FACTORS INFLUENCING SITE OCCUPANCY OF BATS ON MANAGED-PINE LANDSCAPES IN THE COASTAL PLAIN OF THE SOUTHEASTERN UNITED STATES

by

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(Under the Direction of Steven B. Castleberry)

ABSTRACT

Bats are ecologically important inhabitants of forest landscapes in the southeastern United States. These forests account for the majority of regional land cover, much of which is actively managed for forest products. Although many owners of managed-pine forests are committed to preserving biodiversity, responsible management is hampered by a paucity of data concerning bat ecology in these landscapes. To address the lack of data and improve management, my objectives were to evaluate an acoustic identification method and elucidate factors that influence foraging bats in Coastal Plain managed-pine forests. I used cross-validation to assess performance of K-nearest neighbor analysis as a method to classify unknown bat calls. Overall accuracy of K-nearest neighbor was 83% and species-specific accuracy ranged from 51% to 96%. Results suggest that K-nearest neighbor should be considered a viable call identification method. I used Anabat II detectors to survey and determine presence of multiple bat species across managed-pine forest landscapes. I used program PRESENCE to evaluate plausibility of occupancy models based on Akaike's Information Criterion and estimate influence of factors on detection and occupancy. Plausibility of detection and occupancy factors was supported over null models. Detection probabilities of resident bats decreased with increasing amounts of vegetation at sample points. Results suggest that investigations concerning the influence of factors on bat occupancy should account for variable detection. Increasing insect abundances increased the probability of occupancy by bats, but the most plausible measure of insect abundance was species-specific. Small-scale vegetation abundance was negatively related to occupancy. Management activities in managed-pine forests that reduce small-scale vegetation clutter and increase insect abundance are likely to benefit resident bat species. Plausibility of landscape-scale factors influencing probability of occupancy was supported, but plausible factors were species-specific. Landscape-scale factors with evidence supporting their potential influence included un-thinned stands of intermediate age, distance to water sources, road density, patch richness, amount of edge, and percentage of stands older than 30 years. Bats respond to landscape conditions, but managing a single landscape attribute likely will not benefit all members of the bat community. However, maintaining a diverse landscape apparently provides habitat for a diverse bat community.

INDEX WORDS: Acoustic survey, AIC, Anabat, bat-insect relationship, bat-landscape relationship, K-nearest neighbor classification, occupancy models

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INTRODUCTION AND LITERATURE REVIEW

INTRODUCTION

Bats are one of the most diverse and speciose groups of mammals (Laerm et al. 2000, Jones et al. 2009) performing many vital functions within the ecosystems they inhabit, such as insect control (Kalka et al. 2008), pollination (Molina-Frinear and Equiarte 2003), and seed dispersal (Medellin and Goana 1999). Insectivorous bats in the United States are worth an estimated $23 billion to the agriculture industry alone (Boyles et al. 2011) by reducing insect damage to crops that would otherwise require chemical insecticide agents that may have ecological and social costs (Cleveland et al. 2006). Additionally, bats can be valuable as ecological and environmental indicators provided sufficient baseline data are collected and monitoring programs are implemented (Jones et al. 2009).

Forest landscapes are important to virtually all bat species within the southeastern U.S., and many species in the region exclusively use forests to fulfill their life history requirements (Miller et al. 2003). The importance of these landscapes may increase as *Geomyces destructans*, the fungus thought to be the causative agent of white-nose syndrome (Gargas et al. 2009), spreads into the region. Cave dependent populations infected by the fungus have experienced precipitous declines (Blehert et al. 2009), but forest dependent populations appear unaffected thus far and are likely less susceptible to large population declines from *G. destructans*. Some southeastern species exhibit roosting flexibility and are capable of using both caves and forests depending on availability (Hurst and Lacki 1999, Trousdale and Beckett 2005, M. Clement University of Georgia pers. comm.). The regional impact of the fungus on roost-flexible species may depend on the health of forest populations (USFS 2010). Additionally, as the fungal pathogen spreads (Zimmerman 2009), forest populations of all species may play a critical role in maintaining the vital ecosystem functions bats perform.

Much of the research on forest bats in the Southeast has concentrated on publicly owned lands (e.g., Menzel et al. 1998, Menzel et al. 2003, Britzke et al. 2003, O'Keefe et al. 2009), which may not be representative of privately owned forests in the region and therefore limited in utility. Publicly owned forests only comprise approximately 13% of the forest land cover in the southern U.S. and typically are less intensively managed than the remaining forests privately owned by individuals, families, trusts, and other unincorporated groups (60%) or corporations (27%; Smith et al. 2009). Forest management activities alter stand and landscape conditions but provide an economic incentive to maintain forest land cover (McComb 2008) and reduce conversion rates to agricultural or urban/suburban land cover that is often detrimental to native wildlife populations and biodiversity conservation (McKinney 2002, Dunn 2004). However, managing forests concurrently for timber production and biodiversity conservation requires data that are largely lacking in reference to bats on actively managed forest landscapes (Lacki et al. 2007).

LITERATURE REVIEW

Call Analysis

Acoustic research methods have increased in use and sophistication following the pioneering work by Griffin (1958) and realization that echolocation calls could be used to differentiate species (Fenton and Bell 1981, Ahlen and Baagoe 1999). The importance and use of acoustic methods in research may increase as a result of white-nose syndrome. The outbreak of white-nose syndrome in the U.S. may have originated from fungal spores transported on clothing and equipment used by cavers or researchers in Europe (Puechmaille et al. 2010). Therefore, capturing and handling bats increases the likelihood of subsequently spreading fungal spores (U.S. FWS 2011). Consequently, an increased emphasis has and will continue to be placed on acoustic identification and survey techniques to limit spread of the fungus by researchers.

Methods used to identify bats based on recorded echolocation calls can generally be categorized as qualitative or quantitative. While every identification method has strengths and limitations, quantitative techniques are desirable because of increased objectivity, repeatability, and transferability over qualitative methods (Vaughan et al. 1997, Barclay 1999, Robbins and Britzke 1999, Redgwell et al. 2009). Rigorous application of scientific principles to identification of free-flying bats from acoustic recordings is not universal, and many researchers use non-repeatable qualitative methods for identification. However, few researchers possess the experience or resources to accurately identify echolocation calls qualitatively (Zorpette 1999).

The most commonly used quantitative method, discriminant function analysis (DFA; Gannon et al. 2004), is easy to implement and is widely available (Papadatou et al. 2008). However, alternative classification methods may perform better when multivariate normality is violated (Press and Wilson 1978, Parson and Jones 2000) as is often the case with bat calls (e.g., Russo and Jones 2002, Fukui et al. 2004, Preatoni et al. 2005, Papadatou et al. 2008). Artificial neural networks (ANN; Parsons 2001, Parsons and Jones 2000, Preatoni et al. 2005), machine learning (Skowronski and Harris 2006), and synergetic pattern recognition (Obrist et al. 2004), have been used effectively to identify bat calls, but have not been widely adopted because of inconclusive classification improvements over DFA, advanced software and extensive training requirements, or the need for further method refinements prior to widespread use (Parsons and Jones 2000, Obrist et al. 2004, Papadatou et al. 2008). Performance of additional quantitative classification methods have been investigated such as classification and regression trees (Preatoni et al. 2005), but are generally considered inferior to DFA (but see Gannon et al. 2004). Discovery of an accurate quantitative classification method that is widely available, easy to use, and has minimal underlying assumptions, will benefit managers facing the daunting yet critical task of identifying unknown bat calls.

Insects and Vegetation Clutter

Predator fitness is closely linked to foraging decisions (Stephen and Krebs 1986), and decisions about alternative foraging locations may be influenced by physical habitat characteristics (Hopcraft et al. 2005), abundance of prey items (Ives et al. 1993), or a combination of both (Sleep and Brigham 2003). Species-specific characteristics of wing morphology and echolocation call influence flight speeds, maneuverability, and ability of bats to discriminate between prey and non-prey items (Aldridge and Rautenbach 1987). Therefore, optimal habitat conditions and prey items may differ among foraging bat species. Failure to acquire sufficient resources may result in reduced reproductive output (Burles et al. 2009) or likelihood of survival (Thomas et al. 1990) in temperate region bats.

On a small-scale, site occupancy by foraging bats is often attributed to the amount of structural complexity (Ford et al. 2005, Loeb and O'Keefe 2006). Increased occupancy and activity in areas of reduced vegetation structure is commonly found in forested landscapes including bottomland forests (Menzel et al. 2002), mixed forests (Loeb and O'Keefe 2006), and managed-pine dominated landscapes (Ford et al. 2006). The negative influence of structural clutter on foraging has also been demonstrated experimentally (Sleep and Brigham 2003). However, habitat variables alone are often insufficient to fully understand species' ecology (Morrison 2001).

Failure by bats to conform to predictions of habitat use based on morphology alone may be partially attributable to effects of prey densities (Tibbels and Kurta 2003, Ford et al. 2005). Some studies have found a positive relationship between indices of bat foraging activity and insect abundances (Anthony et al. 1981, Rautenbach et al. 1996, Kusch et al. 2004, Fukui et al. 2006) while others indicate a lack of relationship between foraging activity and insect abundance (Ober and Hayes 2008). One factor hampering our ability to understand insect/bat relationships is an inability to accurately measure prey availability, attributable to a lack of knowledge concerning discriminatory capabilities of foraging bats. Many bat species actively select prey (Brigham 1990), but it is unclear if the selection is based on size, insect taxon, or both. Some diet studies have suggested that bats discriminate among prey items by taxon (Buchler 1976, Agosta et al. 2003), whereas others suggest that selection is based on size (Barclay and Brigham 1991, Barclay and Brigham 1994).

It is likely that decisions regarding selection of foraging areas are based on a combination of vegetation characteristics and prey abundances as both factors contribute to small-scale foraging efficiencies (Aldridge and Rautenbach 1987, Salcedo et al. 1995). Sleep and Brigham (2003) found that less maneuverable bat species did not exploit areas of high insect abundance with high amounts of clutter. Meyer et al. (2004) found that bat activity patterns followed the spatial and temporal activity patterns of lepidopteran prey, but habitat characteristics had the most pronounced effect. Among similar habitat types, Wickramsinghe et al. (2004) found that differences in bat activity were related to differences in insect abundances. Despite many inherent challenges, understanding links between foraging bats and prey availability has been recognized as an important research area, particularly within forested landscapes (Lacki et al. 2007).

Landscape Influences on Bat Occupancy

Landscape characteristics potentially influence the distribution, abundance, and activity of many animals, including bats. Therefore, management of bats across large areas requires an understanding of important landscape characteristics and how they influence foraging habitat selection (Walsh and Harris 1996, Brooks and Ford 2006). A landscape management approach is effective if species are motile and can use the landscape at a scale that prevents management activities from inhibiting movement between suitable habitat patches or within areas of sufficient resources (MacNally and Bennett 1997). Bats are capable of moving across unsuitable habitat types and commuting between favorable areas of the landscape (Bernard and Fenton 2003) making concurrent management of forest landscapes for sustainable resources and sustainable bat populations possible if important landscape characteristics are known.

Landscape-scale studies are relatively rare, but previous studies suggest that bats respond to landscape characteristics when selecting habitats. Walsh and Harris (1996) found that landscape-scale habitat types (i.e., intensively farmed arable, pastural, upland) influenced bat activity in Britain. In Switzerland, Jaberg and Guisan (2001) used a database of bat records and a geographic information system (GIS) to examine the influence of landscape characteristics on bat distribution across a 786 km^2 area. Their results indicate the importance of elevation, vegetation type, and lake habitats on species distributions. Duff and Morrell (2007) found that the amount of edge habitat, distance to lakes, and elevation influenced mist-net captures in a California recreation area. Additional investigations suggest the importance of fragmentation and urbanization on bats (Duchamp et al. 2004, Ghert and Chelsvig 2004, Gorreson and Willig 2004). Although these previous studies indicate the potential influence of landscape-scale habitat characteristics on bats, they are not directly relevant to managed-pine dominated landscapes because of geographic and landscape differences, scale, and factors investigated.

Investigations conducted in forested landscapes are most informative and provide the most insight for managers of pine forest landscapes. In one of few replicated landscape studies, Erickson and West (2003) did not find evidence to support significant influence of landscapes on acoustic bat activity at points (n=22) in Washington and Oregon although they concluded that proximity to certain landscape types likely influenced activity. However, Yates and Muzika (2006) found support for the influence of landscape characteristics (abundance of non-forest habitat types, patch size, patch complexity, amount of edge, and interspersion of forest types) on site-occupancy of foraging bats in Missouri forests. In Sumter National Forest, a mixed forest in the Upper Piedmont and Mountain physiographic regions of South Carolina, Loeb and O'Keefe (2006) found support for a single landscape factor (distance to roads) on overall site-occupancy, but a greater influence of small-scale vegetation density. However, they acknowledged that the strong influence of vegetation density they observed may be due, in part, to acoustic detectability. Similarly, Ford et al. (2006) found that vegetation density influenced occupancy in South Carolina, but also found that proximity of sample points to water influenced site-occupancy by most species.

Many of these previous investigations do not indicate a strong influence of landscape characteristics on occupancy, but landscape variables and the habitat mosaic may have a greater influence on bat habitat use in intensively-managed landscapes (Erickson and West 2003, Ford et al. 2006, Miles et al. 2006). However, landscape-level investigations in managed-pine forest of the southeastern U.S. are limited. In a foraging study conducted in managed-pine forests in Mississippi, Elmore et al. (2005) tracked actively foraging bats and found evidence to support the importance of water sources in these forests although they did not exhibit a preference among habitat types investigated. Although roost-site preferences do not indicate foraging-site preferences, several roost-site selection studies conducted in managed-pine forests across the southeastern U.S. also suggest that landscape-level factors influence the choices bats make in these forest landscapes. For example, Elmore et al. (2004) found evidence suggesting that red bats (*Lasiurus borealis*) in intensively-managed pine landscapes in Mississippi chose diurnal roosts based in part on distances to streamside management zones, forest edges, stand types, and water sources. In the Ouachita Mountains of central Arkansas, Perry et al. (2007, 2008) found evidence of species-specific selection of roost sites based on both stand and landscape characteristics including distances to forest habitat types, stands of particular age classes, water sources, roads, and percentage of the landscape composed of various habitat or stand types. Hein et al. (2008) found that Seminole bats (*L. seminolus*) in an intensively-managed pine landscape in South Carolina chose roost sites based on the distance to forested corridors, edge (or road), open habitat types, and mature pine stands. Elucidating landscape factors that influence foraging choices in addition to these important roost-site preferences will allow managers to better manage bats in managed-pine forest landscapes.

OBJECTIVES AND GUIDE TO THE DISSERTATION

Many of the managed-pine forest landscapes in the southeastern U.S. Coastal Plain are concurrently managed for sustainable harvest of wood and conservation of biodiversity. However, managing for healthy bat populations is challenging because of the paucity of data concerning factors that influence foraging locations in managed-pine landscapes. Additionally, bat research in general is hampered by continued use of non-transferrable or repeatable qualitative methods to classify bat calls and identify species from acoustic data. The goal of this project was to provide land managers with the data and call analysis methodology required to better manage forest landscapes and provide suitable foraging habitat for resident bat species.

The dissertation is organized as a series of manuscript-style chapters addressing the goals of this project. Chapter 2 is an evaluation of K-nearest neighbor classification as a method to quantitatively classify calls from a suite of resident Coastal Plain forest bat species. I used a library of known reference calls to evaluate the accuracy of the K-nearest neighbor approach and compared results to those achieved with the most commonly used quantitative classification method, discriminant function analysis. This manuscript will be submitted to the *Wildlife Society Bulletin.*

Chapter 3 is an investigation into the influence of insect abundance and small-scale vegetation characteristics on site-occupancy of foraging bats. I sampled insects, vegetation characteristics, and bats at points in three replicated study areas. I used occupancy models and an information-theoretic approach to evaluate suites of vegetation and insect-based models, and to estimate effects of parameters. This manuscript will be submitted to *Forest Ecology and Management.*

Chapter 4 is an investigation into the influence of landscape-scale factors on site-occupancy of foraging bats. I sampled vegetation characteristics and bats at sample points in addition to characteristics of the surrounding landscape. I included data from replicated study areas under diverse ownership across the Coastal Plain so that inferences could be made to managed-pine forests in the region. I used occupancy models and an information-theoretic approach to evaluate the plausibility of vegetation and landscape-based models and estimate effects of parameters. This manuscript will be submitted to *Forest Ecology and Management.*

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CHAPTER 2

K-NEAREST-NEIGHBOR CLASSIFICATION TO IDENTIFY BAT CALLS: PERFORMANCE WITH A SUITE OF COASTAL PLAIN FOREST SPECIES AND COMPARISON TO DISCRIMINANT FUNCTION ANALYSIS[1]

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ABSTRACT

The primary purpose of many acoustic surveys for bats is to determine and monitor species presence. A critical step in this process is accurate identification of species based on echolocation calls. Many quantitative approaches have been used to identify calls such as artificial neural networks, classification trees, machine learning, and synergetic pattern recognition. The most common quantitative approach to identification is discriminant function analysis (DFA). Although DFA may not be the most accurate quantitative approach, it is commonly used because it is considered less complex and more available than alternative methods. Another relatively simple and widely available alternative method is K-nearest-neighbor analysis (KNN). We used KNN and DFA to classify bat calls associated with Coastal Plain forests and compared accuracy rates. KNN achieved an overall call accuracy rate of 82.5 percent, 9.9 and 7.6 percentage points higher than linear and quadratic DFA rates, respectively. Our results, along with the underlying assumptions and capabilities of KNN analysis, indicate that KNN analysis should be given strong consideration when the primary objective is identification of unknown bat calls.

INTRODUCTION

Identification of bats based on call characteristics remains an imperfect science and topic of debate among bat researchers (Barclay 1999), but the practice is likely to persist until better methods of identification are available. All acoustic identification methods involve comparisons of unknown calls to a reference library of known calls, either quantitatively or qualitatively (Britzke 2003). Few researchers possess the experience or resources to accurately identify echolocation calls qualitatively (Zorpette 1999). Betts (1998) found that among researchers with qualitative identification experience, half performed significantly worse than the classification accuracy expected from randomly assigning identities. Additionally, self assessments of ability to make qualitative identifications were negatively related to classification accuracy. Even preliminary determination of call type (search, approach, or terminal phases; Griffin 1958) can be highly subjective (Weller et al. 1998). Therefore, quantitative techniques are desirable over qualitative methods because of increased objectivity, repeatability, and transferability (Vaughan et al. 1997, Barclay 1999, Robbins and Britzke 1999, Redgwell et al. 2009).

The most common quantitative approach to call identification is discriminant function analysis (DFA; Gannon et al. 2004). Examples of either linear or quadratic forms of DFA being used for bat call analysis are widespread (e.g., Parsons and Jones 2000, Britzke 2003, Fukui et al. 2004, Schirmacher 2006, Corcoran 2007, Papadatou et al. 2008, Hein et al. 2009). DFA allows the user to determine which call characteristics are most influential in discriminating between species in addition to classifying unknown calls. Additionally, linear discriminant functions can be used in the absence of the original function-generating data set thereby promoting transferability (Papadatou et al. 2008). However, DFA is a parametric approach and call data typically violate the underlying multivariate normality assumption (e.g., Russo and Jones 2002, Fukui et al. 2004, Preatoni et al. 2005, Papadatou et al. 2008). Although DFA is considered robust to violations of normality (Dillon and Goldstein 1984), alternative classification methods may perform better when multivariate normality is violated (Press and Wilson 1978).

Alternative quantitative classification approaches, such as artificial neural networks (ANN; Parsons 2001, Parsons and Jones 2000, Preatoni et al. 2005), machine learning (Skowronski and Harris 2006), and synergetic pattern recognition (Obrist et al. 2004), have been used to identify bat calls. These alternative approaches have not been widely adopted because of inconclusive classification improvements over DFA, advanced software and extensive training requirements, or the need for further method refinements prior to widespread use (Parsons and Jones 2000, Obrist et al. 2004, Papadatou et al. 2008). Performance of other quantitative methods such as classification and regression trees has been investigated (Preatoni et al. 2005), but they generally are considered inferior to DFA (but see Gannon et al. 2004).

Another potentially alternative method that is computationally simple and widely available is K-nearest-neighbor analysis (KNN; Hand 1982). In contrast to DFA and other parametric approaches, KNN is a nonparametric classifier that does not require assumptions about underlying data distributions. Non-parametric classification methods often perform better than parametric methods (Peterson et al. 1999, Olden and Jackson 2002), and are particularly useful when classification rather than interpretation is the primary objective (Peterson et al. 1999). In general, comparisons between KNN, neural networks, and a variety of other classification methods have found KNN to be among the better classifiers producing lower error rates than alternative classification methods (Ripley 1994, Taylor and Henery 1994). KNN classification is based on the assumption that call characteristics of members of a class (e.g., species) are similar and therefore should be located closely within statistical space (Cover and

Hart 1967, Peterson et al. 1999). Observations are classified based on identities of a predefined number of closest known neighbors. KNN is commonly available in many statistical software packages (e.g., SAS, R, MatLab), and the minimal prerequisite training and knowledge requirements are similar to DFA.

Given the need to further refine quantitative methods for classifying bat calls recorded during acoustic surveys, our objective was to test performance of KNN as a quantitative method to classify bat calls and compare cross validation accuracy rates of KNN with the most commonly used quantitative methods, linear and quadratic DFA. Accuracy of call identifications is dependent on variability encompassed by the reference library and suite of potential species (Britzke 2003). Reference libraries comprised of species with dissimilar echolocation calls, either true differences among species or artificial differences resulting from the particular calls included, are likely to exhibit higher overall and species-specific accuracy rates that reference libraries collected from species with similar echolocation calls, regardless of the classification method used. Therefore, we evaluated performance of all methods using the same suite of species and library of reference calls.

METHODS

Reference Call Library

We obtained from Chris Corben, designer of the ANABAT system (Titley Scientific, East Brisbane, Australia), a reference library of calls (Gannon et al. 2004) recorded with ANABAT from individuals through a variety of methods including hand releases, visual identification of free-flying individuals, emergence from known roosts, and zip lines (Chris Corben, formerly of Titley Electronics, pers. comm.). The library is comprised of calls recorded across the United States and therefore likely to exhibit greater variance than a geographically restricted library. While use of a local reference library is often encouraged (Papadatou et al. 2008), inter-specific variation is more significant than geographic intra-specific variations (O'Farrell et al. 2000, Murray et al. 2001) eliminating the absolute necessity of a local reference library. We used multiple calls from the same sequences for analyses thereby introducing problems of pseudoreplication (Hurlbert 1984). However, comparisons between classification methods using the same pseudoreplicated data set are still valid (Preatoni et al. 2005).

We included in our reference collection calls from species that we considered to be summer residents of forests within the southeastern U.S. Coastal Plain including: *Corynorhinus rafinesquii* (CORA, Rafinesque's big-eared bat), *Eptesicus fuscus* (EPFU, big brown bat), *Lasiurus borealis* (LABO, eastern red bat), *L. seminolus* (LASE, Seminole bat), *L. cinereus* (LACI, hoary bat), *Nycticeus humeralis* (NYHU, evening bat), *Perimyotis subflavus* (PESU, tri-colored bat), *Tadarida brasiliensis* (TABR, Brazilian free-tailed bat), and *Myotis austroriparius* (MYAU, southeastern myotis). This suite of resident species was determined based on mist-net captures of bats on nine study areas located in the coastal plain (Bender et al. unpublished data), literature reports, and from personal communication with other biologists familiar with the region. While additional species are likely to be found in the region, they are migrants or rare in Coastal Plain forests and thus were not considered typical summer residents and were not included in our analyses.

We created a customized ANALOOK (v 4.9; Titley Scientific, East Brisbane, Australia) filter to retain only search phase calls following the methods and criteria of Britzke and Murray (2000). We followed terminology used by Britzke (2003), in which "calls" were individual sound pulses, a combination of which comprised a "call sequence." We used ANALOOK to automatically calculate and extract call parameters from all calls within retained files. Call parameters included maximum frequency (Fmax), minimum frequency (Fmin), duration (Dur), mean frequency (Fmean), initial slope (S1), slope of flattest portion (Sc), frequency where slope changes from S1 to Sc (Fk), frequency of flattest portion (Fc), time into call when Fc reached (Tc), time into call when Fk reached (Tk), and degree of curvilinearity (Qk). O'Farrell et al. (2000) provides a more complete explanation of call parameters calculated by ANALOOK. Automated filtering and parameter calculation increase objectivity and repeatability while reducing influence of researcher experience (Obrist et al. 2004) which may have significant impact on classification errors (Gannon et al. 2004). Additionally, maintaining objectivity throughout the quantitative identification process is an expressed goal of many research projects (Parsons and Jones 2000, Russo and Jones 2002).

Call Classification

The expected error rate is the most appropriate tool to evaluate a classification method (Lachenbruch 1975). Therefore, we used this metric to compare DFA (linear and quadratic) and KNN classifiers. Leave-one-out cross validation is considered a nearly unbiased estimator of out-of-sample error (Fukunaga and Kessel 1971), and provides a measure of predictive ability without excessive variance (Efron 1983). Our leave-one-out cross validation procedure involved withholding one call from the data set, generating a model with the remaining data, and then using the model to classify the withheld call. The process is repeated until all calls have been classified. The resulting confusion matrix (Table 2.1) displays percentages of observations classified correctly and incorrectly into each alternative category (e.g., suite of possible species). Confusion matrices permit calculation of overall, mean, and species-specific error rates for each classification method. To facilitate comparisons to other research and to permit more intuitive reporting of results, we present accuracy rates (1 minus error rate) rather than error rates.

Species with high accuracy rates likely have unique call characteristics, while species with lower accuracy rates likely have call characteristics that are similar to those species that they were incorrectly classified as.

We used SAS software (v 8.2, SAS Institute Inc., Cary, North Carolina, USA) for all statistical analyses. To classify calls using the KNN approach we used PROC DISCRIM with the METHOD = NONPARAMETRIC option and specified KNN analysis with the option K = a pre-specified number of neighbors. The most appropriate and best performing call parameters for classification likely depend on the suite of species being investigated. Therefore, we examined overall cross validation error rates (i.e., percentage of the total known calls incorrectly classified) from 11 candidate models (Table 2.2) to determine the best performing model. The candidate set included call parameters previously used to quantitatively classify bat calls from the southeastern U.S. (Britzke 2003) and other additive combinations of call parameters thought to vary among species (Fenton and Bell 1981, Russo and Jones 2002; Table 2.2). We used a SAS macro (J.T. Peterson, U.S. Geological Survey, Athens, Georgia, USA) to plot overall leave-one-out cross validation error rates by the number of neighbors to determine optimal number of neighbors. We calculated error rates from 1 to 50 neighbors for each potential candidate model. We defined optimal number of neighbors (K) as the K that resulted in the lowest overall error rate. If multiple levels of K produced the same minimum error rate, we selected the lowest K. We considered the best-predicting model in the candidate set to be the model with the lowest overall cross validation error rate when the optimal number of K was used to identify calls.

We used PROC DISCRIM to perform both linear and quadratic DFA classifications with the 11 candidate models. The POOL option was used to define DFA form (POOL = YES, linear; POOL = NO, quadratic), and the CROSSVALIDATE option was used to conduct the leave-one-out cross validation procedure. Papadatou et al. (2008) found that linear and quadratic DFA forms performed equally well as bat call classifiers, although the covariance matrix was better suited to the quadratic DFA form. However, classification performance and most appropriate DFA form may vary depending on the data set and suite of species being investigated. To determine the most appropriate form and test if the findings from Papadatou et al. (2008) applied to our data we used the POOL = TEST option to determine which DFA form (linear or quadratic) was best suited to our data. This SAS option requests Bartlett's modification of the likelihood ratio test of the homogeneity of within-group covariance matrices at the 0.10 significance level (SAS Institute Inc. 2010). A significant test statistic indicates that quadratic DFA is most appropriate, given the data. Linear DFA uses the pooled covariance matrix while quadratic DFA uses within-group covariance matrices for discriminant function calculations. Most previous research that used DFA used only one DFA form (e.g., Russo and Jones 2002), failed to test the covariance structure (Britzke 2003), or did not report the specific DFA form used (e.g., Obrist et al. 2004). Therefore, we report results from both DFA forms to allow for comparisons.

RESULTS

Our reference library contained 13,356 calls from 482 total sequences (Table 2.3). Two species, *L. borealis* and *L. seminolus*, are acoustically similar (Chris Corben, formerly of Titley Electronics, pers. comm., Susan Loeb, U.S. Department of Agriculture-Forest Service, pers. comm.). Therefore, we pooled them into one species group (LAsp) prior to analysis following recommendations of Barclay (1999).

We determined 10 to be the optimal number of neighbors in our KNN analysis for 9 of the candidate models based on overall error rates generated with our optimal K macro (Figure

2.1). The remaining 2 models had substantially higher error rates for all levels of K (1-50), indicating generally inferior classification performance. The optimal number of neighbors varied between these models (Fmax + Fmin, 44 neighbors; Fmax + Fmin + Fmean, 17). Overall accuracy rates for the KNN analysis ranged from 56.5 to 82.5% (Table 2.2). The model with the highest overall accuracy rate, and therefore the model we defined as the best-performing model, incorporated 10 call parameters: Fmax, Fmin, Fmean, Tk, Fk, Qk, Tc, Fc, S1, and Sc. Accuracy rates for the top model varied by species ranging from 50.8% (LAsp group) to 96% (CORA) correct classification (Table 2.4) with a mean species accuracy rate of 80.6%.

Call data were better suited to a quadratic DFA form than to a linear form based on the homogeneity of variance test, and quadratic DFA generally outperformed linear DFA. Overall accuracy rates for quadratic DFA models ranged from 55.5 to 74.9%, and the best-performing model included; Dur, Fmax, Fmin, Fmean, Tk, Fk, Qk, Tc, Fc, S1, and Sc (Table 2.2). Species accuracy for the best quadratic model ranged from 33.3% (LAsp) to 88.3% (PESU) and had a mean accuracy of 71.3% (Table 2.4). Linear DFA overall accuracy rates ranged from 49.2 to 72.6%, the best model included; Fmax, Fmin, Fmean, Tk, Fk, Qk, Fc, S1, and Sc (Table 2.2). The best-performing linear model had a mean accuracy rate of 66.6% and ranged from 33.6% (LAsp.) to 85.1% (PESU; Table 2.4). Mean accuracy of the best quadratic DFA model was 5 points higher than the best linear DFA model (72% and 67%, respectively; Table 2.4). The quadratic DFA had higher classification rates than linear for all species, except NYHU, and both DFAs had classification rates > 70% for 5 species.

KNN classification exhibited mean and overall accuracy improvements of 14.0% and 9.9%, respectively, over linear DFA, and mean and overall improvements of 8.8% and 7.6%, respectively, over quadratic DFA (Table 2.4). KNN species classification accuracy was superior in every case to linear DFA (range 2.2 - 26.7%), and all cases except PESU when compared to quadratic DFA (-0.94 - 20.2%).

DISCUSSION

The number of species with accuracy rates > 70% is an often cited statistic when determining effectiveness of quantitative analysis methods (e.g., Russo and Jones 2002, Britzke 2003). K-nearest neighbor analysis produced accuracy rates > 70% in seven of the eight species/groups investigated. Improvements over DFA indicate that classification performance with KNN analysis may be comparable to artificial neural networks (ANN), which have effectively been used to quantitatively identify bat calls (e.g., Parsons 2001, Wickramasinghe et al. 2003). Parsons and Jones (2000) compared ANN to quadratic DFA when classifying 12 bat species in Britain and found that overall, ANN accuracy rates were 6 percentage points higher than quadratic DFA rates. However, subsequent analyses with the same data set indicated that performance of DFA and ANN varied depending on parameter extraction and network training procedures (Redgwell et al. 2009). Preatoni et al. (2005) compared accuracy rates of four quantitative methods of call identification (DFA, cluster analysis, artificial neural networks, and classification/regression trees) using calls from species recorded in Italy. DFA outperformed ANN (overall accuracy at species level 77% and 64% respectively), whereas cluster analysis and classification/regression trees were far less accurate (45% and 41%, respectively).

Despite potential classification improvements over DFA, ANNs have not been commonly used for call identification primarily because of increased complexity (Papadatou et al. 2008), difficulty in quantifying classification uncertainty (Preatoni et al. 2005), and computational power required for network training (Obrist et al. 2004). Our overall improvement of 7.6% over quadratic DFA is comparable to the increase in accuracy of ANN over DFA demonstrated by

Parsons and Jones (2000), and the software, training, and computational resources required for KNN analysis are similar to that required for classification using DFA. Furthermore, classification uncertainty on a call-by-call basis is easily quantified with KNN by calculating posterior probabilities of group membership based on the identity of the known neighbors.

Classification methods with improvements over DFA greater than those achieved with KNN have been developed, but widespread application is unlikely. Obrist et al. (2004) compared pattern recognition to DFA for classification of 26 bat species found in Switzerland and achieved an overall accuracy rate 12% points higher than DFA. While pattern recognition resulted in greater improvements over DFA than our KNN approach, the complex synergetic classification algorithm and software, extensive training and filtering process, and stated need to conduct more cross validation work (Obrist et al. 2004) will likely limit use of this approach. Machine learning methods have resulted in the greatest classification improvement over DFA (16% versus 0.4% classification error; Skowronski and Harris 2006). However, the authors acknowledged limitations, primarily the large reference library required because of the number of parameters used by machine learning models (DFA = 20 parameters, machine learning model = 1425). Additionally, results were based on an assumption of ideal recording conditions and a suite of geographically separated species. The authors note that machine learning classification methods require substantially more time and computational complexity than DFA and may only be suitable for full-spectrum recording systems (Skowronski and Harris 2006). The requirements and limitations are likely to eliminate this classification method as a viable option for many research projects, particularly those using the ANABAT system.

Our results indicate the best-performing suite of call parameters is likely to vary among methods, and parameter choice affects overall accuracy rates and discrepancies between alternative methods. Therefore, we suggest that performance of multiple suites of parameters (models) be investigated and some model selection procedure be incorporated so that accuracy can be maximized. A model selection approach has been incorporated by some (Russo and Jones 2002), but many previous studies have failed to do so (e.g., Britzke 2003, Preatoni et al. 2005, Obrist et al. 2004). Although we used overall classification error to evaluate models, alternative error rates may be more appropriate depending on research or monitoring objectives. For instance, if the objective is to assess potential occupancy of an area by a particular species then the suite of model parameters and optimal number of neighbors should be chosen so that calls of that species are accurately classified and calls from alternative species are not improperly classified as the target species.

KNN analysis possesses several advantages as a quantitative classification method for bat calls over alternative methods. We demonstrated higher accuracy rates than DFA, and our improvements were comparable or superior to improvements exhibited by ANNs. Beyond classification performance, another advantage of using KNN as a classifier is the ability to easily calculate posterior probabilities for each classified call based on the identity of known neighbors. These posterior probabilities represent an estimate of classification confidence in addition to cross validation accuracy rates, and may be more appropriate measures of the probability that an individual call has been identified correctly than overall percent species identification rates traditionally used in DFA and ANN applications (Russo and Jones 2002). Probability thresholds can be used to eliminate calls or effectively create an “unknown” category when calls are classified with low confidence, thereby addressing one of the major concerns expressed by proponents of qualitative classification methods. Most quantitative methods such as DFA and ANN are unable to place a call into an unknown category, although a recently developed classification method (support vector machine) that does not have this constraint shows promise for accurate call analysis in the future (Redgwell et al. 2009). Additionally, posterior probability estimates can be directly incorporated into statistical analyses to account for misclassification when investigating factors that influence occupancy (Royle and Link 2006). We did not incorporate posterior probabilities into our analysis because we knew the true identity of all calls and wanted to maintain an equal number classified by each method for comparison purposes. We recommend use of a posterior probability threshold with data collected in the field as a conservative approach to identification. Depending on the objectives and consequences of misidentifications the threshold value can be adjusted. However, a higher threshold will result in more calls being placed in the unknown category.

The KNN classification method is suitable for data collected with the ANABAT system and processed with ANALOOK software, both of which are in widespread use and financially and logistically feasible for many research projects (Britzke 2003). Although access to a reference library is necessary (in contrast to linear DFA), KNN performs well with the ANABAT recorded reference library already accessible to many researchers. The ability to classify calls without access to the reference library is a potential benefit of using linear DFA (Papadatou et al. 2008). However, our results indicate that the equivalent classification performance achieved by Papadatou et al. (2008) using linear and quadratic DFA is likely to depend on the suite of species investigated. Therefore, the potential benefits of using linear DFA for call identification are likely offset by lower accuracy rates and violated assumptions.

MANAGEMENT IMPLICATIONS

Our findings suggest that KNN classification is an accurate quantitative method to identify calls made by bat species associated with southeastern U.S. coastal plain forests, recorded using the ANABAT system, and processed using ANALOOK. However, managers should be aware that performance of any classification method varies with the suite of species investigated, recording methods employed, recording conditions, call measurements used, and software used to process and measure call characteristics. Our results indicate that managers should incorporate a model selection procedure because we demonstrated that classification performance varies among models. Further research is required to assess KNN classification performance with alternative suites of species, recording hardware, or processing software. However, our results indicate that managers should consider KNN as an accurate, available, and suitable method to quantitatively identify unknown bat calls.

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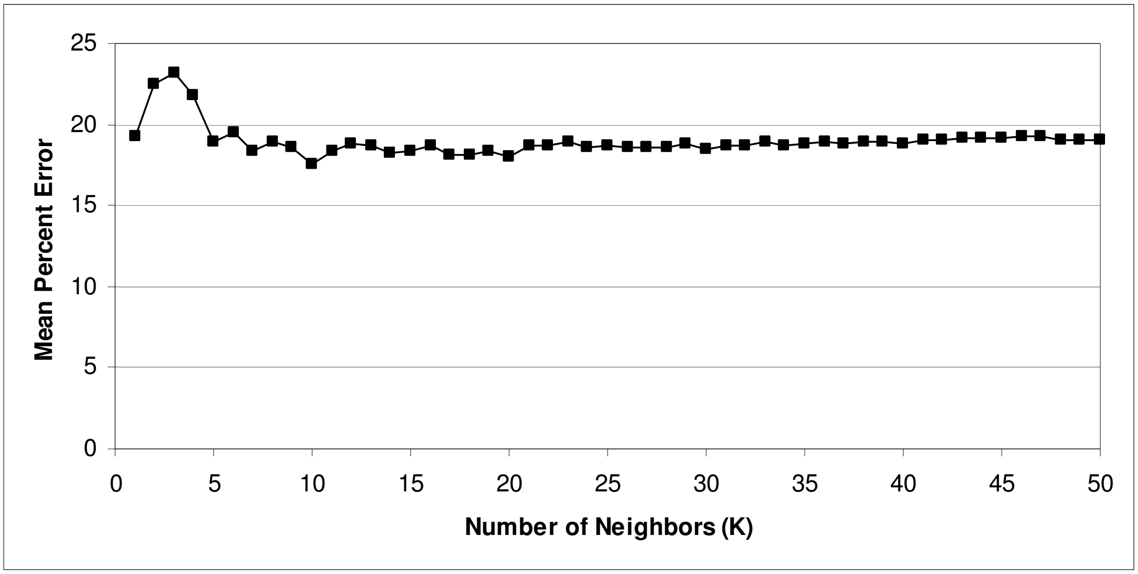

Figure 2.1: Sample plot of overall classification error (i.e., percentage of the total known calls incorrectly classified) by number of neighbors. Optimal K is defined as the number of neighbors that produces the lowest overall classification error (e.g., optimal K=10). The optimal K is used to predefine the number of neighbors used in K-nearest-neighbor classification.

Table 2.1: Confusion matrix resulting from leave-one-out cross validation with K-nearest neighbor classification of calls from a suite of bat species from the southeastern U.S. Coastal Plain. The bold type diagonal row indicates the percentage of correctly classified calls, all others represent percent misclassifications. The suite of species include big brown (EPFU), eastern red and Seminole group (LAsp.), hoary (LACI), evening (NYHU), tri-colored (PESU), Brazilian free-tailed (TABR), Rafinesque's big-eared (CORA), and southeastern myotis (MYAU).

	Classified into								
Known	EPFU	LAsp.	LACI	NYHU	PESU	TABR	CORA	MYAU	Total # classified
EPFU	**74.8**	0.1	3.4	0.3	0.1	20.5	0.8	0.1	1427
LAsp.	0.1	**50.8**	0.0	24.1	17.3	0.0	0.1	7.5	1021
LACI	3.9	0.0	**89.0**	0.3	0.0	6.8	0.0	0.0	589
NYHU	0.3	10.4	0.0	**83.7**	2.5	0.1	0.5	2.4	2381
PESU	0.0	7.6	0.0	2.1	**87.3**	0.0	0.1	2.9	3293
TABR	19.3	0.1	7.2	0.3	0.0	**71.6**	1.4	0.1	1106
CORA	1.3	0.0	0.0	0.4	0.0	0.0	**96.0**	2.2	225
MYAU	0.2	3.0	0.0	0.9	0.1	0.1	2.3	**91.6**	3314

Table 2.2: Overall leave-one-out cross validation accuracy rates for 11 candidate models used to classify bat calls from the southeastern U.S. Coastal Plain using linear discriminant function analysis (DFA), quadratic DFA, and K-nearest neighbor analysis (KNN). Call parameters were automatically calculated using ANALOOK software including call duration (Dur), initial slope (S1), slope of flattest call section (Sc), maximum frequency (Fmax), minimum frequency (Fmin), mean call frequency (Fmean), frequency where slope changes from S1 to Sc (Fk), frequency of flattest part of call (Fc), time when Fk reached (Tk), time when Fc reached (Tc), and significance of change from S1 to Sc (Qk). Bold type indicates best performing model for each method.

	Method		
Candidate Model	Linear DFA	Quadratic DFA	KNN
Fmax, Fmin, Fmean, Tk, Fk, Qk, Tc, Fc, S1, Sc	71.83	73.07	**82.50**
Dur, Fmax, Fmin, Fmean, Tk, Fk, Qk, Tc, Fc, S1, Sc	71.74	**74.87**	82.37
Fmax, Fmin, Fmean, Tk, Fk, Qk, Fc, S1, Sc	**72.59**	70.20	82.12
Dur, Fmax, Fmin, Fmean, Tk, Fk, Tc, Fc, S1, Sc	70.58	73.83	81.50
Fmax, Fmin, Fmean, Fk, Fc, Sc	68.59	66.79	81.29
Dur, Fmax, Fmin, Fk, Tc, Fc, Sc	67.32	71.68	81.27
Dur, Fmax, Fmin, Tk, Fk, Qk, S1, Sc	68.54	73.84	81.12
Dur, Fmax, Fmin, Tk, Qk, S1, Sc	67.21	72.61	79.00
Dur, Fmin, Fc, S1, Sc	68.34	70.54	78.85
Fmax, Fmin, Fmean	59.61	62.49	73.47
Fmax, Fmin	49.24	55.53	56.45

Table 2.3: Species, number of sequences, and number of calls comprising the reference library of ANABAT recorded calls used to classify bat calls from the southeastern U.S. Coastal Plain. Calls were collected by C. Corben (formerly of Title Electronics, Australia) from bats through a variety of methods including hand releases, zip lines, free flying bats, and roost emergences. Species include big brown (EPFU), eastern red and Seminole group (LAsp.), hoary (LACI), evening (NYHU), tri-colored (PESU), Brazilian free-tail (TABR), Rafinesque's big-eared (CORA), and southeastern myotis (MYAU).

Species	Sequences	Calls
MYAU	102	3314
PESU	75	3293
NYHU	61	2381
EPFU	42	1427
TABR	108	1106
LAsp.	42	1021
LACI	43	589
CORA	9	225
Total	482	13356

Table 2.4: Overall, mean, and species/group leave-one-out cross validation accuracy rates for the best performing models used to classify echolocation calls of a suite of bat species from the southeastern U.S. Coastal Plain. Classification methods include linear discriminant function analysis (L-DFA), quadratic DFA (Q-DFA), and K-nearest neighbor analysis (KNN). Overall accuracy calculated as the total correctly classified/total classified, and mean is the average accuracy for all species/groups including; big brown (EPFU), eastern red and Seminole group (LAsp), hoary (LACI), evening (NYHU), tri-colored (PESU), Brazilian free-tail (TABR), Rafinesque's big-eared (CORA), and southeastern myotis (MYAU). Improvement over (IO) L-DFA and Q-DFA represents the difference in accuracy rates between KNN and alternative methods.

			Species							
Method	Overall	Mean	EPFU	LAsp.	LACI	NYHU	PESU	TABR	CORA	MYAU
Best L-DFA	72.59	66.55	57.95	33.59	69.44	80.43	85.12	58.05	69.33	78.46
Best Q-DFA	74.87	71.75	54.59	33.30	85.23	74.38	88.25	63.11	90.67	84.49
Best KNN	82.50	80.59	74.77	50.83	88.96	83.66	87.31	71.61	96.00	91.55
IO L-DFA	9.91	14.04	16.82	17.24	19.52	3.23	2.19	13.56	26.67	13.09
IO Q-DFA	7.63	8.83	20.18	17.53	3.73	9.28	-0.94	8.50	5.33	7.06

CHAPTER 3

INFLUENCE OF INSECT PREY AVAILABILITY AND VEGETATION STRUCTURE ON SITE-OCCUPANCY OF COASTAL PLAIN FOREST BATS[2]

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[2] Bender, M. J., S. B. Castleberry, D. A. Miller, and T. B. Wigley. To be submitted to Forest Ecology and Management

ABSTRACT

Site-occupancy of bats across forested landscapes often has been linked to vegetation clutter. Clutter alone may not sufficiently explain observed occupancy as abundance of insect prey likely has a strong influence on distribution of foraging insectivorous bats. However, inconclusive evidence concerning relevant measures of prey availability hampers understanding how insect abundance influences site-occupancy by bats. Therefore, we sampled insects, vegetation characteristics, and presence/absence of bat species across multiple pine-dominated landscapes in the Coastal Plain of the southeastern United States to determine how these small-scale factors influence site-occupancy by foraging bats. We used Akaike's Information Criterion to evaluate plausibility of models from a set of candidate models that estimated occupancy and detection probabilities while incorporating vegetation and insect predictor variables. Site-occupancy of foraging bats was better explained by a combination of vegetation characteristics and insect abundance than either separately, and vegetation structure appears to have stronger influence than prey availability. The most appropriate measure of available prey remains unclear, but our data suggest that insect taxon is more influential that insect size. Management activities in managed-pine forests that reduce vegetation clutter and increase insect abundance are likely to benefit resident bat species. Additionally, results suggest that researchers should not assume detection probabilities are constant temporally, geographically, or across sample locations that differ in vegetation structure.

INTRODUCTION

Predator fitness is closely linked to foraging decisions (Stephen and Krebs 1986), and decisions about alternative foraging locations may be influenced by physical habitat characteristics (Hopcraft et al. 2005), abundance of prey items (Ives et al. 1993), or a combination of both (Sleep and Brigham 2003). Foraging decisions made by bats influence ability of individuals to acquire sufficient resources to meet immediate energetic demands and accumulate fat stores. Failure to acquire sufficient resources may result in reduced reproductive output (Burles et al. 2009) or decreased likelihood of survival (Thomas et al. 1990) in temperate region bats. Many species exhibit foraging site fidelity (Rydell 1989, Clark et al. 1993, Duchamp et al. 2004, Hillen et al. 2009) and individuals may use agonistic behavior to reduce competition within foraging areas (Belwood and Fullard 1984, Rydell 1989, Barlow and Jones 1997). These consequences and behaviors suggest that selection of foraging location has direct fitness implications for insectivorous bats. A better understanding of how bats choose foraging areas is required to identify important habitat features and evaluate management prescriptions that potentially alter foraging habitat.

Species-specific characteristics of wing morphology and echolocation call influence flight speeds, maneuverability, and ability of bats to discriminate between prey and non-prey items (Aldridge and Rautenbach 1987). Therefore, optimal habitat conditions and prey items may differ among foraging bat species. As hypothesized based on morphology, vegetation clutter or similar measures of vegetation structure are often important habitat variables when discriminating between occupied and apparently unoccupied acoustic sample points (Ford et al. 2005, Loeb and O'Keefe 2006), which is one method to discern importance of factors that may influence distribution patterns (MacKenzie et al. 2006). However, habitat variables alone are often insufficient to fully understand species' ecological relationships (Morrison 2001). Thus, Morrison (2001) recommends going beyond habitat associations and also investigating resources associated with the habitat. For bats, the primary resource is insect prey, and failure of habitat use to conform to predictions based on morphology alone may be partially attributable to effects of prey densities (Tibbels and Kurta 2003, Ford et al. 2005). Despite many inherent challenges, understanding links between foraging bats and prey availability has been recognized as an important research area, particularly within forested landscapes (Lacki et al. 2007).

Predator distributions are influenced by abundance of prey resources (Colwell and Landrum 1993, Ives et al. 1993), and studies have found a positive relationship between indices of bat foraging activity and insect abundances (Anthony et al. 1981, Rautenbach et al. 1996, Kusch et al. 2004). However, acoustic indices of activity have limitations because of an inability to determine number of individuals contributing to activity measures (Barclay and Bell 1988), which may partially account for results indicating a lack of relationship between foraging activity and insect abundance (Ober and Hayes 2008). In general, foraging activity is not constant throughout the night (Hayes 1997). Foraging bouts may be minimized so that only immediate energetic demands are met (Barclay 1989) or may be governed by the need to periodically stop foraging to facilitate digestion (Barclay 1982). Therefore, increasing activity indices could represent increased effort by a few individuals (representing relatively poor/inefficient foraging conditions) or many individuals using the foraging area for short times before returning to night roosts (representing efficient foraging conditions). Additionally, acoustic data may be systematically biased because ability to detect echolocation calls may vary by habitat type and incorrectly indicate activity differences unless variable detection is considered (Patriquin et al. 2003).

One method to account for limitations of acoustic surveys is to use presence/absence data to investigate influence of insect abundances on site-occupancy of bats, but this approach rarely has been used (Ford et al. 2006). Recently-developed occupancy modeling approaches allow researchers to examine factors that influence detection and occupancy with presence/absence data (MacKenzie et al. 2006). This approach acknowledges that, although detection of a species indicates presence, non-detection does not always equate to species absence and that detectability may vary among sampling locations (MacKenzie et al. 2002). The ability to account for variable detection is important to bat researchers using presence/absence type data because probability of detecting most bat species acoustically is generally <1 (Duchamp et al. 2006, Gorreson et al. 2008, Weller 2008), and traditional logistic regression models are sensitive to even low levels of nondetections (Gu and Swihart 2003).

Another factor hampering our ability to understand insect/bat relationships is an inability to accurately measure prey availability, attributable to a lack of knowledge concerning discriminatory capabilities of foraging bats. Many bat species actively select prey (Brigham 1990), but it is unclear if selection is based on size, insect taxon, or both. Some diet studies suggest that bats discriminate among prey items by taxon (Buchler 1976, Agosta et al. 2003), whereas others suggest that size is the relevant factor (Barclay and Brigham 1991, Barclay and Brigham 1994). A recent field study by Ober and Hayes (2008) suggested importance of size for some species groups, but their results were largely inconclusive.

It is likely that decisions regarding selection of foraging areas are based on a combination of vegetation characteristics and prey abundances as both factors contribute to foraging efficiencies (Aldridge and Rautenbach 1987, Salcedo et al. 1995). Sleep and Brigham (2003) experimentally tested influence of clutter and insect abundance on foraging activity and found that less maneuverable bat species may not be capable of exploiting areas of high insect abundance with high amounts of clutter. Meyer et al. (2004) found that bat activity patterns followed the spatial and temporal activity patterns of lepidopteran prey, but habitat characteristics had the most pronounced effect. Among similar habitat types, Wickramsinghe et al. (2004) found that differences in bat activity were related to differences in insect abundances.

Our objective was to examine relationships between site-occupancy of bats and insect abundance. We specifically investigated if overall insect abundance, ordinal richness, abundance of size classes, or abundance of taxonomic orders best explained the observed presence/absence of resident bat species. Secondarily, we determined if vegetation characteristics, insect abundance, or a combination of the two best discriminated between occupied and apparently unoccupied sites. Lastly, we evaluated relative plausibility of occupancy models that included detection factors and the constant/perfect detection model assumed by traditional logistic regression.

METHODS

Data Collection

During summer 2008 we sampled 25 points systematically chosen from a 900 x 900 m grid in each of three managed-pine forest landscapes (n = 75) located in the Coastal Plain of the southeastern U.S. (near Greenville, Alabama; Shallotte, North Carolina; and Washington, North Carolina). Loblolly pine (*Pinus taeda*) was the dominant tree species in all landscapes, and management activities were "typical" of plantation forestry operation in the southeastern U.S. Although management activities are based on site conditions and modified to meet demands of individual stands, typical regional management activities include clear-cutting of managed stands at 20-30 years, mechanical and/or chemical site preparation, and reforestation using 1 to 2-year-old nursery stock typically planted in raised beds at a stocking rate of approximately 450 to 700 trees per acre (Gresham 2002). Competing vegetation is reduced as needed through herbicide applications, fire, or mechanically and most stands are periodically thinned. These intensively-managed stands comprised ≥ 70% of area within sampled landscapes with streamside management zones, roads, wildlife openings, and other non-forest habitat types accounting for the remaining area. We collected data in each landscape for approximately 1 month prior to moving to the next location (Greenville 12 May – 5 June; Shallotte 16 June – 12 July; Washington 17 July – 13 August, 2008).

We passively recorded bat echolocation calls at each point for two nights using an Anabat II frequency division bat detector (Titley Scientific, East Brisbane, Australia) coupled with a zero-crossing interface module (ZCAIM). We stored each Anabat II/ZCAIM combination in a waterproof plastic container and stored data on a compact flash (CF) card, which we downloaded daily. We directed Anabat II microphones towards the area of least vegetation clutter, 45° from horizontal using a 5.1 cm PVC elbow, and 1.5 m above the forest floor on a camera tripod to maximize call quality and quantity (Weller and Zabel 2002). We programmed detectors to begin sampling 30 min prior to civil sunset and end sampling 30 min after civil sunrise. We conducted acoustic sampling for two nights at each point and consecutively when possible to minimize temporal variability. We randomly assigned detectors to points on a nightly basis to randomize equipment bias, and any data collected during nights with rain events were not retained.

We created a customized ANALOOK (v 4.9; Titley Scientific, East Brisbane, Australia) filter to retain only search phase calls following the methods and criteria of Britzke and Murray (2000). We used ANALOOK to automatically calculate and extract call parameters from retained files to increase objectivity and repeatability while reducing influence of researcher experience (Obrist et al. 2004), which may have significant impact on classification errors (Gannon et al. 2004).

We quantitatively identified unknown calls with a reference library of known calls using a K-nearest-neighbor classification approach (Bender et al. unpublished data). We included 8 species/groups as potential residents of southeastern U.S. Coastal Plain forest landscapes based on mist-net captures (Bender unpublished data); big brown bat (*Eptesicus fuscus*), eastern red + Seminole group (*Lasiurus borealis* + *L. seminolus*), hoary bat (*L. cinereus*), evening bat (*Nycticeius humeralis*), tri-colored bat (*Perymyotis subflavus*), Rafinesque's big-eared bat (*Corynorhinus rafinesquii*), Brazilian free-tailed bat (*Tadarida brasiliensis*), and southeastern myotis (*Myotis austroriparius*). Overall call classification accuracy based on leave-one-out cross validation was 83% and mean species accuracy was 81%, ranging from 51% to 96% (Bender et al. unpublished data; Table 3.1). However, species identifications were based on the sequence of calls within each unknown call file rather than on individual calls. Therefore, we used three-fold cross validation of the reference library to estimate sequence classification accuracy. To accomplish this, we randomly selected one third of reference sequences with a random number generator and used them as our test data. Calls from the remaining two-thirds of sequences were used to train the classification model. We repeated this process until all sequences containing ≥ 5 calls were classified. We used the posterior classification probabilities averaged across all calls in a sequence to assign sequence identities. Sequence accuracies averaged across the three iterations ranged by species from 72% to 100% (Table 3.1). Each sequence recorded in the field with ≤ 4 calls or that did not result in identification with an average posterior classification probability ≥ 0.5 was eliminated.

We collected insects using a variation of a flight intercept trap (Tripplehorn and Johnson 2005) mounted on a portable frame 1.5 m above the forest floor. Traps consisted of a 1 m^2 screen panel with a collection device above and below the intercept panel. A small amount of liquid dish soap was added to water in the collection devices to break the surface tension and facilitate insect euthanasia (Tripplehorn and Johnson 2005). Passive insect collection methods capture fewer individuals than methods that employ an attractant such as a light source (Bontadina et al. 2008). However, a passive design is likely less biased than designs using chemical or light attractants. Flight intercept traps produce insect captures similar to alternative passive sampling methods including sticky and suction traps (Sleep and Brigham 2003) and were desirable because of logistic considerations.

We set insect traps within 15 m of acoustic sampling points in locations likely to minimize influence on bat activity or detectability (i.e., not in front of bat detectors or in flight corridors leading to detectors). We collected insects and reset traps each morning so that each sample represents captures for approximately 24 hours. Insects were preserved in 90% ethanol until identification. We used a dissecting microscope to measure and identify all winged insects captured to order based on dichotomous keys (Arnett 1985, Tripplehorn and Johnson 2005); taxonomy follows Tripplehorn and Johnson (2005). We measured insect lengths to the nearest millimeter from the anterior portion of the head to the last abdominal segment and placed each into one of three size classes (≤ 2 mm, 3-6 mm, and ≥ 7 mm long; Ober and Hayes 2008).

Insect sampling was conducted concurrently with acoustic sampling whenever possible. On rare occasions ($n = 9$ nights, 6%) we were unable to sample concurrently because of equipment malfunctions. However, acoustic and insect sampling at each point was always conducted within 2 days in similar weather conditions. We sampled insects at 10 points for an additional night (i.e., three nights), and for a single night at one point because of trap damage during subsequent attempts. Insect predictor variables represent average nightly abundances for each point. One sample point was dropped from analyses because reoccurring trap failures (i.e., repeatedly broken by wind gusts) prevented insect sampling.

We measured percent canopy cover using a convex spherical densiometer (Ben Meadows Company, Janesville, WI), averaging measurements taken at the acoustic sample point and 4 additional locations 5 m from the point in each of the cardinal directions. We measured basal area (m^2/ha) using a 10-factor prism centered at the acoustic detector point. We measured vegetation clutter using methods based conceptually on a Nudds board (Nudds 1977), estimating percent coverage using a 1-m^2 panel raised approximately 4.5 m above the ground and 4.5 m from the sample point in each cardinal direction and in the sampling direction of the acoustic detector.

Statistical Analyses

We interpreted detection of a species during the sampling season (i.e., time period encompassing repeated sampling visits) as an indication that members of that species "used" rather than constantly "occupied" the sample point during the season, which is a valid relaxation of the closure assumption of occupancy models (MacKenzie et al. 2006). Although we use the terms "site-occupancy" and "use" interchangeably, data represent the influence of predictor variables on use of sample points by foraging bats. All modeling steps were performed separately for each bat species investigated. Correlation between predictor variables was assessed and no correlated variables (Pearson's correlation coefficient $|r| > 0.70$) were used in the same model to reduce multicollinearity concerns (Moore and McCabe 1993).

We first investigated influence of sampling date, study site, and vegetation structure on acoustic detection of bats. Eight competing models were generated to represent plausible hypotheses concerning influence of these parameters on detection by including them as predictor variables (Table 3.2). We constructed 3 candidate models to reflect our hypothesis that detection probability is related to vegetation structure. We predicted that detection probabilities would decrease as measures of vegetation structure increased (Weller and Zabel 2002). Another plausible hypothesis is that detection is related to sampling date (Hein et al. 2009), and we predicted that later sampling dates would have higher detection probabilities because of increased population sizes as juveniles become volant and with increased activity related to mating behaviors (Parsons et al. 2003) and/or foraging prior to autumn (Seidman and Zabel 2001). We explored both a quadratic and linear relationship between sampling date and detection, but found that a linear relationship was more plausible based on Akaike's Information Criterion values (AIC; Akaike 1973). We created a model to reflect our hypothesis that study site might influence detection because of historic conditions, local population levels, or unmeasured characteristics of the landscape and surrounding areas. We constructed 2 candidate models representing our hypotheses that detection may be related to additive combinations of the most plausible measure of vegetation structure and either sample site or sample date (Table 3.2). Lastly, we included the null model which assumed that detection probability was constant and that none of the factors measured had an influence on detecting a species provided it was present. We held the occupancy portion of models constant by using the null occupancy model when evaluating plausibility of detection models (Olson et al. 2005, Kroll et al. 2007, Kroll et al. 2008, Mattsson and Marshall 2009, Hansen et al. 2011). The most parsimonious detection model for each species was incorporated into subsequent occupancy models (Amelon 2007, Kroll et al. 2007, Kroll et al. 2008, Hein et al. 2009, Hansen et al. 2011).

In our second analysis, we determined the most plausible insect abundance-based occupancy model. We developed 11 candidate models reflecting our hypotheses regarding influence of prey abundances on site-occupancy by foraging bats (Table 3.3). Our hypotheses were that bats choose foraging locations (and therefore the probability of use increases) based on 1) overall abundance of insects, 2) insect richness, 3) abundance of individual orders, or 4) abundance within size classes. The null model assumed that probability of site-occupancy was equal across the landscape and that the predictor variables measured at sample points had no influence on occupancy. No additive combinations of variables were modeled because measures of insect abundances were often correlated. Models were evaluated with and without a binary coded (0, 1) study area variable to determine if unmeasured study site characteristics had an influence on site-occupancy. Thus, we evaluated 22 candidate models relating prey abundances to site-occupancy by bats.

Our third analysis examined relative plausibility of insect, vegetation, or combined insect + vegetation factors on site occupancy. The first step involved determining the most plausible vegetation-based model: canopy cover, vegetation clutter, or basal area. No additive combinations of these measures were modeled to minimize number of parameters estimated and because preliminary analyses indicated correlations between these variables (Pearson's $|r| > 0.70$). We retained only the most parsimonious model for the next step, which involved creating and evaluating a candidate set of models (Table 3.4) including our previously determined confidence set of insect-based models, the most plausible vegetation-based model, and models including the vegetation measure in addition to insect abundances, along with the null model.

We explored the plausibility of interactions between insect and vegetation factors, but found that that modeling predictor variables as additive combinations was more appropriate than modeling interactions between predictors based on AIC values.

We used Program PRESENCE (MacKenzie et al. 2002) to evaluate our candidate model sets and estimate detection and occupancy parameters for each species. We used Akaike's Information Criterion adjusted for small sample size (AICc; Hurvich and Tsai 1989) to evaluate the relative plausibility of all candidate sets of models. We specified AICc in PRESENCE by changing effective sample size to our number of sample points (n = 74; Schmidt 2005). Models that did not converge were eliminated from further analyses (Long et al. 2007). We defined our confidence set of models as those with ΔAICc values ≤ 2.0, which indicates substantial support (Burnham and Anderson 2004, Perry et al. 2008). We also calculated model weights (ω_i) to estimate weight of evidence for models and used the ratio of these weights to asses likelihood of one model over another (Burnham and Anderson 2001).

We incorporated model selection uncertainty in our final analyses by averaging parameter estimates and standard errors across our confidence set of models for all parameters included in the confidence set to create a composite model (Burnham and Anderson 2002, Perry et al. 2008). We calculated odds ratios from the model averaged parameter estimates and 90% confidence intervals around the odds ratios to determine relationship to site-occupancy, assess variability within the data (Gardner and Altman 1986), and evaluate biological significance of parameters given the data (Gerard et al. 1998). We made inferences based on relative Information Criterion (ICc) rankings (either AICc or QAICc), model weights, and composite model parameter estimates and confidence intervals.

We assessed model goodness-of-fit in PRESENCE with 1000 bootstraps using the most parameterized model within the confidence set (MacKenzie and Bailey 2004). If lack of fit was determined (i.e., greater dispersion than the underlying distribution assumes), we used the overdispersion parameter (c-hat; observed test statistic/average bootstrapping test statistic) to calculate quasi-AICc (QAICc) values which were then used to evaluate model plausibility (Burnham and Anderson 2001). Standard errors from overdispersed models were adjusted using the square root of the c-hat value (MacKenzie and Bailey 2004).

RESULTS

We collected, identified to order, and placed into size class 4008 insects captured during 159 trapping periods. Combined captures included members from 12 insect orders. Seven orders (Dictyoptera, Hemiptera, Isoptera, Neuroptera, Orthoptera, Psocoptera, and Zoraptera) were never abundant (i.e., < 15 individuals at point with highest abundance) and were eliminated as potential occupancy factors. Therefore, abundance of five insect orders including; Coleoptera, Diptera, Hymenoptera, Lepidoptera, and Thysanoptera were included as predictor variables along with abundance within size classes and vegetation measures (Table 3.5). Total insect abundance was negatively but weakly correlated with basal area, percent clutter, and percent canopy cover (Pearson's $r = -0.37$, -0.39, and -0.50, respectively; $P < 0.01$). This weak negative correlation between insect abundances and measures of vegetation structure was consistent for all order and size class abundances, except abundance of thysanopterans which generally exhibited no relationship to vegetation structure (Pearson's $r = 0.00$, 0.10, and -0.14, respectively; $P \geq 0.25$).

We detected at least one identifiable bat call at 78% (58/74) of surveyed points. *Nycticeus humeralis* was detected at the greatest number of points (56.8%, n = 42), followed by the *L.*

borealis + *L. seminolus* group (54.1%, n = 40). *Eptesicus fuscus* was detected at 36 points (48.7%), *P. subflavus* at 30 (40.5%), *M. austroriparius* at 19 (25.7%), and *T. brasiliensis* at 16 (21.6%). Because *Corynorhinus rafinesquii* was never detected and *L. cinereus* was only detected at 3 points (4.1%) they were excluded from modeling efforts. Based on simple means, sample points with confirmed bat occupancy were characterized by lower levels of basal area, canopy cover, and clutter and greater or equal insect abundances than apparently unoccupied points (Appendix A).

The most plausible detection model differed among species investigated (Table 3.6). However, the null model, which assumed equal probability of detection at all sites given the species was present, received little empirical support for any species (ΔAICc ≥ 7) indicating the plausibility of measured factors and importance of accounting for detection when investigating site-occupancy. Mean estimated detection probability using the most plausible model from the insect + vegetation model set differed among species. Among the species investigated, detection probability was highest for *N. humeralis* (0.71 after a single sample night, 0.91 after two sample nights), followed by the *L. borealis* + *L. seminolus* group (0.67, 0.89), *P. subflavus* (0.57, 0.82), *E. fuscus* (0.47, 0.72), *T. brasiliensis* (0.44, 0.69), and was lowest for *M. austroriparius* (0.20, 0.36).

The most parsimonious insect-based occupancy model differed among bat species investigated (Table 3.6). Abundance of at least one insect taxonomic order was included in the confidence set for all bat species and abundance of an insect size class was included as a parameter in the confidence set of models for three species (*E. fuscus* and *T. brasiliensis* = medium, *M. austroriparius* = small; Table 3.7). The confidence sets of models for the *L. borealis* + *L. seminolus* group and *M. austroriparius* included the null model (Table 3.6). Model averaged estimates and odds ratios for all bat species indicated a positive relationship between increasing insect abundances and probability of use.

The vegetation occupancy model with the strongest empirical support for 4 species (*P. subflavus*, *L. borealis* + *L. seminolus* group, *N. humeralis*, and *M. austroriparius*; Table 3.8) was amount of vegetation clutter. The canopy cover model for *T. brasiliensis* did not converge and was eliminated from the analysis. The most parsimonious model for each species had substantial support receiving ICc weights ranging from 52.5 – 83.8% of the total weight (Table 3.8). The top models were 1.7 – 5.2 times more likely to be the best model than the second ranked models.

Among the candidate sets that included both insect and vegetation based models, the top performing model for three species included vegetation as the single occupancy parameter (*E. fuscus*, *P. subflavus*, *L. borealis* + *L. seminolus* group), while the remaining top models included an additive combination of the vegetation parameter and abundance of an insect order (Table 3.9). The confidence sets for *L. borealis* + *L. seminolus* group and *M. austroriparius* again included the null occupancy model indicating that, given our data, none of the models and predictor variables investigated had strong empirical support for their influence on site-occupancy (Table 3.9).

Detection of *E. fuscus* was positively related to Julian date, and negatively related to increasing percentage of vegetation clutter at sample points (Table 3.10). Abundance of medium-sized insects (3-6 mm) was the most plausible insect-based occupancy model. However, there was strong support for total abundance, lepidopteran abundance, and coleopteran abundance (Table 3.7). Model averaged estimates indicated a positive yet imprecise influence of these measures of abundance on probability of *E. fuscus* occurrence. The composite model from our candidate set generated from insect and vegetation parameters included one occupancy parameter (canopy cover) with confidence intervals that did not overlap zero, indicating useful information for predicting site-occupancy of *E. fuscus* (Table 3.10). Odds of *E. fuscus* using a point decreased from 1.9 to 3.2 times for every one percent increase in canopy cover.

Detection of *P. subflavus* was positively related to Julian date and percent vegetation clutter, although the confidence interval for vegetation clutter contained zero (Table 3.10). The most plausible insect-based model, which accounted for 66% of AICc weight, indicated a strong but imprecise positive relationship between lepidopteran abundance and probability of occurrence (Table 3.7). The confidence set from our combined candidate set for *P. subflavus* bats contained a single model that included clutter as the single occupancy predictor variable (Table 3.9). Model averaged parameter estimates suggested that *Perimyotis subflavus* was from 1.1 to 1.3 times less likely to use a sample point for every percentage increase in vegetation clutter (Table 3.10).

Basal area at the sample point was the most plausible *N. humeralis* detection parameter, but estimates indicated a weak negative relationship to detection probability (Table 3.10). Insect-based models indicated importance of hymenopterans along with overall insect richness, both of which were positively associated with use, along with importance of study site (Table 3.7). A single model containing clutter and hymenopteran abundance as occupancy predictor variables comprised the confidence set for *N. humeralis* from the combined candidate set (Table 3.9). This single model accounted for 90% of cumulative AICc weight and was 17.2 times more likely to be the best than the next best model. *Nycticeus humeralis* was 7.37 times more likely to use a sample point for each additional hymenopteran captured per night, and slightly (1.06 times) less likely for every percentage increase in vegetation clutter (Table 3.10).

Estimates for all data associated with *T. brasiliensis* detection and occupancy were imprecise (Table 3.10). Within the composite model created from the combined candidate set, the confidence interval surrounding the estimate for influence of Julian date on detection indicated a positive relationship and was the only interval that did not include zero (Table 3.10). Estimates from the insect only model set indicated a positive relationship between coleopterans, lepidopterans, and medium sizes insect abundances and *T. brasiliensis* site-occupancy (Table 3.7). Confidence intervals for all occupancy parameters within our composite model surrounded one, indicating an inability to predict site-occupancy based on these factors.

DISCUSSION

Our results support the general conclusion that foraging bats are positively influenced by increasing insect abundances (Kunz 1973, Hayes 1997, O'Donnell 2000, Wickramsinghe et al. 2004). However, the most appropriate measure of available prey to predict site-occupancy by bats remains unclear as multiple abundance measures appeared in confidence sets and varied by species. We found that site-occupancy of foraging bats was frequently better explained by a combination of vegetation characteristics and insect abundance than by either separately. Additionally, our data support recent research suggesting that detection probabilities for elusive animals should not be assumed constant temporally (Hein et al. 2008), geographically (Nichols et al. 1998), or across sample locations that differ in vegetation characteristics (Bailey et al. 2004, Amelon 2007).

Insect abundances contribute to foraging efficiencies of insectivorous bats (Racey and Swift 1985) and are likely to influence foraging decisions. In our study, this hypothesis was supported by the higher abundance of insects captured at points with confirmed occupancy and by the positive relationship between occupancy and abundance of insects for all species.

However, insect abundance as we measured it does not appear to have a consistently strong influence on foraging location choices. Because of large confidence intervals associated with insect parameter estimates, our data suggest that insect abundance alone is not sufficient to predict site-occupancy in Coastal Plain forest landscapes unless precision of parameter estimates can be improved. We hypothesize that the inability of insect predictor variables to improve model performance over our null model for Southeastern myotis may be related to a strong affinity for certain habitat types rather than insect abundance or vegetation characteristics (Ford et al. 2006). Lack of substantial increase in plausibility over the null model for the *L. borealis* + *L. seminolus* group models may be related to the high degree of foraging plasticity noted for this species group (Elmore et al. 2005). However, the relationship may also be confounded because we combined two species into one phonic group although differences in behavior (Menzel et al. 1998) and diet (Carter et al. 2004) have been documented. This source of uncertainty and inability to discriminated between these two species based on echolocation calls is common (Menzel et al. 2002, Menzel et al. 2005, Ford et al. 2006), yet hampers our ability to discern the influence of insect abundance on site-occupancy.

Inconclusive results for some species groups were also obtained by Ober and Hayes (2008) in a similar study investigating influence of insect abundance on indices of bat activity in Oregon forests. Our combined results suggest that alternative factors unrelated to insect abundance may be more influential to foraging bats, possibly because insects may be ubiquitously distributed in sufficient abundances during summer (Racey and Swift 1985) which limits their influence on foraging decisions. Stronger influences may be observed in seasons or geographic areas characterized by lower insect abundances or across landscapes that exhibit greater variability in insect abundances than what we observed.

It remains unclear if bats discriminate between prey items, and are therefore more likely to use sites based on insect size classes or taxa (Ober and Hayes 2008). Our results generally support the hypothesis that prey discrimination is likely based on taxon characteristics (Agosta et al. 2003) rather than size (Barclay and Brigham 1994). Model-averaged parameter estimates indicated a stronger influence per unit change of taxa abundances than size classes for *E. fuscus* and *T. brasiliensis*, and the confidence sets for *N. humeralis* and *P. subflavus* bats included only taxa-based factors. However, correlations between size classes and taxa (Pearson's correlation coefficient $|r| > 0.70$; small – dipteran abundance, medium – coleopteran and hymenopteran abundances) make interpretation difficult because of possibly confounded results. Additionally, our results may have been influenced by the size classes we chose to model. Although we placed our insects into size classes based on previous research (Ober and Hayes 2008), these size classes may not be biologically relevant to all species. Alternative and possibly more biologically relevant size classes may reveal a greater importance of prey size than our data suggest. Assuming that Coastal Plain forest bats actually discriminate based on taxon characteristics as our data suggest, this level of discrimination may not apply to all habitat types or geographic regions. Barclay and Brigham (1994) found that as the density of foraging bats increases individuals become less discriminant in the prey they pursue, possibly because of acoustic interference or increased competition. Therefore, the relatively low amount of bat foraging activity associated with southeastern U.S. forests (Menzel et al. 2005, Loeb and O'Keefe 2006) and abundance of insects may allow for discrimination among taxa rather than more coarse discrimination by size.

Probability of occurrence was always positively related to abundance of insect taxa, but the taxon (or taxa) of importance varied by species. Results indicated the importance of lepidopterans and coleopterans for *E. fuscus* and *T. brasiliensis*, lepidopterans for *P. subflavus*, and hymenopterans along with taxa richness for *N. humeralis*. Diet studies confirm the potential for these insect orders to influence foraging decisions as they have been commonly documented as prey. Coleopterans often constitute a large portion of the prey consumed by *E. fuscus* (Agosta et al. 2003, Feldhamer et al. 2009) and lepidopterans and coleopterans were the most commonly consumed prey items by *E. fuscus* in western Oregon (Ober and Hayes 2008). Diet similarities between *E. fuscus* and *T. brasiliensis* were expected as their call structure and body morphology are similar. Diet studies confirm that *P. subflavus* consume lepidopterans and a diversity of other soft bodied prey (Carter et al. 2003, Feldhamer et al. 2009), although we found lepidopteran abundance to be the only important insect order supported by our data. The occurrence of *N. humeralis* was positively related to hymenopteran abundance which is supported in diet studies (Whitaker and Clem 1992, Carter et al. 2004) and in habitat types similar to those examined in this study (Bender et al. 2009). Although site-occupancy was modeled without additive combinations of insect predictor variables, diet studies indicate a diverse diet for all species we investigated. Therefore, bats may respond to abundance of multiple insect orders simultaneously and importance of prey items may vary seasonally (Agosta et al. 2003, Fukui et al. 2006) or even nightly.

We found that insect abundances and vegetation structure were weakly and negatively correlated, similar to within-stand results from Tibbels and Kurta (2003). In apparent contrast to our results, Kalcounis and Brigham (1995) captured more insects in a cluttered habitat type (white spruce forest) than in an uncluttered habitat type (open fescue field) in Saskatchewan, Canada. These contrasting results suggest that the assumption that insect abundance increases with vegetation clutter (Aldridge and Rautenbach 1987) may not apply within forest landscapes.

Furthermore, in managed-pine landscapes the relationship is likely reversed with insect abundance being higher in areas with reduced vegetation clutter than in areas with high amounts of vegetation clutter (Tibbels and Kurta 2003) and may be related to insect-repelling compounds synthesized by coniferous trees (Kalcounis et al. 1999).

Sample points with decreased amounts of clutter generally were more likely to be used by foraging bats. Although morphological differences are often useful for classifying species as clutter or open-adapted species (Aldridge and Rautenbach 1987), and representatives of each group were present in our study (Menzel et al. 2005), all species (except *M. austroriparius*) were more likely to use points with reduced vegetation clutter. This pattern of higher activity or site-occupancy in areas of reduced vegetation structure regardless of morphological predictions is commonly found in forested landscapes including bottomland forests (Menzel et al. 2002), mixed forests (Loeb and O'Keefe 2006), and managed-pine dominated landscapes (Ford et al. 2006), but does not hold true in all forest landscapes (Ford et al. 2005). Although morphology suggests that species are most adapted to foraging in particular habitat types, behavioral flexibility to exploit areas that promote efficient foraging is expected (Aldridge and Rautenbach 1987). Provided that insect abundances are relatively similar, areas with reduced vegetation structure may be easier to navigate which enables more efficient foraging and therefore represents preferred foraging habitat (Grindal and Brigham 1998). Importance of structural complexity on foraging is likely more influential in forest landscapes, particularly in forest landscapes with high stand densities, than less structurally complex land-cover types such as orchards, suburban, and pasture lands.

Our data support previous conclusions that foraging is related to both habitat characteristics and prey abundance (Wickramsinghe et al. 2003, Meyer et al. 2004, Wickramsinghe et al. 2004). Results suggest that, in general, vegetation structure may be more important to foraging bats in forests than insect abundances, similar to conclusions of Meyer et al. (2004) and Grindal and Brigham (1998). However, there is little empirical evidence to support influence of insect abundance or small-scale vegetation characteristics on occupancy of some resident species in these managed forest landscapes. The high degree of variability within the data for *T. brasiliensis* may be related to foraging behaviors of this species which is well documented in its ability to forage high above the forest floor (Davis et al. 1962, Williams et al. 1973, Claire et al. 1984, McCracken et al. 2008). Therefore, our vegetation and insect sampling protocol may be poorly suited to accurately measuring the insect community and structural characteristics experienced by foraging *T. brasiliensis* individuals.

Detection probabilities and important predictors were species-specific. We found that sample date was positively related to detection for 3 of our resident species (*E. fuscus, P. subflavus,* and *T. brasiliensis*). This positive relationship between detection probability and later sampling dates within the summer season is supported by results from South Carolina (Hein et al. 2009) and Missouri (Yates and Muzika 2006, Amelon 2007). The observed influence of sample date on detection suggests that studies spanning long time periods should consider the temporal influence on detection and make inferences accordingly. Our results caution against assuming that vegetation clutter does not influence sampling effectiveness (Loeb and O'Keefe 2006) or detection probabilities (Hein et al. 2008) unless supported by data. Although Patriquin et al. (2003) found that vegetation clutter has minimal impact on detectability of 40 Khz sound in forest environments, our data suggest that vegetation did impact our ability to detect species with calls in this range (*P. subflavus* and *N. humeralis*). Others have noted the negative influence of vegetation on detectability (Amelon 2007) and number of identifiable sequences (Ford et al.

2005). However, Yates and Muzika (2006) did not find understory density to be an important detection probability parameter. These conflicting results may be related to the widely different measures of vegetation clutter used across studies, which may vary in ability to accurately and equally describe the amount of vegetation clutter (O'Keefe 2009). At a minimum, field protocols of orienting acoustic detectors towards the area of least clutter should be maintained to increase detection probabilities (Weller and Zabel 2002, Patriquin et al. 2003). Ideally, we suggest that differential detectability be accounted for whenever possible.

Our insect sampling protocol introduced biases that had an unknown effect on the results obtained. All insect sampling methods are biased towards capturing prey of certain sizes or behaviors (Tripplehorn and Johnson 2005). However, because of logistical constraints, we were forced to sample both diurnal and nocturnal insects. The number of exclusively diurnal insects comprised an unknown portion of the insects collected although they were unavailable as prey to bats. Our sampling was restricted to aerial insects which is appropriate because the species we investigated are considered aerial hawkers. However, gleaning prey from vegetation may be more widespread than expected in morphologically capable species (Feldhamer et al. 2009). Lastly, insects were sampled just above the forest floor although vertical stratification of the insect community within managed forests has been documented (Su and Woods 2001).

To partially account for variability in foraging activity within nights, among nights, and seasonally (Hayes 1997) we used site-occupancy as a variable of interest as opposed to bat passes/hour (Hogberg et al. 2002), pulses/hour (O'Keefe 2009), or minutes of activity/night (Ober and Hayes 2008). We assumed that sample points were closed to occupancy changes during the brief sampling time required to acoustically sample for two nights or that the occupancy changes were random, both of which are valid for our modeling approach

(MacKenzie et al. 2006). Others have partitioned nights into multiple time periods to facilitate estimation of both occupancy and detection parameters (Duchamp 2006, Yates and Muzika 2006, Amelon 2007). Given that many species exhibit peaks of foraging activity (Hayes 1997) or forage during certain times of the night (Rydell et al. 1996) we believed it was more appropriate to sample multiple nights than to consider portions of each night as separate observation periods. However, our use of an entire night as a sampling visit limited the number of visits we could make to each sample point as well as the number of points sampled. Therefore, the likelihoods of false absence were higher than recommended when investigating habitat preferences (MacKenzie et al. 2006).

Alternative analytical approaches may be more appropriate when attempting to elucidate the relationship between insect abundance, vegetation characteristics, and site-occupancy by foraging bats. Although our stepwise method of determining the most parsimonious detection model and then incorporating it into subsequent models is often used, alternative methods (i.e., investigating all possible detection and occupancy parameter combinations or using a general set of occupancy parameters while determining the most plausible detection model) may be more appropriate and influence results and interpretations. Additionally, we investigated the potential influence of study sites on detection and occupancy by investigating the plausibility of models that incorporated study site as a fixed effect. Although models incorporating study-site as a factor influencing site-occupancy did not receive empirical support, post-hoc analysis of variance on the most parsimonious insect + vegetation model revealed spatial dependence among sample points for some of the species investigated. Therefore, although we investigated the influence of study site as a fixed effect, it may be more appropriate to include study site as a random effect, particularly if researchers are interested in making inferences to landscapes beyond those investigated. Incorporating the study site as a random effect and accounting for spatial dependence may improve parameter estimates and standard errors and more appropriately partition variance (Moore and Swihart 2005). However, PRESENCE does not allow for random effects models so researchers interested in incorporating random effects into models should use alternative software programs (e.g., MARK, Moore and Swihart 2005).

MANAGEMENT IMPLICATIONS

Overall, our results indicate that increasing insect abundance, regardless of how measured, has a positive influence on site-occupancy of foraging bats. Therefore, assessing impact of management activities on insect abundance may be a less costly and more feasible approach than attempting to monitor the bat community directly. Additionally, indices of insect abundance may already be available as some landowners sample to assess presence or density of insect pests. Reduction in vegetation appears beneficial to the majority of resident species. Management activities that reduce basal area, canopy cover, and vegetation clutter, such as stand thinnings or planting at lower stocking densities, are likely to benefit the bat community.

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Table 3.1: Leave-one-out cross validation accuracy for single calls and three-fold cross validation accuracy for sequences containing ≥ 5 calls of all species/groups considered residents of Coastal Plain forests of the southeastern U.S., summer 2008. Accuracy rates were calculated by iteratively withholding a portion of the known reference library of calls and using the remaining portion for classification.

Species	**≥ 5 call sequence accuracy**	**single call accuracy**
C. rafinesquii	100	96
M. austroriparius	100	92
P. subflavus	99	87
L. cinereus	97	89
N. humeralis	97	84
T. brasiliensis	89	72
E. fuscus	80	75
L. borealis + *L. seminolus* group	72	51

Table 3.2: Hypotheses relating the influence of vegetation characteristics, survey date, and site effects to detection probabilities of bats sampled May-August 2008 in managed pine forests of the southeastern U.S. Coastal Plain, their expected influence on detection probabilities, and models reflecting the hypotheses and considered as the candidate set.

Hypothesis	Expected influence	Model
Detection probability is dependent on vegetation characteristics at the survey point	Detection probability will decrease with increasing amounts of structural clutter	Canopy cover Basal area Vegetation clutter
Detection probability is survey specific depending on population reproductive status and mean temperature both of which are dependent on survey date	Detection probability will increase with increasing survey dates	Julian date
Detection probability is dependent on the underlying population size and structure which is a function of many unknown or unmeasured factors but likely to vary geographically by study site	Detection probability will vary in an unknown fashion because of site level differences	Site
Detection probability is an additive combination of the influence of vegetation characteristics and survey date or site	Detection probability will increase with decreasing amounts of structural clutter, later dates, and the site influence is unknown	Best vegetation only model + Julian date Best vegetation only model + site
Detection probability is equal at all sites provided they are occupied, or none of the measured predictor variables influence detection probabilities	Null model will perform better than or equal to models including predictors	Null model (·)

Table 3.3: Candidate set of models generated to investigate the influence of alternative measures of insect abundance on site occupancy of bats sampled May-August 2008, hypothetical relationships, and expected influence of increasing abundances in managed pine forests of the southeastern U.S. Coastal Plain.

Hypothesis	Expected influence	Model
Site occupancy is simply related to the overall abundance of insects rather than abundance of preferred items.	Probability of site-occupancy will increase with overall abundance of aerial insects.	Total
Areas with high insect richness may be limited in managed pine forests. Insect richness may be more important to foraging bats and influence site occupancy in these forests more than abundances of particular orders, sizes, or overall.	Probability of site occupancy will increase with increasing richness of captured insects.	Richness
Bats discriminate between prey items based on insect taxon and therefore site occupancy will be related to abundances of preferred insect taxa.	Probabilities of site occupancy will increase with increasing abundances of preferred taxa. Because preferences vary by bat species, the response to taxa abundances will vary by species.	Abundance of individual insect orders; Coleopteran Diptera Hymentoptera Lepidoptera Thysanoptera
Bats discriminate between prey items based on insect size because of echolocation call characteristics, jaw morphology, and limitations to the discriminatory capacity while foraging. Therefore, site occupancy will be related to abundances of preferred insect size classes.	Probabilities of site occupancy will increase with increasing abundances of a preferred size class. Because preferences vary by bat species, the response to size class abundances will vary by species.	Abundance of size class; Small Medium Large
Probability of site occupancy is equal at all sites, or none of the measured insect abundances influence the probability of site occupancy.	Null model will perform better than or equal to models including predictors	Null model (·)

Table 3.4: Candidate set generated to investigate the relative influence of insect-based, vegetation-based, or combined models on probabilities of bat occurrence sampled May-August 2008, hypothetical relationships, and expected outcomes in managed pine forests of the southeastern U.S. Coastal Plain.

Hypothesis	Expected influence	Model
Site-occupancy depends on the vegetation characteristics at the sample point that may influence maneuverability, insect community, and foraging efficiency	Occupancy probabilities will increase or decrease depending on species morphological constraints and foraging strategy	Best Vegetation Model
Site-occupancy depends on the abundance of preferred prey items, either overall, richness, taxon, or size class depending on the species.	Occupancy probabilities will increase with the abundance of preferred prey items.	Species-specific insect confidence set
Site-occupancy depends on the additive influence of preferred prey abundance and vegetation characteristics. Occupancy is related to both these because their combined influence determines the foraging efficiency at the point.	Occupancy probabilities will increase with the abundance of preferred prey items + preferred vegetation characteristics and will be species specific.	Insect confidence set + vegetation measure
Probability of site occupancy is equal at all sites, or none of the measured insect or vegetation predictor variables influence the probability of site occupancy	Null model will perform better than or equal to models including predictors	Null model (·)

Table 3.5: Mean, standard error, and range of insect size classes (small ≤ 2 mm, medium 3-6 mm, large ≥7 mm) and vegetation factors measured at 74 sample points in Coastal Plain managed-pine forests of the southeastern U.S., summer 2008.

Variable*	**Mean**	**Standard Error**	**Range**
Small insects	8.03	1.35	0.5 - 67.0
Medium insects	12.69	1.26	1.5 - 54.0
Large insects	4.40	0.38	0.0 - 16.0
Coleopterans	4.59	0.43	0.0 - 21.0
Dipterans	11.12	1.52	0.5 - 85.0
Hymenopterans	4.46	0.78	0.0 - 42.5
Lepidopterans	1.80	0.30	0.0 - 18.0
Thysanopterans	0.83	0.31	0.0 - 18.0
Total insects	25.10	2.52	4.5 - 126.0
Order richness	4.82	0.13	2.5 - 7.0
Basal area (m^2/ha)/.23	67.43	7.17	0.0 - 200
Percent vegetation clutter	24.20	2.86	0.0 - 85.0
Percent canopy cover	54.41	4.35	0.16 - 96.88

*Insect variables represent average number of individuals captured per sample point per 24 hour period with passive flight intercept traps.

Table 3.6: Model, number of parameters (K), Akaike's Information Criterion adjusted for small sample size (AICc), difference of AICc between a model and the model with the lowest AICc value (ΔAICc), and model weight (ω_i) for the confidence set (ΔAICc < 2.0) of insect based models used to predict occupancy (ψ) given detection probability (ρ) of bats sampled May-August 2008 in manage-pine forests of the southeastern U.S. Coastal Plain. Occupancy parameters represent the richness or abundance of insect orders, size classes, or totals from sample points averaged from ≥ 2 samples/point.

Species	**Model**	**K**	**AICc**	**ΔAICc**	ω_i
**E. fuscus*	ψ (medium), ρ (Julian date + clutter)	5	65.94	0.00	0.1899
	ψ (total), ρ (Julian date + clutter)	5	66.31	0.37	0.1578
	ψ (lepidoptera), ρ (Julian date + clutter)	5	67.09	1.15	0.1068
	ψ (coleoptera), ρ (Julian date + clutter)	5	68.14	1.91	0.0731
**P. subflavus*	ψ (lepidoptera), ρ (Julian date + clutter)	5	93.35	0	0.267
L. borealis + seminolus	ψ (diptera), ρ (basal area + site)	6	156.57	0	0.173
	ψ (·), ρ (basal area + site)	5	157.35	0.78	0.1171
	ψ (richness), ρ (basal area + site)	6	157.8	1.23	0.0935
N. humeralis	ψ (hymenoptera), ρ (basal area)	4	151.74	0	0.5202
	ψ (site, richness), ρ (basal area)	6	152.35	0.61	0.3835
T. brasiliensis	ψ (coleoptera), ρ (basal area + Julian date)	5	102.73	0	0.1945
	ψ (lepidoptera), ρ (basal area + Julian date)	5	103.19	0.46	0.1546
	ψ (medium), ρ (basal area + Julian date)	5	104.2	1.47	0.0933
M. austroriparius	ψ (small), ρ (site)	5	121.15	0	0.1346
	ψ (thysanoptera), ρ (site)	5	121.21	0.06	0.1306
	ψ (·), ρ (site)	4	121.24	0.09	0.1286
	ψ (diptera), ρ (site)	5	121.53	0.38	0.1113
	ψ (total), ρ (site)	5	122.46	1.31	0.0699
	ψ (lepidoptera), ρ (site)	5	122.63	1.48	0.0642
	ψ (large), ρ (site)	5	122.71	1.56	0.0617

* Denotes evaluation using quasi-AICc because of overdispersion within the data (c-hat > 1.0).

Table 3.7: Model averaged occupancy estimates and standard errors, lower and upper 90% confidence intervals on parameter estimates, odds ratios (OR), and lower and upper 90% confidence intervals on odds ratios for parameters included in the confidence set of models used to predict occupancy of bat species sampled May-August in managed pine forests of the southeastern U.S. Coastal Plain. The confidence set are those with empirical support given the candidate set generated from insect-based models in Table 3.6.

Species	**Parameter**	**Estimate**	**Std. Error**	**Lower 90**	**Upper 90**	**OR**	**Lower OR**	**Upper OR**
E. fuscus	ψ (intercept)	-3.45	4.33	-10.55	3.66			
	medium	0.60	0.43	-0.10	1.31	1.82	0.90	3.69
	total	0.69	0.68	-0.43	1.80	1.99	0.65	6.08
	lepidoptera	2.34	1.67	-0.40	5.09	10.42	0.67	162.45
	coleoptera	0.81	0.73	-0.39	2.00	2.24	0.68	7.40
P. subflavus	ψ (intercept)	-1.29	1.43	-3.63	1.04			
	lepidoptera	6.73	7.31	-5.26	18.71	833.39	0.01	133344613.66
L. borealis + seminolus	ψ (intercept)	-0.03	0.97	-1.62	1.57			
	diptera	0.06	0.04	-0.01	0.13	1.06	0.99	1.14
	richness	0.44	0.31	-0.07	0.95	1.55	0.93	2.59
N. humeralis	ψ (intercept)	-5.64	3.92	-12.07	0.79			
	hymenoptera	1.72	0.63	0.68	2.75	5.56	1.97	15.63
	richness	1.83	0.64	0.78	2.87	6.20	2.17	17.70
	Shallotte	1.53	0.92	0.02	3.03	4.60	1.02	20.73
	Washington	3.99	1.51	1.52	6.47	54.15	4.56	642.46
T. brasiliensis	ψ (intercept)	-1.25	1.16	-3.15	0.65			
	coleoptera	0.41	0.23	0.03	0.78	1.50	1.03	2.18
	lepidoptera	0.72	0.49	-0.09	1.52	2.05	0.92	4.58
	medium	0.11	0.08	-0.01	0.24	1.12	0.99	1.27
M. austroriparius	ψ (intercept)	-0.03	0.83	-1.40	1.34			
	small	0.07	0.06	-0.02	0.16	1.07	0.98	1.17
	thysanoptera	2.33	2.47	-1.72	6.38	10.27	0.18	588.36
	diptera	0.04	0.04	-0.02	0.10	1.04	0.98	1.11
	total	0.02	0.02	-0.01	0.05	1.02	0.99	1.05
	lepidoptera	0.15	0.19	-0.16	0.45	1.16	0.85	1.58
	large	0.15	0.23	-0.23	0.52	1.16	0.80	1.69

Table 3.8: Model, number of parameters (K), Akaike's information criterion adjusted for small sample size (AICc), difference of AICc between a model and the model with the lowest AICc value (ΔAICc), and model weight (ω_i) for the candidate set of vegetation based models used to predict occupancy (ψ) given detection probability (ρ) of bats sampled May-August 2008 in managed pine forests of the southeastern U.S. Coastal Plain. Occupancy parameters represent the % canopy cover, basal area, or % vegetation clutter measured at sample points. All models incorporate the previously determined most parsimonious detection model.

Species	**Model**	**K**	**AICc**	**ΔAICc**	**ω_i**
**E. fuscus*	ψ(canopy),ρ(Julian date, clutter)	5	65.31	0	0.6585
	ψ(basal area),ρ(Julian date, clutter)	5	66.69	1.38	0.3303
	ψ(clutter),ρ(Julian date, clutter)	5	73.46	8.15	0.0112
**P. subflavus*	ψ(clutter),ρ(Julian date, clutter)	5	109.78	0	0.7747
	ψ(canopy),ρ(Julian date, clutter)	5	112.73	2.95	0.1772
	ψ(basal area),ρ(Julian date, clutter)	5	115.34	5.56	0.0481
L. borealis + seminolus	ψ(clutter),ρ(basal area, site)	6	156.31	0	0.7049
	ψ(basal area),ρ(basal area, site)	6	159.27	2.96	0.1605
	ψ(canopy),ρ(basal area, site)	6	159.62	3.31	0.1347
N. humeralis	ψ(clutter),ρ(basal area)	4	155.3	0	0.5876
	ψ(canopy),ρ(basal area)	4	156.35	1.05	0.3476
	ψ(basal area),ρ(basal area)	4	159.71	4.41	0.0648
T. brasiliensis	ψ(basal area),ρ(basal area, Julian date)	5	103.88	0	0.8382
	ψ(clutter),ρ(basal area, Julian date)	5	107.17	3.29	0.1618
M. austroriparius	ψ(clutter),ρ(site)	5	121.35	0	0.525
	ψ(canopy),ρ(site)	5	122.51	1.16	0.294
	ψ(basal area),ρ(site)	5	123.48	2.13	0.181

* Denotes evaluation using quasi-AICc because of overdispersion within the data (c-hat > 1.0).

Table 3.9: Model, number of parameters (K), Akaike's information criterion adjusted for small sample size (AICc), difference of AICc between a model and the model with the lowest AICc value (ΔAICc), and model weight (ω_i) for the confidence set of insect-based, vegetation-based, and combined models used to predict occupancy (ψ) given detection probability (ρ) of bats sampled May-August 2008 in managed pine forests of the southeastern U.S. Coastal Plain. All models incorporate the previously determined most parsimonious detection model.

Species	**Model**	**K**	**AICc**	**ΔAICc**	**ω_i**
**E. fuscus*	ψ(canopy),ρ(Julian date, clutter)	5	62.33	0	0.3165
	ψ(coleoptera, canopy),ρ(Julian date, clutter)	6	63.33	1	0.192
	ψ(lepidoptera, canopy),ρ(Julian date, clutter)	6	63.88	1.55	0.1458
**P. subflavus*	ψ(clutter),ρ(Julian date, clutter)	5	116.51	0	0.662
L. borealis + seminolus	ψ(clutter),ρ(basal area, site)	6	156.31	0	0.2609
	ψ(diptera),ρ(basal area, site)	6	156.57	0.26	0.2291
	ψ(.),ρ(basal area, site)	5	157.35	1.04	0.1551
	ψ(diptera, clutter),ρ(basal area, site)	7	157.57	1.26	0.1389
	ψ(richness),ρ(basal area, site)	6	157.8	1.49	0.1238
N. humeralis	ψ(hymenoptera, clutter),ρ(basal area)	5	144.44	0	0.9028
T. brasiliensis	ψ(coleoptera, basal area),ρ(basal area, Julian date)	6	100.79	0	0.3725
	ψ(medium, basal area),ρ(basal area, Julian date)	6	102.26	1.47	0.1786
	ψ(coleoptera),ρ(basal area, Julian date)	5	102.73	1.94	0.1412
M. austroriparius	ψ(diptera, clutter),ρ(site)	6	120.23	0	0.1566
	ψ(small, clutter),ρ(site)	6	120.47	0.24	0.1389
	ψ(total, clutter),ρ(site)	6	121.04	0.81	0.1044
	ψ(small),ρ(site)	5	121.15	0.92	0.0988
	ψ(thysanoptera),ρ(site)	5	121.21	0.98	0.0959
	ψ(.),ρ(site)	4	121.24	1.01	0.0945
	ψ(clutter),ρ(site)	5	121.35	1.12	0.0894
	ψ(diptera),ρ(site)	5	121.53	1.30	0.0817

* Denotes evaluation using quasi-AICc because of overdispersion within the data (c-hat > 1.0).

Table 3.10: Model averaged estimates and standard errors, lower and upper 90% confidence intervals on parameter estimates, odds ratios (OR), and lower and upper 90% confidence intervals on odds ratios for occupancy parameters included in the confidence set of models used to predict occupancy of bat species sampled May-August 2008 in managed pine forests of the southeastern U.S. Coastal Plain. Detection probabilities were modeled using the most parsimonious model for each species (See Table 3.7).

Species	**Parameter**	**Estimate**	**Std. Error**	**Lower 90**	**Upper 90**	**OR**	**Lower OR**	**Upper OR**
E. fuscus	ψ (intercept)	83.98	13.47	61.89	106.07			
	coleoptera	1.02	0.73	-0.18	2.22	2.77	0.83	9.24
	lepidoptera	3.49	2.98	-1.40	8.38	32.80	0.25	4356.93
	canopy	-0.91	0.16	-1.17	-0.66	0.40	0.31	0.52
	p (intercept)	-10.62	0.98	-12.23	-9.01			
	Julian date	0.06	0.01	0.05	0.07	1.06	1.05	1.07
	percent clutter	-0.02	0.02	-0.05	0.01	0.98	0.95	1.01
P. subflavus	ψ (intercept)	3.98	1.76	1.10	6.87			
	clutter	-0.14	0.05	-0.23	-0.05	0.87	0.80	0.95
	p (intercept)	-6.95	0.55	-7.85	-6.05			
	Julian date	0.04	0.00	0.03	0.04	1.04	1.03	1.04
L. borealis + seminolus	ψ (intercept)	0.49	0.94	-1.05	2.02			
	clutter	-0.02	0.01	-0.05	0.00	0.98	0.95	1.00
	diptera	0.05	0.04	-0.02	0.12	1.05	0.98	1.13
	richness	0.44	0.31	-0.07	0.95	1.55	0.93	2.59
	p (intercept)	0.63	0.77	-0.63	1.90			
	basal area	-0.02	0.01	-0.03	-0.01	0.98	0.97	0.99
	Shallotte	1.81	0.77	0.56	3.07	6.13	1.75	21.50
	Washington	2.62	0.88	1.17	4.06	13.70	3.23	58.06

Table 3.10 (continued): Model averaged estimates and standard errors, lower and upper 90% confidence intervals on parameter estimates, odds ratios (OR), and lower and upper 90% confidence intervals on odds ratios for occupancy parameters included in the confidence set of models used to predict occupancy of bat species sampled May-August 2008 in managed pine forests of the southeastern U.S. Coastal Plain. Detection probabilities were modeled using the most parsimonious model for each species (See Table 3.6).

Species	**Parameter**	**Estimate**	**Std. Error**	**Lower 90**	**Upper 90**	**OR**	**Lower OR**	**Upper OR**
N. humeralis	ψ (intercept)	-1.50	1.06	-3.25	0.25			
	clutter	-0.06	0.03	-0.10	-0.02	0.94	0.90	0.98
	hymenoptera	2.00	0.76	0.74	3.25	7.37	2.10	25.83
	p (intercept)	1.42	0.33	0.88	1.96			
	basal area	-0.01	0.00	-0.01	0.00	0.99	0.99	1.00
T. brasiliensis	ψ (intercept)	-0.55	1.59	-3.16	2.06			
	basal area	-0.04	0.03	-0.08	0.01	0.96	0.92	1.01
	coleoptera	-0.04	0.21	-0.38	0.31	0.96	0.68	1.36
	medium	0.13	0.10	-0.03	0.29	1.14	0.97	1.33
	p (intercept)	-5.71	0.72	-6.89	-4.53			
	Julian date	0.03	0.00	0.02	0.03	1.03	1.02	1.03
	basal area	0.01	0.02	-0.02	0.03	1.01	0.98	1.03
M. austroriparius	ψ (intercept)	-0.98	1.52	-3.47	1.50			
	diptera	0.07	0.06	-0.03	0.16	1.07	0.97	1.18
	clutter	0.79	1.37	-1.47	3.04	2.19	0.23	20.86
	small	0.10	0.08	-0.04	0.23	1.10	0.96	1.26
	total	0.05	0.04	-0.02	0.12	1.05	0.98	1.13
	thysanoptera	2.33	2.47	-1.72	6.38	10.27	0.18	588.37
	p (intercept)	-3.54	1.05	-5.27	-1.81			
	Shallotte	2.97	1.10	1.17	4.77	19.40	3.21	117.36
	Washington	2.72	1.12	0.89	4.56	15.21	2.43	95.32

CHAPTER 4

INFLUENCE OF LANDSCAPE CHARACTERISTICS ON SITE-OCCUPANCY OF FORAGING BATS IN COASTAL PLAIN MANAGED-PINE FOREST LANDSCAPES[3]

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[3] Bender, M. J., S. B. Castleberry, D. A. Miller, and T. B. Wigley. To be submitted to Forest Ecology and Management

ABSTRACT

Effect of small-scale factors on foraging activity of bats is a well-studied aspect of bat ecology, but data on landscape effects are largely lacking. Few large-scale studies relevant to Coastal Plain managed-pine forests of the southeastern U.S. are available, and many acoustic studies fail to account for imperfect detection of foraging bats. Without data at all spatial scales that properly account for imperfect detection, ability to fully evaluate potential effects of forest management activities on bats is severely limited. Therefore, we used occupancy models to examine influence of small-scale vegetation and large-scale spatial factors on foraging patterns of bats in managed-pine forests of the southeastern Coastal Plain while accounting for imperfect detection. Results indicate that responses to investigated factors were largely species-specific. In general, basal area at the sample point, sampling date, and sample site influenced detection of foraging bats. Small-scale vegetation increases generally had a negative influence on occupancy. Landscape-scale factors with evidence supporting their potential influence on foraging activity included un-thinned stands of intermediate age, distance to water sources, road density, patch richness, amount of edge, and percentage of stands older than 30 years. Based on our results, managing a single landscape attribute likely will not benefit all members of the bat community. However, maintaining a diverse landscape provides quality foraging habitat for a diverse bat community.

INTRODUCTION

Bat communities are increasingly recognized for their economic importance (Boyles et al. 2011), as vital components of healthy forest environments (O'Shea et al. 2003), and as a significant component of terrestrial vertebrate diversity (Laerm et al. 2000). The relative ecological and economic importance of forest-dwelling species may increase as white-nose syndrome, the destructive fungal disease predominantly associated with cave hibernacula, causes precipitous declines in many cave dependent populations (Smith et al. 2009). Even before onset of white-nose syndrome, forest managers were increasingly expected to consider the bat community in management decisions (Miller et al. 2003), but a paucity of bat research conducted in managed-pine forests continues to make this a challenging task.

Forest management is a continuum that ranges from minimal forestry activities, typical of publicly-owned forests in the Southeast, to forests managed intensively to sustainably produce goods and services. Although amount of forest land cover in the Coastal Plain of the southeastern U.S. has remained relatively constant over the past half century, there has been a shift to more intensive management (Wear and Greis 2002) that provides an economic incentive to maintain forest land cover (McComb 2008). Approximately 98 million acres of commercially productive forests in the southern U.S. are now owned by individuals, families, the forestry industry, or other corporations (Wear and Greis 2002), and much of this area is actively managed. These managed-forest landscapes are dynamic with management activities being conducted throughout much of the year, resulting in alteration of roosting and foraging habitats for bats (Lacki et al. 2007). Information concerning ecology of bats in managed-forest landscapes would help managers evaluate management activities and policy issues that may affect bat communities (Arnett 2003).

Alteration of forest structure enhances foraging habitat for some bat species yet degrades foraging habitat for others (Aldridge and Rautenbach 1987, Patriquin and Barclay 2003), making management of the community challenging. Additionally, managing forests to meet small-scale habitat requirements for bats (e.g., roost tree characteristics, within-stand foraging conditions) generally is not feasible across large and dynamic landscapes. However, the motility of bats allows them opportunities to persist in these landscapes provided suitable resources are available at a larger scale. Therefore, creating desirable foraging conditions for multiple species in managed-pine landscapes can be achieved through stand-level management activities conducted with a landscape-scale perspective so that suitable stands are appropriately distributed across the landscape.

Data necessary to identify landscape conditions suitable to foraging bats in Coastal Plain managed-pine forests of the southeastern U.S. are largely lacking. Most Coastal Plain studies investigating bat-habitat relationships have used telemetry and focused on roost structures (e.g., Menzel et al. 2001a, Menzel et al. 2001b, Elmore et al. 2004, Hein et al. 2005, Trousdale and Beckett 2005, Miles et al. 2006). While roosting habitat has long been considered a limiting factor for bat populations (Humphrey 1975), much information concerning the equally important foraging habitat component of bat biology is anecdotal and insufficient for effective management (Ford et al. 2005). Foraging studies are often difficult to conduct because of the small size, vagility, and nocturnal nature of bats (Duff and Morrell 2007). One method to assess habitat associations for foraging bats is to compare occupied and unoccupied points sampled acoustically at night when most activity is foraging related (MacKenzie et al. 2006). It is statistically important that differences in detectability between sample points be accounted for when using this approach (Gu and Swihart 2004, MacKenzie et al. 2006). Relatively recent statistical and software advances allow researchers to simultaneously investigate and account for factors that influence occupancy and detection probabilities. These advances are relevant to acoustic surveys of bats because most species are imperfectly detected (Duchamp et al. 2006, Yates and Muzika 2006, Amelon 2007, Hein et al. 2009) and false absences may influence results and inferences unless accounted for in analyses (Gu and Swihart 2004).

Although limited in relevance to managed-pine landscapes or lacking in replication, previous research indicates the potential influence of landscape characteristics on bats. Previous studies using telemetry have indicated importance of water sources (Elmore et al. 2005), bottomland hardwoods (Trousdale and Beckett 2005), and young pine stands (Menzel et al. 2001b) in pine-dominated landscapes of the southeastern Coastal Plain. Acoustic data from the Coastal Plain indicates importance of riparian and seral stages (early and late) for foraging bats in pine-dominated landscapes (Menzel et al. 2005a). Additional research in coniferous forests indicates importance of edges (Hein et al. 2008, Hein et al. 2009), roads (Loeb and O'Keefe 2006), and thinned stands (Humes et al. 1999) to foraging bats. Outside of the southeastern Coastal Plain, point- and stand-level variables were better predictors of activity and occupancy than landscape variables in landscapes that were not intensively managed (Erickson and West 2003, Ford et al. 2006, Loeb and O'Keefe 2006). However, landscape variables and the habitat mosaic may have a greater influence on intensively managed landscapes because of the potential for reduced small-scale heterogeneity and possibility of limited roosting structures (Erickson and West 2003, Ford et al. 2006, Miles et al. 2006).

Foraging bats are ecologically and financially important in the landscapes they inhabit and land owners interested in sustainable forestry practices are committed to providing quality foraging habitat for bats. However, limited data hamper ability of managers to evaluate management decisions that may influence foraging bats. Our objective was to characterize landscape-level foraging associations of bats in managed-pine forests of the southeastern Coastal Plain and to elucidate factors important to foraging bats that could be considered in management decisions. We sampled multiple landscapes to include management and geographic variability so that inferences might be applicable to a wide range of intensively-managed pine landscapes in the region.

METHODS

Study Areas

We sampled six intensively-managed forest landscapes in corporate ownership/management across five states (Alabama, South Carolina, North Carolina, Georgia, and Arkansas) in the Coastal Plain of the southeastern U.S. during summer (May – August) 2007 and 2008. We collected data from each study area for approximately 1 month prior to moving to the next location. Owner/management companies at the time of sampling included MeadWestvaco Corp., International Paper Co., Weyerhaeuser Co., Resource Management Service LLC., and Plum Creek Timber Co. Inc. Landscapes were predominantly loblolly pine (*Pinus taeda*) plantations interspersed with streamside management zones and other less intensively managed areas dominated by hardwoods or a mix of pine and hardwood tree species. Typical management activities in production stands included clear-cutting at 20-30 years, mechanical and/or chemical site preparation, and reforestation using 1 to 2-year-old nursery stock typically planted in raised beds at a stocking rate of approximately 450 to 700 trees per acre (Gresham 2002). Competing vegetation was reduced through herbicide applications and most stands were periodically thinned. All landowners were participants in a sustainable forestry certification program (Sustainable Forestry Initiative 2010).

The southeastern Coastal Plain physiographic region of the U.S. encompasses diverse habitat types and environmental conditions (Hubbard et al. 2004). However, the region is generally characterized as flat and having warm temperatures and high rainfall, particularly during the summer (Hubbard et al. 2004). Soils of the region are highly variable in the amount of organic matter and permeability (Hubbard et al. 2004) resulting in a diverse regional vegetation community. However, forests dominate the regional land-cover and agriculture (cropland, forest, or pasture) is the primary land use (Wear and Greis 2002, Hubbard et al. 2004). A thorough discussion of the sampled sub-regions (southern mixed forest and outer coastal plain mixed ecosystem provinces) is provided by Bailey (1995).

At each study area, we surveyed 22-36 sample points (average = 26.3). When spatial data were available prior to arriving at each site, we used ArcMap 9.3 (ESRI, Redlands, CA) to overlay the study area and surrounding areas with 900 x 900 m spaced points. When spatial data were unavailable, we chose a starting point and manipulated global positioning system (GPS) coordinates to create appropriately spaced points. Point spacing was based on bat biology and logistical considerations. We hypothesized that, although the 63 ha encompassed by the 450 m radius circular area surrounding each point is not likely to contain all of an individual's home range movements, it is reasonable to assume that this area is large enough to encompass a core area that constitutes most of an individual's foraging movements. Our assumption is supported by telemetry data and estimates indicating that 85% core areas of insectivorous forest bats are roughly 6% of the total home range size used during approximately 15 days of tracking (O'Donnell 2001). A systematic sampling approach was employed to the greatest extent possible by sampling points regardless of habitat type, distance to roads, or accessibility. However, we eliminated points that were logistically impossible to access (i.e., isolated by water) and those with non-corporate ownerships within the 450 m circular buffer unless alternative points were not available.

Acoustic Detection

At each sample point, we passively recorded bat echolocation calls using Anabat II frequency division bat detectors coupled with a zero-crossing interface module (ZCAIM). We stored data on a compact flash (CF) card and we downloaded daily. We stored each Anabat II/ ZCAIM combination in a waterproof plastic container to protect equipment from environmental conditions. We directed Anabat II microphones in the area of least vegetation clutter, 45˚ from horizontal using a 5.08 cm PVC elbow. We placed detectors approximately 1.5 m above the forest floor on a camera tripod to maximize call quality and quantity (Weller and Zabel 2002). We programmed detectors to begin sampling 30 min prior to civil sunset and end sampling 30 min after civil sunrise. Initial acoustic sampling was conducted for 2 consecutive nights when possible to minimize temporal variability. We sampled additional nights opportunistically to include a greater diversity of sampling conditions and improve occupancy and detection estimates. We did not sample during rain and heavy wind because of low bat activity during these conditions. We randomly assigned detectors to sampling points on a nightly basis to minimize equipment bias.

We created a customized ANALOOK (v 4.9; Titley Scientific, East Brisbane, Australia) filter to retain only search phase calls following methods and criteria of Britzke and Murray (2000). We used ANALOOK to automatically calculate and extract call parameters from retained files. Automated filtering and parameter calculation increase objectivity and repeatability while reducing influence of researcher experience (Obrist et al. 2004), which may have significant effects on classification errors (Gannon et al. 2004).

We used a K-nearest neighbor approach to identify calls individually based on a reference library of calls from potential species (Bender, unpublished data). We included 8 species/groups as potential residents of Coastal Plain forest landscapes based on mist-net captures (Bender, unpublished data) including Big Brown Bat (*Eptesicus fuscus*), Eastern Red + Seminole Bat group (*Lasiurus borealis* + *L. seminolus*), Hoary Bat (*L. cinereus*), Evening Bat (*Nycticeius humeralis*), Tri-colored Bat (formerly Eastern Pipistrelle, *Perymyotis subflavus*), Rafinesque's Big-eared Bat (*Corynorhinus rafinesquii*), Brazilian Free-tailed Bat (*Tadarida brasiliensis*), and Southeastern Myotis (*Myotis austroriparius*). Species identifications were based on the full sequence of calls within each call file rather than on identification of individual calls. We used average posterior classification probabilities from each sequence to assign identities. Each sequence that did not result in identification with a posterior classification probability ≥ 0.5 was eliminated. Visual examination of these eliminated files suggested they resulted from recordings of multiple individuals, non-bat ultrasonic sounds, or poor quality calls.

Habitat and Landscape Metrics

We measured 3 components of local vegetation structure at each sample point. We measured percent canopy cover using a convex spherical densiometer (Ben Meadows Company, Janesville, WI), averaging measurements taken at the acoustic sample point and 4 additional locations 5 m from the point in each of the cardinal directions. We estimated basal area (m^2/ha) of overstory trees using a 10-factor prism centered at the acoustic detector point. We characterized vegetation clutter using methods based conceptually on a Nudds board (Nudds 1977), estimating percent coverage of a 1-m^2 panel raised approximately 4.5 m above the ground and 4.5 m from the sample point in each cardinal direction and in the direction of orientation for the acoustic detector.

We used ArcMap 9.3 and Fragstats (McGarigal et al. 2002) to compute landscape metrics from company-provided and publicly available data (Table 4.1). We corrected data when ground-truthing indicated discrepancies (i.e., updated age of stands to reflect recent harvests). We measured landscape composition metrics using a 450 m radius circular buffer around sample points and landscape configuration metrics using euclidean distances. Edge was defined as the boundary between any two of six habitat classes including nonforest (i.e., roads, food plots, utility lines, etc.) and multiple age-based forest classes (0-9, 10-19, 20-30, 30-40, >40 years old). We did not investigate influence of distance to edge because we were primarily interested in large-scale factors and previous research indicates that distance to edge has only localized effects on foraging bats (Krusic et al. 1996). We considered the possibility that edge and road density should be modeled quadratically to better represent the relationship between these variables and occupancy. However, preliminary analyses indicated that linear relationships were more plausible based on AIC scores.

Predictor variable values were rescaled by multiplying/dividing by multiples of ten so that the ranges of values for each predictor were on relatively the same scale (Table 4.2; Donovan and Hines 2007). We decided to rescale rather than standardize predictor variables because of the difficulties associated with back-transforming and interpreting standardized estimates (Field et al. 2001). Preliminary analyses using predictor variables that were not rescaled resulted in non-convergence for many models because of the disparate scales of predictors. Rescaling continuous parameters has no effect on the slope of regression models and is equivalent to expressing distance measurements in meters rather than kilometers. However, rescaling influences interpretation because per/unit parameter effects may not be biologically relevant. Therefore, predictor effects are best illustrated by plotting effects across the range of observed values or by rescaling parameter estimates.

Statistical Analyses

We used an information theoretic approach to evaluate a candidate set of occupancy models for each species. Occupancy models allow for simultaneous estimation of probability of occupancy (ψ) and detection (ρ) and are useful when investigating influence of covariates on each (MacKenzie et al. 2006). Results should be interpreted as use rather than occupancy because species presence at each point was assumed to vary randomly within sample season (i.e., duration encompassing repeated sampling visits; MacKenzie et al. 2006)

Our candidate models were generated from hypotheses concerning factors that potentially influence site occupancy and detection (Tables 4.3 – 4.4). We used only uncorrelated predictor variables (Pearson's $|r| \leq 0.70$) to avoid problems associated with multicollinearity. We eliminated canopy cover from all analyses because it was correlated with basal area, which we retained because it is readily available to forest managers. We used PRESENCE version 2.4 software (Hines 2006) to calculate Akaike's information criterion adjusted for small sample sizes (AICc) that we subsequently used to evaluate our set of models and determine the most plausible given our data set. To assess goodness-of-fit we used the methods developed by MacKenzie and Bailey (2004) with 1000 bootstraps. If lack of fit was indicated (c-hat value > 1) we used quasi-AIC values (QAIC) to evaluate models. We inflated standard errors by the square root of c-hat whenever QAIC values were used (MacKenzie and Bailey 2004, Donovan and Hines 2007).

We used a general set of predictor variables in the occupancy portion of all models (i.e., ψ = distance to water + distance to stand 10-19 + dist. to roads + TE + % 30 plus + % 0-9 + % thinned + % clutter) when determining the most plausible detection model. We assessed model goodness-of-fit using the general occupancy set and our global set of detection parameters (i.e., ρ = site + basal area + julian date + % clutter) to determine if QAIC values should be used to evaluate plausibility of detection models. We did not use the global set of occupancy parameters because PRESENCE was unable to reach convergence or produced nonsensical parameter estimates in preliminary analyses using the global set of predictors. Poor performance with the global set may be related to the large number of estimated parameters (Hines 2006). We incorporated the most plausible detection model into all occupancy models (Table 4.4). By determining the most parsimonious detection model prior to investigating occupancy hypotheses, we prevented evaluation of an excessively large set of models (Yates and Muzika 2006, Hein et al. 2009, Long et al. 2010).

Covariate modeling was used to evaluate *a priori* hypotheses about influence of landscape and site measurements on probabilities of site occupancy (Tables 4.3 – 4.4). We assessed fit using the global set of occupancy parameters along with the most plausible detection model previously determined. We used a reduced global model to assess fit for analysis of the *T. brasiliensis* data because the full global model did not reach convergence. Using the most general model to assess fit and using the associated c-hat to adjust standard errors is recommended when lack-of-fit is detected (MacKenzie et al. 2006). We conducted an analysis of variance (ANOVA) and TUKEY test on the residuals (observed minus expected values) by study site for each species to determine if it was appropriate to pool data from our various study sites. To incorporate model selection uncertainty, we model-averaged parameter estimates and created a composite model that included parameters from all plausible models (i.e., Akaike weights within 10 % of the most plausible model).

RESULTS

We detected presence of bats at 80% (126/158) of sample points during 385 detector nights. We sampled 115 points two nights and the remaining points were sampled from 3-6 nights to improve parameter estimates. All species were detected at each of the 6 study areas except *Corynorhinus rafinesquii* and *L. cinereus,* which were rarely detected at 2 and 3 study areas, respectively.

The two phonic groups detected at the greatest number of sample points (*L. borealis* + *L. seminolus* group, n = 97; and *N. humeralis,* n = 99) comprised the species/group most commonly captured in concurrent mist net sampling (89 and 99 individuals, respectively; Appendix B). Species intermediate in both number of sample points occupied and individuals captured in mistnets included *T. brasiliensis* (44 points; 7 individuals), *M. austroriparius* (54; 16), *E. fuscus* (70; 7), and *P. subflavus* (71; 18). The two species represented by the lowest number of captures obtained from mist nets (n = 1; *C. rafinesquii* and *L. cinereus*) also occupied the lowest number of acoustic sample points (2 and 11 occupied acoustic points, respectively; Appendix B). We were unable to model influence of predictor variables on *C. rafinesquii* and *L. cinereus* because of the low number of sites apparently occupied.

The goodness-of-fit test (MacKenzie and Bailey 2004) indicated that data for all species were overdispersed (i.e., more variation than predicted by underlying statistical distributions; Burnham and Anderson 2001). Therefore, QAICc values were used to evaluate model plausibility and standard errors were inflated by the square root of the c-hat parameter from 1000 bootstraps. ANOVA and TUKEY test results did not indicate spatial autocorrelation, therefore data from all sampling locations (n=158) were pooled across sample sites.

Detection

Basal area (BA) was the parameter most commonly included in the detection portion of species models for 4 of the 7 species investigated and the most plausible detection model for 3 species included basal area as the single detection parameter (Table 4.5). Model averaged estimates and 90% confidence intervals suggest that increasing levels of basal area had a negative effect on probability of detecting the *L. borealis* + *L. seminolus* group (Table 4.6). The direction of effect on *M. austroriparius* and *N. humeralis* was less certain because of confidence intervals that overlapped zero. However, model averaged estimates suggest that increasing basal area had a positive influence on *M. austroriparius* detection and a negative influence on *N. humeralis* detection (Table 4.6). Basal area and Julian date were included in the most parsimonious detection model for *E. fuscus*. Increasing basal area had a negative effect on detection while later dates positively influenced detection (Table 4.6). The positive relationship between later dates and probability of detection was similar for *T. brasiliensis*. Sampling site was included in the most plausible detection model for both *T. brasiliensis* and *P. subflavus* suggesting that detection probabilities varied by site (Table 4.6). However, estimates were imprecise and the direction of effect was largely uninterpretable (i.e., confidence intervals overlapping 0).

Eptesicus fuscus Occupancy

Data supported plausibility of a single occupancy model for *E. fuscus* that included total edge as the single parameter estimated. Increasing amounts of edge in the surrounding landscape had a negative effect on occupancy (Figure 4.1). This model received a QAICc weight greater than 0.88 indicating substantial support as the most plausible among the candidate set investigated (Table 4.5). This best model was at least 15 times more likely to be the best model than the other models investigated indicating little evidence to support plausibility of alternative models within our candidate set.

Lasiurus borealis + L. seminolus **Occupancy**

Data indicated strong support (i.e., ΔQAICc within 2 points of most plausible model) for the null *L. borealis* + *L. seminolus* group occupancy model (Table 4.5), and 18 models were included in the confidence set. Parameters in the composite model with confidence intervals that did not overlap 0 were patch richness, vegetation clutter, and basal area; all were negatively related to probability of occupancy (Table 4.6). Estimates and confidence intervals slightly overlapping zero indicated a positive influence of distance to water and a negative influence of total edge on probability of occupancy (Table 4.6). The direction of effect for the remaining 9 parameters was indistinguishable because of large confidence intervals overlapping 0 (Table 4.6).

Myotis austroriparius **Occupancy**

The confidence set of models for *M. austroriparius* lacked substantial support for a single or relatively small number of superior models. The most plausible model was approximately 1.2 times more likely than the second best model, and 11 models were included in the confidence set including the null model. Percent of stands within 450 m ≥ 30 years old, distance to water, and distance to unthinned stands aged 10-19 generally had a positive relationship to occupancy, while remaining parameters exhibited a generally negative relationship (Table 4.6). However, percent stands aged ≥30 years and percent vegetation clutter were the only parameters with confidence intervals that did not overlap zero (Table 4.6).

Nycticeus humeralis **Occupancy**

The composite model for *N. humeralis* included two measures of vegetation structure (basal area and percent clutter) at the sample point as occupancy parameters (Table 4.6). Estimates indicate that increasing vegetation structure negatively influenced probability of occupancy by *N. humeralis* (Table 4.6, Figures 4.2 – 4.3). The percent clutter model was approximately 3 times more likely than the basal area model to be the most plausible given our data. There was little evidence to support other models.

Perymyotis subflavus **Occupancy**

Probability of occupancy declined as amount of basal area, vegetation clutter, and percentage of unthinned stands aged 10-19 increased (Table 4.6, Figure 4.4). A negative relationship between occupancy and increases in road density received marginal support. However, the confidence interval for the estimate overlapped zero (Table 4.6). Probability of occupancy increased with increasing distances to water, but the remaining parameters included in the composite model (distance to stands ≥ 30 years and percent ≥ 30 years) were too variable to determine direction of effect (Table 4.6).

Tadarida brasiliensis **Occupancy**

Probability of occupancy was negatively related to all three parameters included in the composite model; basal area, vegetation clutter, and patch richness (Table 4.6). Confidence intervals for vegetation clutter and patch richness indicate variability and that the direction of the effect was not always negative, although a negative trend was apparent (Table 4.6). The effect of increasing basal area was more consistent in its negative effect on probability of occupancy (Table 4.6).

Generalized Species Occupancy

Overall, measures of vegetation structure at the sample point (vegetation clutter and basal area) were the most common occupancy parameters in composite species models. Each of these parameters was present in the composite model for all species investigated except *E. fuscus*, and consistently indicated that increasing vegetation clutter and/or basal area adversely affected occupancy probability (Table 4.6). Composition metrics of total edge, patch richness, percent unthinned stands aged 10-19, and percent aged ≥ 30 years were each found in three composite models, as were the configuration metrics of distance to water and distance to stands ≥ 30 years. Increasing distances to water consistently had a positive relationship to occupancy, while increasing amounts of edge, patch richness, and % unthinned stands aged 10-19 consistently had a negative effect on species occupancy in composite models that contained these parameters. The general influence of stands ≥ 30 years of age (either distance to or percentage of) could not be determined as the confidence intervals either largely overlapped zero and/or the effect varied by species. The composition metric of road density and configuration metric of distance to unthinned 10-19 year old stands were each found in two composite models, but effects were too variable to speculate on their general influence on site occupancy. All remaining occupancy parameters were only present in a single composite model.

DISCUSSION

Consistent with our predictions and findings from previous researchers, increasing amounts of vegetation clutter and basal area at sample points generally had a negative influence on detection of forest bat species. Although Patriquin et al. (2003) and Yates and Muzika (2006) found that vegetation clutter has minimal impact on detectability of bats in forests, our data suggest that vegetation did impact our ability to detect bats. Others also have noted this negative influence of vegetation on detectability (Amelon 2007) and number of identifiable sequences (Ford et al. 2005). Therefore, assuming equal detectability among sample points may not be appropriate and efforts should be made to account for variable detection as even low levels of non-detection can influence results and inferences (Gu and Swihart 2004).

Increasing amounts of vegetation at sample points had a negative influence on occupancy probability regardless of species' ecomorphology. Similarly, Yates and Muzika (2006) found that occurrences of *L. borealis* and *P. subflavus*, both of which are categorized as clutter-adapted species (Menzel et al. 2005a), were inversely related to basal area in Missouri forests. The benefits of reducing clutter in forest landscapes for most aerial foragers has been demonstrated experimentally (Brigham et al. 1997), and in field studies (Ford et al. 2006, Loeb and O'Keefe 2006, Loeb and Waldrop 2008). Although clutter reduction may lead to increased insect abundance resulting in increased foraging activity (Tibbels and Kurta 2003), the influence of vegetation may be largely independent of insect abundance (Adams et al. 2009, Morris et al. 2010). Preliminary analyses did not support a relationship between overall insect abundance and vegetation indices within our data (Bender, unpublished data), although vegetation density may influence insect community structure (Allgood et al. 2009, Ober and Hayes 2009). Therefore, the negative influence of increasing vegetation clutter is likely related to difficulties associated with tracking prey while simultaneously monitoring location of obstacles (Simmons et al. 1979) rather than insect abundance.

The negative effect of vegetation density on foraging apparently extends beyond sample points to the landscape scale. We found that points across the landscape characterized by shorter distances to, or a greater abundance of, unthinned stands aged 10-19 years had a reduced probability of occupancy by foraging bats. This negative relationship has been documented at the stand-level and has been attributed to inefficient foraging condition (Loeb and O'Keefe 2006), although foraging may take place above the canopy (Kalcounis et al. 1999) or at the stand margins (Morris et al. 2010). At the landscape-scale, Perry et al. (2008) found that diurnal roosts were less likely to be located in managed-pine landscapes with increasing amounts of closed-canopy stands. Because roost site selection may be influenced by proximity of food resources (Kunz and Fenton 2003), observations made by Perry et al. (2008) may have been influenced by an aversion to foraging in these closed-canopy stands that were functionally similar to our unthinned 10-19 age habitat type.

The observed negative relationship between occupancy and distance to water contradicts our predictions. We know of no biological reason that sources of water would negatively influence site-occupancy by foraging bats unless the increased activity typically associated with aquatic habitats (Brooks and Ford 2005, Menzel et al. 2005b, Vindigni et al. 2009) is produced by individuals that vacate the surrounding landscape. If this is the case, sample points within the vicinity of water but beyond the area of increased activity would have a low probability of occupancy but this effect would likely diminish with increasing distances from the water source. A more plausible alternative is that our results were influenced by the large scale of our project that prevented mapping all ephemeral water sources. Therefore, modeled distance from sample points to water may not be representative of the actual distance to all sources of water available to foraging bats. This limitation is difficult to avoid in a large scale project because bats have been documented using even the most ephemeral of water sources such as flooded road ruts (Menzel et al. 2001a) that would be virtually impossible to census and map. Additionally, aquatic areas as a source of drinking water may be only marginally important to many bat species during foraging bouts because a significant portion of water intake can be obtained from prey (Nueweiler 2000). Results generally suggest that water may not be a limiting resource for bats in the Coastal Plain of the southeastern U.S.

Contrary to our predictions, increasing amounts of edge in the landscape surrounding a sample point had a negative influence on the probability of occupancy by *E. fuscus*. Although Muzika and Yates (2006) found similar results for northern long-eared bats (*Myotis septentrionalis*), this species is generally associated with contiguous forest (Owen et al. 2003) while *E. fuscus* is generally considered an open-adapted species (Menzel et al. 2005a) known to forage along edges in southeastern Coastal Plain managed-pine forests (Hein et al. 2009). At a small-scale, edges represent preferred foraging areas for many species (Grindal and Brigham 1999, Hein et al. 2009). Foraging bats may benefit from concentrated insect abundances (Lewis 1970, Pasek 1988) and navigational ease (Simmons et al. 1979) that permits efficient foraging and high levels of foraging activity (Grindal and Brigham 1999, Morris et al. 2010). However, small-scale effects may not be consistent across all relevant scales (Stephens et al. 2003). At the landscape-scale, the positive influence of edges on foraging *E. fuscus* appears to diminish as the amount of edge habitat increases. *Eptesicus fuscus* forages in stand interiors and along edges (Morris et al. 2010) often to a higher degree than predicted based on ecomorphology (Hein et al. 2009). Therefore, this species may choose foraging areas that balance amounts of edge with amount of interior habitat. We did not differentiate between hard and soft edges that may differ in their foraging suitability (Morris et al. 2010) and may have influenced our results, but any definition of edge likely has similar limitations.

The percent of landscape composed of stands ≥ 30 years was positively related to *M. austroriparius* occupancy. This species roosts in hardwood tree species (Carver and Ashley 2008), and appropriate roost trees would be found in our habitat type consisting of stands ≥ 30 years old that were often streamside management zones. Proximity to suitable roosts may influence foraging decisions (Crampton and Barclay 1998). The apparently reduced importance of older stands among the other species investigated may be related to a greater propensity to roost in foliage (Menzel et al. 1998) or in stands younger than 20-25 years (Elmore et al. 2004, Hein et al. 2008).

Many landscape characteristics do not appear to consistently influence occupancy by foraging forest bats. Patch richness is likely more relevant to investigations of landscape factors that influence species richness and diversity of the community (Fahrig et al. 2011) rather than probability of occupancy, which was our primary interest. We predicted that roads would influence occupancy probability but could not determine direction of effect for either road density or distance to roads. Roads are well documented as a habitat feature used for foraging and commuting by bats in small-scale investigations (Grindal and Brigham 1998, Hein et al. 2009), but Loeb and O'Keefe (2006) found that probability of occupancy declined with proximity to roads when examined at the landscape scale. This influence of scale on road effects may partially account for our inability to determine a direction of effect for road density or distance to roads. Additionally, we did not map and measure all linear landscape features that may be perceived by bats as similar to roads (e.g., forest trails, temporary roads, hard edges, and thinned strips). Modeling the distance to, and density of, all features that may be functionally similar to roads may have revealed a stronger relationship between foraging bats and road-like landscape features.

MANAGEMENT IMPLICATIONS

Our results suggest that managed-pine landscapes in the southeastern Coastal Plain provide sufficient resources and habitat for the majority of bat species in the region. Responses to landscape characteristics were species-specific suggesting that no single management prescription will benefit all members of the bat community. However, management activities that decrease vegetation structure, particularly within stands of intermediate age, should serve to increase the suitability of managed forest landscapes to the forest bat community. One caveat to this suggestion is that if insect prey abundance and diversity is adversely affected by vegetation reduction activities (Haddad et al. 2001), the net effect on the bat community also may be negative.

Landscape composition appears to influence bat occupancy more than landscape configuration, which indicates that important habitat types are present in sufficient abundance (Ritchie et al. 2009) in managed-pine landscapes of the Southeast. Therefore, maintaining diverse habitat types and increasing amount of important habitat types should be the goal rather than attempting to manage placement of habitat types. This independence from configuration is likely related to the highly motile nature of bats and their capacity to commute significant distances between required habitat types (Elmore et al. 2005). However, managers should make decisions so that the diversity and composition of stands be evaluated at scales relevant to foraging bats.

When planning landscapes suitable for foraging bats, managers should consider the percentage of the landscape comprised of unthinned intermediate-aged stands because of the negative relationship to occupancy. Retention of older stands and corridors as roost sites may be important (Miles et al. 2006, Hein et al. 2008), but there is little evidence that these stands influence foraging habitat use, except by *M. austroriparius*. Importance of older stands may depend on the bat species of interest, their dependence on hardwood or mature trees, and prevalence of these features in the landscape. Our results suggest that the bat community requires a mix of foraging and roosting habitats, which managers can best accomplish by creating and maintaining diverse habitat conditions across the landscape.

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Table 4.1: Name and description of occupancy predictor variables examined to determine the relationship to bat occupancy on six study sites in the Coastal Plain of the southeastern U.S., summer 2007-2008.

Predictor name	**Description**
Water	Euclidean distance (km) to the nearest permanent water
Dist unthin 10-19	Euclidean distance (km) to nearest stand aged 10-19 yrs
Dist 30plus	Euclidean distance (km) to stands aged ≥ 30 years
Dist Road	Euclidean distance (km) to nearest road
PR	Richness of patch types based on stand age class within 450 m circular buffer surrounding sample points
SIDI	Simpson's index of diversity
Rd density	Density of roads (km/km^2) within 450 m circular buffer
TE	Total edge (km) within 450 m buffer
%30plus	Percent of 2.5 m cells within the 450 m circular buffer around each point aged ≥ 30 years
%unthin 10-19	Percent of 2.5 m cells within the 450 m circular buffer around each point aged 10-19 years
%0-9	Percent of 2.5 m cells within the 450 m circular buffer around each point aged 0-9 years
%thinned	Percent of 2.5 m cells within the 450 m circular buffer around each point that had been thinned or pruned within 5 years
BA	Basal area (m^2/ha)
%clutter	Percent of vegetation clutter

* 450m buffer areas were independent between points and considered an appropriate foraging area size

Table 4.2: Mean, range, unit of measurement, and scalar for occupancy predictor variables measured at six managed-pine forest sites in the Coastal Plain of the southeastern U.S. during summer 2007-2008 and used to investigate influence on foraging bats. Scaled values were required for analysis software to reach optimization and produce logical parameter estimates.

Predictor	**units/scalar**	**Mean**	**Range**
Water	km	0.56	0.00-2.97
Dist unthin 10-19	km	0.57	0.00-2.89
Dist 30plus	km	0.21	0.00-1.91
Dist Road	km	0.13	0.00-0.52
PR	richness/10	0.43	0.20-0.60
SIDI	N/A	0.51	0.02-0.77
Rd density	$(km/km^2)*100$	0.27	0.00-0.83
TE	km/10	0.70	0.09-1.71
%30plus	percent/100	0.21	0.00-0.92
%unthin 10-19	percent/100	0.16	0.00-0.97
%0-9	percent/100	0.38	0.00-0.99
%thinned	percent/100	0.12	0.00-0.99
BA	$(m^2/ha)/23$	0.72	0.00-2.40
%clutter	percent/100	0.23	0.00-0.99

Table 4.3: Occupancy predictor variables and predicted relationship to probability of site occupancy by foraging bats at six managed-pine forest sites in the Coastal Plain of the southeastern U.S. during summer 2007-2008.

Predictor	**Predictor name**	**Hypothesis**	**Predicted relationship**
Percent Vegetation Clutter	clutter	Inhibits efficient foraging	-
Basal Area	BA	Inhibits efficient foraging	-
Stands aged 0-9 yrs	%0-9 Dist 0-9	Promotes efficient foraging	+
Unthinned stands 10-19 yrs	%unthin 10-19 Dist unthin10-19	Overly cluttered for efficient foraging	-
Stands 30 plus yrs	%30plus Dist 30plus	Roosting habitat	+
Roads	Rd density Dist roads	Promotes foraging and navigation	+
Stands thinned within 5 yrs	%thinned	Permits foraging regardless of stand age	+
Total Edge	TE	Navigation, increased prey	+
Patch Richness	PR	Fulfill multiple requirements	+
Simpson's Diversity Index	SIDI	Diversity of patches	+
Distance to closest water	Dist water	Often limited resource in managed forests, preferred foraging habitat for some species	-

Table 4.4: List of occupancy models and associated number of parameters evaluated using Akaike's Information Criterion to investigate the influence of landscape factors on site-occupancy of bats in Coastal Plain managed-pine forest landscapes during summer 2007-2008.

Model	**# parameters**
BA	4
Clutter	4
%0-9	4
%unthin 10-19	4
% 30plus	4
%thinned	4
TE	4
Rd density	4
PR	4
SIDI	4
%30plus + %unthin 10-19	5
%0-9 + %thinned + Rd density	6
%30plus + %0-9 + %thinned + Rd density	7
dist water	4
dist road	4
dist unthin 10-19	4
dist 30plus	4
dist water + dist 30plus	5
dist water + dist 30plus + dist road	6
Global	17
(.)	3

Table 4.5: Quasi –Akaike's Information Criterion adjusted for small sample size (QAICc), delta QAICc, QAICc weight (**ω_i**), and number of parameters (K) for top performing (QAICc ≤ 2) site occupancy models of bats within managed-pine forest landscapes of the southeastern Coastal Plain, 2007-2008. Models included occupancy (ψ) and detection (ρ) parameters.

Model	**QAICc**	**ΔQAICc**	**ω_i**	**K**
E. fuscus				
ψ (TE), ρ (date, BA)	266.60	0.00	0.8875	5
L. borealis + *L. seminolus* group				
ψ (water), ρ (BA)	354.50	0.00	0.1589	4
ψ (PR), ρ (BA)	354.65	0.15	0.1474	4
ψ (BA), ρ (BA)	354.97	0.47	0.1256	4
ψ (clutter), ρ (BA)	355.26	0.76	0.1087	4
ψ (TE), ρ (BA)	356.18	1.68	0.0686	4
ψ (.), ρ (BA)	356.50	2.00	0.0585	3
M. austroriparius				
ψ (%30plus, %Unthin10-19.), ρ (BA)	206.80	0.00	0.2333	5
ψ (%30plus), ρ (BA)	207.24	0.44	0.1872	4
ψ (clutter), ρ (BA)	207.91	1.11	0.1339	4
N. humeralis				
ψ (clutter), ρ (BA)	292.81	0.00	0.6625	4
P. subflavus				
ψ (clutter), ρ (site)	269.15	0.00	0.2918	8
ψ (water), ρ (site)	270.00	0.85	0.1908	8
ψ (% unthin10-19), ρ (site)	270.88	1.73	0.1229	8
T. brasiliensis				
ψ (BA), ρ (date, site)	134.53	0.00	0.5109	9

Table 4.6: Model averaged parameter estimates, standard errors (SE), and 90% confidence intervals for occupancy (ψ) and detection (ρ) parameters contained in species composite models and averaged over the confidence set of models (QAICc weight ≥ 10% most plausible model) for bats in Coastal Plain managed-pine forests of the southeastern U.S., summer 2007-2008.

Species	**Parameter name**	**Estimate**	**SE**	**90% UPPER CI**	**90% LOWER CI**
E. fuscus	ψ intercept	3.9279	-1.2241	1.9204	5.9354
	TE	-4.5749	-1.4348	-6.9279	-2.2219
	ρ intercept	-2.4883	-0.5119	-3.3278	-1.6489
	date	0.0193	-0.0020	0.0160	0.0226
	BA	-1.6167	-0.3471	-2.1860	-1.0474
L. borealis + seminolus	ψ intercept	1.6891	1.0989	3.4913	-0.1132
	water	1.1578	0.7519	2.3909	-0.0753
	PR	-6.6082	-3.6770	-12.6385	-0.5778
	BA	-1.0601	-0.4518	-1.8011	-0.3191
	clutter	-1.9980	-0.9794	-3.6042	-0.3917
	TE	-1.3031	-0.8414	-2.6829	0.0768
	dist 30plus	0.0836	1.2760	2.1763	-2.0091
	%Unthin10-19	-1.6585	1.3401	0.5393	-3.8562
	Rd density	-1.6820	-1.8969	-4.7929	1.4289
	SIDI	-1.5912	-2.2787	-5.3283	2.1458
	%30plus	0.8509	1.4371	3.2077	-1.5060
	dist Unthin10-19	0.1490	-0.4538	-0.5952	0.8932
	dist Roads	-0.6089	2.7382	3.8817	-5.0995
	% 0-9	0.1866	-1.0188	-1.4842	1.8575
	% thinned	-0.1006	-1.4925	-2.5483	2.3472
	ρ intercept	1.2854	0.2663	1.7222	0.8486
	BA	-1.2127	0.3348	-0.6637	-1.7617
N. humeralis	ψ intercept	2.1388	0.4285	2.8416	1.4360
	Clutter	-3.9275	-1.1430	-5.8020	-2.0530
	BA	-1.8691	-0.5331	-2.7434	-0.9948
	ρ intercept	1.5120	0.5861	2.4732	0.5508
	BA	-1.1940	2.8519	3.4831	-5.8711

Table 4.6: (continued)

Species	**Parameter name**	**Estimate**	**SE**	**90% UPPER CI**	**90% LOWER CI**
M. austroriparius	ψ intercept	-0.0983	0.7991	1.2123	-1.4089
	% 30plus	2.8565	1.4954	5.3089	0.4041
	%Unthin10-19	-2.2775	1.4394	0.0832	-4.6381
	clutter	-2.5128	-1.2658	-4.5887	-0.4369
	BA	-1.2116	-0.8280	-2.5695	0.1464
	water	0.9426	0.7479	2.1691	-0.2839
	TE	-1.3264	-0.9134	-2.8243	0.1715
	PR	-3.8328	-2.9169	-8.6165	0.9510
	dist 30plus	-1.2371	-1.1748	-3.1637	0.6895
	dist Unthin 10-19	0.4946	-0.4759	-0.2860	1.2751
	ρ intercept	-0.7548	0.4652	0.0082	-1.5177
	BA	0.8755	0.5778	1.8231	-0.0720
P. subflavus	ψ intercept	0.4495	0.6002	1.4338	-0.5348
	clutter	-2.5336	-1.0281	-4.2197	-0.8476
	water	1.0992	0.5682	2.0310	0.1675
	%Unthin10-19	-2.7962	1.3029	-0.6594	-4.9330
	BA	-0.7805	-0.3815	-1.4062	-0.1548
	dist 30plus	-0.3675	-1.0101	-2.0240	1.2891
	% 30plus	-0.2654	-1.4349	-2.6187	2.0879
	Rd Density	-2.7530	-1.8282	-5.7512	0.2453
	ρ intercept	-0.2543	0.5348	0.6229	-1.1314
	site PC-AR	2.6992	1.0782	4.4675	0.9309
	site WV-SC	1.0934	0.6991	2.2399	-0.0530
	site RMS-AL	-1.4246	0.8552	-0.0221	-2.8272
	site RMS-NC	0.3804	0.7283	1.5749	-0.8140
	site WE-NC	0.8861	0.7071	2.0458	-0.2736
T. brasiliensis	ψ intercept	1.4829	1.2693	3.5646	-0.5989
	BA	-1.9140	-0.8565	-3.3186	-0.5093
	clutter	-3.0647	-2.0200	-6.3774	0.2481
	PR	-8.7249	-7.6321	-21.2416	3.7919
	ρ intercept	-8.2255	1.0711	-6.4689	-9.9821
	date	0.0436	0.0030	0.0485	0.0387
	site PC-AR	0.8400	1.2232	2.8459	-1.1660
	site WV-SC	-2.1480	1.1712	-0.2273	-4.0688
	site RMS-AL	-0.2985	1.4095	2.0131	-2.6102
	site RMS-NC	-0.3907	1.1406	1.4798	-2.2612
	site WE-NC	-1.5833	1.1653	0.3278	-3.4943

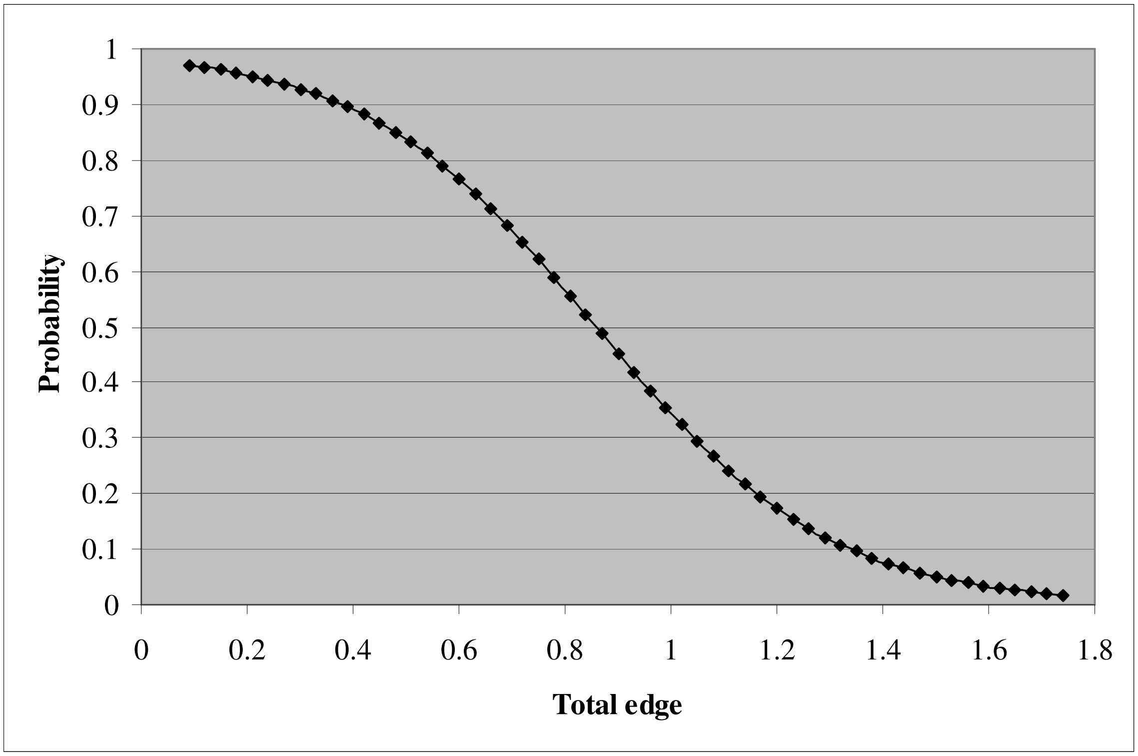

Figure 4.1: Influence of total edge (km per km^2/10 of edge within 450 m circular buffer around sample points) on the probability of occupancy by *Eptesicus fuscus* over the range of observed total edge values. Probability is calculated from the intercept and total edge parameter estimate obtained from the single plausible occupancy model for *E. fuscus*.

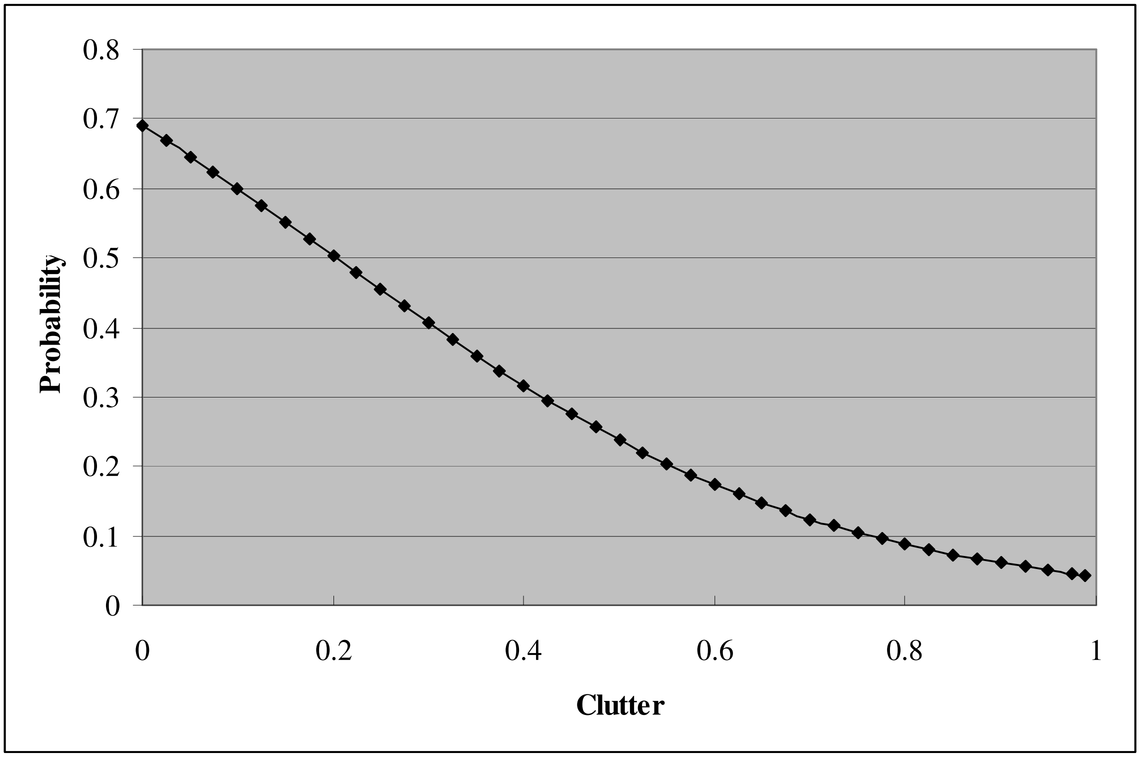

Figure 4.2: Influence of clutter (percent vegetation clutter/100) on the probability of occupancy by *Nycticeus humeralis* over the range of observed values. Probabilities are based on the composite model using model averaged estimates and holding all other variables at the mean of their observed values.

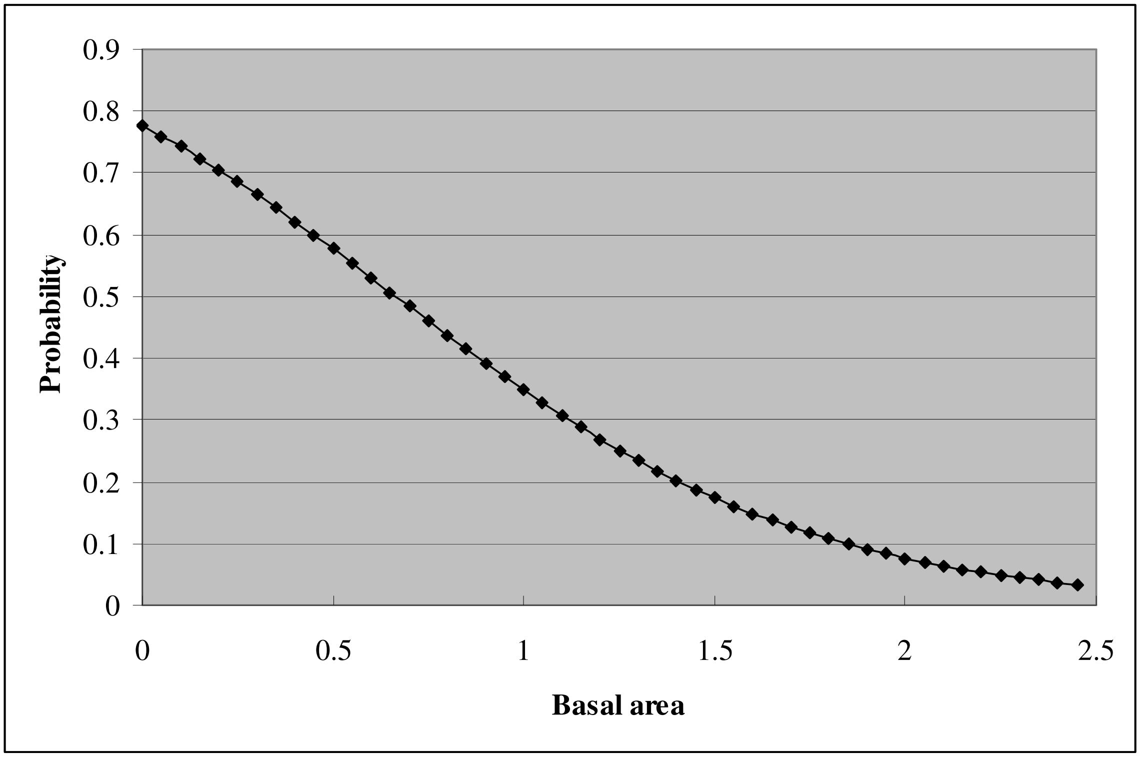

Figure 4.3: Influence of basal area [(m^2/ha)/23] on the probability of occupancy by *Nycticeus humeralis* over the range of observed values. Probabilities are based on the composite model using model averaged estimates and holding all other variables at the mean of their observed values.

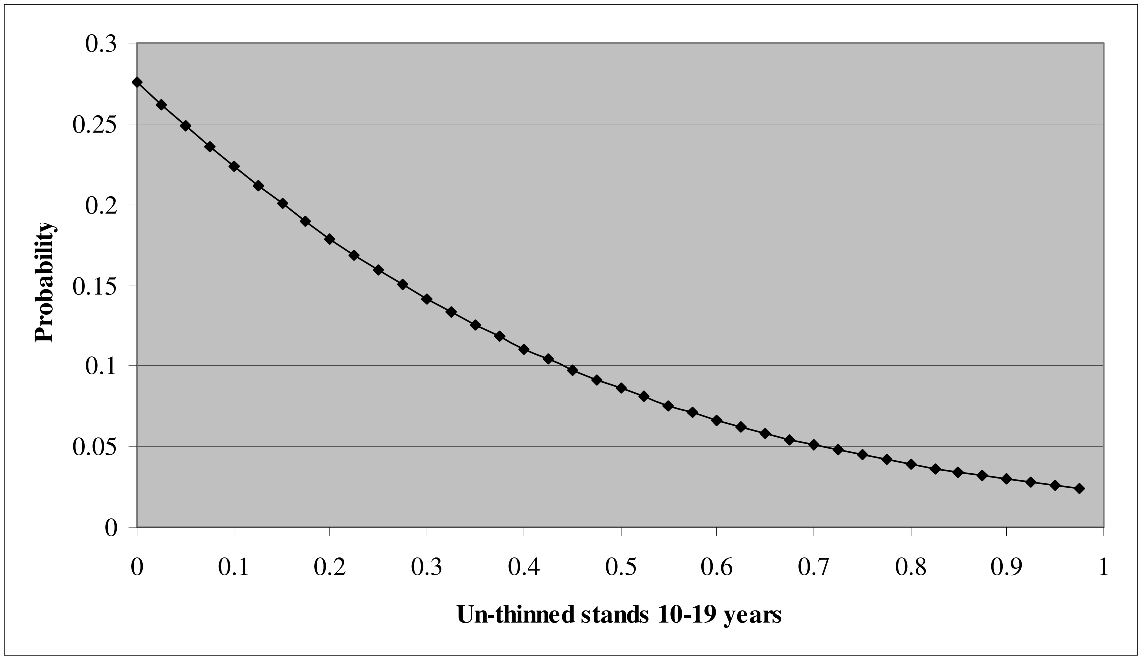

Figure 4.4: Influence of unthinned stands aged 10-19 years (percentage/100 within 450 m circular buffer) on probability of occupancy by *Perimyotis subflavus* over the range of observed values. Probabilities are based on the composite model using model averaged estimates and holding all other variables at the mean of their observed values.

CHAPTER 5

SUMMARY AND MANAGEMENT IMPLICATIONS

Privately owned forests account for roughly 90% of the forest land-cover in the southeastern U.S. (Wear and Greis 2002). Many of these privately-owned forests are managed for timber production to meet the growing demands of the market (Wear and Greis 2002). Although landscape- and stand-scale characteristics in managed landscapes may differ from unmanaged forests (Hansen et al. 1991), timber production provides an economic incentive to maintain forest land-cover and prevent conversion to land uses that are less favorable to wildlife (McComb 2008). Therefore, managed-pine forest landscapes represent an opportunity to provide suitable habitat for many wildlife species in the Southeast, particularly for bats because of their motility and capacity to traverse unfavorable habitat types (Bernard and Fenton 2003). However, limited information on bat-habitat associations in managed pine systems hampers the ability of managers to maintain bat diversity and create suitable habitat conditions. Therefore, the overall objective of my research was to provide land managers with data necessary to better manage forest landscapes and provide suitable foraging habitat for resident bat species.

Call analysis

Acoustic surveys for bats often are used to determine and monitor species presence within a landscape. A critical step in this process is accurate identification of species based on echolocation calls. Quantitative identification methods are desirable (Redgewell et al. 2009), but the most commonly used quantitative method, discriminant function analysis (DFA; Gannon et al. 2004), may not be the most accurate or appropriate alternative. Therefore, my first objective was to test performance of K-nearest neighbor analysis (KNN) as a quantitative method to classify bat calls and compare cross validation accuracy rates of KNN with DFA. My results demonstrated that K-nearest-neighbor analysis is a viable quantitative identification alternative for bat calls from the Coastal Plain of the southeastern U.S. I achieved an overall classification accuracy rate of 82.5%. Species-specific accuracy rates ranged from 51% to 96% and seven species had rates ≥ 70%. This non-parametric KNN approach is not limited by normality assumptions (Peterson et al. 1999) and was more accurate than the commonly used DFA alternative (Gannon et al. 2004). The improvements over DFA were comparable or superior to results from alternative quantitative methods (e.g., artificial neural networks, Parsons and Jones 2000; pattern recognition algorithms, Obrist et al. 2004) which land managers and researchers alike rarely use because of data requirements, lack of availability, and computational complexity (Papadatou et al. 2008).

My results indicate that the suite of parameters used to classify calls influences classification accuracy of KNN and DFA approaches. Therefore, I suggest that researchers using quantitative classification approaches investigate the performance of multiple suites of parameters (models) so that accuracy can be maximized. Researchers also should be aware that the optimal classification model likely will depend on the suite of resident bat species and the objective of the research. Although determining the best method to classify bat calls is beyond the scope of my research, researchers should consider KNN analysis when searching for an accurate, available, and suitable method to quantitatively classify unknown bat calls.

Insect and local vegetation effects

A paucity of relevant information concerning foraging ecology of forest bats is available to managers of Coastal Plain forests in the southeastern U.S. However, management activities conducted within managed-pine landscapes may influence foraging efficiencies by altering stand structure and insect abundance (Aldridge and Rautenbach 1987, Hollifield and Dimmick 1995). Foraging decisions made by bats may influence survival and fitness of individuals and likely influences habitat use (Kusch et al. 2004, Burles et al. 2009). Understanding the responses of foraging bats to insect abundances and vegetation characteristics may help managers provide suitable foraging conditions through stand-level activities. In response to the lack of foraging information, my second objective was to investigate the relationship between insect abundance and stand structure on foraging bats.

My results suggest that managed-pine landscapes in the Coastal Plain of the southeastern U.S. provide sufficient resources and habitat for the majority of bat species in the region. Acoustic and mist-net results confirmed the presence of nine species including *Corynorhinus rafinesquii, Eptesicus fuscus*, *Lasiurus borealis*, *L. seminolus*, *L. cinereus*, *Nycticeus humeralis*, *Perimyotis subflavus*, *Tadarida brasiliensis*, and *Myotis austroriparius*. Approximately 80% of acoustic sample points were used by at least one bat species suggesting that much of these managed-pine landscapes are suitable for foraging bats. Based on acoustic and mist-net data, *N. humeralis* and members of the *L. borealis* + *L. seminolus* group were most commonly encountered, whereas *L. cinereus* and *C. rafinesquii* were rarely encountered.

My results add to existing evidence suggesting that many insectivorous bat species are positively influenced by increasing insect abundances (Kusch et al. 2004). In general, hypotheses suggesting that foraging bats discriminate among prey items based on taxon characteristics (Buchler 1976, Agosta et al. 2003) appear more plausible than size based discriminations (Barclay and Brigham 1991, Barclay and Brigham 1994). However, the most appropriate measure of available prey (i.e., measure of insect abundance relevant to foraging bats) remains unclear and likely varies by species. Additionally, parameter estimates suggest that insect abundance does not have a strong influence on foraging location choices and insect abundance alone is not sufficient to predict site-occupancy in Coastal Plain forest landscapes.

I found that site-occupancy of foraging bats frequently was better explained by a combination of small-scale vegetation characteristics and insect abundance rather than either separately. Sample points occupied by at least one bat species had reduced canopy cover, basal area, and vegetation clutter and higher insect abundances than unoccupied points. However, the most plausible model for *E. fuscus, P. subflavus,* and the *L. borealis+L. seminolus* group indicated that vegetation characteristics alone were more plausible than models that included both insect abundance and vegetation characteristic parameters. Therefore, managers primarily should focus on management prescriptions that reduce the amount of vegetation structure and, secondly, on actions that possibly increase insect abundances such as increasing herbaceous plant cover (Campbell et al. 2007) or abundance of deciduous cover in riparian areas (Ober 2006).

Bats likely choose foraging areas based on decisions made at multiple scales (Yates and Muzika 2006). Elucidating the large-scale factors that influence occupancy will help managers direct stand-level management activities with a landscape-scale perspective so that suitable foraging conditions are appropriately distributed across the landscape. This landscape approach may be particularly effective with bats because their motility allows them to traverse unsuitable habitat types and use resources that are dispersed across the landscape (Bernard and Fenton

2003). Therefore, my third objective was to evaluate the plausibility of landscape-scale variables that might influence foraging bats.

Landscape effects

Landscape-scale characteristics appear to influence foraging decisions made by many forest bats. However, I found that responses to landscape characteristics were species-specific suggesting that no single management prescription will benefit all members of the bat community. Additionally, the landscape-scale factors investigated did not appear to affect foraging activity of all species and the effects of small-scale vegetation characteristics often produced more consistent negative effects. In general, my landscape-scale results suggest that percentage of area in un-thinned stands of intermediate age and increasing road density, patch richness, and amount of edge are negatively related to occupancy, while the percentage of area in stands older than 30 years and distance to water sources are positively related to occupancy in managed-pine forests. In general, landscape composition (i.e., the abundance of habitat types) appeared more plausibly related to bat occupancy than landscape configuration (i.e., the distance to habitat types or features), which indicates that important habitat types are present in sufficient abundance (Ritchie et al. 2009) in managed-pine landscapes of the Southeast.

My results suggest that management activities that reduce canopy cover and vegetation clutter in the midstory, increase insect abundances, and result in diverse landscape conditions are most likely to benefit the bat community as a whole. However, management efforts to improve foraging habitat for specific species will depend on the species of interest. Future efforts designed to elucidate the influence of landscape changes on foraging may benefit from an adaptive management approach in which management actions are prescribed and resulting effects on the bat community monitored and evaluated so that knowledge is advanced and subsequent actions can be modified (Stankey et al. 2005).

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Appendix A. Mean covariate values (+/- 90% confidence interval value) at points occupied (O) and apparently unoccupied (U) by bats after two sampling visits sampled May-August 2008 in managed-pine forests of the southeastern U.S. Coastal Plain. Covariates include mean abundance of insects captured with passive flight intercept traps including Coleopterans (Col), Dipterans, Hymenopterans (Hym), Lepidopterans (Lep), Thysanopterans (Thy), total, insect order richness (Richness), small size class (≤ 2 mm), medium size class (3 – 6 mm), and large size class (≥ 7 mm). Vegetation characteristics at points include basal area, mean percent vegetation clutter (Clutter), and mean percent canopy cover (Canopy).

Species		**Col**	**Dipterans**	**Hym**	**Lep**	**Thy**	**Total**	**Richness**
OVERALL	O	5.02 (0.86)	12.46 (3.00)	5.45 (1.58)	1.88 (0.57)	0.93 (0.64)	28.29 (4.91)	5.05 (0.22)
	U	3.03 (0.80)	6.24 (3.30)	0.86 (0.21)	1.51 (0.98)	0.49 (0.59)	13.51 (4.79)	4.00 (0.44)
E. fuscus	O	5.41 (1.12)	14.98 (4.43)	5.20 (1.29)	2.17 (0.86)	0.38 (0.22)	30.68 (6.66)	5.08 (0.29)
	U	3.81 (0.85)	7.46 (2.08)	3.75 (2.19)	1.45 (0.50)	1.27 (0.97)	19.80 (4.68)	4.58 (0.29)
L. borealis + seminolus	O	4.76 (1.05)	13.43 (4.07)	5.16 (1.44)	1.88 (0.80)	0.46 (0.21)	28.11 (6.17)	5.03 (0.27)
	U	4.39 (0.95)	8.40 (2.43)	3.63 (2.23)	1.70 (0.54)	1.27 (1.09)	21.55 (5.27)	4.58 (0.32)
N. humeralis	O	5.40 (1.15)	13.88 (3.91)	6.31 (2.05)	2.00 (0.72)	0.83 (0.71)	31.29 (6.21)	5.23 (0.25)
	U	3.52 (0.51)	7.49 (2.33)	2.03 (0.90)	1.54 (0.65)	0.84 (0.75)	16.97 (4.03)	4.29 (0.30)
P. subflavus	O	5.32 (1.39)	16.57 (5.17)	5.32 (1.51)	2.49 (1.03)	0.92 (0.76)	33.49 (7.77)	5.27 (0.32)
	U	4.09 (0.72)	7.40 (1.83)	3.87 (1.90)	1.33 (0.41)	0.77 (0.70)	19.37 (4.01)	4.52 (0.25)
T. brasiliensis	O	7.27 (2.17)	20.03 (8.78)	6.54 (2.45)	3.43 (1.81)	0.68 (0.47)	40.83 (13.08)	5.23 (0.44)
	U	3.85 (0.60)	8.66 (1.81)	3.88 (1.48)	1.35 (0.34)	0.88 (0.64)	20.75 (3.39)	4.71 (0.23)
M. austroriparius	O	5.30 (1.78)	16.82 (8.03)	5.32 (2.16)	2.38 (1.60)	0.48 (0.33)	32.89 (11.92)	4.95 (0.46)
	U	4.34 (0.74)	9.15 (1.78)	4.16 (1.57)	1.60 (0.38)	0.95 (0.68)	22.40 (3.66)	4.78 (0.23)

Appendix A (continued). Mean covariate values (+/- 90% confidence interval value) at points occupied (O) and apparently unoccupied (U) by bats after two sampling visits sampled May-August 2008 in managed-pine forests of the southeastern U.S. Coastal Plain. Covariates include mean abundance of insects captured with passive flight intercept traps including Coleopterans (Col), Dipterans, Hymenopterans (Hym), Lepidopterans (Lep), Thysanopterans (Thy), total, insect order richness (Richness), small size class (≤ 2 mm), medium size class (3 – 6 mm), and large size class (≥ 7 mm). Vegetation characteristics at points include basal area, mean percent vegetation clutter (Clutter), and mean percent canopy cover (Canopy).

Species		**Small**	**Medium**	**Large**	**Basal Area**	**Clutter**	**Canopy**
OVERALL	O	8.95 (2.66)	14.54 (2.47)	4.83 (0.73)	51.38 (11.57)	19.04 (4.58)	44.96 (7.63)
	U	4.69 (3.32)	6.00 (1.50)	2.82 (0.99)	125.63 (22.57)	42.91 (11.31)	88.64 (8.96)
E. fuscus	O	10.26 (3.47)	15.73 (3.03)	4.69 (0.95)	40.56 (11.96)	16.13 (5.36)	40.55 (9.29)
	U	5.91 (2.74)	9.81 (2.64)	4.12 (0.87)	92.89 (17.58)	31.85 (7.09)	67.54 (9.66)
L. borealis + seminolus	O	8.81 (3.19)	14.77 (2.89)	4.56 (0.88)	49.00 (12.99)	16.62 (4.94)	46.40 (8.89)
	U	7.11 (3.08)	10.24 (2.84)	4.20 (0.91)	89.12 (19.07)	33.13 (7.77)	63.83 (11.09)
N. humeralis	O	9.87 (3.39)	16.36 (3.03)	5.09 (0.98)	40.95 (12.71)	13.08 (4.75)	37.36 (8.85)
	U	5.61 (2.44)	7.88 (1.94)	3.48 (0.61)	102.19 (17.08)	38.80 (6.95)	76.78 (8.11)
P. subflavus	O	11.98 (4.24)	16.60 (3.53)	4.97 (1.10)	41.00 (13.83)	10.85 (3.79)	40.26 (9.75)
	U	5.34 (2.16)	10.02 (2.32)	4.01 (0.74)	85.45 (16.09)	33.30 (6.61)	64.05 (9.38)
T. brasiliensis	O	14.18 (6.89)	21.18 (5.76)	5.48 (1.75)	23.75 (12.82)	13.22 (7.83)	29.84 (13.42)
	U	6.33 (1.99)	10.35 (1.84)	4.10 (0.64)	79.48 (13.55)	27.23 (5.44)	61.18 (7.77)
M. austroriparius	O	12.17 (6.25)	15.94 (5.34)	4.86 (1.49)	55.79 (19.42)	22.29 (7.41)	54.57 (13.02)
	U	6.60 (2.02)	11.57 (2.06)	4.23 (0.68)	71.45 (14.37)	24.86 (5.81)	54.35 (8.57)

Appendix B. Mist net captures from Coastal Plain managed-pine forests of the southeastern U.S., summers 2006-2008. Species captured include *Corynorhinus rafinesquii* (CORA), *Eptesicus fuscus* (EPFU), *Lasiurus borealis* (LABO), *L. cinereus* (LACI), *L. seminolus* (LASE), *Myotis austroriparius* (MYAU), *Nycticeus humeralis* (NYHU), *Perimyotis subflavus* (PESU), *L. borealis or L. seminolus* escape prior to confirmed identification (LA?), *Tadarida brasiliensis* (TABR).

			Species										
Year	State	General Location	CORA	EPFU	LABO	LACI	LASE	MYAU	NYHU	PESU	LA?	TABR	**Total**
2006	SC	3km NW of Tuckertown	1	1	21		8	2	22				**55**
	GA	3km NW of Townsend			2		4		10	2	1		**19**
	MS	6km SW of Scooba		1	20		6		8	3			**38**
2007	GA	13km SW of Bainbridge			1		23	5	17			1	**47**
	AR	18km E of Crossett	1		11	1	1	6	8	11			**39**
	SC	11km N of Ravenel		2	4		17		32	4		3	**62**
2008	AL	16km SW of Greenville		1	1			4	16	1		1	**24**
	NC	11km NNW of Shallotte			8		5	1	1	2			**17**
	NC	15km NE of Greenville		4	19				25			2	**50**
		Total	**2**	**9**	**87**	**1**	**64**	**18**	**139**	**23**	**1**	**7**	**351**