breadth, and body size in bats: Why are aerial insectivorous bats so small? *American Naturalist* 137:693-703.
- Barclay, R. M. R., and R. M. Brigham. 1994. Constraints on optimal foraging: a field test of prey discrimination by echolocating insectivorous bats. *Animal Behavior* 48:1013-1021.

- Barron, David N. 1992. The analysis of count data: overdispersion and autocorrelation. *Sociological Methodology* 22:179-220.
- Bliss, C. I., R. A. Fisher. 1953. Fitting the negative binomial distribution to biological data. *Biometrics* 9:176-200.
- Bogdanowicz, W., R. D. Csada, and M. B. Fenton. 1997. Structure of noseleaf, echolocation, and foraging behavior in the Phyllostomidae (Chiroptera). *Journal of Mammalogy* 78:942-953.
- Brigham, R. M., S. D. Grindal, M. Firman, and J. Morissette. 1997. The influence of structural clutter on activity patterns of insectivorous bats. *Canadian Journal of Zoology* 74:422-427.
- Campbell, L. A., J. G. Hallett, and M. A. O'Connell. 1996. Conservation of bats in managed forests: use of roosts by *Lasionycteris noctivagans*. *Journal of Mammalogy* 77:976-984.
- Cadenasso, M. L., and S. T. A. Pickett. 2000. Linking forest edge structure to edge function: mediation of herbivore damage. *Journal of Ecology* 88:31-44.
- Cadenasso, M. L., and S. T. A. Pickett. 2001. Effect of edge structure on the flux of species into forest interiors. *Conservation Biology* 15:91-97.
- Carter, T. C., M. A. Menzel, B. R. Chapman, and K. V. Miller. 2003. Partitioning of food resources by syntopic eastern red (*Lasiurus borealis*), seminole (*L. seminolus*) and evening (*Nycticeius humeralis*) bats. *American Midland Naturalist* 151:186-191.
- Clark, B. S., D. M. Leslie, Jr., and T. S. Carter. 1993. Foraging activity of adult female ozark big-eared bats (*Plecotus townsendii ingens*) in summer. *Journal of Mammalogy* 74:422-427.
- Crampton, L. H., and R. M. R. Barclay. 1998. Selection of roosting and foraging habitat by bats in different-aged aspen mixedwood stands. *Conservation Biology* 12:1347-1358.
- Crome, F. H. J., and G. C. Richards. 1988. Bats and gaps: Microchiropteran community structure in a Queensland rain forest. *Ecology* 69:1960-1969.

- Cunningham, Ross B., D.B. Lindenmayer. 2005. Modeling count data of rare species: some statistical issues. *Ecology* 86:1135-1142.
- Donovan, T. M., P. W. Jones, E. M. Annand, and F. R. T. Iii. 1997. Variation in local-scale edge effects: mechanisms and landscape context. *Ecology* 78:2064-2075.
- Eby, P. 1998. An analysis of diet specialization in frugivorous *Pteropus poliocephalus* (Megachiroptera) in Australian subtropical rainforest. *Australian Journal of Ecology* 23:443-456.
- Elmore, L. W., D. A. Miller, and F. J. Vilella. 2005. Foraging area size and habitat use by red bats (*Lasiurus borealis*) in an intensively managed pine landscape in Missouri. *The American Midland Naturalist* 153:405.
- Ewers, R.M. and Didham, R.K. 2006. Confounding factors in the detection of species responses to habitat fragmentation. *Biological Reviews* 81: 117-142.
- Fagan, W. F., R. S. Cantrell, and C. Cosner. 1999. How habitat edges change species interactions. *American Naturalist* 153:165-182.
- Faure, P.A., J.H. Fullard, J.W. Dawson. 1993. The gleaning attacks of the northern long-eared bat, *Myotis septentrionalis*, are relatively inaudible to moths. *Journal of Experimental Biology* 178:173-189.
- Fellers, G. M., and E. D. Pierson. 2002. Habitat use and foraging behavior of Townsend's big-eared bat (*Corynorhinus townsendii*) in coastal California. *Journal of Mammalogy* 83:167-177.
- Fenton, M. B. 1990. The foraging behavior and ecology of animal-eating bats. *Canadian Journal of Zoology* 68:411-422.
- Fenton, M. B. 1997. Science and the conservation of bats. *Journal of Mammalogy* 78:1-14.
- Fenton, M. B., and W. Bogdanowicz. 2002. Relationships between external morphology and foraging behavior: bats in the genus *Myotis*. *Canadian Journal of Zoology* 80:1004-1013.

- Fenton, M. B., D. H. M. Cumming, I. L. Rautenbach, G. S. Cumming, M. S. Cumming, G. Ford, R. D. Taylor, J. Dunlop, M. D. Hovorka, D. S. Johnston, C. V. Portfors, M. C. Kalcounis, and Z. Mahlanga. 1998a. Bats and the loss of tree canopy in African woodlands. *Conservation Biology* 12:399-407.
- Fenton, M. B., I. L. Rautenbach, J. Rydell, H. T. Arita, J. Ortega, S. Bouchard, M. D. Hovorka, B. Lim, E. Odgren, C. V. Portfors, W. W. Scully, D. M. Syme, and M. J. Vonhof. 1998b. Emergence, echolocation, diet and foraging behavior of *Molossus ater* (Chiroptera: Molossidae). *Biotropica* 30:314-320.
- Fenton, M. B., and D. W. Thomas. 1980. Dry-season overlap in activity patterns, habitat use, and prey selection by sympatric African insectivorous bats. *Biotropica* 12:81-90.
- Fraver, S. 1994. Vegetation responses along edge-to-interior gradients in the mixed hardwood forests of the Roanoke River Basin, North Carolina. *Conservation Biology* 8:822-832.
- Forman, R. T. T., and M. Godron. 1981. Patches and structural components for a landscape ecology. *BioScience* 31:733-740.
- Gehrt, S. D., and J. E. Chelso. 2003. Bat activity in an urban landscape: patterns at the landscape and microhabitat scale. *Ecological Applications* 13:939-950.
- Griffin, D. R., F.A. Webster, C.R. Michael. 1960. The echolocation of flying insects by bats. *Animal Behaviour* 8:141-154.
- Grindal, S. 1999. Habitat use by bats, *Myotis spp.*, in Western Newfoundland. *Canadian Field-Naturalist* 113:258-263.
- Grindal, S., and R. Brigham. 1999. Impacts of forest harvesting on habitat use by foraging insectivorous bats at different spatial scales. *Ecoscience* 6:25-34.
- Guldin, J. M., and T. B. Wigley. 1998. Intensive management-can the south really live without it? Transactions of the 63rd North American Wildlife and Natural Resources conference, Orlando, FL. Washington, DC: Wildlife Management Institute.
- Herlin, I. S. 2001. Approaches to forest edges as dynamic structures and functional concepts. *Landscape Research* 26:27-43.

- Heske, E. J. 1995. Mammalian abundances on forest-farm edges versus forest interiors in southern Illinois: is there an edge effect? *Journal of Mammalogy* 76:562-568.
- Hickey, M. B. C., L. Acharya, and S. Pennington. 1996. Resource partitioning by two species of Vespertilionid Bats (*Lasiurus cinereus* and *Lasiurus borealis*) feeding around street lights. *Journal of Mammalogy* 77:325-334.
- Ho, S., H. Nassef, N. Pornsinsirak, Y.-C. Tai, and C.-M. Ho. 2003. Unsteady aerodynamics and flow control for flapping wing flyers. *Progress in Aerospace Sciences* 39:635-681.
- Hogberg, L. K., K. J. Patriquin, and R. M. R. Barclay. 2002. Use by bats of patches of residual trees in logged areas of the boreal forest. *American Midland Naturalist* 148:282-288.
- Hutchinson, J., and M. Lacki. 2000. Selection of day roosts by red bats in mixed mesophytic forests. *Journal of Wildlife Management* 64:87-94.
- Irwin, L. L., and T. B. Wigley. 1993. Toward an experimental basis for protecting forest wildlife. *Ecological Applications* 3:213-217.
- Jaberg, C., and A. Guisan. 2001. Modelling the distribution of bats in relation to landscape structure in a temperate mountain environment. *Journal of Applied Ecology* 38:1169-1181.
- Jones, G. 1990. Prey selection by the greater horseshoe bat (*Rhinolophus ferrumequinum*): optimal foraging by echolocation? *Journal of Animal Ecology* 59:587-602.
- Jones, G., M. Morton, P. Hughes, and R. Budden. 1993. Echolocation, flight morphology and foraging strategies of some West African hipposiderid bats. *Journal of Zoology* 230:385-400.
- Jung, T., I. Thompson, R. Titman, and A. Applejohn. 1999. Habitat selection by forest bats in relation to mixed-wood stand types and structure in central Ontario. *Journal of Wildlife Management* 63:1306-1319.
- Kalcounis-Ruppell, M. C., J. M. Psyllakis, and R. M. Brigham. 2005. Tree roost selection by bats: an empirical synthesis using meta-analysis. *Wildlife Society Bulletin* 33:1123-1132.

- Kalcounis, M. C., and R. M. Brigham. 1995. Intraspecific variation in wing loading affects habitat use by little brown bat (*Myotis lucifugus*). *Canadian Journal of Zoology* 73:89-95.
- Kalcounis, M. C., and R. M. Brigham. 1998. Secondary use of aspen cavities by tree-roosting big brown bats. *Journal of Wildlife Management* 62:603-611.
- Kalcounis, M. C., K. A. Hobson, R. M. Brigham, and K. R. Hecker. 1999. Bat activity in the boreal forest: importance of stand type and vertical strata. *Journal of Mammalogy* 80:673-682.
- Kalcounis-Rüppell, M.C., V.H. Payne, S.R. Huff, A.L. Boyko. 2007. Effects of wastewater treatment plant effluent on bat foraging ecology in an urban stream system. *Biological Conservation* 138:120-130.
- Krusic, R., M. Yamasaki, C. Neefus, and P. Pekins. 1996. Bat habitat use in White Mountain National Forest. *Journal of Wildlife Management* 60:625-631.
- Kusch, J., C. Weber, S. Idelberger, and T. Koob. 2004. Foraging habitat preferences of bats in relation to food supply and spatial vegetation structures in a western European low mountain range forest. *Folia Zoology* 53:113-128.
- Kuusipalo, J., and J. Kangas. 1994. Managing biodiversity in a forestry environment. *Conservation Biology* 8:450-460.
- Lambert, Diane. 1992. Zero-inflated poisson regression, with an application to defects in manufacturing. *Technometrics* 34:1-14.
- Law, B., and M. Chidel. 2002. Tracks and riparian zones facilitate the use of Australian regrowth forest by insectivorous bats. *Journal of Applied Ecology* 39:605-617.
- Mager, K. J., and T. A. Nelson. 2001. Roost-site selection by eastern red bats (*Lasiurus borealis*). *American Midland Naturalist* 145:120-126.
- Malcolm, J. R. 1994. Edge effects in central Amazonian forest fragments. *Ecology* 75:2438-2445.

- Martin, Tara G., B. A. Wintle, J.R. Rhodes, P. M. Kuhnert., S.A. Field, S.J. Low-Choy, A.J. Tyre. and H.P. Possingham. 2005. Zero tolerance ecology: improving ecological inference by modelling the source of zero observations. *Ecology Letters* 8: 1235-1246.
- Matlack, Glenn R., 1994. Vegetation dynamics of the forest edge -- trends in space and successional time. *The Journal of Ecology* 82:113-123
- Menzel, J. M., M. A. Menzel, J. C. Kilgro, W. M. Ford, J. W. Edwards, and G. F. McCracken. 2005. Effect of habitat and foraging height on bat activity in the coastal plain of South Carolina. *Journal of Wildlife Management* 69:235-245.
- Menzel, M., T. Carter, J. Menzel, W. Mark Ford, and B. Chapman. 2002. Effects of group selection silviculture in bottomland hardwoods on the spatial activity patterns of bats. *Forest Ecology and Management* 162:209-218.
- Meyer, C. F. J., C. J. Schwarz, and J. Fahr. 2004. Activity patterns and habitat preferences of insectivorous bats in a West African forest-savanna mosaic. *Journal of Tropical Ecology* 20:397-407.
- Miles, Adam C., S.B. Castleberry, D.A. Miller, L.M. Conner. 2006. Multi-scale roost-site selection by evening bats on pine-dominated landscapes in southwest Georgia. *Journal of Wildlife Management* 70:1191-1199.
- Miller, Darren A. 2003. Species diversity, reproduction, and sex ratios of bats in managed pine forest landscapes of Mississippi. *Southeastern Naturalist* 2:59-72.
- Miller, Darren A., E. B. Arnett, M. J. Lacki. 2003. Habitat management for forest-roosting bats of North America: A critical review of habitat studies. *Wildlife Society Bulletin* 31: 30-44.
- NCSSF, 2005. *Global Markets Forum Summary report of the National Commission on Science for Sustainable Forestry* (NCSSF), Washington, DC.
- Norberg, U. M., and J. M. V. Rayner. 1987. Ecological morphology and flight in bats (Mammalia; Chiroptera): wing adaptations, flight performance, foraging strategy and echolocation. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences* 316:335-427.
- Odum, Eugene P. 1985. Trends expected in stressed ecosystems. *Bioscience* 35:418-422.

- O'Donnell, C. F. J. 2000. Influence of season, habitat, temperature, and invertebrate availability on nocturnal activity of the New Zealand long-tailed bat (*Chalinolobus tuberculatus*). *New Zealand Journal of Zoology* 27:207-221.
- O'Donnell, C. F. J., and J. A. Sedgeley. 1999. Use of roosts by the long-tailed bat, *Chalinolobus tuberculatus*, in temperate rainforest in New Zealand. *Journal of Mammalogy* 80:913-923.
- Owen, Sheldon F., M. A. Menzel, W.M. Ford, B.R. Chapman, K.V. Miller, J.W. Edwards, P.B. Wood. 2003. Home-range size and habitat used by the northern myotis (*Myotis septentrionalis*) *American Midland Naturalist* 150: 352-359
- Parsons, S., A. M. Boonman, M.K. Obrist. 2000. Advantages and disadvantages of techniques for transforming and analyzing Chiropteran echolocation calls. *Journal of Mammalogy* 81: 927-938.
- Patriquin, K. J., and R. M. R. Barclay. 2003. Foraging by bats in cleared, thinned and unharvested boreal forest. *Journal of Applied Ecology* 40:646-657.
- Ratcliffe, John M., J.W. Dawson. 2003. Behavioural flexibility: the little brown bat, *Myotis lucifugus*, and the northern long-eared bat, *M. septentrionalis*, both glean and hawk prey. *Animal Behaviour* 66:847-856.
- Roberts, M. R. and F. S. Gilliam. 1995. Disturbance effects on herbaceous layer vegetation and soil nutrients in *Populus* forests of northern lower Michigan. *Journal of Vegetative Science* 6:903-912.
- Russ, J., and W. Montgomery. 2002. Habitat associations of bats in Northern Ireland: implications for conservation. *Biological Conservation* 108:49-58.
- Schnitzler H. U., E. Kalko. 2001. Echolocation by insect-eating bats. *Bioscience* 51:557-569.
- Sileshi, G. 2006. Selecting the right statistical model for analysis of insect count data by using information theoretic measures. *Bulletin of Entomological Research* 96:479-488.
- Simmons J.A, M.B. Fenton, M.J. O'Farrell. 1979. Echolocation and the pursuit of prey by bats. *Science* 203:16-21.



- Saunders, M. B., and R. M. R. Barclay. 1992. Ecomorphology of insectivorous bats: a test of predictions using two morphologically similar species. *Ecology* 73:1335-1345.
- Schlaepfer, M. A., and T. A. Gavin. 2001. Edge effects on lizards and frogs in tropical forest fragments. *Conservation Biology* 15:1079-1090.
- Schultz, R. P. 1999. Loblolly -- the pine for the twenty-first century. *New Forests* 17:71.
- Sharitz, R. R., L. R. Boring, D. H. V. Lear, and J. E. Pinder, III. 1992. Integrating ecological concepts with natural resource management of southern forests. *Ecological Applications* 2:226-237.
- Sleep, D. J. H., and R. M. Brigham. 2003. An experimental test of clutter tolerance in bats. *Journal of Mammalogy* 84:216-224.
- Sousa, Wayne P. 1984. The role of disturbance in natural communities. *Annual Review of Ecological Systems* 15:353-391.
- Swystun, M. B., J. M. Psyllakis, and M. Brigham. 2001. The influence of residual tree patch isolation on habitat use by bats in central British Columbia. *Acta Chiropterologica* 3:197-201.
- Tibbels, A. E., and A. Kurta. 2003. Bat activity is low in thinned and unthinned stands of red pine. *Canadian Journal of Forest Resources* 33:2436-2442.
- Vaughan, N., G. Jones, and S. Harris. 1997. Habitat use by bats (Chiroptera) assessed by means of a broad-band acoustic method. *The Journal of Applied Ecology* 34:716-730.
- Verboom, B., and K. Spoelstra. 1999. Effects of food abundance and wind on the use of tree lines by an insectivorous bat, *Pipistrellus pipistrellus*. *Canadian Journal of Zoology* 77:1393-1401.
- Vincent, P. J., J. M. Haworth. 1983. Poisson regression models of species abundance. *Journal of Biogeography* 10:153-160.
- Walsh, A. L., and S. Harris. 1996. Foraging habitat preferences of Vespertilionid bats in Britain. *The Journal of Applied Ecology* 33:508-518.

- Watts, B. D., and M. D. Wilson. 2005. The use of pine plantations by worm-eating warblers in coastal North Carolina. *Southeastern Naturalist* 4:177-187.
- Weller, Theodore J., C. J. Zabel. 2002. Variation in bat detections due to detector orientation in a forest. *Wildlife Society Bulletin*. 30: 922-930.
- Weyerhaeuser Company and the Environmental Defense Fund, *A Partnership in Conservation*, published by the Environmental Defense Fund, 1997.  
Environmental Defense Fund, 2500 Blue Ridge Road, Raleigh, NC 27607.
- White, Gary C., R.E. Bennetts. 1996. Analysis of frequency count data using the negative binomial distribution. *Ecology* 77: 2549-2557.
- Wigley, T. Bently, William M. Baughman, Michael E. Dorcas, John A. Gerwin, J. Whitfield Gibbons, David C. Guynn, Jr., Richard A. Lancia, Yale A. Leiden, Michael S. Mitchell, and Kevin R. Russell. 2000. Contributions of intensively managed forests to the sustainability of wildlife communities in the south. In: *Sustaining southern forests: the science of forest assessment*. Southern Forest Resource Assessment.
- Wilson, M. D., B. D. Watts, and B. J. Paxton. 2000. Breeding bird communities of the Parker Tract hardwood forest swamps: Year 2000 report. Center for Conservation Biology Research Report, CCBRR-00-07.
- Wunder, L., and A. B. Carey. 1996. Use of the forest canopy by bats. *Northwest Science* 70.
- Yahner, R. H. 1988. Changes in wildlife communities near edges. *Conservation Biology* 2:333-339.