

**Bat Habitat Ecology Using Remote Acoustical Detectors at the Army National
Guard Maneuver Training Center - Fort Pickett, Blackstone, Virginia.**

Michael J. St. Germain

Thesis submitted to the faculty of the Virginia Polytechnic Institute and State University
in partial fulfillment of the requirements for the degree of

Master of Science
In
Fisheries and Wildlife

Marcella J. Kelly (Chair)
Dean F. Stauffer
W. Mark Ford

25 April 2012

Keywords: activity index, AnaBat, detection probability, *Eptesicus fuscus*, *Lasiurus borealis*, military lands, *Myotis lucifugus*, *Myotis septentrionalis*, *Nycticeius humeralis*, occupancy, *Perimyotis subflavus*, proportion of area occupied, spatial co-occurrence, species interaction factor, temporal overlapping, two species modeling

Copyright © 2012 by Michael J. St. Germain

Bat Habitat Ecology Using Remote Acoustical Detectors at the Army National Guard Maneuver Training Center - Fort Pickett, Blackstone, Virginia.

Michael J. St. Germain

ABSTRACT

Bats occupy diverse and unique niches and are regarded as important components in maintaining ecosystem health. They are major consumers of nocturnal insects, serve as pollinators, seed disperser, and provide important economic benefits as consumers of agricultural and forest pest insects. Establishing community- and population-level data, and understanding species interactions is especially important in changing landscapes and for species whose populations levels are threatened by outside factors of anthropomorphic disturbance from hibernacular visitation to energy production and fungal pathogens. For these reasons I have set out to establish habitat use patterns, detection probabilities, spatial and temporal occupancy, and investigate species interactions. This thesis is broken down into three distinct chapters each intended to be a stand-alone document. The first establishes the basic ecology from natural history accounts, provides an overview of the various sampling strategies, and gives a comprehensive description of the study area. The second sets out to identify the factors influencing detection probabilities and occupancy of six sympatric bat species and provide insight into habitat use patterns. The third examines spatial and temporal activity patterns and investigates species interactions. This study can provide understanding into the secretive and poorly understood patterns of free flying bats across the landscape. It can also deliver useful information to land managers regarding potential changes in landscape practices for the conservation of bat species.

TABLE OF CONTENTS

Chapter 1

Bat Habitat Ecology Using Remote Acoustical Detectors at the Army National Guard Maneuver Training Center - Fort Pickett, Blackstone, Virginia. 1

ABSTRACT 1

INTRODUCTION 3

Natural History of North American Insectivorous Bats 5

Overall Sampling Strategies 8

OBJECTIVES 12

GENERAL SAMPLING METHODS 12

General Capture Methods 12

General Acoustic Sampling Methods 14

STUDY SITE 18

Dominant Vegetation Classifications on ARNG-MTC Fort Pickett 20

The Natural History of the Bats on Fort Pickett 22

Species Examined During the Scope of this Study 23

LITERATURE CITED 25

Chapter 2

Detection Probabilities, Occupancy, and Factors Influencing Bat Species Occurrence on Ft. Pickett Army National Guard Maneuver Training Center, Blackstone, Virginia. 52

ABSTRACT 52

INTRODUCTION 54

Study Site 58

METHODS 58

A Priori Hypothesis 58

Acoustic Bat Detection 58

Acoustic Activity Index-site covariate 61

Habitat Structure-site covariate 61

Prey Availability-site covariate 62

Environmental Factors-sampling covariates 63

Model Construction and Testing 64

Determining Detection Probabilities and Predicting Occurrence 65

Geographic Prediction of Occupancy Across the Landscape 67

RESULTS 68

Summary of Effort 68

Summary of Variables 68

Single Species Models 69

Eptesicus fuscus (Big brown bat) 70

Lasiurus borealis (Eastern red bat) 71

Myotis lucifugus (Little brown myotis) 71

Myotis septentrionalis (Northern long-eared myotis) 72

Nycticeius humeralis (Evening bat) 72

Perimyotis subflavus (Eastern pipistrelle) 73

DISCUSSION	73
CONCLUSION	76
LITERATURE CITED	79
 Chapter 3	
Patterns and Dynamics of Bat Co-occurrence Through Time and Space	108
ABSTRACT	108
INTRODUCTION	110
<i>A Priori Hypothesis</i>	114
STUDY SITE	115
METHODS	115
<i>Acoustic Bat Detection</i>	115
<i>Spatial Activity</i>	117
<i>Temporal Activity</i>	118
<i>Spatial co-occurrence</i>	119
<i>Temporal co-occurrence</i>	121
RESULTS	122
<i>Summary of Effort</i>	122
<i>Spatial Activity</i>	122
<i>Temporal Activity</i>	123
<i>Spatial co-occurrence</i>	124
<i>Temporal co-occurrence</i>	125
<i>Individual species spatial and temporal occurrence relative to other bats</i>	125
<i>Eptesicus fuscus</i> (Big brown bat)	126
<i>Lasiurus borealis</i> (Eastern red bat)	127
<i>Myotis lucifugus</i> (Little brown myotis)	129
<i>Myotis septentrionalis</i> (Northern long-eared myotis)	131
<i>Nycticeius humeralis</i> (Evening bat)	132
<i>Perimyotis subflavus</i> (Eastern pipistrelle)	134
DISCUSSION	135
<i>Eptesicus fuscus</i> (Big brown bat)	136
<i>Lasiurus borealis</i> (Eastern red bat)	137
<i>Myotis lucifugus</i> (Little brown myotis)	137
<i>Myotis septentrionalis</i> (Northern long-eared myotis)	138
<i>Nycticeius humeralis</i> (Evening bat)	138
<i>Perimyotis subflavus</i> (Eastern pipistrelle)	139
CONCLUSION	142
LITERATURE CITED	144
APPENDIX A Dominant Vegetation Classifications on ARNG-MTC Fort Pickett	175
APPENDIX B Natural history summary for all 13 species with the potential to occur on ARNG-MTC Ft. Pickett, Blackstone, Virginia.	178
APPENDIX C Pairwise comparisons for species activity for each habitat type	195
APPENDIX D Two-species models to examine species spatial co-occurrence	198

List of Tables

Table 1.1. Species with special concerns potentially found on ARNG-MTC Fort Pickett	47
Table 1.2. Bat species examined on ARNG-MTC Fort Pickett and associated method of detection during the 2006-2007 survey.	48
Table 2.1. <i>A priori</i> hypotheses affecting bat species occurrence and detection in 2007 on ARNG-MTC Ft. Pickett, Blackstone, Virginia.	85
Table 2.2. Summary of activity index (number of one minute time blocks) for each bat species at every sampling location on ARNG-MTC Ft. Pickett, Blackstone, Virginia during the 2007 summer sampling season.	86
Table 2.3. Top and competing occupancy and detection probability models for six vespertilionid bat species occurring on ARNG-MTC Ft. Pickett, Blackstone, Virginia in 2007. Models were constructed using program PRESENCE V 4.1. Psi represents occupancy and p represents detection probability. Competing models are characterized and having a $\Delta AIC < 2$.	89
Table 2.4. Untransformed beta estimates of coefficients for covariates derived from top (bold) and competing models for six bat species on ARNG-MTC Ft. Pickett Blackstone, Virginia in 2007. Positive value represents a positive relationship and a negative value represents and inverse relationship. Values are a non-linear magnitude of the relationship.	90
Table 3.1. Mean acoustic activity levels (number of 1 minute time blocks) per hour over 10 hour night (95% confidence intervals) by species, physiognomic cover type, and flyway presence on ARNG-MTC Ft. Pickett, Blackstone, Virginia in 2007. The sample size (n) equals the number of sites that include the physiognomic habitat/cover and flyway type. ANOVA's were conducted on the samples for among type comparisons. Ranks with the same letters were not significantly different ($p < 0.05$, Tukey Kramer's pairwise comparisons)	166
Table 3.2. Top two-species spatial co-occurrence models for each paired combination of species interactions on ARNG-MTC, Ft. Pickett, Blackstone, Virginia in 2007. The ΔAIC in this case represents the difference between the top model and the next closest model.	167

List of Figures

Figure 1.1. Location of Army National Guard Maneuver Training Center (ARNG-MTC) Fort Pickett within Virginia (St. Germain 2012).	49
Figure 1.2. Major physiognomic habitat classifications on Army National Guard Maneuver Training Center (ARNG-MTC) Fort Pickett, Virginia (St. Germain 2012).	50
Figure 1.3. Sonograms for each of the six species included for analysis (St. Germain 2012).	51
Figure 2.1. Physiognomic habitat cover types and acoustic sampling locations on ARNG-MTC Ft. Pickett, Blackstone, Virginia in 2007 (St. Germain 2012).	91
Figure 2.2. Acoustic sampling locations on ARNG-MTC Fort Pickett, Blackstone, Virginia. Sampling occurred at a subset of these locations in 2006 and at all locations in 2007 (St. Germain 2012).	92
Figure 2.3. Height class volumetric vegetation density by habitat type on ARNG-MTC Ft. Pickett, Blackstone, Virginia in 2007. Estimations used braun-blanquet cover class midpoints over 20 points per sampling location (St. Germain 2012).	93
Figure 2.4. Volumetric vegetation density by habitat type on ARNG-MTC Ft. Pickett, Blackstone, Virginia in 2007. All height classes combined using braun-blanquet cover class midpoints over 20 points per site (St. Germain 2012).	93
Figure 2.5. Average insect biomass by habitat type type on ARNG-MTC Ft. Pickett, Blackstone, Virginia in 2007. Biomass is summarized as insect dry weight in grams (St. Germain 2012).	94
Figure 2.6. Global occupancy estimates derived from best model for the 6 species examined during 2007 on ARNG-MTC Ft. Pickett, Blackstone, Virginia. This estimate was based on the top models for all habitats installation wide (St. Germain 2012).	95
Figure 2.7. Proportion of area occupied (Ψ) and detection probability (p) stratified by habitat types for <i>Eptesicus fuscus</i> Big brown bat on ARNG-MTC Ft. Pickett, Blackstone, Virginia in 2007 (St. Germain 2012).	96
Figure 2.8. Proportion of area occupied (Ψ) and detection probability (p) stratified by habitat types for <i>Lasiurus borealis</i> Eastern red bat on ARNG-MTC Ft. Pickett, Blackstone, Virginia in 2007 (St. Germain 2012).	97
Figure 2.9. Proportion of area occupied (Ψ) and detection probability (p) stratified by habitat types for <i>Myotis lucifugus</i> , Little brown bat on ARNG-MTC Ft. Pickett, Blackstone, Virginia in 2007 (St. Germain 2012).	98
Figure 2.10. Proportion of area occupied (Ψ) and detection probability (p) stratified by habitat types for <i>Myotis septentrionalis</i> Northern long-eared myotis on ARNG-MTC Ft. Pickett, Blackstone, Virginia in 2007 (St. Germain 2012).	99
Figure 2.11. Proportion of area occupied (Ψ) and detection probability (p) stratified by habitat types for <i>Nycticius humeralis</i> Evening bat on ARNG-MTC Ft. Pickett, Blackstone, Virginia in 2007 (St. Germain 2012).	100
Figure 2.12. Proportion of area occupied (Ψ) and detection probability (p) stratified by habitat types for <i>Perimyotis subflavus</i> Eastern pipistrelle on ARNG-MTC Ft. Pickett, Blackstone, Virginia in 2007 (St. Germain 2012).	101
Figure 2.13. Species distribution map for <i>Eptesicus fuscus</i> Big brown bat on ARNG-MTC Ft. Pickett, Blackstone, Virginia in 2007. Distributions are represented as the proportion of area occupied (Ψ) based on top species models derived from program PRESENCE (St. Germain 2012).	102
Figure 2.14. Species distribution map for <i>Lasiurus borealis</i> Eastern red bat on	103

ARNG-MTC Ft. Pickett, Blackstone, Virginia in 2007. Distributions are represented as the proportion of area occupied (Ψ) based on top species models derived from program PRESENCE (St. Germain 2012).	
Figure 2.15. Species distribution map for <i>Myotis lucifugus</i> , Little brown bat on ARNG-MTC Ft. Pickett, Blackstone, Virginia in 2007. Distributions are represented as the proportion of area occupied (Ψ) based on top species models derived from program PRESENCE (St. Germain 2012).	104
Figure 2.16. Species distribution map for <i>Myotis septentrionalis</i> Northern long-eared myotis on ARNG-MTC Ft. Pickett, Blackstone, Virginia in 2007. Distributions are represented as the proportion of area occupied (Ψ) based on top species models derived from program PRESENCE (St. Germain 2012).	105
Figure 2.17. Species distribution map for <i>Nycticeius humeralis</i> Evening bat on ARNG-MTC Ft. Pickett, Blackstone, Virginia in 2007. Distributions are represented as the proportion of area occupied (Ψ) based on top species models derived from program PRESENCE (St. Germain 2012).	106
Figure 2.18. Species distribution map for <i>Perimyotis subflavus</i> Eastern pipistrelle on ARNG-MTC Ft. Pickett, Blackstone, Virginia in 2007. Distributions are represented as the proportion of area occupied (Ψ) based on top species models derived from program PRESENCE (St. Germain 2012).	107
Figure 3.1. <i>A priori</i> hypothesis regarding spatial co-occurrence based on morphology, natural history, echolocation call structure and habitat use among six vespertilionid species on ARNG-MTC Ft. Pickett, Blackstone, Virginia in 2007 (St. Germain 2012).	168
Figure 3.2. Temporal activity patterns for six sympatric bat species based on average activity index on ARNG-MTC Ft. Pickett, Blackstone, Virginia in 2007 (St. Germain 2012).	169
Figure 3.3. Average nightly activity index for six sympatric bat species by major physiognomic habitat type on ARNG-MTC Ft. Pickett, Blackstone, Virginia in 2007 (St. Germain 2012).	170
Figure 3.4. Spatial co-occurrence based on two-species occupancy models among six vespertilionid species on ARNG-MTC Ft. Pickett, Blackstone, Virginia in 2007. Δ AIC represents the difference between the top model and the next best model (St. Germain 2012).	171
Figure 3.5. Temporal activity based on kernel density estimates among six vespertilionid species on ARNG-MTC Ft. Pickett, Blackstone, Virginia in 2007. Various smoothing factors are represented, Light grey $c=0.25$, Solid line $c=1.0$, dotted line $c=1.25$ (St. Germain 2012).	172
Figure 3.6. Two-species temporal overlap (Δ) based on kernel density estimates among six vespertilionid species on ARNG-MTC Ft. Pickett, Blackstone, Virginia in 2007. The solid line represents species in column, dotted line denotes species in row (St. Germain 2012).	173
Figure 3.7. Overall results of spatial, temporal and activity co-occurrence for six sympatric bat species on ARNG-MTC Ft. Pickett, Blackstone, Virginia in 2007 (St. Germain 2012) .	174

Chapter 1

Bat Habitat Ecology Using Remote Acoustical Detectors at the Army National Guard Maneuver Training Center - Fort Pickett, Blackstone, Virginia.

“Beautiful, isn’t she, Lucius? A microphone and high frequency generator-receiver.”

—Bruce Wayne

ABSTRACT

Bats occupy diverse and unique niches and are regarded as important components in maintaining ecosystem health. They are major consumers of nocturnal insects, serve as pollinators, seed disperser, and provide important economic benefits as consumers of agricultural and forest pest insects. Bats have been proposed as good indicators of the integrity of natural communities because they integrate a number of resource attributes and may show population declines quickly if a resource attribute is missing. Establishing community- and population-level data, and understanding species interactions is especially important in changing landscapes and for species whose populations levels are threatened by outside factors of anthropomorphic disturbance from hibernacular visitation to energy production and fungal pathogens. For these reasons I have set out to establish habitat use patterns, detection probabilities, spatial and temporal occupancy, and investigate species interactions. This thesis is broken down into three distinct chapters each intended to be a stand-alone document. The first establishes the basic ecology from natural history accounts, provides an overview of the various sampling strategies, and gives a comprehensive description of the study area. The second sets out to identify the factors influencing detection probabilities and occupancy of six sympatric bats species and provide insight into habitat use patterns. The third examines spatial and temporal activity patterns and investigates species interactions. This study can provide

understanding into the secretive and poorly understood patterns of free flying bats across the landscape. It can also deliver useful information to land managers regarding potential changes in landscape practices for the conservation of bat species.

Key words: acoustical detector, activity index, AnaBat, Big brown bat, Eastern pipistrelle, Eastern red bat, Evening bat, *Eptesicus fuscus*, Ft. Pickett, insect biomass, *Lasiurus borealis*, military lands, mist net, *Myotis lucifugus*, *Myotis septentrionalis*, Northern long-eared myotis, *Nycticeius humeralis*, *Perimyotis subflavus*,

INTRODUCTION

The tremendous variety of foods that bats (Order Chiroptera) exploit, coupled with the various foraging techniques and roosting structures they utilize have led to remarkable abundance and diversity patterns for the Order (Patterson et al. 2003). Bats occupy diverse and unique niches and are regarded as important components in maintaining ecosystem health (Marcot 1996, O'Shea and Bogan 2003). They are major consumers of nocturnal insects, serve as pollinators, and act as seed dispersers. Bats can provide important economic benefits as consumers of agricultural and forest pest insects (O'Shea and Bogan 2003, Boyles et al. 2011). Insectivorous bats in the United States consume large numbers of insect pests that would otherwise cost the agriculture and forestry industries millions of dollars in insecticide control (Pierson 1998) and higher crop yields (Cleveland et al. 2006). Given their important role, many aspects of their basic ecology are still unknown. One reason for this is the difficulty encountered in studying volant, nocturnal creatures.

Many bat species within the eastern United States depend on forested environments to meet at least one portion of their life history requirements. Some species referred to as “forest roosting bats”, utilize forests to meet their entire habitat needs (e.g., foraging, roosting, pup-rearing) for at least part of their annual cycle (i.e., some bats roost in caves during the hibernation period but use forests exclusively during the summer (Miller et al. 2003). Most of the bat species occurring in Virginia will utilize forested environments to meet seasonal resource requirements.

Bats have been proposed as good indicators of the integrity of natural communities because they integrate a number of resource attributes (e.g., roosting, watering, and feeding habits), and thus may show population declines quickly if a resource attribute is missing (Hutson et al. 2001). Some bat populations worldwide are experiencing declines due to adverse effects of human population growth and associated deforestation, conversion of natural habitats to forest and agricultural monocultures, water, soil, and air pollution, and introductions of xenobiotics and exotic species (Kunz and Fenton 2003). Of the 45 species of bats known to occur in the United States, 11 are listed, either as endangered ($n = 3$), vulnerable or threatened ($n = 4$), or near threatened or species of concern ($n = 4$) by the International Union for Conservation of Nature and Natural Resources (IUCN 2007).

Natural resource managers throughout North America have placed increasing emphasis on understanding the impact of forest management practices on populations and behavior of bats (Menzel et al. 2005b). Subsequently land managers, both public and private, are increasingly expected to provide habitat to maintain or promote bat community diversity in forested and other natural landscapes (Miller et al. 2003). The continued decline of several bat species associated with forested environments underscores the need for an increased understanding of habitat relationships for North American bats (Fenton 1997, O'Shea et al. 2003, Menzel et al. 2005a). These relationships have been identified as one of the informational gaps hindering our understanding of how to better manage natural systems for bats (Arnett 2003).

With increased pressures on natural environments for a variety of resources, a critical component of land management planning should include an understanding of how changes across the landscape affect bat distributions and population levels. My goal was to determine the influence of landscape composition and structure at multiple scales on bats species occurrence across the landscape on Army National Guard Maneuver Training Center (ARNG-MTC) Fort Pickett, Virginia. This project will assist ARNG-MTC Fort Pickett in accomplishing stewardship objectives designed to protect bat species while also ensuring the continued availability, maintenance, and function of quality military training land. In addition, such information will prove valuable to other land managers in making critical decisions regarding land use practices.

Natural History of North American Insectivorous Bats

Bats are a remarkably abundant and widespread taxon. Nearly global in distribution, bats have successfully adapted to life in virtually every terrestrial environment except the arctic and polar regions, and comprise the second largest mammalian order; only Rodentia includes a greater number of species (Nowak 1994). Bats represent approximately 1/5 of all mammalian species with an estimated ~1100 species (Kunz and Lumsden 2003, Simmons and Conway 2003, Wilson and Reeder 2003). Although bats reach their highest densities in tropical and subtropical areas, they are frequently abundant members of the temperate faunas of the United States (Vaughn 1986). However, as result of their small size, nocturnal lifestyle and cryptic nature, bats

are difficult to study and can be an easily overlooked component of the overall biotic community.

Despite the great ecological diversity among bat species, many bats show some common behaviors and preferences. For example, when foraging, many bat species will frequently feed over water (streams, ponds, ephemeral sources like road ruts), and along edges (forest edges, cliffs or ravines, or among buildings) (Barbour and Davis 1969). These patterns allow ecologists to monitor free-living bat populations using a variety of methods.

Bats, similar to other animals, collect, communicate, and interpret information using a wide range of sensory cues, including, hearing, vision, olfaction, and touch (Smith 1977). Hearing is not necessarily the dominant sense in the orientation and communication for bats (Altringham and Fenton 2003), although sound plays an important role for the microchiropteran bats through means of echolocation (Griffin 1958). Echolocation signals primarily serve to deliver the echo information that a bat needs to solve different tasks it encounters while commuting and foraging, by giving the bats a three dimensional acoustic visualization of their environment.

Most species in the eastern United States can be distinguished by their echolocation call structure. The most common species-specific call type is referred to as the “search-phase” calls. These can be thought of as echolocation calls produced when a bat is not involved in any other type of behavior, such as pursuit of prey, rather the bat is

simply navigating or activity foraging through the environment. However, there are some features of the echolocation calls that are not species specific, but rather situation-specific (Siemers 2002, Szewczak 2002). Echolocation calls can change depending on how far a bat is flying from other objects in its vicinity, or how cluttered the environment is (Corben 2002). Thus a bat flying in the open, zero clutter, will typically produce its flattest, lowest-frequency calls (expressed as frequency in kiloHertz (kHz) over time in milliseconds (ms)). At the other extreme, most bats produce steeper calls of shorter duration when flying in extreme clutter, in close proximity to other objects (Corben 2002). These characteristics are species specific and can vary to some degree given the conditions and species.

Calls can also be influenced by environmental conditions as the sound waves travel through the air, such as reflections, atmospheric absorption / attenuation, and geometric spreading (Pettersson 2002). Although some species produce calls that can be confused with other species, most species' repertoires exhibit a portion that is diagnostic and thus identifiable to the species level (Britzke and Murray 2000, Britzke et al. 2002, Corben 2002, Miller 2002).

Bat activity is not uniformly distributed through the night and will vary depending on the season and reproduction cycle. For most species, several distinct periods of activity occur (Thomas and West 1989). Activity is highest during the first 60 minutes that correspond with dispersal away from roosts and the first feeding period (Anthony and Kunz 1977, Swift 1980). Activity often declines after this, but marked peaks may occur around midnight and again toward dawn (Thomas and West, 1989). Bergallo *et al.*

(2003) have documented the benefits of conducting all night automated surveys to determine period of highest activity.

Overall Sampling Strategies

Summertime bat sampling using acoustics is typically conducted between the beginning of May and the end of August. The time of year or stage of the reproductive cycle will influence sampling in several ways (Thomas and West 1989). There are different energetic requirements between males and females during various reproductive cycles (e.g., more trips are made by females to maternity roosts during lactation) and when the young are recruited into the flying population (Thomas and West 1989). These activities may give the impression of higher levels of bat activity than other times even though there was no actual change in the number of bats present (Ministry of Environment 1998). Environmental conditions also influence bat activity. (e.g., Grindal et al. 1992). The presence of precipitation, strong winds, or temperatures below 10°C may result in a decrease in levels of bat activity. No sampling should be done on nights with heavy precipitation, moderate to strong winds, or when the ambient temperature at sunset is below 10°C.

The unique ecology and behavior of bats present challenges to sampling in the field. Bats are volant, nocturnal, often avoid being trapped repeatedly (Kunz and Kurta 1988), exhibit temporal and spatial heterogeneity (Thomas and West 1989, Hayes 1997), and demonstrate sexual dimorphism in habitat use (Barclay 1991). It is virtually impossible to determine the absolute abundance of bats present in an area (except

possibly at colonial roost sites) because they are so infrequently re-captured, and even comparisons of relative abundance of different species either within an area or between areas is difficult (Thomas and LaVal 1988, Thomas and West 1989, Ministry of Environment 1998). Current sampling techniques available for bats during the non hibernacular period are primarily qualitative surveys and not suited for quantitative censuses (Thomas and West 1989, Ministry of Environment 1998).

The two major classes of sampling for bats are physical capture and acoustic detection. Physical capture is accomplished through the use of mist nets and harp traps originally designed by (Constantine 1958), and later modified by (Tuttle 1974), although other techniques are available (LaVal and LaVal 1977, Youngston and McKenzie 1977, Fenton and Bell 1979, Kunz and Kurta 1988, Padgett and Rose 1991, Miller 2001). The capture of bats allows for positive species identification (see: Hall 1981, Nagorsen and Brigham 1993, Wilson and Reeder 1993), age and sex classification, mensural data collection, assessment of reproductive status/cycles (Phillips and Inwards 1985, Anthony 1988, Racey 1988, Lumsden and Bennett 1995) patterns of movement (e.g., Dwyer 1966) and survival estimates (e.g., Thompson 1987). However, not all species and sexes have equal catchability (Barclay 1991). Different capture techniques also have their own inherent biases. Harp traps have been shown to be more effective than mist nets at capturing bats, and bats using high frequency echolocation calls may be more difficult to trap than species emitting low frequency signals (Berry et al. 2004). Studies by (Henry et al. 2004) showed some species significantly favored canopy or understory, and some

were opportunistic regarding vertical stratification. This can lead to a sampling bias due to the difficulty of capturing canopy foraging species.

Detection is primarily achieved through the use of ultrasonic acoustic detectors. Acoustic sampling has proven to be an effective means of identifying free flying bats (O'Farrell 1997, O'Farrell and Miller 1997, O'Farrell et al. 1999a, O'Farrell and Gannon 1999, O'Farrell and Miller 1999, O'Farrell et al. 1999b). Acoustic sampling provides a more complete picture of bat activity than does capture in mist nets (Rautenbach et al. 1996, Duffy et al. 2000) and has been shown to be more effective than physical capture for determining presence of certain groups of bats (Kalko 1997, O'Farrell and Gannon 1999). Acoustic data collection can also be automated (e.g., Hayes 1997, O'Farrell 1998) allowing monitoring over long periods or at multiple locations simultaneously without an on-site observer. Acoustic surveys are the most expedient means of gathering landscape level, community level, and long-term data for bats (O'Farrell and Miller 1999, Hayes 2000, Ochoa et al. 2000). Identification from detectors, however, may be less reliable than capture records for some species (e.g., Mills et al. 1996, Law et al. 1998, Murray et al. 1999b, Livengood et al. 2002), but more efficient for others (e.g., O'Farrell et al. 1999b). Also habitat structure has a great influence on levels of bat activity (Thomas 1988, Hayes and Adam 1996). Acoustical detection therefore is influenced by differences in the range of detection for various habitats (Patriquin et al. 2000).

Nonetheless, the use of ultrasonic detectors has gained acceptance as a convenient and efficient method of conducting bat surveys where the main objective is to detect and

identify presence of bat species (Thomas 1988, Bettes 1998, Britzke and Murray 2000, Duffy et al. 2000, Larson and Hayes 2000, O'Farrell et al. 2000, Prevett 2002). It should be noted that *individuals* can not be identified with acoustic detectors, but rather presence of various species can be detected.

All survey methods have their benefits and potential biases. Currently there is no one method that is most effective for determining presence or relative abundance of all bats. The best strategy for the most thorough assessment of a free-living bat population over a large area is to use a combination of these techniques (Kalko et al. 1996, Kuenzi and Morrison 1998, Ministry of Environment 1998, O'Farrell and Gannon 1999, Duffy et al. 2000, Miller 2001, Johnson et al. 2002). The demographic data provided by physical capture techniques cannot be derived from less-intrusive sampling methods. Historically, species richness may have been more accurately measured during mist-netting than ultrasonic detection because some species had to be grouped together due to similarities in their calls (e.g. *Myotis* spp.) and could only be differentiated in hand. However, recent developments in acoustic call analyses have allowed many more species to be differentiated acoustically (Britzke et al. 2002). Ultrasonic detection efforts compliment the potential biases of trapping by sampling in areas where mist-netting is difficult, or when species are present that are not successfully sampled by the nets due to net placement, configuration, or the nature of the individuals. The combined use of ultrasonic detection and trapping techniques also allows for the potential to improve detection accuracy through the creation of ultrasonic reference recordings (Thomas and West 1989) from animals captured in-hand.

In this study, I used a combination of capture techniques to confirm species presence and to further develop accurate acoustic filters for species identification. The primary data sets used to meet the specific objectives of this study are derived from passive acoustical data collected across the landscape.

OBJECTIVES

1. Chapter 2: Determine the factors influencing bat occurrence, and predict bat species occurrence across the landscape.
2. Chapter 3: Examine temporal activity patterns, habitat use, and investigate species interactions.

GENERAL SAMPLING METHODS

General Capture Methods

For the capture portion of this study I employed a non-random design. The major objective was to choose survey areas where bats are most likely to occur. Mist nets and harp traps were set to maximize the capture probability of bats (Kunz and Kurta 1988). I targeted flight corridors, creeks, perennial road ruts, wildlife ponds, and other potential foraging areas (Kunz and Kurta 1988, Murray et al. 1999a). To increase probability of capture, strategies for net/trap set include using gaps in the vegetation that are potential flyways enabling the vegetation to act as a funnel.

I deployed an array of mist nets (38 mm mesh, reduced bag, nylon; Avinet Inc, Dryden, NY, USA) and harp traps (Austbat 4.2m³; FaunalTech/Austbat, Mount Taylor, Victoria, Australia), at capture sampling sites. Mist net heights were all 2.6m tall but vary in length: 2.6m, 6m, 9m, and 12m. Whenever possible a custom personally designed and constructed high net system was used. In this situation, a series of pulleys attached to tall poles, are used to stack nets on top of each other. This doubles the effective capture area from 2.6m high to 5.2m x the length of the net. I recorded the species, sex, time, and trap type for each capture. To calculate capture per unit effort I record net time (opened and closed), size, and number of nets utilized. The number of bats caught per net hour (per trap-hour) (Morena and Halfetter 2000) was analyzed and reported for each sample site. One net hour is equivalent to one 6m length of net/hour and 1 harp trap / hour (Ministry of Environment 1998). Capture rates have been documented to decrease with consecutive trap nights (Kunz and Brock 1975). Therefore, most sites were sampled without replication to maximize effort per area and to eliminate bias from previously captured individuals. Detailed locations (UTM coordinates in WGS 84) were recorded for each sampling site with a Garmin 12XL GPS Unit. All spatial data is stored in an ARC-GIS 9.2 geodatabase for analysis (ESRI, Redlands, California).

I collected the following information from all animals captured: species following description provided by (Harvey et al. 1999), sex, reproductive condition, age by ossification of wing joints (young of year / adult), tooth wear (as a surrogate for adult age), body mass (to the nearest 0.1g), and the length of the forearm. All animals were handled humanely following guidelines of the American Society of Mammalogists

(Animal Care and Use Committee 1998), and methods used for handling bats conformed to guidelines set forth by the Institutional Animal Care and Use Committee at Virginia Polytechnic Institute and State University (IUCAC # FIW07-035) and both federal (TE102410-0) and state permitting (VaDGIF #028832, #028833). Upon release of the captured individual, acoustic signatures were collected to provide additional information to the local call library for that species.

General Acoustic Sampling Methods

For ultrasonic acoustic detection at the trap site, I used a remotely mounted microphone connected to the Anabat II detector and Compact Flash-Zero Crossing Analysis Interface Module (CF-ZCAIM) (Titley Electronics, Ballina, New South Wales, Australia). These units were activated when the first mist net and harp trap were opened and were turned off when the last mist net/harp trap was closed. The Anabat detector was deployed within the center of the trap array typically no further than ~30m from the nets. The placement was chosen with the objective of capturing as many calls as possible (e.g. Hayes and Hounihan 1994). The microphone placement was ~1.4 meters off the ground, and oriented in the direction of fewest trees (Weller and Zabel 2002) at a ~45° angle (Duffy et al. 2000). Sensitivity of the Anabat detector was set at six to minimize stream and insect noises (Hayes 1997) but sometimes adjustments were needed. All acoustic emissions are recorded to the internal compact flash card with a date and time stamp on each file. All recorded calls were transferred from the CF cards to desktop computer for identification and analysis. Additional units on site were used to actively track released individuals for obtaining additional acoustic call, when possible.

Initially I conducted active acoustic sampling using an Anabat II bat detector linked to a laptop computer with a Mini6 Zero Crossing Analysis Interface Module (ZCAIM) using the software Anabat6, and later with the Anabat SD1 linked to a PDA (HP iPAQ hx2100). For active recordings of bats, an on-site observer continuously directed the microphone opportunistically to follow the flight path of an individual bat. These actively recorded calls are primarily used to construct local call libraries from known hand released individuals (Britzke 2002).

I used passive sampling as the primary sampling strategy for determining detection probabilities, activity levels, species occurrence and species interactions. Passive monitoring used remotely mounted microphones connected to the Anabat II detector and Compact Flash-Zero Crossing Analysis Interface Module (CF-ZCAIM). These units are not built to withstand harsh environmental conditions from the manufacturer, therefore, I constructed secure housing systems using recycled 100 cartridge, 0.50 caliber military ammunition cans. I constructed microphone extension cables and microphone housing units “AnaMike bat hats” to protect both the device and microphone from the elements. These allowed the units to be securely housed in the metal box while permitting waterproof extension of the microphone to directly record bat calls without the need for a reflection plate. Battery life was extended by the use of 12 volt 7.5Ah rechargeable batteries which also required the construction of special wiring harnesses to power the devices. This allowed for monitoring up to 21 days without the

need for battery replacement. Through personal experience using conventional methods, I found one 9 volt, and 4 AA batteries are required for 2 nights of sampling.

Passive acoustic monitoring allowed for simultaneous sampling of multiple sites without the need for an on-site observer (Britzke 2002, Corben 2002). The placement of the microphone element was chosen with the objective of capturing as many calls as possible (e.g. Hayes and Hounihan 1994). The microphone placement was ~1.4 meters off the ground, and oriented in the direction of fewest trees (Weller and Zabel 2002) at a ~45° angle (Duffy et al. 2000). Passive units were programmed to activate recording at the onset of civil twilight (before sunset) and shut down at the end of civil twilight at sunrise. All recorded calls were transferred from the CF cards to a desktop computer for identification and analysis.

Species identifications for passive sampling analysis were based on subjective comparison of call sequences to vocal signature vouchers (O'Farrell et al. 1999b) and follow taxonomy described by (Harvey et al. 1999). Specific filters were created for each species verified for the area as well as for those species that possibly could occur in the area. These filters were constructed using standard parameters (e.g., minimum, maximum and characteristic frequencies etc.) based upon calls of vocal signatures of known species with a minimum of five pulses required for identification. Identification of bats was possible using information in acoustic libraries compiled locally on each sampling site, other available libraries collected throughout the U.S., and published echolocation call parameters. The Scan utility function of the AnaLookW (Beta version

3.2h dated 25 August 2005) software (Corben 2005) and constructed filters was used for species identification.

All complete vocal sequences, including those that could not be identified (i.e., “unknowns”) were archived digitally. Although all calls obtained were examined, only those sequences that contained frequency and structural characteristics known for a particular species for determining identifications were used. If there was doubt or overlap with other species, sequences were disregarded. However, I kept track of the number of unidentifiable calls to determine number of undetectable calls versus detectable calls. Data analysis uses the Acoustic Activity Index (AI) as described by Miller 2001.

$$AI = \sum_i^n P$$

The AI is calculated by summing up the number of one-minute time blocks for which the species was detected (n) as being present (P). Dividing by the unit effort for the survey standardizes the AI. The AI is standardized by hours of survey time to allow comparison between dates and sites.

This study involved direct field investigations and synthesis based on collected field data coupled with natural history of bats within the Mid-Atlantic region. The field investigations concentrated on determining the spatial and temporal distribution of bats across the landscape, and to determine what factors influence the detectability occurrence, and distribution of bats. Second, investigations were conducted to examine

potential interspecific competitive interactions of bat species occurring on the landscape. Each of these forms a separate paper within this thesis focusing on understanding the ecological aspects of bats in the Mid-Atlantic. A series of sampling methods and analytic frameworks were applied to achieve these objectives. Finally, based on the results of field investigations, critical ecological components are identified and predictive maps of species occurrence created. These results can assist natural resource managers in making critical land use decisions with regards to the conservation of particular bat species.

STUDY SITE

Army National Guard Maneuver Training Center (ARNG-MTC) Fort Pickett is located in the Nottoway drainage of the lower Piedmont in southeastern Virginia (Figure 1.1). The base is approximately 100 kilometers (62 miles) southwest of Richmond and five kilometers (3.1 miles) east of the town of Blackstone. It lies within the counties of Brunswick, Dinwiddie, and Nottoway. Fort Pickett is approximately 36 km (22 mi) from the fall line where the Piedmont physiographic region transitions to the Coastal Plain physiographic region. It consists of 16870 ha (41,690 acres) of both open and forested live-fire and maneuver training lands.

Regionally, the vegetation of the ARNG-MTC Fort Pickett area is part of the oak-hickory-pine (*Quercus* sp – *Carya* sp – *Pinus* sp) region described by Braun (1950). Many of the plant species are typical of the southeastern Piedmont, with some distinct Coastal Plain influences (Dorr 2007). Furthermore, because of the unique land use of controlled and training induced wildfires on ARNG-MTC Fort Pickett, there are several

occurrences of rare and endangered species (Emrick and Murray 2001). The fauna is also characteristic of the Piedmont region. The Virginia Gap Analysis program has identified ARNG-MTC Fort Pickett as an area which provides vital habitat for the overall biodiversity of the piedmont of Virginia.

Unique ecosystem characteristics at ARNG-MTC Fort Pickett support occurrences of rare native plant communities. These rare and unique plant communities are primarily maintained by prescribed fire and training-caused wildfires. A majority of the training-caused wildfires occur within the Controlled Access Area (CAA) on an annual or biannual basis. These fires are usually moderately intense ground fires that are allowed to burn unhindered within the CAA; only rarely do they result in intense crown fires. As a result, a unique mosaic of pyric disclimax plant communities, such as loblolly pine savannas (*Pinus teada*), oak-hickory woodlands and little bluestem grasslands, has developed within the CAA (Emrick and Murray 2001).

The description of forest resources is in large part based upon the Forest and Wildlife Habitat Inventory (1987). This inventory characterized 13,720 ha (33,892 acres) as forested land and included all forested land in the CAA and forested wetlands. The majority of the hard mast producing stands, pine and pine-oak stands are located on well-drained sites varying in location from coves to ridge tops. The mixed hardwoods generally occupy slightly more mesic sites. On well-drained sites, previous management of the site is the primary factor that determines current species composition, with pine and pine-oak mixes most common on abandoned agricultural fields. Hardwoods

generally occur in areas that have not been managed for agricultural purposes for over 100 years. Hunter (1995) identified and described four general forest site types at ARNG-MTC Fort Pickett: pine, pine/hardwood mix, upland hardwood, and bottomland hardwood.

Dominant Vegetation Classifications on ARNG-MTC Fort Pickett

There are 6 major physiognomic habitat types classified on ARNG-MTC Fort Pickett (Dorr 2007). These have been classified as: Coniferous Forests (CF), Developed / Cantonment Areas (DA), Deciduous Hardwood Forest (DF), Forested Wetlands e.g. bottomland hardwood forests (FW), Grassland / Shrublands (GS), and Wetlands with surface water present (WL). There are a few unique communities that also occur within the Controlled Access Area (CAA) (see Figure 1.2.). Detailed vegetation descriptions can be found in Appendix A.

Coniferous Forests (CF): This coniferous forest cover type is very common at Fort Pickett-MTC and is almost exclusively dominated by loblolly pine (*Pinus taeda*). Loblolly pine comprises over 80% of the basal area in this cover type.

Developed / Cantonment Areas (DA): The cantonment area encompasses most of the buildings (barracks, dining halls, maintenance areas, warehouses, etc.) at ARNG-MTC Fort Pickett. Blackstone army airfield (BAAF), helicopter landing zones and the ammunition supply point (ASP) are all also located within the cantonment area. Within

the cantonment area there are also several buildings that are abandoned and in various states of decay.

Deciduous Hardwood Forest (DF): The deciduous hardwood forest cover type is the most variable of all the cover types at ARNG-MTC Fort Pickett. This type occurs on a variety of sites with black oak (*Quercus velutina*) being more prevalent on the drier more exposed sites and northern red oak (*Quercus rubra*) more common on the less exposed wetter sites.

Forested Wetlands - Bottomland Hardwood Forests (FW): This cover type occurs on frequently flooded bottomlands and alluvial plains of major rivers. It is especially common along the Nottoway River floodplain at ARNG-MTC Fort Pickett in deep coarse textured soils.

Grassland / Shrublands (GS): The open areas at Fort Pickett-MTC exist because of the training requirements of the military and are maintained in an early successional status by training activities, prescribed fire, drum-chopping, and mowing. Typically this complex comprises a mosaic of warm and cold season grasslands (Emrick and Murray 2001).

Open Water Wetlands (WL): Wetlands are defined as those areas that are inundated or saturated by surface ground water at a frequency and duration to support vegetation typically adapted for life in saturated soil conditions. Here, open water

wetlands are classified as ponds, streams, rivers, and swamps that may contain emergent vegetation but do not have an overstory canopy.

Rare communities within the Controlled Access Area: These communities occur with some frequency in the Controlled Access Area (CAA). The CAA serves as buffer zone for various live fire ranges resulting in frequent training caused wildfires, which in turn, maintain these communities.

The Natural History of the Bats on Fort Pickett

Bats are an especially diverse group whose distribution is influenced by very specific habitat requirements and/or seasonal variation. At least 13 species have ranges that include the Piedmont of Virginia, and so represent species that could potentially be found in the ARNG-MTC Fort Pickett area (VAFWIS 2005). These species include: *Corynorhinus rafinesquii* (eastern big-eared bat), *Corynorhinus townsendii virginianus* (Virginia big-eared bat), *Eptesicus fuscus* (big brown bat), *Lasionycteris noctivagans* (silver-haired bat), *Lasiurus borealis* (eastern red bat), *Lasiurus cinereus* (hoary bat), *Lasiurus seminolus* (Seminole bat), *Myotis leibii* (eastern small-footed myotis), *Myotis lucifugus* (little brown myotis), *Myotis septentrionalis* (northern myotis), *Myotis sodalis* (Indiana bat), *Nycticeius humeralis* (evening bat), and *Perimyotis subflavus* (eastern pipistrelle) (Whitaker and Hamilton 1998). A comprehensive list of all potential species on ARNG-MTC Fort Pickett and those positively identified can be found in Table 1.4. (St. Germain 2008a).

Two of these species are listed as federally endangered: *Myotis sodalis* (Indiana bat), and the Townsends big-eared bat sub-species *C. townsendii virginianus* (Virginia big-eared bat) (Harvey 1986). These are also considered endangered or vulnerable under the global microbat action plan (Hutson et al. 2001). Three others are of state management concern (Table .1) (Roble 2003, VAFWIS 2005). Detailed descriptions of each species' natural history can be found in Appendix B and Table 1.3.

Species Examined During the Scope of this Study

For the scope of this study, I initially surveyed for all 13 species that could potentially occur in the region: *Corynorhinus rafinesquii* (eastern big-eared bat), *Corynorhinus townsendii virginianus* (Virginia big-eared bat), *Eptesicus fuscus* (big brown bat), *Lasionycteris noctivagans* (silver-haired bat), *Lasiurus borealis* (eastern red bat), *Lasiurus cinereus* (hoary bat), *Lasiurus seminolus* (Seminole bat), *Myotis leibii* (eastern small-footed myotis), *Myotis lucifugus* (little brown myotis), *Myotis septentrionalis* (northern myotis), *Myotis sodalis* (Indiana myotis), *Nycticeius humeralis* (evening bat), and *Perimyotis subflavus* (eastern pipistrelle).

The primary mode of identification in this study is acoustical recording of species specific search phase calls. At this time, high quality representative search phase calls are not available for: *Corynorhinus rafinesquii* (eastern big-eared bat), *Lasiurus seminolus* (Seminole bat), nor, *Myotis leibii* (eastern small-footed myotis), with which to construct filters. These species may still be present on ARNG-MTC Fort Pickett although unless high quality signature vocalizations are obtained, they will not be included in this

study. *Lasionycteris noctivagans* (silver-haired bat) is a migratory species known to winter in the region. It has been confirmed as occurring but only during the winter (St. Germain 2005, St. Germain and Miller 2007), therefore also will not be included. There is some indication the call structures for *Corynorhinus townsendii virginianus* (Virginia big-eared bat) and *Corynorhinus rafinesquii* (eastern big-eared bat) may be very similar. It is possible that the filters I have to identify the *Corynorhinus townsendii virginianus* may indeed be misidentifying calls as *Corynorhinus rafinesquii*, so for the purposes of this study I combined the two into *Corynorhinus sp.*

There were limited detections attained for *Corynorhinus sp* and *Lasiurus cinereus* (hoary bat) on ARNG-MTC Ft. Pickett (St. Germain 2008). The low sample sizes did not allow for species modeling to occur therefore both of these species were excluded from further analysis.

Combining capture records for species on the installation (Table 1.2), very low detection rates (St. Germain 2008), and limited ability to identify some species acoustically, 6 species remain for further analysis. These species include: *Eptesicus fuscus* (big brown bat), *Lasiurus borealis* (eastern red bat), *Myotis lucifugus* (little brown myotis), *Myotis septentrionalis* (northern myotis), *Nycticeius humeralis* (evening bat), and *Perimyotis subflavus* (eastern pipistrelle). Representative echolocation sonograms for these six species can be found in Figure 1.3.

LITERATURE CITED

- Aldridge, H. D. J. N. and I. L. Rautenbach. 1987. Morphology, echolocation, and resource partitioning in insectivorous bats. *Journal of Animal Ecology* **56**.
- Altringham, J., D. and M. B. Fenton. 2003. Sensory ecology and the communication in the Chiroptera. Pages 90-127 *in* T. H. Kunz and M. B. Fenton, editors. *Bat Ecology*. University of Chicago Press, Chicago.
- ANHC. 2005. Mammals of Special Concern (dated 16 March 2005)
<http://www.naturalheritage.com/pdf/ANIMALS-Mammals-2005.pdf>. Arkansas Natural Heritage Commission, Little Rock, AR.
- Animal Care and Use Committee. 1998. Guidelines for the capture, handling, and care of mammals as approved by the American Society of Mammalogists. *Journal of Mammalogy* **79**:1416-1431.
- Anthony, E. L. P. 1988. Age Determination in Bats. Pages 47-58 *in* T. H. Kunz, editor. *Ecological and behavioral methods for the study of bats*. Smithsonian Institution Press, Washington, DC.
- Anthony, E. L. P. and T. H. Kunz. 1977. Feeding strategies of the little brown bat (*Myotis lucifugus*) in southern New Hampshire. *Ecology* **58**:775-786.
- Arita, E. 1997. Species composition and morphological structure of the bat fauna of Yucatan, Mexico. *Journal of Animal Ecology* **66**:83-97.
- Arlettaz, R. 1999. Habitat selection as a major resource partitioning mechanism between the two sympatric sibling bat species *Myotis myotis* and *Myotis blythii*. *Journal of Animal Ecology* **68**:460-471.

- Arnett, E., B. 2003. Advancing science and partnerships for the conservation of bats and thier habitats. *Wildlife Society Bulletin* **31**:2-5.
- Arnett, E., B. 2008. Patterns of bat fatalities at wind energy facilities in North America. *Journal of Wildlife Management* **72**:61-78.
- Bailey, L., L., J. Hines, E., J. Nichols, D., and D. MacKenzie, I. 2007. Sampling design trade-offs in occupancy studies with imperfect detection: Examples and software. *Ecological Applications* **17**:281-290.
- Bailey, L., L., J. Reid, A., E. Forsman, D., and J. Nichols, D. 2009. Modeling co-occurrence of northern spotted and barred owls: Accounting for detection probaility differences. *Biological Conservation* **142**:2983-2989.
- Barbour, R. W. and W. H. Davis. 1969. *Bats of America*, Lexington, KY.
- Barclay, R. M. R. 1985. Long- versus short- range foraging strategies of hoary (*Lasivirus cinereus*) and silver-haired (*Lasionycteris noctivigans*) bats and the consequence of prey selection. *Canadian Journal of Zoology* **63**:2507-2515.
- Barclay, R. M. R. 1991. Population structure of temperate zone insectivorous bats in relation to foraging behaviour and energy demand. *Journal of Animal Ecology* **60**:165-178.
- Bergallo, H. G., C. E. L. Esberard, M. A. R. Mello, V. Lins, R. Mangolin, G. G. S. Melo, and M. Baptista. 2003. Bat species richness in Atlantic Forest: What is the minimum sampling effort? *Biotropica* **35**:278-288.
- Berry, N., W. O'Connor, M. W. Holderied, and G. Jones. 2004. Detection and avoidance of harp traps by echolocating bats. *Acta Chiropterologica* **6**:335-346.

- Bettes, B., J. 1998. Effects of Interindividual Variation in Echolocation Calls on Identification of Big Brown and Silver-haired Bats. *Journal of Wildlife Management* **62**:1003-1010.
- Blehert, D., S., A. Hicks, C., M. Behr, C. Meteyer, U., B. Berlowski-Zier, M., E. L. Buckles, T. Coleman, H., S. Darling, R., A. Gargas, R. Niver, J. Okoniewski, C., R. Rudd, J., and W. Stone, B. 2009. Bat White-nosed syndrome: an emerging fungal pathogen? *Science* **323**:227.
- Britzke, E. R. 2002. Designing monitoring programs using frequency-division bat detectors: active versus passive sampling. Pages 79-83 *in* R. Brigham, Mark, E. K. V. Kalko, C. Jones, S. Parsons, and H. J. G. A. Limpens, editors. *Bat Echolocation Research: tools, techniques, and analysis*. Bat Conservation International, Austin, Texas.
- Britzke, E. R. and K. L. Murray. 2000. A quantitative method for selection of identifiable search-phase calls using the Anabat System. *Bat Research News* **41**:33-36.
- Britzke, E. R., K. L. Murray, B. M. Hadley, and L. W. Robins. 1999. Bat activity as measured with the Anabat system. *Bat Research News* **40**:89.
- Britzke, E. R., K. L. Murray, J. S. Heywood, and L. W. Robbins. 2002. Acoustic Identification. Pages 221-227 *in* A. Kurta and J. Kennedy, editors. *The Indiana Bat: Biology and Management of an Endangered Species*. Bat Conservation International, Austin, Texas.
- Broders, H. G., G. M. Quinn, and G. J. Forbes. 2003. Species status, and the spatial and temporal patterns of activity of bats in southwest Nova Scotia, Canada. *Northeastern Naturalist* **10**:383-398.

- Brooks, R., T. and W. M. Ford. 2006. Introduction to the special section - Bat habitat use in eastern North American temperate forests: stand, site, and landscape effects. *Journal of Wildlife Management* **70**:1171-1173.
- Burnham, K. P. and D. R. Anderson. 1998. Model selection and inference: a practical information-theoretic approach. Springer-Verlag, New York, New York.
- Burnham, K. P. and D. R. Anderson. 2004. Multimodel inference: understanding AIC and BIC in model selection. *Sociological Methods & Research* **33**:261-304.
- Carter, T. C. 2006. Indiana bats in the midwest: The importance of Hydric Habitats. *Journal of Wildlife Management* **70**:1185-1190.
- Carter, T. C., M. A. Menzel, S. F. Owen, J. W. Edwards, J. M. Menzel, and W. M. Ford. 2003. Food habits of seven species of bats in the Allegheny Plateau and Ridge and Valley of West Virginia. *Northeastern Naturalist* **10**:83-88.
- Choate, J. R., J. K. Knox Jr., and C. Jones. 1994. Handbook of Mammals of the Southcentral States. Louisiana State University Press, Baton Rouge, LA.
- Cleveland, C., J., M. Betke, P. Federico, J. Frank, D., T. Hallman, G., J. Horn, J. Lopez Jr, D., G. McCracken, F, R. Medellin, A., A. Moreno-Valdez, Sansone, Chris, G., J. Westbrook, K, and T. H. Kunz. 2006. Economic value of the pest control service provided by Brazilian free-tailed bats in south-central Texas. *Frontiers in Ecology and the Environment* **4**:238-243.
- Constantine, D. G. 1958. An automatic bat collecting device. *Journal of Wildlife Management* **22**:17-22.
- Cooper, R. J. and R. C. Whitmore. 1990. Arthropod sampling in ornithology. *Studies in Avian Biology* **12**:29-37.

- Corben, C. 2002. Zero-crossings analysis for bat identification: an overview. Pages 95-107 in R. Brigham, Mark, E. K. V. Kalko, C. Jones, S. Parsons, and H. J. G. A. Limpens, editors. Bat Echolocation Research: tools, techniques and analysis. Bat Conservation International, Austin, Texas.
- Corben, C. 2005. AnalookW (Beta version 3.2h dated 25 August 2005). URL http://users.lmi.net/corben/WinAnalook.htm#AnaLookW_Content.
- Davis-Klopfer, M. 2008. AnaMichelle. Virginia Tech, Blacksburg, Virginia.
- Dorr, J., L. V. R. Emrick, P. Swint, and E. Pokorski. 2007. Army National Guard - Maneuver Training Center Fort Pickett vegetative communities map and vegetation classification system. CMI-MLD R-46 Conservation Management Institute - Military Lands Division, College of Natural Resources, Virginia Polytechnic Institute and State University, Blacksburg, Virginia.
- Duffy, A. M., L. F. Lumsden, C. R. Caddle, R. R. Chick, and G. R. Newell. 2000. The efficacy of Anabat ultrasonic detectors and harp traps for surveying microchiropterans in south-eastern Australia. *Acta Chiropterologica* **2**:127-144.
- Dwyer, P. D. 1966. The population pattern of *Miniopterus schreibersii* (Chiroptera) in north-eastern New South Wales. *Australian Journal of Zoology* **14**:1073-1137.
- Ellison, L. E., T. J. O'Shea, M. A. Bogan, A. L. Everette, and D. Schneider, M. 2003. Existing data on colonies of bats in the United States: Summary and analysis of the U.S. Geological Survey's bat population database. Pages 127-237 in T. J. O'Shea and M. A. Bogan, editors. Monitoring trends in bat populations of the United States and Territories: problems and prospects. U.S. Geological Survey,

- Biological Resources Discipline, Information and Technology Report,
USGS/BRD/ITR--2003-0003.
- Emrick, V. R. and R. L. Murray, editors. 2001. Integrated Natural Resource Management
Plan Fort Pickett Maneuver Training Center, Blackstone, Virginia. Conservation
Management Institute- Military Lands Division at Virginia Polytechnic Institute
and State University, Blacksburg, Virginia.
- Evans, D., E., W. Mitchel, A., and R. Fischer, A. 1998. Species Profile: Indiana bat
(*Myotis sodalis*) on military installations in the Southeastern United States.
Technical Report SERDP 98-3,. U. S. Army Engineer Waterways Experiment
Station, Vicksburg, MS.
- Feldhamer, G. A., B. C. Thompson, and C. J. A. 2003. Wild Mammals of North America:
biology, management, and conservation. The Johns Hopkins University Press,
Baltimore, Maryland.
- Fenton, M. B. 1982. Echolocation calls and patterns of hunting bats and habitat use of
bats (Microchiroptera) from Chillagoe, North Queensland. Australian Journal of
Zoology **30**:417-425.
- Fenton, M. B. 1997. Science and the conservation of of bats. Journal of Mammalogy
78:1-14.
- Fenton, M. B. and G. P. Bell. 1979. Echolocation and feeding behaviour in four species
of myotis (Chiroptera). Canadian Journal of Zoology **57**:1271-1277.
- Findley, J. S. 1993. Bats, a community perspective. Cambridge University Press,
Cambridge, UK.

- Findley, J. S. and H. Black. 1983. Morphological and dietary structuring of a Zambian insectivorous bat community. *Ecology* **64**:625-630.
- Ford, W. M., J. M. Menzel, M. Menzel, A., J. W. Edwards, and J. C. Kilgo. 2006. Presence and absence of bats across habitat scales in the upper coastal plain of South Carolina. *Journal of Wildlife Management* **70**:1200-1209.
- Ford, W. M., M. A. Menzel, J. L. Rodrigue, J. M. Menzel, and J. B. Johnson. 2005. Relating bat species presence to simple habitat measures in a central Appalachian forest. *Biological Conservation* **126**:528-539.
- Franklin, A., B., T. M. Shenk, D. R. Anderson, and K. P. Burnham. 2001. Statistical model selection: an alternative to null hypothesis testing. *in* T. M. Shenk and A. Franklin, B., editors. *Modeling in natural resource management: development interpretation and application*. Island Press, Washington, DC.
- Gehrt, S. D. and J. E. Chelsvig. 2004. Species-specific patterns of bat activity in an urban landscape. *Ecological Applications* **14**:625-635.
- Gerber, B., D. 2010. Comparing density analysis and carnivore ecology in Madagascar's southeastern rainforest. Virginia Polytechnic Institute and State University.
- Gorrensens, P. M., A. C. Miles, C. M. Todd, F. J. Bonoccorso, and T. J. Weller. 2008. Assessing bat detectability and occupancy with multiple automated echolocation detectors. *Journal of Mammology* **89**:11-17.
- Gotelli, N., J. 2000. Null model analysis of species co-occurrence patterns. *Ecology* **81**:2606-2621.
- Gressitt, J. L. and M. K. Gressitt. 1962. An improved malaise trap. *Pacific Insects* **4**:87-90.

- Griffin, D. R. 1958. Listening in the dark. Yale University Press, New Haven, Connecticut.
- Grindal, S. D., T. S. Collard, R. M. Brigham, and R. M. R. Barclay. 1992. The influence of precipitation on the design of echolocation-monitoring studies. *Journal of Mammalogy* **78**:514-524.
- Hall, L. S. 1981. The Biogeography of Australian Bats. 41 edition.
- Harvey, M. J. 1986. Arkansas Bats: A Valuable Resource. Arkansas Game and Fish Commission.
- Harvey, M. J., J. S. Altenbach, and T. L. Best. 1999. Bats of the United States. Arkansas Game and Fish Commission, Little Rock, Arkansas.
- Harvey, M. J. and R. K. Redman. 2001. Endangered bats of Arkansas: distribution, status, and ecology (2000 - 2001) W-56-R. Tennessee Technological University, Cookeville, TN.
- Hayes, J. P. 1997. Temporal variation in activity of bats and the design of echolocation-monitoring studies. *Journal of Mammalogy* **78**:514-524.
- Hayes, J. P., editor. 2000. Assumptions and practical considerations in the design and interpretation of echolocation-monitoring studies. *Acta Chiropterologica*.
- Hayes, J. P. and M. D. Adam. 1996. The influence of logging riparian areas on habitat use by bats in western Oregon. Pages 185-198 *in* R. M. R. Barclay and R. M. Brigham, editors. Bats and Forest symposium. Ministry of Forestry, Victoria, British Columbia.
- Hayes, J. P. and P. Hounihan. 1994. Field use of the Anabat II bat-detector system to monitor activity. *Bat Research News* **35**:1-3.

- Henry, M., P. Barriere, A. Gautier-Hion, and M. Colyn. 2004. Species composition, abundance and vertical stratification of a bat community (Megachiroptera : Pteropodidae) in a West African rain forest. *Journal of Tropical Ecology* **20**:21-29.
- Hickey, M., Brian, C., L. Acharya, and S. Pennington. 1996. Resource partitioning by two species of vespertilionid bats (*Lasiurus cinereus* and *Lasiurus borealis*) feeding around street lights. *Journal of Mammalogy* **77**:325-334.
- Hines, J., E. 2005. Program PRESENCE. USGS Patuxent Wildlife Research Center, Laurel, Maryland.
- Hurlbert, S., H. 1978. The measurement of niche overlap. *Ecology* **59**:67-77.
- Husar, S., L. 1976. Behavioural character displacement: Evidence of food partitioning in insectivorous bats. *Journal of Mammalogy* **57**:331-338.
- Hutson, A. M., S. P. Mickleburgh, and P. A. Racey. 2001. Microchiropteran bats: global status survey and conservation action plan. Gland, Switzerland and Cambridge: IUCN/SSC Chiroptera Specialist Group. IUCN:258.
- Hutto, R. L. 1990. Measuring the availability of food resources. *Studies in Avian Biology*:20-28.
- IUCN. 2007. International Union for the Conservation of Nature and Natural Resources: Redlist 2006. <http://www.iucnredlist.org/>.
- Johnson, J. B., M. A. Menzel, J. W. Edwards, and W. M. Ford. 2002. A comparison of 2 acoustical bat survey techniques. *Wildlife Society Bulletin* **30**:931-936.

- Jung, T. S., I. D. Thompson, R. D. Titman, and A. P. Applejohn. 1999. Habitat selection by forest bats in relation to mixed-wood stand types and structure in central Ontario. *Journal of Wildlife Management* **63**:1306-1319.
- Kalko, E. K. V. 1997. Diversity in tropical bats. Pages 13-43 *in* Proceedings from the International Symposium on Biodiversity and Systematics in Tropical Ecosystems. Zoologisches Forschungsinstitut und Museum Alexander Koenig, Bonn, 357 pp.
- Kalko, E. K. V., C. O. Hnadle Jr., and D. Hnadle, editors. 1996. Organization, diversity, and long-term dynamics of a Neotropical bat community. Academic Press, New York.
- Kuenzi, A. J. and M. L. Morrison. 1998. Detection of bats by mist-nets and ultrasonic Sensors. *Wildlife Society Bulletin* **26**:307-311.
- Kunz, T. H. 1973. Resource utilization: temporal and spatial components of bat activity in central Iowa. *Journal of Mammalogy* **54**:14-31.
- Kunz, T. H. and C. E. Brock. 1975. A COMPARISON OF MIST NETS AND ULTRASONIC DETECTORS FOR MONITORING FLIGHT ACTIVITY OF BATS. *Journal of Mammalogy* **56**:907-911.
- Kunz, T. H. and M. B. Fenton. 2003. Preface. Pages xiii-xix *in* T. H. Kunz and M. B. Fenton, editors. *Bat Ecology*. University of Chicago Press, Chicago.
- Kunz, T. H. and A. Kurta. 1988. Capture Methods and Holding Devices. Pages 1-29 *in* T. H. Kunz, editor. *Ecological and Behavioral methods for the study of bats*. Smithsonian Institution Press, Washington, DC.

- Kunz, T. H. and L. F. Lumsden. 2003. Ecology of cavity and foliage roosting bats. Pages 3-89 in T. H. Kunz and M. B. Fenton, editors. *Bat Ecology*. University of Chicago Press, Chicago.
- Kurta, A., J. Kath, E. L. Smith, R. Foster, M. W. Orick, and R. Ross. 1993a. A maternity roost of the endangered Indiana bat (*Myotis sodalis*) in an unshaded hollow sycamore tree (*Plantanus occidentalis*). *American Midland Naturalist* **130**:405-407.
- Kurta, A., D. King, J. A. Teramino, J. M. Stribley, and K. F. Williams. 1993b. Summer roosts of the endangered Indiana bat (*Myotis sodalis*) on the northern edge of its range. *American Midland Naturalist* **129**:132-138.
- Larson, D. J. and J. P. Hayes. 2000. Variability in sensitivity of AnaBat II bat detectors and a method of calibration. *Acta Chiropterologica* **2**:209-213.
- LaVal, R. K. and M. L. LaVal. 1977. Reproduction and behavior of the African banana bat (*Pipistrellus nanus*). *Journal of Mammalogy* **58**:403-410.
- Law, B., J. Anderson, and M. Chidel. 1998. A bat survey in state forests on the south-west slopes region of New South Wales with suggestions of improvements for future surveys. *Australian Zoologist* **30**:467-479.
- Livengood, K., R. Drobney, and C. Corben. 2002. The evaluation of call parameters for three Missouri *Myotis* species. Report to Missouri Department of Conservation - Research Unit, Columbia, Missouri.
- Loeb, S., C. and J. O'Keefe, M. 2006. Habitat use by forest bats in South Carolina in relation to local, stand, and landscape characteristics. *Journal of Wildlife Management* **70**:1210-1218.

- Luiselli, L. 2006. Site occupancy and density of sympatric Gaboon viper (*Bitis gabonica*) and nose-horned viper (*Bitis nasicornis*). *Journal of Tropical Ecology* **22**:555-564.
- Lumsden, L. F. and A. F. Bennett. 1995. Bats of a semi-arid environment in south-eastern Australia: biogeography, ecology and conservation. *Wildlife Research* **22**:217-240.
- MacKenzie, D., I. 2005. What are the issues with presence - absence data for wildlife managers? *Journal of Wildlife Management* **69**:849-860.
- MacKenzie, D., I., L. Bailey, L., and J. Nichols, D. 2004. Investigating species co-occurrence patterns when species are detected imperfectly. *Journal of Animal Ecology* **73**.
- MacKenzie, D., I., J. Nichols, D., J. Hines, E., M. Knutson, G., and A. Franklin, B. 2003. Estimating site occupancy, colonization, and local extinction when a species is detected imperfectly. *Ecology* **84**:2200-2207.
- MacKenzie, D., I., J. Nichols, D., G. Lachman, B., S. Droege, J. A. Royle, and C. Langtimm, A. 2002. Estimating site occupancy rates when detection probabilities are less than one. *Ecology* **83**:2248-2255.
- MacKenzie, D., I., J. Nichols, D., J. A. Royle, K. Pollock, H., L. Bailey, L., and J. Hines, E. 2006. *Occupancy Estimation and Modeling, Inferring Patterns and Dynamics of Species Occurrence*. Elsevier Academic Press, New York.
- MacKenzie, D., I. and J. A. Royle. 2005. Designing occupancy studies: general advice and allocating survey effort. *Journal of Applied Ecology* **42**.
- Marcot, B. G. 1996. An ecosystem context for bat management : a case study of the interior Columbia River Basin. *in* R. M. R. Barclay and R. M. Bringham, editors.

- Bats and forest symposium. British Colombian Ministry of Forestry, Victoria, Canada.
- Menzel, J. M., W. M. Ford, M. A. Menzel, T. C. Carter, J. E. Gardner, J. D. Garner, and J. E. Hofmann. 2005a. Summer habitat use and home-range analysis of the endangered Indiana bat. *Journal of Wildlife Management* **69**:430-436.
- Menzel, J. M., M. A. Menzel, J. C. Kilgo, W. M. Ford, J. W. Edwards, and G. F. McCracken. 2005b. Effect of habitat and foraging height on bat activity in the Coastal Plain of South Carolina. *Journal of Wildlife Management* **69**:235-245.
- Miller, B. W. 2001. A method for determining relative activity of free flying bats using a new activity index for acoustic monitoring. *Acta Chiropterologica* **3**:93-105.
- Miller, B. W. 2002. Acoustic surveys and Non-phylostomid neotropical bats: How effective are they? Pages 58-63 *in* R. Brigham, Mark, E. K. V. Kalko, C. Jones, S. Parsons, and H. J. G. A. Limpens, editors. *Bat Echolocation Research: tools, techniques, and analysis*. Bat Conservation International, Austin Texas.
- Miller, D., A., E. Arnett, B., and M. J. Lacki. 2003. Habitat management for forest-roosting bats of North America: a critical review of habitat studies. *Wildlife Society Bulletin* **31**:30-44.
- Mills, D. J., T. W. Norton, H. E. Parnaby, R. B. Cunningham, and H. A. Nix. 1996. Designing surveys for microchiropteran bats in complex forested landscapes - a pilot study from south-eastern Australia. *Forest Ecology and Management* **85**:149-161.

- Ministry of Environment. 1998. Inventory Methods for Bats No. 20. Standards for Components of British Columbia's Biodiversity. Ministry of Environment, Victoria, British Columbia.
- Morena, C., E. and G. Halfetter. 2000. Assessing the completeness of bat biodiversity inventories using species accumulation curves. *Journal of Applied Ecology* **37**:149-151.
- Murray, K. L., E. R. Britzke, B. M. Hadley, and L. W. Robbins. 1999a. A comparison of acoustic sampling and mist netting in assessing bat species presence. *Bat Research News* **40**:96.
- Murray, K. L., E. R. Britzke, B. M. Hadley, and L. W. Robbins. 1999b. Surveying bat communities: a comparison between mist nets and the Anabat II bat detector system. *Acta Chiropterologica* **1**:105-112.
- Nagorsen, D. W. and R. M. Brigham. 1993. Royal British Columbia Museum Handbook: Bats of British Columbia.
- Nichols, J., D. and K. U. Karanth. 2002. Statistical concepts: assessing spatial distributions. Pages 29-38 *in* K. U. Karanth and J. Nichols, D., editors. *Monitoring Tigers and Their Prey: A Manual for Wildlife Managers, Researchers, and Conservationists*. Center for Wildlife Studies, Bangalore, India.
- Nowak, R., M. 1994. *Walker's Bats of the World*. Johns Hopkins University Press, Baltimore, Maryland.
- O'Farrell, M. J. 1997. Use of echolocation calls for the identification of free-flying bats. *Transactions of the western section of the wildlife society* **33**:1-8.

- O'Farrell, M. J. 1998. A Passive monitoring system for Anabat II using a laptop computer. *Bat Research News* **39**:147-150.
- O'Farrell, M. J., C. Corben, W. L. Gannon, and B. W. Miller. 1999a. Confronting the Dogma: A Reply. *Journal of Mammalogy* **80**:297-302.
- O'Farrell, M. J., C. J. Corben, and W. L. Gannon. 2000. Geographic variation in the echolocation calls of the Hoary Bat (*Lasiurus cinereus*). *Acta Chiropterologica* **2**:185-195.
- O'Farrell, M. J. and W. L. Gannon. 1999. A comparison of acoustic versus capture techniques for the inventory of bats. *Journal of Mammalogy* **80**:24-30.
- O'Farrell, M. J. and B. W. Miller. 1997. A new examination of echolocation calls of some Neotropical bats (Emballonuridae and Mormoopidae). *Journal of Mammalogy* **78**:954-963.
- O'Farrell, M. J. and B. W. Miller. 1999. Use of vocal signatures for the inventory of free-flying neotropical bats. *Biotropica* **31**:507-516.
- O'Farrell, M. J., B. W. Miller, and W. L. Gannon. 1999b. Qualitative identification of free-flying bats using the Anabat detector. *Journal of Mammalogy* **80**:11-23.
- O'Shea, T. J. and M. A. Bogan. 2003. Monitoring trends in bat populations of the United States and Territories: problems and prospects. Page 274 *in* T. J. O'Shea and M. A. Bogan, editors. U.S. Geological Survey, Biological Resources Discipline, Information and Technology Report, USGS/BRD/ITR--2003-0003.
- O'Shea, T. J., M. A. Bogan, and L. E. Ellison. 2003. Monitoring trends in bat populations of the United States and territories: status of the science and recommendations for the future. *Wildlife Society Bulletin* **31**:16-29.

- Ochoa, G. J., M. J. O'Farrell, and B. W. Miller. 2000. Contribution to acoustic methods to the study of insectivorous bat diversity in protected areas from northern Venezuela. Pages 171-183 *in* W. L. Gannon and W. Bogdanowicz, editors. Contributions to the study of Bats: field use of acoustic detectors. Acta Chiropterologica.
- Padgett, T., M. and R. Rose, k. 1991. Bats (Chiroptera: Vespertilionidae) of the Great Dismal Swamp of Virginia and North Carolina. *Brimleyana* **17**:17-25.
- Patriquin, K., L. Hogberg, B. Chruszcz, and R. Barclay. 2000. The influence of habitat type on the ability to detect bats with anabat II detectors. *Bat Research News* **41**:133.
- Patterson, B., D., M. Willig, R., and R. Stevens, D. 2003. Trophic strategies, niche partitioning, and patterns of ecological organization. Pages 536-579 *in* T. H. Kunz and M. B. Fenton, editors. *Bat Ecology*. University of Chicago Press, Chicago.
- Persson, L. 1985. Asymmetrical competition: Are larger animal competitively superior? *American Naturalist* **126**:261-266.
- Pettersson, L. 2002. The properties of sound and bat detectors. Pages 9-12 *in* R. Brigham, Mark, E. K. V. Kalko, C. Jones, S. Parsons, and H. J. G. A. Limpens, editors. *Bat Echolocation Research: tools, techniques, and analysis*. Bat Conservation International, Austin, Texas.
- Phillips, W. R. and S. J. Inwards. 1985. The annual activity and breeding cycles of Gould's Long-eared Bat. *Australian Journal of Zoology* **33**:111-126.
- Pianka, E., R. 1980. Guild structure in desert lizards. *Oikos* **35**:194-201.

- Pierson, E. D. 1998. Tall trees, deep holes, and scarred landscapes: conservation biology of North American bats. Pages 309-325 *in* T. H. Kunz and P. A. Racey, editors. Bat Biology and Conservation. Smithsonian Institution Press, Washington DC.
- Pimm, S. L., M. Rosenzweig, L., and W. A. Mitchell. 1985. Competition and food selection: field-tests of a theory. *Ecology* **66**:798-807.
- Prevett, P. 2002. Anabat-computer survey for microbats: sampling considerations, call identification and analysis. *Bat Research News* **43**:21.
- R-Development-Core-Team. 2008. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- Racey, P. A. 1988. Reproductive assessment in bats. Pages 31-43 *in* T. H. Kunz, editor. Ecological and Behavioural Methods for the Study of Bats. Smithsonian Institution Press, 533pp., Washington DC.
- Rautenbach, I. L., M. B. Fenton, and M. J. Whiting. 1996. Bats in riverine forest and woodlands; a latitudinal transect in southern Africa. *Canadian Journal of Zoology* **74**:312-322.
- Richmond, O., M., J. Hines, E., and S. Beissinger, R. 2010. Two-species occupancy models: an new parameterization applied to co-occurrence of secretive rails. *Ecological Applications* **20**:2036-2046.
- Ridout, M., S. and M. Linkie. 2009. Estimating overlap of daily activity patterns from camera trap data. *Journal of Agricultural, Biological, and Environmental Statistics* **14**:322-337.

- Roble, S. M. 2003. Natural Heritage Resources of Virginia: Rare Animal Species. Natural Heritage Technical Report 03-04, Virginia Department of Conservation and Recreation, Division of Natural Heritage, Richmond, Virginia.
- Root, R., B. 1967. Niche exploitation pattern of the blue-gray gnatcatcher. *Ecological Monographs* **37**:317-350.
- Rosenzweig, M., L. 1995. Species diversity in space and time. Cambridge University Press, Cambridge, UK.
- Schmid, F. and A. Schmidt. 2006. Nonparametric estimation of the coefficient of overlapping - theory and empirical application. *Computational Statistics and Data Analysis* **50**:1583-1596.
- Schoener, T., W. 1974. Resource partitioning in ecological communities. *Science* **185**:27-39.
- Schoener, T., W. 1982. The controversy over interspecific competition. *American Scientist* **70**:586-595.
- Schwartz, C. W. and E. R. Schwartz. 1981. Flying Mammals, Order *Chiroptera*. The Wild Mammals of Missouri. University of Missouri Press and Missouri Department of Conservation, Columbia, MO.
- Sealander, J. A. and G. A. Heidt. 1990. Arkansas Mammals: Their natural history, classification, and distribution. University of Arkansas Press.
- Siemers, B., M. 2002. Bats in the field and in a flight cage: recording and analysis of thier echolocation calls and behavior. Pages 107-120 *in* R. Brigham, Mark, E. K. V. Kalko, C. Jones, S. Parsons, and H. J. G. A. Limpens, editors. Bat Echolocation

- Research: tools, techniques, and analysis. Bat Conservation International, Austin, Texas.
- Simmons, N., B. and T. Conway, M. 2003. Evolution of ecological diversity in bats. Pages 493-535 *in* T. H. Kunz and M. B. Fenton, editors. Bat Ecology. University of Chicago Press, Chicago.
- Smith, W. J. 1977. The behavior of communicating. Harvard University Press, Cambridge, Massachusetts.
- St Germain, M. J. and R. M. Murray-Schneider. 2012. Grassland bird diversity and density on ARNG-MTC Ft. Pickett, Blackstone, Virginia. Conservation Management Institute, College of Natural Resources and Environment, Virginia Polytechnic Institute and State University, Blacksburg, Virginia. **Technical Report**:1-24.
- St. Germain, M., J. 2005. Pilot Planning Level Survey of Bat Species at ARNG-MTC Fort Pickett, Blackstone, Virginia. CMI-MLD R-30a, Conservation Management Institute - Military Lands Division, College of Natural Resources, Virginia Polytechnic Institute and State University., Blacksburg, Virginia.
- St. Germain, M., J. 2008a. Bats of Fort Pickett, Blackstone, Virginia. Conservation Management Institute-Virginia Tech College of Natural Resources and Environment. CMI-MLD R-67. 21p.
- St. Germain, M., J. and B. W. Miller. 2005. Bat survey for Fort Chaffee MTC, Fort Smith, Arkansas. CMI-MLD R-38, Conservation Management Institute - Military Lands Division, College of Natural Resources, Virginia Polytechnic Institute and State University., Blacksburg, Virginia.

- St. Germain, M., J. and B. W. Miller. 2007. Bat species assemblage at Army National Guard Maneuver Training Center Fort Pickett, Blackstone, Virginia. CMI-MLD R-59 20070718
- St. Germain, M. J. 2008b. Bat Species Assemblage on ARNG-MTC fort Pickett, Blackstone, Virginia. Technical Report CMI-MLD R 39.
- Sunarto. 2011. Ecology and restoration of Sumartan tigers in forest and plantation landscapes. Virginia Polytechnic Institute and State University.
- Swift, S. M. 1980. Activity patterns of pipistrelle bats (*Pipistrellus pipistrellus*) in northeast Scotland. *Journal of Zoology of London* **190**:285-295.
- Swift, S. M. and P. A. Racey. 1983. Resource partitioning in two species of vespertilionid bats (chiroptera) occupying the same roost. *Journal of Zoology of London* **200**:249-259.
- Szewczak, J., M. 2002. Advanced analysis techniques for identifying bat species. Pages 121-127 *in* R. Brigham, Mark, E. K. V. Kalko, C. Jones, S. Parsons, and H. J. G. A. Limpens, editors. *Bat Echolocation Research: tools, techniques, and analysis*. Bat Conservation International, Austin, Texas.
- Thomas, D. W. 1988. The distribution of bats in different ages of Douglas-fir forests. *Journal of Wildlife Management* **52**:619-628.
- Thomas, D. W. and R. K. LaVal. 1988. Survey and Census Methods. Pages 77-89 *in* T. H. Kunz, editor. *Ecological and Behavioral Methods for the Study of Bats*. Smithsonian Institution Press, 533 pp, Washington DC.

- Thomas, D. W. and S. West, D. 1989. Wildlife-habitat relationships: sampling procedures for Pacific Northwest vertebrates. PNW-GTR-243, USDA Forest Service, Portland, OR.
- Thompson, M. J. A. 1987. Longevity and Survival of female pipistrelle bats (*Pipistrellus pipistrellus*) on the Vale of York, England. Journal of Zoology of London **211**:209-214.
- Townes, H. 1962. Design for a malaise trap. Proceeding of the Entomological Society Washington **64**:253-262.
- Townes, H. 1972. A light-weight malaise trap. Entomological News **83**:239-247.
- Tuttle, M. D. 1974. An improved trap for bats. Journal of Mammalogy **55**:475-477.
- VAFWIS. 2005. Virginia Fish and Wildlife Information Service. Virginia Department of Game and Inland Fisheries, Richmond, VA
<http://vafwis.org/WIS/ASP/home.asp?sID=64394&ln=I>.
- Vaughn, T. A. 1959. Functional morphology of three bats: Eumops, Myotis, Macrotus. University of Kansas Publishing, Museum of Natural History, 12:1-153.
- Vaughn, T. A. 1986. Mammals. Saunders College Publishing, Orlando, FL.
- Vojta, C., D. 2005. Old dog, new tricks: innovations with presence - absence information. Journal of Wildlife Management **69**:845-848.
- Weller, T. J. and C. J. Zabel. 2002. Variation in bat detections due to detector orientation in a forest. Wildlife Society Bulletin **30**:922-930.
- Whitaker, J. O. J. and W. J. J. Hamilton. 1998. Order Chiroptera. Mammals of the Eastern United States. Comstock Publishing Associates of Cornell University Press, Ithaca, NY.

- Williams, J., A., M. J. O'Farrell, and B. Riddle, R. 2006. Habitat use by bats in a riparian corridor of the mojave desert in southern Nevada. *Journal of Mammalogy* **87**:1145-1153.
- Wilson, D. E. and D. M. Reeder. 1993. *Mammal Species of the World*. Smithsonian Institute Press, Washington DC.
- Wilson, D. E. and D. M. Reeder, editors. 2003. *Mammal species of the world: a taxonomic and geographic reference*. 2nd edition. Smithsonian Institute Press, Washington, D.C.
- Wolda, H. 1990. Food availability for an insectivore and how to measure it. *Studies in Avian Biology* **13**:38-43.
- Yates, M. D. and R. M. Muzika. 2006. Effect of forest structure and fragmentation on site occupancy of bat species in Missouri Ozark forests. *Journal of Wildlife Management* **70**:1238-1248.
- Youngston, W. K. and N. L. McKenzie. 1977. An improved bat collecting technique. *Bulletin of the Australian Mammalian Society* **3**:20-21.

Table 1.1. Species with special concerns potentially found on ARNG-MTC Fort Pickett (Roble 2003, VAFWIS 2005)

Scientific Name	Common Name	Federal Status ⁽¹⁾	State Status ⁽²⁾	Global Rank ⁽³⁾	State Rank ⁽⁴⁾
<i>Myotis leibii</i>	Eastern small-footed bat	-	-	G3	S1
<i>Myotis sodalis</i>	Indiana bat	LE	LE	G2	S1
<i>Corynorhinus rafinesquii</i>	Rafinesque's big-eared bat	-	LE	G3G4	S2
<i>macrotis</i>					
<i>Corynorhinus townsendii</i>	Virginia big-eared bat	LE	LE	G4T2	S1
<i>virginianus</i>					

1. Federal status abbreviation codes:

LE – Listed federally as an endangered species

2. State status abbreviation codes (Virginia Department of Game and Inland Fisheries):

LE – Listed as state endangered

3. Global Rank: The Division of Natural Heritage estimate of abundance on a global scale. Ranking codes are:

G1- Critically imperiled globally because of extreme rarity – especially vulnerable to extinction

G2- Imperiled globally because of rarity - vulnerable to extinction

G3- very rare – susceptible to becoming extinct

G4- common- apparently secure globally- may be rare within range and periphery

G5- very common- demonstrably secure globally-- may be rare within range and periphery

T#- sub specific taxon rank

4. State Rank

S1- Extremely rare - vulnerable to extirpation

S2- Very rare - susceptible to becoming extirpated

Table 1.2. Bat species examined on Army National Guard Maneuver Training Center (ARNG-MTC) Fort Pickett, Virginia, and associated method of detection during the 2006-2007 survey.

Common Name	Scientific Name	Status	roost	capture	acoustic
Eastern big-eared bat	<i>Corynorhinus rafinesquii</i>	FS SE	.	.	possible
Virginia big-eared bat	<i>Corynorhinus townsendii</i>	FE SE	.	.	unknown
* Big brown bat	<i>Eptesicus fuscus</i>		X	X	X
Silver-haired bat	<i>Lasionycteris noctivagans</i>		.	.	X
* Eastern red bat	<i>Lasiurus borealis</i>		.	X	X
Hoary bat	<i>Lasiurus cinereus</i>		.	.	X
Seminole bat	<i>Lasiurus seminolus</i>		.	.	unknown
Small-footed myotis	<i>Myotis leibii</i>	FS	.	.	unknown
* Little brown bat	<i>Myotis lucifugus</i>		X	X	X
Northern long-eared					
* myotis	<i>Myotis septentrionalis</i>		.	.	X
Indiana bat	<i>Myotis sodalis</i>	FE	.	.	
* Evening bat	<i>Nycticeius humeralis</i>		.	.	X
* Eastern pipistrelle	<i>Perimyotis subflavus</i>		.	X	X
* Species included in detailed analysis					
FE Federally Endangered					
FS Federally Sensitive					
SE State Endangered					

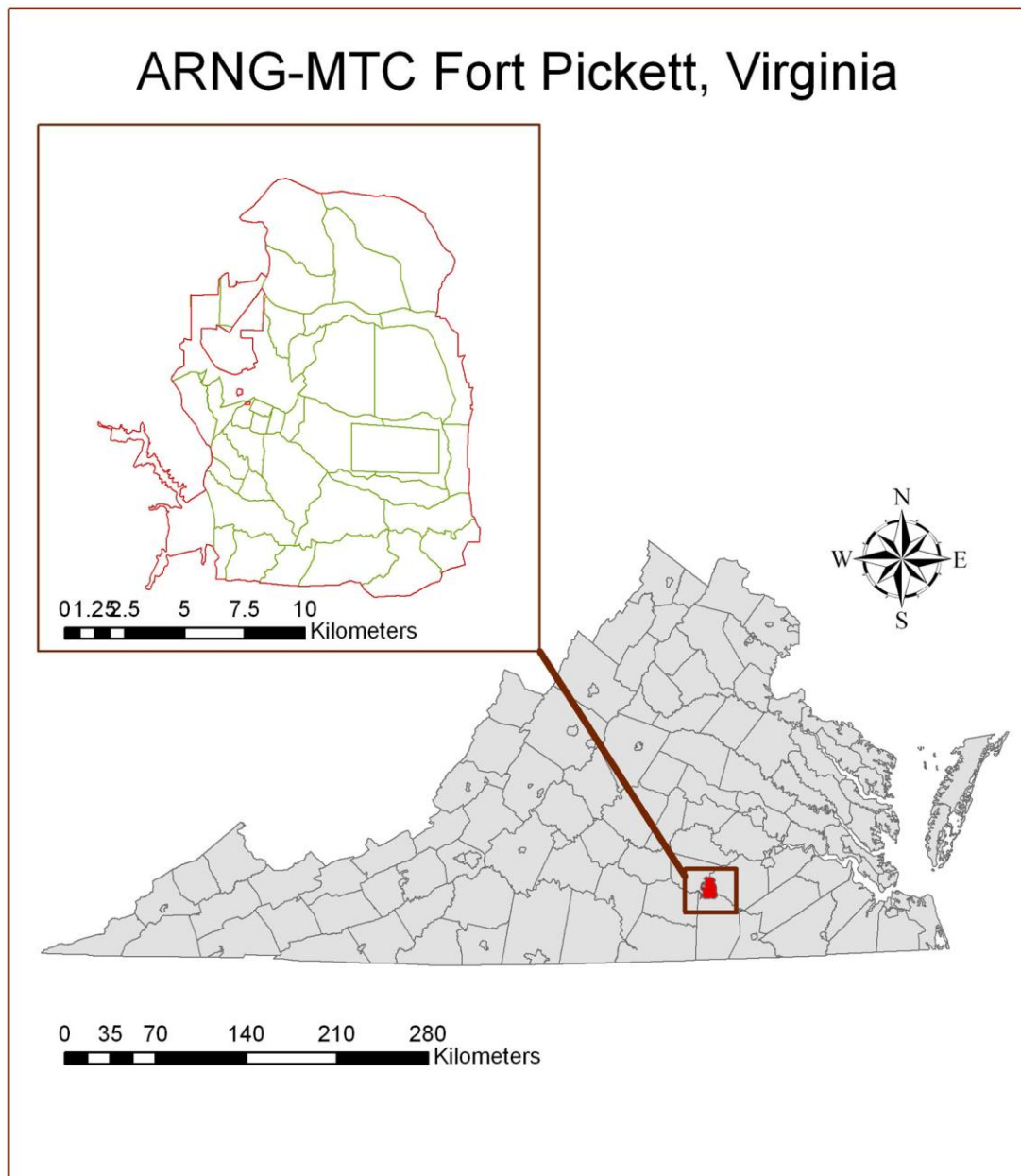


Figure 1.1. Location of Army National Guard Maneuver Training Center (ARNG-MTC) Fort Pickett within Virginia (St. Germain 2012).

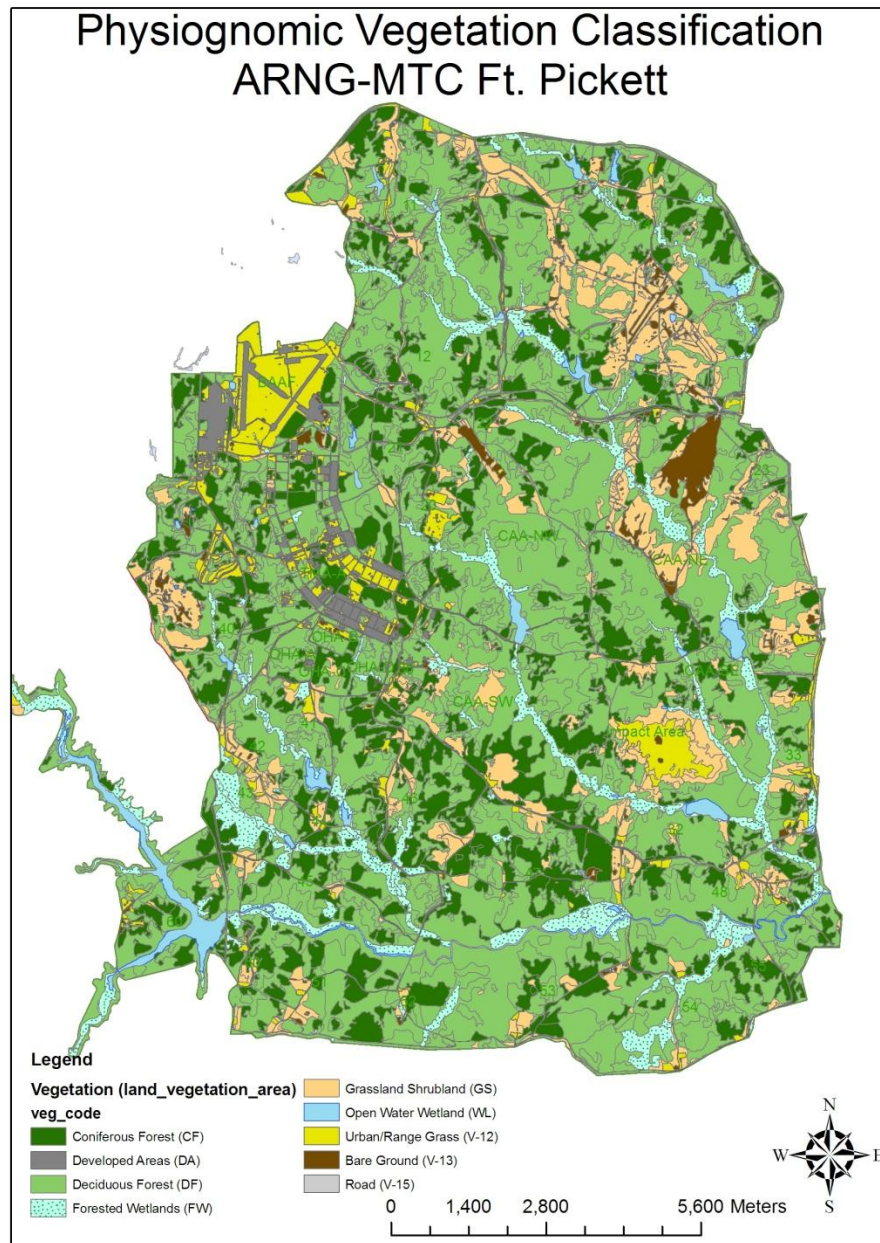


Figure 1.2. Major physiognomic habitat classifications on Army National Guard Maneuver Training Center (ARNG-MTC) Fort Pickett, Virginia (St. Germain 2012).

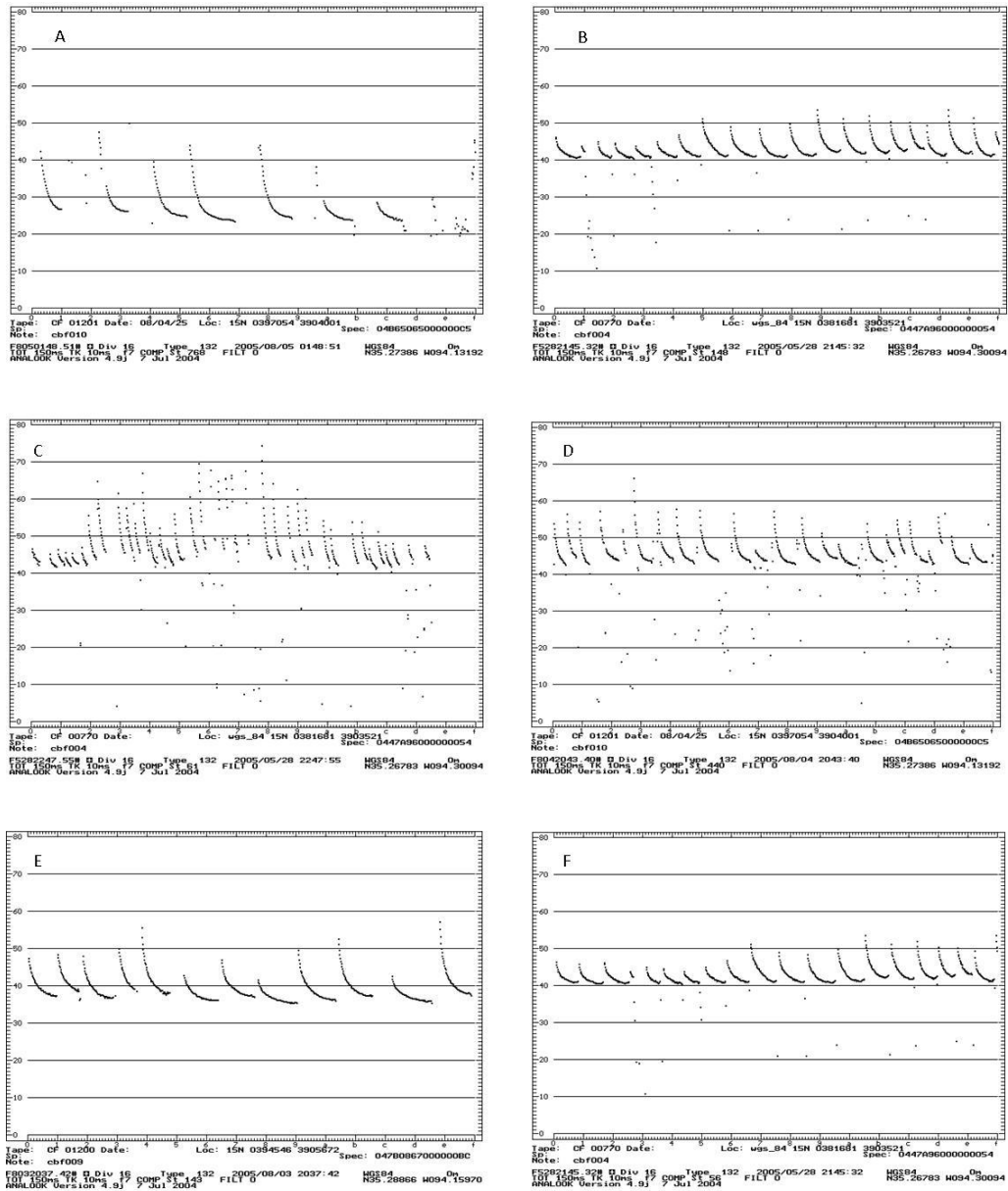


Figure 1.3. Sonograms for each of the six species included for analysis: A: *Eptesicus fuscus* (big brown bat), B: *Lasius borealis* (eastern red bat), C: *Myotis lucifugus* (little brown myotis), D: *Myotis septentrionalis* (northern myotis), E: *Nycticeius humeralis* (evening bat), and F: *Perimyotis subflavus* (eastern pipistrelle).

Chapter 2

Detection Probabilities, Occupancy, and Factors Influencing Bat Species Occurrence on Ft. Pickett Army National Guard Maneuver Training Center, Blackstone, Virginia.

“We cannot stop here, this is bat country!” – Hunter S. Thompson

ABSTRACT

Effective bat conservation and management requires knowledge of habitat use and potential limiting factors for populations at various geographic scales. Our understanding of how most bat species utilize habitat space is little studied and poorly synthesized, making bat conservation difficult. In this study I examine how distributional patterns of bats may be influenced by habitat factors from the micro site to the landscape level. These factors not only include habitat type, and temporal and climatic variables, but also examinations of prey availability, flyway types, and bat activity levels. I quantified the detection probabilities and proportion of area occupied stratified by habitats of six species belonging to the bat community in a mixed grassland forested environment in central Virginia. These species include: *Eptesicus fuscus* (Big brown bat), *Lasiurus borealis* (Eastern red bat), *Myotis lucifugus* (Little brown myotis), *Myotis septentrionalis* (Northern long-eared myotis), *Nycticeius humeralis* (Evening bat), and *Perimyotis subflavus* (Eastern pipistrelle). I used a patch occupancy modeling approach implemented in program PRESENCE from acoustically derived bat activity data collected using an array of AnaBat II acoustical detectors. I found that a combination of reduced vegetation density, lower insect biomass, and high levels of bat activity increased the detection probability of each species. Moon phase or temperature did not have strong effects on

detection. Increased insect biomass and reduced vegetation in combination positively affected site occupancy for all species. I also provide species specific descriptions of detection and occupancy stratified by habitat type increasing our knowledge of bat species ecology within and across habitat types. Predictive maps of species distributions can assist with making landscape level decisions for installation stewardship and management. My acoustical sampling array provided an efficient means to sample the entire bat community simultaneously providing a relatively new means to obtain substantial information on bat species and community ecology.

Key words: acoustical detector, AnaBat, Big brown bat, detection probability, Eastern pipistrelle, Eastern red bat, Evening bat, *Eptesicus fuscus*, insect biomass, *Lasiurus borealis*, military lands, *Myotis lucifugus*, *Myotis septentrionalis*, Northern long-eared myotis, *Nycticeius humeralis*, occupancy, *Perimyotis subflavus*, proportion of area occupied

INTRODUCTION

Gaps in our understanding of bat habitat use are widely acknowledged (Arnett 2003, Miller et al. 2003). Bat conservation and management requires knowledge of habitat use at various geographic and temporal scales, and how potential limiting factors may vary across these scales (Ford et al. 2005). Additionally, our understanding of how most bat species utilize habitat space and other resources is poorly synthesized, hence making bat conservation difficult (Brooks and Ford 2006).

In fragmented landscapes, distributional patterns of bats are influenced by a complex interaction of habitat factors. These factors range in scale from microsite, (i.e. individual tree), to stand-level, to the landscape level. The autecology of an individual species, prey availability, temporal factors, and climate will also have an effect on bat activity. Common to all points on the landscape and across all habitat scales, presence of bats at a single location at any moment can depend on time, temperature, humidity, precipitation, barometric pressure, wind speed, ambient light intensity, and the availability of insects (Barclay 1985, Hayes 1997, Broders et al. 2003, Ford et al. 2006). At smaller habitat scales, activity can be related to proximity of riparian habitat of water source, structural characteristics of the habitat, echolocation characteristics, wing morphology of the bat species, and prey preference (Aldridge and Rautenbach 1987, Jung et al. 1999, Menzel et al. 2005b, Carter 2006).

A number of recent studies have emerged to address some of these processes across spatial and temporal scales and have shown strong linkages between bat activity and both microhabitat and landscape variables (Gehrt and Chelsvig 2004, Ford et al. 2005, Ford et al. 2006, Loeb and O'Keefe 2006, Yates and Muzika 2006). With increased human pressures on ecosystems for a variety of resources, a critical component of landscape management planning should include an understanding of how proposed changes in land use patterns will affect bat species assemblages and distributions. This is especially true now because many bat species are suffering widespread population declines due to white-nose syndrome (Blehert et al. 2009) and any increase in our understanding of bat ecology is desperately needed.

The scope of this study concentrated on 6 of 8 target species whose detection rates had sample sizes adequate for modeling. These species include: *Eptesicus fuscus* EPTFUS (Big brown bat), *Lasiurus borealis* LASBOR (Eastern red bat), *Myotis lucifugus* MYOLUC (Little brown myotis), *Myotis septentrionalis* MYOSEP (Northern long-eared myotis), *Nycticeius humeralis* NYCHUM (Evening bat), and *Perimyotis subflavus* PERSUB (Eastern pipistrelle). For two species, *Lasiurus cinereus* (Hoary bat), and *Corynorhinus sp. (townsendii virginianus or rafenesquii)* (Virginia/ Rafenesque's big-eared bat) there were too few detections and therefore species modeling was not conducted.

Presence/absence data are useful to managers for monitoring populations and identifying important habitats or areas that are of high value to an entire suite of species.

This information, however, has historically been difficult to interpret because animal detectability is not constant in space or time and previous studies assumed equal and complete detectability ($p = 1$) leading potentially to extremely negatively biased estimation of a species presence, especially if detection probabilities ($p < 1$) are not taken into consideration (Vojta 2005). A key issue that a species may be declared “absent” may simply be a result of not detecting the species during the survey period resulting in a “false absence”(MacKenzie 2005). The effect is that the data may reflect the observer’s ability to find the species on the landscape and not where the species actually is on the landscape (MacKenzie 2005). Not all species have equal detectability. Some of these biases can be reduced with a greater concentration of effort with multiple surveys being conducted at a location in shorter time frames. However, increasing the number of sites surveyed at the expense of decreasing the number of repeats surveys may not result in a better design in terms of precision of occupancy estimates (MacKenzie and Royle 2005). Without a sufficient number of repeat surveys the probability of a “false absence” ($= (1 - P)^K$) at a site may be large (MacKenzie et al. 2006). But with a strategy of many repeated site visits, the probability of a false absence decreases exponentially with each survey.

Recent models that incorporate detection probabilities that are less than 1.0 have been developed and have been used to predict occupancy across a landscape. Such models require a determination of detection probabilities by making thorough repeated visits to a site where a species may be detected (MacKenzie et al. 2002). This patch occupancy estimation approach treats each site as the sampling unit, and the detection – nondetection history becomes the equivalent of capture – recapture data in the model

(Nichols and Karanth 2002). These patterns of detection – nondetection permit estimation of detection probabilities and the ultimate parameter of interest, the proportion of the area occupied (PAO) (MacKenzie et al. 2002). Estimating the proportion of sites occupied by a target species is important in both long-term monitoring programs and metapopulation studies (MacKenzie et al. 2003). In a monitoring context, site occupancy probabilities may be used as a metric reflecting the current state of a population. Additionally, the models created can be used to build predictive maps of species occupancy across a landscape, even if the entire landscape was not surveyed.

These occupancy techniques fully recognize that individual identification of animals is not possible. The models have been developed to gain pertinent information on detectability and occupancy by including habitat and/or other variables as co-variates in the detection non-detection histories. Taking this research direction has the potential to advance our understanding of bat ecology, especially in regard to habitat use patterns across a landscape. To date, habitat use analysis has not been conducted in an occupancy modeling framework as done in this study.

Besides single species analysis, species interactions for North American vespertilionids have not been examined using acoustical data, yet the occupancy approach can incorporate such an analysis using the co-occurrence models. This information could yield significant information regarding species behavior relative to presence of other species in the bat guild. I further explore these guild relationships in co-occurrence models in Chapter 3 and limit Chapter 2 primarily to single species analysis

with the exception of including co-bat activity indices as predictors of each single species detection and occupancy.

Study Site

Army National Guard Maneuver Training Center (ARNG-MTC) Fort Pickett is located in the Nottoway drainage of lower Piedmont in southeastern Virginia (Fig 1.1). The army base is adjacent to the community of Blackstone, Virginia, within the counties of Brunswick, Dinwiddie, and Nottoway. Fort Pickett is approximately 36 km (22 mi) from the fall line where the Piedmont physiographic region turns into the Coastal Plain physiographic region. It consists of 41,690 acres (16,870 ha) of both open and forested live-fire and maneuver training lands.

METHODS

A Priori Hypothesis

Habitat use by bats often varies among species depending on their body size, wing morphology, foraging mode, and echolocation call structure (Aldridge and Rautenbach 1987, Patterson et al. 2003). I used this natural history information to construct *a priori* hypothesis (Table 2.1) concerning factors influencing species detection and occurrence.

Acoustic Bat Detection

For ultrasonic acoustic detection, I used a remotely mounted microphone connected to the Anabat II detector and Compact Flash-Zero Crossing Analysis Interface Module (CF-ZCAIM) (Titley Electronics, Ballina, New South Wales, Australia). These

units were programmed to turn on 30 min prior to civil twilight and turn off 30 min after civil sunrise. The sampling locations were chosen using a stratified random design in proportion to availability, however the microphone was placed within 30 m of the locations with the objective of capturing as many calls as possible to increase detectability (e.g. Hayes and Hounihan 1994). The microphone placement was ~1.4 meters off the ground, and oriented in the direction of fewest trees (Weller and Zabel 2002) at a ~45° angle (Duffy et al. 2000). The Anabat units were calibrated each season for sensitivity and set at the respective sensitivity level of ~6. All acoustic emissions were recorded to the internal compact flash card with a date and time stamp on each file. All recorded calls were transferred from the CF cards to desktop computer for identification and analysis. The Scan utility function of the AnaLookW (Beta version 3.2h dated 25 August 2005) software (Corben 2005) and constructed filters were used for species identification.

Acoustic sampling for these analyses occurred from 08 June to 25 August 2007. I sampled each of the six major habitat types on Fort Pickett. Sampling locations were selected randomly for each habitat type for a total of 87 sites (Figure 2.1 and 2.2). These types include: coniferous forest (CF) (n=15), developed areas (DA) (n=7), deciduous forests (DF) (n=16), forested wetlands (FW) (n=14), grassland /shrublands (GS) (n=21), and wetlands with surface water present (WL) (n=14) (see Appendix 1.1 for more complete description). These categories were for *post hoc* model construction and occupancy prediction across the landscape by habitat type.

I used 10 remote detectors for this study. I deployed one detector in each of the habitat types for 3-12 nights per sample. These 3-12 nights were considered the “encounter occasions” in occupancy modeling. Separate sampling at each location was repeated a minimum of 2 times through the study so each site had a minimum of 10 repeat visits. Multiple nights of sampling provide an assessment of temporal variation among habitats. To compare differential habitat use, each habitat type was sampled simultaneously to account for temporal variation (Williams et al. 2006). I followed the general strategy in sampling more sites with fewer surveys for a rare species versus fewer sites for more common species with similar detection probability (MacKenzie et al. 2006). For this study I define “site” as a single location and “replicate” as a group of 6 sites, 1 from each habitat type.

All acoustical data were summarized into detection/non-detection at various temporal scales. This was greatly facilitated by the in-house development of the program AnaMichelle, which takes the output scan files from AnalookW and transfers them into the acoustic activity index (see Chapter 1) and presence non-detection histories at various temporal scales (Davis-Klopfer 2008). For single species models I defined the sampling occasion as 1 night (24hour period = 10 hours of acoustical sampling). I chose 12 nights at random from each of the 87 sites surveyed in 2007 (Fig 2.2) and summarized this into binary values of detection and non-detection for occupancy model construction, thus modeling represents 12 sampling occasions.

My assumptions for the study design are that: all habitats are accessible to all species of bats, proper replication is achieved by sampling a minimum of one representative for each habitat simultaneously for multiple nights, all bats have equal detectability with regard to vertical distribution, and all equipment has equal ability of detecting echolocation calls (Weller 2008).

Acoustic Activity Index-site covariate

The bat activity index (AI) was summarized for each species by an acoustic activity index (Miller 2001) and was calculated as the detection in 1 minute time blocks for each hour surveyed. The summation of one minute time blocks that species was detected during a sampling event was standardized to 10 hours. Summary at each sampling location is represented as an average AI for each species at each location. This represents the relative amount of time that a species was active at the location and time. The average activity was also used as a site covariate in the occupancy models. The actual values were square root transformed to account for non-normal distribution and this variable is labeled “AI” for model parameterization.

Habitat Structure-site covariate

In my study, habitat structure was primarily based on vegetation density. I used 4, 5m long transects radiating out in the 4 cardinal directions from the microphone site. I calculated habitat cover using an estimation based on the midpoint braun-blanket (Braun-Blanquet 1932, 1964) cover classes from 0-2 m, 2.1-4m, 4.1 – 6 m, 6.1-10 m, 10.1 – 15 m, and over 15 m averaged at 1m intervals along that transect (total of 20

points per site). This volumetric density estimation for vegetation coverage was summarized for each habitat type. The categories were then combined to provide an overall value of vegetation density at each site. Comparisons were made between habitat types by the means of analysis of variance with Tukey-Kramer pairwise comparisons (SYSTAT v13.1). The overall average volumetric density for each sampling location formed the site covariate labeled “veg” for occupancy modeling.

Prey Availability-site covariate

When relating food availability to individual presence, one must consider whether the insects sampled are available from the perspective of the bat (Hutto 1990). Bats forage preferentially on certain types of insects due to the bats foraging niches (Wolda 1990, Carter et al. 2003). When measuring food availability for bats that forage on the wing, a method to sample flying insects should be used (Cooper and Whitmore 1990). Given that all the bats of Virginia are nocturnal insectivores, only nocturnal insects were sampled in this study.

I quantified flying insects using custom-built 2 m Malaise style insect traps designed to funnel nocturnal insects into a collection chamber (Gressitt and Gressitt 1962, Townes 1962, 1972) The trap was designed to allow for the capture or non-capture of insects depending on the setting of the collection jar which could be opened or closed. The collection chamber contained Hercon Vaportape®, 10% DDVP as a killing agent. One trap was placed at each of the acoustic sampling sites and run for the duration of the

individual sample, approximately 3 nights. The trap was placed within the 30m buffer of the sampling area.

After collection, insects were retrieved from the Malaise traps and placed into alcohol for lab identification. Insects were identified to family if possible. Once identified, insects were removed from the alcohol and held in a drying oven at seventy degrees Celsius for twenty four hours. Dry weights of insects in grams were then calculated for each sampling night. Summary statistics were used to compare insect biomass estimates between each habitat type by analysis of variance (SYSTAT v13.1). The insect samples are archived within the Virginia Tech Department of Entomology.

The occupancy model variable for the dry weight of insects is labeled “bugs”. Because not all sampling events had even sampling, average dry weights were calculated at the site level and used as a site covariate in the models.

Environmental Factors-sampling covariates

Environmental factors can have a profound effect on bat occurrence at a given site and time. To quantify this effect I collected both landscape level and microsite climatic factors to determine if they influenced detection and/or occupancy. The landscape level variable was moon phase. The moon phase data were obtained through available National Oceanic and Atmospheric Administration (NOAA) data. These data were available as a percent of moon illumination. This value was classified for each sampling occasion and used as a sampling covariate labeled “moon” for the occupancy modeling.

The microsite data were collected by LASCAR EL-USB-2® data loggers attached to each microphone element. These variables recorded temperature (°C) at various temporal scales, I used 1 hour intervals. These data were summarized for each site and sampling occasion. I standardized the temperature to z-scores for normalization and labeled “enrivot” for occupancy modeling.

Model Construction and Testing

A random selection of 12 nights was chosen from each of the 87 sites to create the models (Fig 2.2). I transformed the raw activity data into a binary series for analysis of detection probabilities and occupancy. Detection (1) and non-detection (0) were organized into vectors of detection history for each species per night of sampling. As an example, a version of site F0056 for *Eptesicus fuscus* was 101011110111. If a specific site did not have 12 sampling occasions a value of no-data was assigned (.).

A Priori models were developed based morphological characteristics and published literature on habitat use (Table 2.1.). I used Akaike’s Information Criterion (AIC or AIC_c) and those models with the lowest weight (ω) determine the best model fit (Burnham and Anderson 1998, Franklin et al. 2001). Models within 2 Δ AIC of each other were considered competing models. Models for detection probability were created with a constant occupancy first. Subsequently, these top detection models were then used to model the occupancy.

Determining Detection Probabilities and Predicting Occurrence

I used the program PRESENCE (Hines 2005) to calculate the detection probabilities and proportion of area occupied (PAO) for each species. This program was developed to incorporate information on detectability (i.e. detection probabilities < 1) to make more accurate and precise predictions of the POA from detection/non-detection data (MacKenzie et al. 2002, MacKenzie et al. 2003, MacKenzie et al. 2006). This method has been shown to be effective for modeling other vespertilionid species by means of acoustic signatures (Gorrensens et al. 2008).

To develop models that predict species occurrence across the landscape, I added effects of habitat and environmental variables into the occupancy model. These covariates were then entered into program PRESENCE, which uses logistic regression and logit link incorporating covariates (independent variables) to investigate the relationships between these variables and detection and occupancy probability (response variable). The logistic model can be noted as follows (MacKenzie et al. 2006):

$$\text{logit}(\Psi_i) = \ln(\Psi_i/1 - \Psi_i) = \beta_o + \beta_1 \chi_{i1} + \beta_2 \chi_{i2} + \dots + \beta_u \chi_{iu}$$

where

Ψ_i = the probability of occupancy, or probability of use for i th sampling unit

χ_i = value for covariate u measured at i th sampling unit

β = regression coefficient that determines the size of the effect of the respective covariates, which are to be estimated; β_o is the intercept term.

i = number of sampling units or sites

u = number of covariates entered into the model.

This analysis is very similar to the approach used in Capture – Mark - Recapture models for determination of survival and probability of capture (e.g. program MARK). In this analysis the detection – non detection history of the site becomes the equivalent of capture – recapture data of an individual (Vojta 2005). Occupancy modeling is very flexible as it allows for missing observations, possibly due to sampling logistics or equipment loss/failure, thus not affecting the detection probability estimations (Hines 2005).

I first examined the factors influencing the detection probabilities for each species (p). I examined each variable independently in a univariate model (MacKenzie et al. 2006). These variables include activity level for the species examined (AI - site covariate), volumetric vegetation density (veg - site covariate), insect biomass (bugs - site covariate), temperature (temp - sampling covariate), humidity (humidity – sampling covariate), environment if temperature and humidity are correlated (environ – sampling covariate), and moon illumination (moon – sampling covariate). I then constructed multivariate models using combinations of these covariates on the species detection probability.

The best model of detection probability was used to further examine occupancy (Ψ or Ψ). These variables included in occupancy were habitat types as site covariates (CF- coniferous forest, DA - developed area, DF deciduous forest, FW – forested wetland, GS – grassland shrubland, WL – open water wetland), volumetric vegetation

density (veg-site covariate), insect biomass (bugs - site covariate). I did not feel the biological justification of examining activity level (AI - site covariate), temperature (environ – sampling covariate), and moon illumination (moon – sampling covariate) for occupancy.

The beta estimates of coefficients for covariates were then calculated for the top and competing models for each species. These estimates represent the influence of each of the covariates within model. A positive value represents a positive relationship and a negative value represents an inverse relationship. Because covariate values were standardized by z-score, the Beta values represent a non-linear magnitude in the trends.

Geographic Prediction of Occupancy Across the Landscape

The occupancy estimates derived for the top models for each species were loaded into ArcGIS (ESRI, Redlands, California) for spatial mapping of occupancy across the landscape to predict where species might occur in areas that were not directly surveyed. This was achieved by post-stratifying the data and calculating an occupancy estimate (Ψ) for each habitat strata. These strata were then categorized and projected across the landscape based on available spatial vegetation maps for the installation (Dorr et al. 2007). Some site level details such as, vegetation density and insect biomass, used for modeling occupancy was not available at the scale of the entire installation. Therefore these predictions were based on habitat strata alone.

RESULTS

Summary of Effort

From 08 June to 25 August 2007 at 87 sites, I collected 240,189 bat call files with 11,680 hours (1168 nights) of acoustic monitoring. The 2007 acoustical survey data was used for all data analysis presented herein.

Summary of Variables

Bat activity was summarized for each specific survey location representing average activity for each species at that location (Table 2.2). The AI ranged from a low of 0.0 to a high of 1211.7 minutes for all species combined across the course of the 2007 study.

Volumetric vegetation density was summarized by each height class and habitat type (Figure 2.3) giving an overall representation of habitat structure at different heights. Height classes were pooled for comparisons among habitats (Figure 2.4). Results from the Tukey-Kramer analysis of variance yielded statistical significance ($n=87$, $df = 83$, $\bar{x}=12.137$, $F=10.769$, $\alpha=0.05$, $p=0.000$) with lower vegetation density with grassland /shrublands compared to coniferous forests ($\bar{x}_d = 8.834$, $p=0.001$), deciduous forests ($\bar{x}_d = 8.640$, $p<0.000$), and forested wetlands ($\bar{x}_d = 13.431$, $p<0.000$). A difference at the $\alpha=0.1$ level was detected with higher density between forested wetlands to open water wetlands ($\bar{x}_d = 7.028$, $p=0.068$) and open water wetlands to grassland shrublands ($\bar{x}_d = 6.404$, $p=0.098$).

There was high variability in the capture data for insect biomass (dry weight in grams) among the habitat types (Figure 2.5). Based on the ANOVA Tukey-Kramer pairwise comparisons a difference ($n=110$, $df=106$ $\bar{x}=0.299$, $F=4.691$, $\alpha=0.05$, $p=0.001$), I detected a higher overall biomass in open water wetlands compared to deciduous forests ($\bar{x}_d = -0.349$, $p=0.002$) and forested wetlands ($\bar{x}_d = -0.336$, $p=0.003$).

Single Species Models

Single species detection (p) and occupancy (Ψ) models were executed for each of the six species (Table 2.3). All species had a combination of vegetation density+ insect biomass + species activity index (veg+bugs+AI) as the top models representing detection probabilities. With the addition of AI, high reduction in AIC values occurred as compared to combination of bugs+veg. All species detections were influenced negatively by vegetation density (veg), negatively by insect biomass in dry weight (bugs), and positively for species activity (AI). The univariate models indicated that including the variables of moon illumination (moon), temperature (environ), and insect biomass (bugs) did not perform much better than the standard model (1 group, constant p) for detection ($\sim \Delta AIC < 2$). For all species a positive relationship was observed for detection moon illumination and insect biomass. The relationships to temperature were species specific.

A positive relationship with insect biomass (bugs) was the top influence on most species occupancy (Ψ) once added to the top model for detection (Table 2.4). There were some competing models based on a delta AIC < 2.0 with the inclusion of vegetation density (veg) to insect biomass on occupancy. The global model estimates for each

species occupancy across the installation is based on the top model (p and Ψ) for that species (Figure 2.6). Beta estimates were derived from each of the top and competing models and represent the influence of each of the covariates within the top model (Table 2.4). All species showed a positive relationship to insect biomass and an inverse relationship to vegetation density for site occupancy.

Site covariates of habitat type were post stratified from the original detection/non-detection data then reexamined. The calculations of detection probability and proportion of area occupied for each habitat were constructed based on the top model for each species (Figures. 2.7 to 2.12). The results were then loaded into ArcGIS (ESRI, Redlands, California) for spatial mapping of occupancy across the landscape for each species (Figures 2.13 to 2.18). Classifications were applied to the resulting scale of area occupancy: extremely low $\Psi = 0 - 0.1$, very low $\Psi = 0.101 - 0.25$, low $\Psi = 0.251 - 0.5$, medium $\Psi = 0.501 - 0.75$, high $\Psi = 0.751 - 0.9$, very high $\Psi = 0.901 - 1.0$.

Because each species had variations in response to detection and occupancy by habitat, a more detailed description of the best model(s) is described below for each species.

Eptesicus fuscus (Big brown bat)

The detection probability (p) of *Eptesicus fuscus* (Figure 2.7) was higher in the developed areas ($p=0.60\pm0.15$), grasslands/shrublands ($p=0.68\pm0.04$), and open water wetlands ($p=0.67\pm0.06$) than in the coniferous forests ($p=0.30\pm0.06$), deciduous forests

($p=0.26\pm0.08$) and forested wetlands ($p=0.30\pm0.08$). The habitats with higher detection probabilities tended to be lower in vegetative density as indicated by the beta estimates for detectability (Table 2.4). The overall proportion of area occupied by big brown bats was high to very high ($\Psi=0.73\pm0.15$ - 1.0 ± 0.0) in all habitats except the forested wetlands ($\Psi=0.45\pm0.16$). Across the installation their occupancy was high ($\Psi=0.77\pm0.05$).

Lasiurus borealis (Eastern red bat)

Lasiurus borealis had the highest detection probabilities (Figure 2.8) in the open water wetlands ($p=0.96\pm0.02$) followed by forested wetlands ($p=0.77\pm0.07$), grassland shrublands ($p=0.76\pm0.04$), developed areas ($p=0.75\pm0.06$) with the lowest being deciduous forest ($p=0.48\pm0.06$), and coniferous forests ($p=0.42\pm0.06$). Three models for occupancy were considered competing for *Lasiurus borealis*. These included occupancy as constant, bugs, and bugs + veg (Table 2.3). Occupancy was high ($\Psi>0.751$) in the developed areas, grassland shrublands, open water wetlands, and deciduous forests, medium in the coniferous forests ($\Psi=0.70\pm0.15$) and low in the forested wetlands ($\Psi=0.43\pm0.13$). Among all habitats their occupancy was also high ($\Psi=0.78\pm0.05$).

Myotis lucifugus (Little brown myotis)

Myotis lucifugus exhibited a fairly continuous spread in detection probabilities (Figure 2.9) ranging from the lowest in the deciduous forest ($p=0.51\pm0.06$) and coniferous forests ($p=0.56\pm0.06$), to higher in forested wetlands ($p=0.71\pm0.07$), developed areas ($p=0.81\pm0.06$), grassland shrublands ($p=0.87\pm0.03$), and highest in open water wetlands ($p=0.96\pm0.02$). Occupancy was lowest in forested wetlands

($\Psi=0.36\pm0.13$) and highest in open water wetlands ($\Psi=0.93\pm0.07$), developed areas ($\Psi=1.0\pm0.0$) and the grassland shrubland complex ($\Psi=1.0\pm0.0$). Installation wide *Myotis lucifugus* displayed high occupancy ($\Psi=0.78\pm0.04$).

Myotis septentrionalis (Northern long-eared myotis)

Myotis septentrionalis had some of the lowest detection probabilities ($p=0.31\pm0.08 - 0.49\pm0.7$) of the six species examined in all habitats except the open water wetlands ($p=0.97\pm0.02$) (Figure 2.10). Occupancy estimates with low detection probabilities ($p<0.30$) should be interpreted with caution as it could lead to spurious overestimations of occupancy (MacKenzie et al. 2006). These habitats include the developed areas ($\Psi=0.85\pm0.20$), and the grassland shrublands ($\Psi=1.0\pm0.0$), although the detection estimates were close to 0.30 they were not below (DA $p=0.31\pm0.08$, GS $p=0.32\pm0.04$). *Myotis septentrionalis* is classified as having a medium occupancy level ($\Psi=0.69\pm0.05$) across all habitats.

Nycticeius humeralis (Evening bat)

Nycticeius humeralis was found to have lower detection probabilities in the deciduous forests ($p=0.43\pm0.05$) and coniferous forests ($p=0.56\pm0.06$), than the forested wetlands ($p=0.79\pm0.07$), developed area ($p=0.81\pm0.05$), grassland shrubland matrix ($p=0.87\pm0.03$), and open water wetlands ($p=0.88\pm0.04$). Despite having a high detection probability in the forested wetlands they demonstrated low occupancy ($\Psi=0.29\pm0.12$). Occupancy was estimated at 1.0 for the developed areas, grassland shrublands, and open

water wetlands (Figure 2.11). The evening bat presented a medium level of occupancy across all habitats ($\Psi=0.74\pm0.02$).

Perimyotis subflavus (Eastern pipistrelle)

Perimyotis subflavus followed a similar detection distribution to *Myotis lucifugus* with slightly lower estimates than other species for each habitat. The lowest was in the coniferous forests ($p=0.44\pm0.06$) and deciduous forests ($p=0.48\pm0.06$), with a gradual increase in the developed areas ($p=0.75\pm0.06$), forested wetlands ($p=0.80\pm0.06$), grassland shrublands ($p=0.82\pm0.03$), and finally open water wetlands ($p=0.98\pm0.01$). Patterns of occupancy were also similar with the lowest occurring in forested wetlands ($\Psi=0.43\pm0.13$) and the highest occurring in open water wetlands ($\Psi=0.92\pm0.07$), developed areas and grassland/shrubland complex, each with an occupancy of 100% ($\Psi=1.0\pm0.0$). The overall occupancy for *Perimyotis subflavus* was high ($\Psi=0.81\pm0.04$) (Figure 2.12).

DISCUSSION

Effective bat conservation and management requires knowledge of habitat use and potential limiting factors for populations at various geographic scales (Ford et al. 2005). I found that the most influential variables effecting bat distributions were insect biomass, vegetation density, and the species level of activity, or combinations thereof. This pattern was consistent across all six species examined. The inverse relationship between detection probability and insect biomass is likely attributed to effective foraging. Where insects are more abundant on the landscape bats do not need to spend as much time

actively foraging in the area therefore decreasing detection. Vegetation density also was inversely related to detectability, perhaps due to bats avoiding cluttered environments as indicated by the occupancy estimates. I had expected these results for all species except *Myotis septentrionalis*. Because this species has morphological characteristics adapted for highly maneuverable flight and the ability to hover to obtain water resources from very tight spaces without a direct flight path (personal observation), I hypothesized a positive relationship. This species did however have a low relationship to vegetation density likely due to low amplitude of *Myotis septentrionalis* echolocation call structure. Even though there was lack of strong statistical evidence for vegetation density effect among the habitat types, this may be an artifact of the gross scale at which these data were collected. A more refined data collection technique may be necessary to reveal a meaningful difference in detecting differences at both the between habitat scale and at the species detection and occupancy level. It is perhaps not surprising that activity level would influence detection since this is an index of time the species is within the site. With the addition of AI, high reduction in AIC values occurred

Insect biomass was also an influential covariate in detection probability, but usually only in combinations with other variables, suggesting a complex array of influential factors. Moon illumination did not have an effect on detection in this study as compared to others that found inverse correlations (Hayes 1997, Broders et al. 2003). Those studies, however, referred to effects more associated with physical capture of bats so perhaps represented an artifact of mist net detectability and not activity. Admittedly, my measure of moon illumination was based on NOAA moon phase data

and not a direct measure of ambient light at the sampling period. Perhaps a refined measure of this would result in significant findings. Further examination at the site over all hours of the night would be needed to test if illumination influences bat detectability.

Temperature at this study site was not a significant contributor to detection probabilities however each species exhibited a positive relationship even though this factor was never included in the top model. Perhaps temperature would be a more influential factor at higher latitudes and/or elevations other than the Piedmont of Virginia, or earlier in the year during the emergence cycle or later during fall and pre-hibernacula swarming periods.

Insect biomass was the most influential variable effecting bat occupancy for all species. The resulting top occupancy models indicated positive influences of insect biomass on occupancy based on beta estimates, confirming the hypothesis that these bats like bugs. Vegetation density had an inverse effect on occupancy for only 2 species in combination with the positive effect of insects for *Myotis lucifigus* and *Nycticius humeralis* as determined from competing models.

Proximity to open water resources is an important factor when determining resource utilization of bat species (Carter 2006). This was shown for all species by the high proportion of area occupied for the open water wetlands. For most species occupancy was higher in grasslands and shrublands with the exception of *Myotis septenptionalis*. The developed areas on the military installation also provide important

components for foraging bats. This could be because these habitats are fairly open, provide artificial illumination for insect attraction, are somewhat higher insect biomass, and provide ample roosting opportunities both in trees and abandoned buildings (St. Germain 2008b). This proximity to roosts has been identified as a contributing influence to increased activity for some species (Kunz 1973, Fenton and Bell 1979).

All species had medium to high occupancy across all habitats on the installation (Figure 2.6). This suggests that all these species are widely present across this landscape and utilize a wide variety of habitat throughout the course of an evening. However differences were identified as to the level of use (see Figure 3.4 Chapter 3 of this thesis).

Documentation of species spatial distribution is important and helpful in conservation and management of populations. The constructed occupancy maps will provide natural resource managers beneficial information when making critical land use decisions. This is especially important where species populations are being reduced by widespread outside factors (Arnett 2008, Blehert et al. 2009).

CONCLUSION

This study illustrates that it is possible to quantify detection probabilities and proportion of area occupied stratified by habitats of multiple species simultaneously using an acoustical sampling array. This technique provides a means to sample the entire bat community more efficiently than trapping, which has some inherent capture biases (Thomas and LaVal 1988, Thomas and West 1989, Ministry of Environment 1998).

Knowledge of habitat use across the landscape can provide valuable information for land managers when making decisions regarding landscape alterations derived from changing land use practices. For example, Ft. Pickett is undergoing alterations that include clearing forested environments in favor of opening up more training lands to conduct maneuver practices (St Germain and Murray-Schneider 2012). This study shows that clearing of forested environments may not negatively affect any species at the population level, and in fact, may likely benefit *Eptesicus fuscus*, *Lasiurus borealis*, *Myotis lucifugus* and *Perimyotis subflavus*, however both *Myotis lucifugus* and *Perimyotis subflavus* also have strong ties to water. This can be especially important for *Myotis lucifugus*, a once very common species, whose populations have suffered recent dramatic declines due to high mortality rates resulting from White-nosed syndrome (Blehert et al. 2009). Even though *Lasiurus borealis* is a tree roosting species, added benefits can be derived from these land conversions since their populations are being affected by the production of wind energy facilities (Arnett 2008) if roost trees are not a limiting resource.

This is one of the first study to apply these techniques to this suite of species across the landscape. I have shown that it is an effective means for determining and predicting species occurrence at the micro and macro spatial scales. This study can also provide insight into the factors influencing the occupancy and detection of a species. . My acoustical sampling array provided an efficient means to sample the entire bat community

simultaneously providing a relatively new means to obtain substantial information on bat species and community ecology.

LITERATURE CITED

- Aldridge, H. D. J. N. and I. L. Rautenbach. 1987. Morphology, echolocation, and resource partitioning in insectivorous bats. *Journal of Animal Ecology* **56**.
- Arnett, E., B. 2003. Advancing science and partnerships for the conservation of bats and thier habitats. *Wildlife Society Bulletin* **31**:2-5.
- Arnett, E., B. 2008. Patterns of bat fatalities at wind energy facilities in North America. *Journal of Wildlife Management* **72**:61-78.
- Barclay, R. M. R. 1985. Long- versus short- range foraging strategies of hoary (*Lasivirus cinereus*) and silver-haired (*Lasionycteris noctivigans*) bats and the consequence of prey selection. *Canadian Journal of Zoology* **63**:2507-2515.
- Blehert, D., S., A. Hicks, C., M. Behr, C. Meteyer, U., B. Berlowski-Zier, M., E. L. Buckles, T. Coleman, H., S. Darling, R., A. Gargas, R. Niver, J. Okoniewski, C., R. Rudd, J., and W. Stone, B. 2009. Bat White-nosed syndrome: an emerging fungal pathogen? *Science* **323**:227.
- Broders, H. G., G. M. Quinn, and G. J. Forbes. 2003. Species status, and the spatial and temporal patterns of activity of bats in southwest Nova Scotia, Canada. *Northeastern Naturalist* **10**:383-398.
- Brooks, R., T. and W. M. Ford. 2006. Introduction to the special section - Bat habitat use in eastern North American temperate forests: stand, site, and landscape effects. *Journal of Wildlife Management* **70**:1171-1173.
- Burnham, K. P. and D. R. Anderson. 1998. Model selection and inference: a practical information-theoretic approach. Springer-Verlag, New York, New York.

- Carter, T. C. 2006. Indiana bats in the midwest: The importance of Hydric Habitats. *Journal of Wildlife Management* **70**:1185-1190.
- Carter, T. C., M. A. Menzel, S. F. Owen, J. W. Edwards, J. M. Menzel, and W. M. Ford. 2003. Food habits of seven species of bats in the Allegheny Plateau and Ridge and Valley of West Virginia. *Northeastern Naturalist* **10**:83-88.
- Cooper, R. J. and R. C. Whitmore. 1990. Arthropod sampling in ornithology. *Studies in Avian Biology* **12**:29-37.
- Corben, C. 2005. AnalookW (Beta version 3.2h dated 25 August 2005). URL http://users.lmi.net/corben/WinAnalook.htm#AnaLookW_Contents.
- Davis-Klopfer, M. 2008. AnaMichelle. Virginia Tech, Blacksburg, Virginia.
- Dorr, J., L. V. R. Emrick, P. Swint, and E. Pokorski. 2007. Army National Guard - Maneuver Training Center Fort Pickett vegetative communities map and vegetation classification system. CMI-MLD R-46 Conservation Management Institute - Military Lands Division, College of Natural Resources, Virginia Polytechnic Institute and State University, Blacksburg, Virginia.
- Duffy, A. M., L. F. Lumsden, C. R. Caddle, R. R. Chick, and G. R. Newell. 2000. The efficacy of Anabat ultrasonic detectors and harp traps for surveying microchiropterans in south-eastern Australia. *Acta Chiropterologica* **2**:127-144.
- Fenton, M. B. and G. P. Bell. 1979. Echolocation and feeding behaviour in four species of myotis (Chiroptera). *Canadian Journal of Zoology* **57**:1271-1277.
- Ford, W. M., J. M. Menzel, M. Menzel, A., J. W. Edwards, and J. C. Kilgo. 2006. Presence and absence of bats across habitat scales in the upper coastal plain of South Carolina. *Journal of Wildlife Management* **70**:1200-1209.

- Ford, W. M., M. A. Menzel, J. L. Rodrigue, J. M. Menzel, and J. B. Johnson. 2005. Relating bat species presence to simple habitat measures in a central Appalachian forest. *Biological Conservation* **126**:528-539.
- Franklin, A., B., T. M. Shenk, D. R. Anderson, and K. P. Burnham. 2001. Statistical model selection: an alternative to null hypothesis testing. *in* T. M. Shenk and A. Franklin, B., editors. *Modeling in natural resource management: development interpretation and application*. Island Press, Washington, DC.
- Gehrt, S. D. and J. E. Chelsvig. 2004. Species-specific patterns of bat activity in an urban landscape. *Ecological Applications* **14**:625-635.
- Gorrensens, P. M., A. C. Miles, C. M. Todd, F. J. Bonoccorso, and T. J. Weller. 2008. Assessing bat detectability and occupancy with multiple automated echolocation detectors. *Journal of Mammalogy* **89**:11-17.
- Gressitt, J. L. and M. K. Gressitt. 1962. An improved malaise trap. *Pacific Insects* **4**:87-90.
- Hayes, J. P. 1997. Temporal variation in activity of bats and the design of echolocation-monitoring studies. *Journal of Mammalogy* **78**:514-524.
- Hayes, J. P. and P. Hounihan. 1994. Field use of the Anabat II bat-detector system to monitor activity. *Bat Research News* **35**:1-3.
- Hines, J., E. 2005. Program PRESENCE. USGS Putuxent Wildlife Research Center, Laurel, Maryland.
- Hutto, R. L. 1990. Measuring the availability of food resources. *Studies in Avian Biology*:20-28.

- Jung, T. S., I. D. Thompson, R. D. Titman, and A. P. Applejohn. 1999. Habitat selection by forest bats in relation to mixed-wood stand types and structure in central Ontario. *Journal of Wildlife Management* **63**:1306-1319.
- Kunz, T. H. 1973. Resource utilization: temporal and spatial components of bat activity in central Iowa. *Journal of Mammalogy* **54**:14-31.
- Loeb, S., C. and J. O'Keefe, M. 2006. Habitat use by forest bats in South Carolina in relation to local, stand, and landscape characteristics. *Journal of Wildlife Management* **70**:1210-1218.
- MacKenzie, D., I. 2005. What are the issues with presence - absence data for wildlife managers? *Journal of Wildlife Management* **69**:849-860.
- MacKenzie, D., I., J. Nichols, D., J. Hines, E., M. Knutson, G., and A. Franklin, B. 2003. Estimating site occupancy, colonization, and local extinction when a species is detected imperfectly. *Ecology* **84**:2200-2207.
- MacKenzie, D., I., J. Nichols, D., G. Lachman, B., S. Droege, J. A. Royle, and C. Langtimm, A. 2002. Estimating site occupancy rates when detection probabilities are less than one. *Ecology* **83**:2248-2255.
- MacKenzie, D., I., J. Nichols, D., J. A. Royle, K. Pollock, H., L. Bailey, L., and J. Hines, E. 2006. *Occupancy Estimation and Modeling, Inferring Patterns and Dynamics of Species Occurrence*. Elsevier Academic Press, New York.
- MacKenzie, D., I. and J. A. Royle. 2005. Designing occupancy studies: general advice and allocating survey effort. *Journal of Applied Ecology* **42**.

- Menzel, J. M., M. A. Menzel, J. C. Kilgo, W. M. Ford, J. W. Edwards, and G. F. McCracken. 2005. Effect of habitat and foraging height on bat activity in the Coastal Plain of South Carolina. *Journal of Wildlife Management* **69**:235-245.
- Miller, B. W. 2001. A method for determining relative activity of free flying bats using a new activity index for acoustic monitoring. *Acta Chiropterologica* **3**:93-105.
- Miller, D., A., E. Arnett, B., and M. J. Lacki. 2003. Habitat management for forest-roosting bats of North America: a critical review of habitat studies. *Wildlife Society Bulletin* **31**:30-44.
- Ministry of Environment. 1998. Inventory Methods for Bats No. 20. Standards for Components of British Columbia's Biodiversity. Ministry of Environment, Victoria, British Columbia.
- Nichols, J., D. and K. U. Karanth. 2002. Statistical concepts: assessing spatial distributions. Pages 29-38 *in* K. U. Karanth and J. Nichols, D., editors. *Monitoring Tigers and Their Prey: A Manual for Wildlife Managers, Researchers, and Conservationists*. Center for Wildlife Studies, Bangalore, India.
- Patterson, B., D., M. Willig, R., and R. Stevens, D. 2003. Trophic strategies, niche partitioning, and patterns of ecological organization. Pages 536-579 *in* T. H. Kunz and M. B. Fenton, editors. *Bat Ecology*. University of Chicago Press, Chicago.
- St Germain, M. J. and R. M. Murray-Schneider. 2012. Grassland bird diversity and density on ARNG-MTC Ft. Pickett, Blackstone, Virginia. Conservation Management Institute, College of Natural Resources and Environment, Virginia Polytechnic Institute and State University, Blacksburg, Virginia. **Technical Report**:1-24.

- St. Germain, M. J. 2008. Bat Species Assemblage on ARNG-MTC fort Pickett, Blackstone, Virginia. Technical Report CMI-MLD R 39.
- Thomas, D. W. and R. K. LaVal. 1988. Survey and Census Methods. Pages 77-89 *in* T. H. Kunz, editor. Ecological and Behavioral Methods for the Study of Bats. Smithsonian Institute Press, 533 pp, Washington DC.
- Thomas, D. W. and S. West, D. 1989. Wildlife-habitat relationships: sampling procedures for Pacific Northwest vertebrates. PNW-GTR-243, USDA Forest Service, Portland, OR.
- Townes, H. 1962. Design for a malaise trap. Proceeding of the Entomological Society Washington **64**:253-262.
- Townes, H. 1972. A light-weight malaise trap. Entomological News **83**:239-247.
- Vojta, C., D. 2005. Old dog, new tricks: innovations with presence - absence information. Journal of Wildlife Management **69**:845-848.
- Weller, T. J. and C. J. Zabel. 2002. Variation in bat detections due to detector orientation in a forest. Wildlife Society Bulletin **30**:922-930.
- Williams, J., A., M. J. O'Farrell, and B. Riddle, R. 2006. Habitat use by bats in a riparian corridor of the mojave desert in southern Nevada. Journal of Mammalogy **87**:1145-1153.
- Wolda, H. 1990. Food availability for an insectivore and how to measure it. Studies in Avian Biology **13**:38-43.
- Yates, M. D. and R. M. Muzika. 2006. Effect of forest structure and fragmentation on site occupancy of bat species in Missouri Ozark forests. Journal of Wildlife Management **70**:1238-1248.

Table 2.1. *A priori* hypotheses affecting bat species occurrence and detection in 2007 on ARNG-MTC Ft. Pickett, Blackstone, Virginia

Species	Occurrence	Relationship to Variable (Detection)			
	Habitat Site-cov	Understory density (VEG)	Temperature (ENVIRON)	Moon Illumination (MOON) Sampling- cov	Prey Availability (BUGS) Site-cov
		Site-cov	Sampling-cov		
<i>Eptesicus fuscus</i>	DA WL	-	+	-	+
<i>Lasiurus borealis</i>	DF WL	-	+	-	+
<i>Myotis lucifugus</i>	DA FW	-	+	-	+
<i>Myotis septentrionalis</i>	DF	+	+	-	+
<i>Nycticeius humeralis</i>	WL	-	+	-	+
<i>Perimyotis subflavus</i>	All	-	+	-	+

- Habitat: ALL: all habitats; DA: Developed areas; DF: Deciduous forests; FW: Forested wetlands; WL: Open water wetlands.

Table 2.2. Summary of activity index (number of one minute time blocks) for each bat species at every sampling location on ARNG-MTC Ft. Pickett, Blackstone, Virginia during the 2007 summer sampling season.

Site	Habitat	Flyway	<i>Eptesicus fuscus</i>	<i>Lasiurus borealis</i>	<i>Myotis lucifugus</i>	<i>Myotis septentrionalis</i>	<i>Nycticeius humeralis</i>	<i>Perimyotis subflavus</i>	Relative Activity
F0001	WL	S	0	31.3	9.9	18.1	4.7	65.4	1.45%
F0002	WL	W	1	91.1	32.4	130.3	19.1	129.3	4.52%
F0003	CF	N	0.9	0.1	1.3	0	1.3	0.5	0.05%
F0004	WL	W	5	79.8	51.9	35.3	39.4	104	3.53%
F0006	FW	S	0	0.7	0.3	1.3	0	2	0.05%
F0007	FW	S	0.4	26.4	18.7	38.4	12.3	56.1	1.71%
F0009	WL	W	10	30	163	19	132	52	4.55%
F0011	WL	W	0.7	174.3	115	129.7	45	219	7.66%
F0012	CF	N	0	0.3	0	0.3	0	0.4	0.01%
F0013	FW	S	0.7	9.5	20.2	13.3	17.3	27.5	0.99%
F0014	DA	O	19.4	9.6	13.6	0.3	12.4	4.4	0.67%
F0015	DA	O	122.6	2.8	7.4	0.5	6.8	3.8	1.61%
F0016	DA	R	13.2	44.6	152.8	24.4	111	44.6	4.38%
F0017	DA	R	7.7	5.7	4.7	0	3.3	11.7	0.37%
F0018	GS	O	6.4	21.6	52	2.8	42.6	34.6	1.79%
F0019	DF	S	1.6	16.4	44.6	9.9	39.4	25	1.53%
F0020	WL	W	4.6	26	77	24.4	68.4	36.2	2.65%
F0021	DF	N	0	0.4	0	0.4	0.1	1	0.02%
F0022	WL	W	0	0	0	0	0.2	0	0.00%
F0023	DF	S	0	0	0.1	0.1	0.1	0	0.00%
F0024	GS	O	1.3	11	31.3	0	26	11.3	0.91%
F0025	CF	R	0	0	0	0	0	0	0.00%
F0026	GS	O	8.6	6.9	8.6	0.5	5.1	12.3	0.47%
F0027	GS	O	0.3	0.6	2.3	0.1	2	1.5	0.08%
F0028	DF	R	0.2	0	0	0	0.7	0.2	0.01%
F0030	WL	W	16.5	123.5	112.5	190.5	91	271.5	9.03%
F0032	CF	R	101	0	1	0	0.3	0	1.15%
F0033	DF	N	0	0.1	0	0	0.1	0.1	0.00%
F0034	GS	O	0	4.3	7	0	2.7	3	0.19%
F0035	CF	R	10	0	1	0	0.7	0	0.13%
F0036	DA	O	1.9	18.6	22	0.7	18.4	5	0.75%
F0039	WL	W	2	39.5	87	5	72	30.5	2.64%
F0040	WL	W	13	134	192	124	166	196	9.25%
F0042	WL	S	0.1	2.9	12.4	27.6	12.9	12	0.76%

Table 2.2 continued. Summary of activity index (number of one minute time blocks) for each bat species at every sampling location on ARNG-MTC Ft. Pickett, Blackstone, Virginia during the 2007 summer sampling season.

Site	Habitat	Flyway	<i>Eptesicus fuscus</i>	<i>Lasiurus borealis</i>	<i>Myotis lucifugus</i>	<i>Myotis septentrionalis</i>	<i>Nycticeius humeralis</i>	<i>Perimyotis subflavus</i>	Relative Activity
F0050	FW	N	0	0	0	0	0	0	0.00%
F0051	FW	S	2.8	0.3	0.6	0.6	0.8	0.4	0.06%
F0052	FW	N	0.5	11.5	3.3	0.6	3.7	6.7	0.29%
F0053	FW	N	0	0	0	0.3	0	0	0.00%
F0054	FW	S	0	0	0	0	0	0	0.00%
F0055	FW	N	0.1	0	0	0	0	0	0.00%
F0056	GS	O	7.7	51.9	53.1	8.3	46	43.9	2.36%
F0057	FW	N	0	0	0	0	0	0	0.00%
F0058	DA	O	3.3	4.5	6.6	0.1	6.8	5.2	0.30%
F0060	FW	N	0	0	0	0.3	0	0	0.00%
F0061	FW	N	0	0	0	0	0	0	0.00%
F0062	GS	O	119	0	4.5	0	2.5	0.5	1.42%
F0065	GS	O	11.9	10.8	32	6	26.9	18.5	1.19%
F0066	WL	S	0.7	45.6	49	48.9	39.3	81.9	2.97%
F0067	WL	W	23.9	228.3	74.4	445.4	67.3	372.4	13.58%
F0068	WL	W	2.5	52	52.5	9.8	23.8	71	2.37%
F0070	GS	O	12	5.3	12.1	0.3	8.4	8.6	0.52%
F0072	GS	O	5.5	5.7	8.4	0.5	6.4	6.4	0.37%
F0076	GS	O	12.4	6.1	10.6	1	8.4	9.8	0.54%
F0079	GS	O	2.7	8.2	11.9	1.7	9.4	10.7	0.50%
F0080	DA	O	0.3	0.6	3.3	0	2	0.4	0.07%
F0082	GS	O	4	8	44.3	2.3	34.7	11	1.17%
F0083	GS	O	0.7	1.7	12	0	7.3	2.3	0.27%
F0084	CF	N	0	2.8	5.5	0.8	6.3	3.3	0.21%
F0085	FW	N	0	3.5	0	2	0	3.3	0.10%
F0086	DF	N	0	0	0.3	0.3	0.3	0	0.01%
F0101	DF	S	2.5	0.6	2.2	0	2	1.4	0.10%
F0138	DF	N	0.6	0	0.2	0.2	0.2	0	0.01%
F0232	DF	N	2	35	7.3	0.3	6.7	28.3	0.89%
F0285	CF	N	1.1	0.2	0.4	0	0.4	0.3	0.03%
F0392	DF	O	0.2	0.3	1.9	0	1.5	0.6	0.05%
F0728	DF	N	0	0.3	0	0	0	0.3	0.01%
F0817	CF	N	0	0	0	0	0	0	0.00%
F0835	CF	N	0.8	22	25.8	9.3	19	26.3	1.16%
F0839	CF	R	0.1	0	0.1	0	0.1	0.2	0.01%
F1742	GS	O	1.9	3.4	13.4	0.1	9.5	6	0.38%
F1884	GS	O	0.3	0.3	3.3	0	2	2	0.09%
F1889	GS	O	1	8.7	7	0	4.3	3	0.27%

Table 2.2 continued. Summary of activity index (number of one minute time blocks) for each bat species at every sampling location on ARNG-MTC Ft. Pickett, Blackstone, Virginia during the 2007 summer sampling season.

Site	Habitat	Flyway	<i>Eptesicus fuscus</i>	<i>Lasiurus borealis</i>	<i>Myotis lucifugus</i>	<i>Myotis septentrionalis</i>	<i>Nycticeius humeralis</i>	<i>Perimyotis subflavus</i>	Relative Activity
F5282	DF	N	0.3	11.5	0.3	0	1	3.8	0.19%
F5445	GS	O	1.7	15.5	30	0.3	28.5	16.2	1.03%
F5779	DF	N	1	6.4	2.9	0.9	3.6	0.1	0.17%
F5873	CF	N	0.1	0.6	1.3	0	1.2	0.7	0.04%
F5952	CF	R	6.8	1.2	9.3	0.3	8.5	2.3	0.32%
F6707	GS	O	22.6	7.6	18.3	2.1	11.7	7.1	0.78%
F6769	DF	N	0.1	15.9	19.9	4.6	17.3	24.3	0.92%
F6811	CF	R	0	0	0	0	0	0	0.00%
F6867	GS	O	54	2.1	9.4	0.3	6.7	3.3	0.85%
F6873	CF	R	0.3	2.3	4.3	0.1	4.4	1.3	0.14%
F6875	DF	N	0.2	22	16.2	2	20.6	11.6	0.81%
F7078	DF	N	4	0.2	0	0	0	0.3	0.05%
F7169	CF	R	0	9.8	1.5	2	3.2	3	0.22%
F8056	GS	O	3.7	0.7	7	0.8	6.8	3.7	0.25%
F9999	FW	S	0	0	0	0	0	0	0.00%
% Activity			7.45%	17.09%	20.27%	15.12%	15.83%	24.24%	1

Habitat: CF: Coniferous forests; DA: Developed areas; DF: Deciduous forests; FW: Forested wetlands; GS: Grasslands / Shrublands; WL: Open water wetlands.

Flyway: N: None; O: Open; R: Road; S: Stream; W: Open water:

Table 2.3. Top and competing occupancy and detection probability models for six vespertilionid bat species occurring on ARNG-MTC Ft. Pickett, Blackstone, Virginia in 2007. Models were constructed using program PRESENCE V 4.1. Psi represents occupancy and p represents detection probability. Competing models are characterized and having a $\Delta AIC < 2$.

Species	Top Model	AIC	ΔAIC	AIC wgt	Model Likelihood	no.Par.	$-2 \times \text{LogLike}$
<i>Eptesicus fuscus</i>	psi(bugs),p(veg+bugs+AI)	610.53	0	0.5381	1	4	602.53
	psi(bugs+veg), p(veg+bugs+AI)	610.91	0.38	0.445	0.827	5	600.91
<i>Lasiurus borealis</i>	psi(.), p(veg+bugs+AI)	524.09	0	0.658	1	4	516.09
	psi(bugs.),p(veg+bugs+AI)	526.07	1.98	0.2445	0.3716	4	518.07
	psi(bugs+veg), p(veg+bugs+AI)	527.91	3.82	0.0974	0.1481	5	517.91
<i>Myotis lucifugus</i>	psi(bugs+veg),p(veg+bugs+AI)	577.64	0	0.9627	1	5	567.64
<i>Myotis septentrionalis</i>	psi(bugs),p(veg+bugs+AI)	519.78	0	0.6486	1	4	511.78
	psi(bugs+veg), p(veg+bugs+AI)	521.11	1.33	0.3336	0.5143	5	511.11
<i>Nycticus humeralis</i>	psi(bugs+veg),p(veg+bugs+AI)	523.8	0	0.8211	1	5	513.8
	psi(bugs),p(veg+bugs+AI)	526.87	3.07	0.1769	0.2155	4	518.87
<i>Perimyotis subflavus</i>	psi(bugs),p(veg+bugs+AI)	530.26	0	0.6327	1	4	522.26
	psi(bugs+veg),p(veg+bugs+AI)	531.79	1.53	0.2944	0.4653	5	521.79
	psi(.),p(veg+bugs+AI)	534.68	4.42	0.0694	0.1097	4	526.68

Table 2.4. Untransformed beta estimates of coefficients for covariates derived from top (bold) and competing models for six bat species on ARNG-MTC Ft. Pickett Blackstone, Virginia in 2007. Positive value represents a positive relationship and a negative value represents and inverse relationship. Values are a non-linear magnitude of the relationship.

Species	Top Model	bugs		veg		veg		bugs		AI	
		$\alpha\Psi$	SE $\alpha\Psi$	$\alpha\Psi$	SE $\alpha\Psi$	βp	SE βp	βp	SE βp	βp	SE βp
<i>Eptesicus fuscus</i>	psi(bugs),p(veg+bugs+AI)	7.779	2.229	.	.	-0.622	0.114	-2.198	0.339	0.439	0.066
	psi(bugs+veg), p(veg+bugs+AI)	7.930	2.439	-0.486	0.392	-0.597	0.115	-2.173	0.338	0.438	0.066
<i>Lasiurus borealis</i>	psi(.), p(veg+bugs+AI)	1.653	0.341	.	.	-0.506	0.123	-0.859	0.367	0.532	0.067
	psi(bugs.),p(veg+bugs+AI)	5.929	1.995	.	.	-0.491	0.120	-1.009	0.373	0.549	0.069
	psi(bugs+veg), p(veg+bugs+AI)	5.929	2.099	-0.123	0.318	-0.486	0.120	-1.009	0.378	0.549	0.069
<i>Myotis lucifugus</i>	psi(bugs+veg),p(veg+bugs+AI)	8.601	2.634	-0.901	0.387	-0.331	0.129	-0.977	0.367	0.538	0.064
<i>Myotis septentrionalis</i>	psi(bugs),p(veg+bugs+AI)	4.919	1.663	.	.	-0.196	0.123	-2.801	0.394	0.700	0.087
	psi(bugs+veg), p(veg+bugs+AI)	4.816	1.578	-0.258	0.316	-0.180	0.125	-2.773	0.402	0.697	0.088
<i>Nycticus humeralis</i>	psi(bugs+veg),p(veg+bugs+AI)	14.910	4.421	-1.002	0.488	-0.512	0.121	-0.775	0.339	0.522	0.062
	psi(bugs),p(veg+bugs+AI)	12.244	3.231	.	.	-0.534	0.122	-0.781	0.340	0.531	0.062
<i>Perimyotis subflavus</i>	psi(bugs),p(veg+bugs+AI)	10.524	3.116	.	.	-0.394	0.116	-1.239	0.349	0.559	0.069
	psi(bugs+veg),p(veg+bugs+AI)	11.007	3.400	-0.265	0.390	-0.389	0.116	-1.240	0.349	0.559	0.069
	psi(.),p(veg+bugs+AI)	1.954	0.391	.	.	-0.399	0.121	-1.075	0.377	0.543	0.071

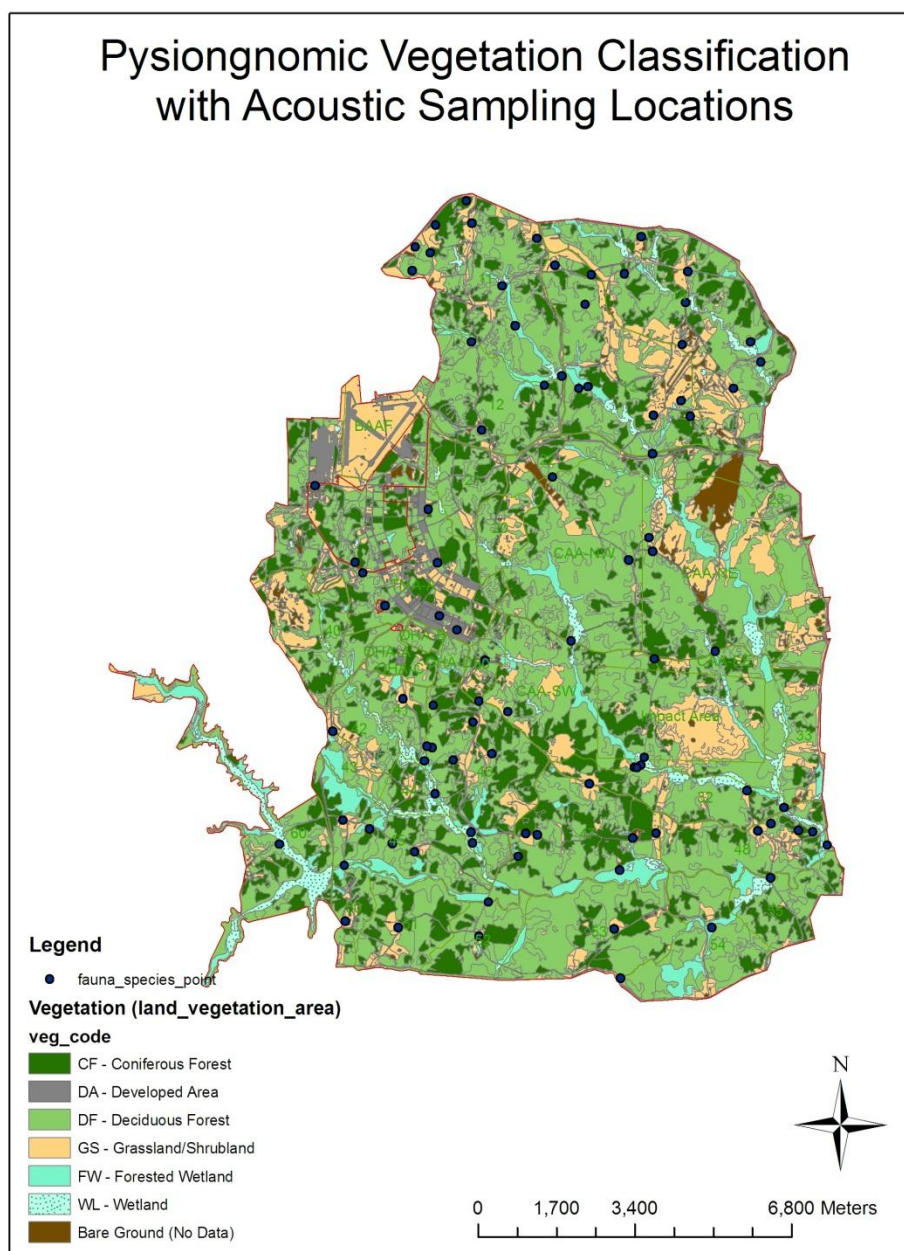


Figure 2.1. Physiognomic habitat cover types and acoustic sampling locations on ARNG-MTC Ft. Pickett, Blackstone, Virginia in 2007 (St. Germain 2012).

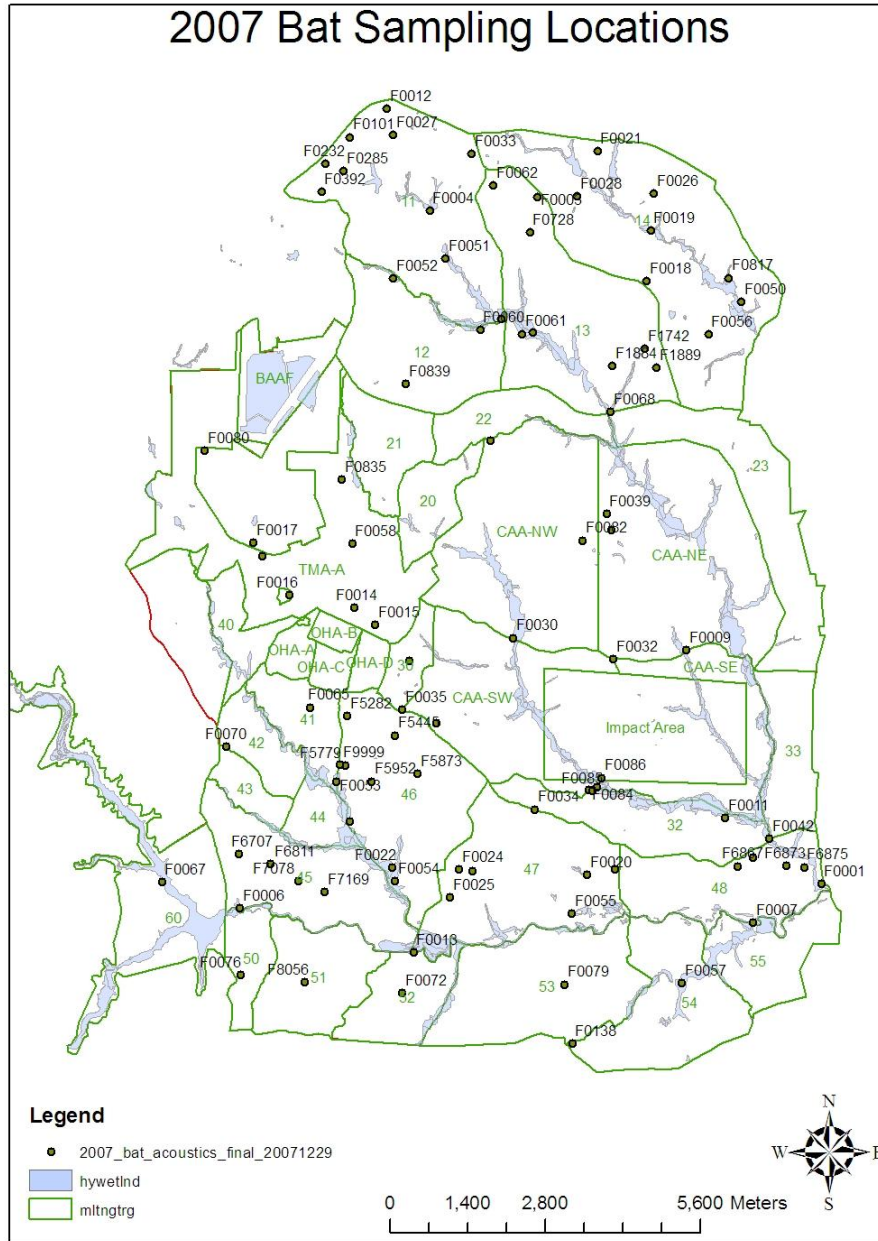


Figure 2.2. Acoustic sampling locations on ARNG-MTC Fort Pickett, Blackstone, Virginia. Sampling occurred at a subset of these locations in 2006 and at all locations in 2007 (St. Germain 2012).

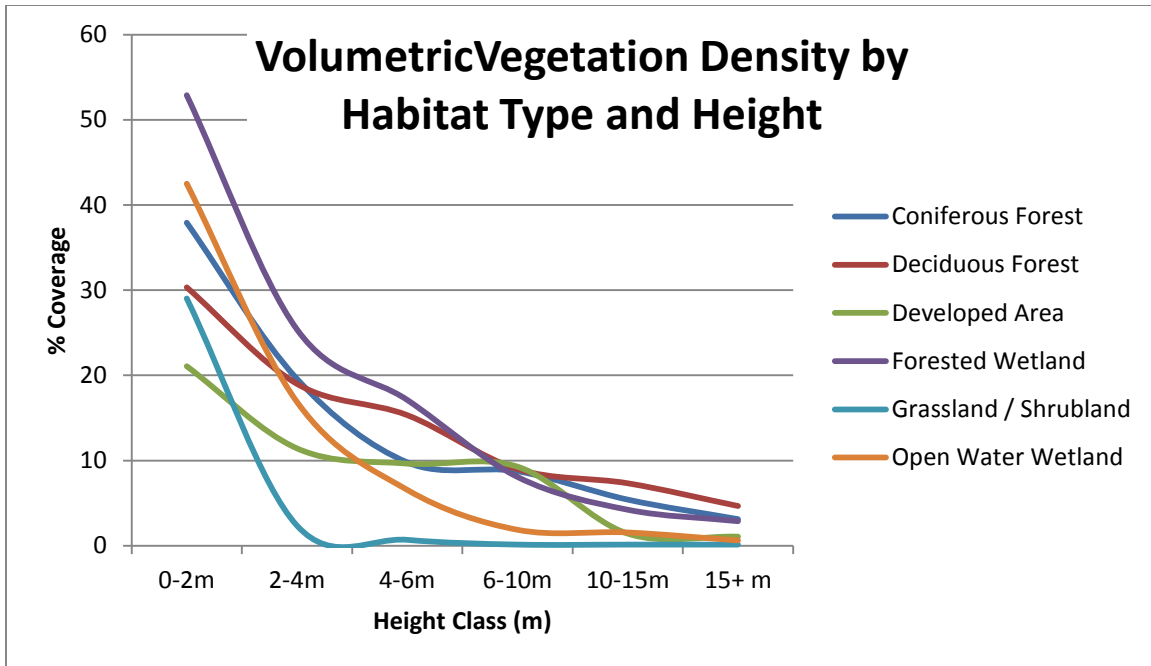


Figure 2.3. Height class volumetric vegetation density by habitat type on ARNG-MTC Ft. Pickett, Blackstone, Virginia in 2007. Estimations used braun-blanket cover class midpoints over 20 points per sampling location (St. Germain 2012).

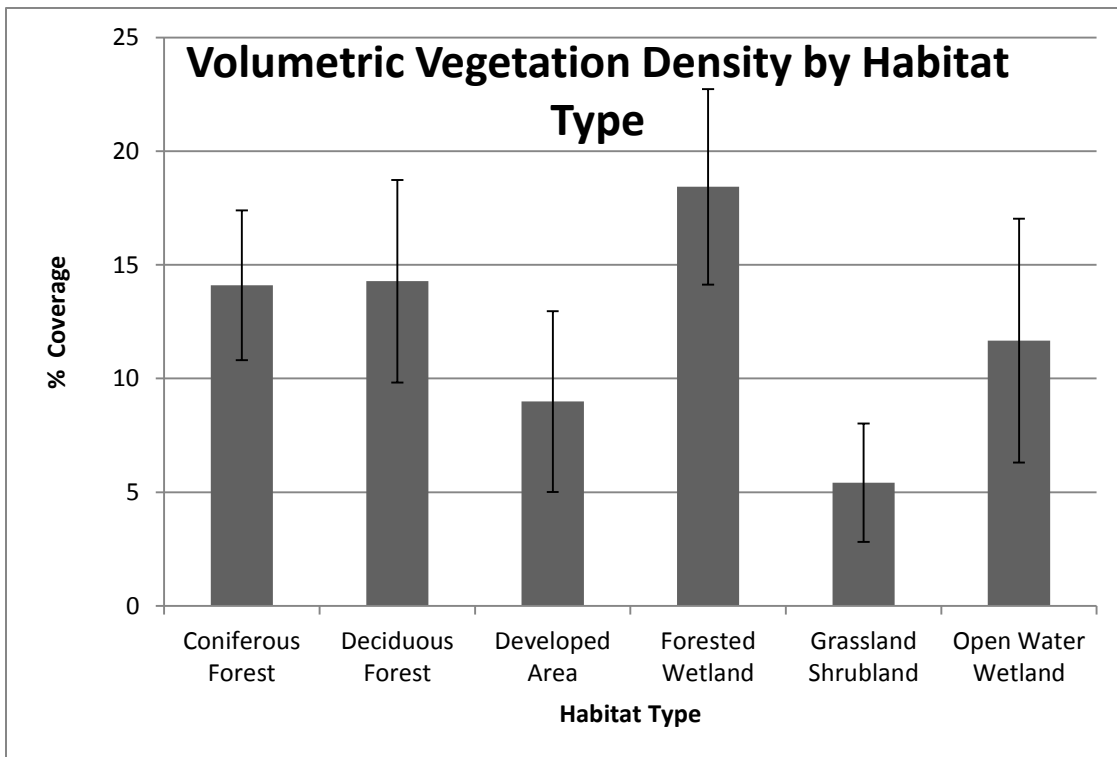


Figure 2.4. Volumetric vegetation density by habitat type on ARNG-MTC Ft. Pickett, Blackstone, Virginia in 2007. All height classes combined using braun-blanket cover class midpoints over 20 points per site (St. Germain 2012).

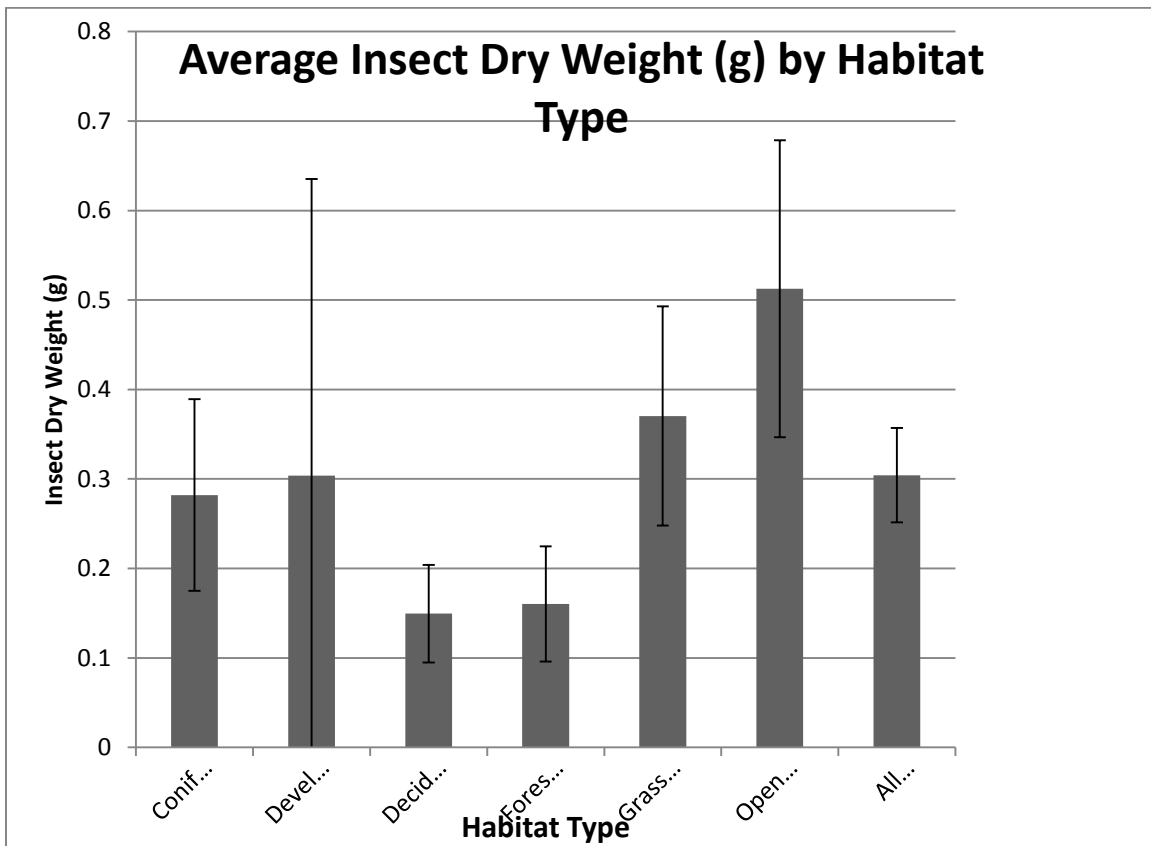


Figure 2.5. Average insect biomass by habitat type type on ARNG-MTC Ft. Pickett, Blackstone, Virginia in 2007. Biomass is summarized as insect dry weight in grams (St. Germain 2012).

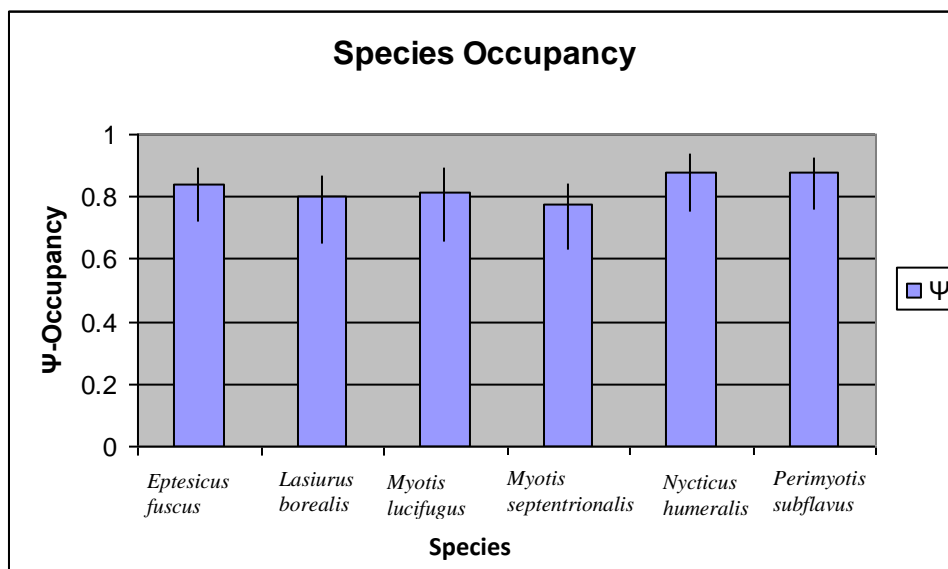


Figure 2.6. Global occupancy estimates derived from best model for the 6 species examined during 2007 on ARNG-MTC Ft. Pickett, Blackstone, Virginia. This estimate was based on the top models for all habitats installation wide (St. Germain 2012).

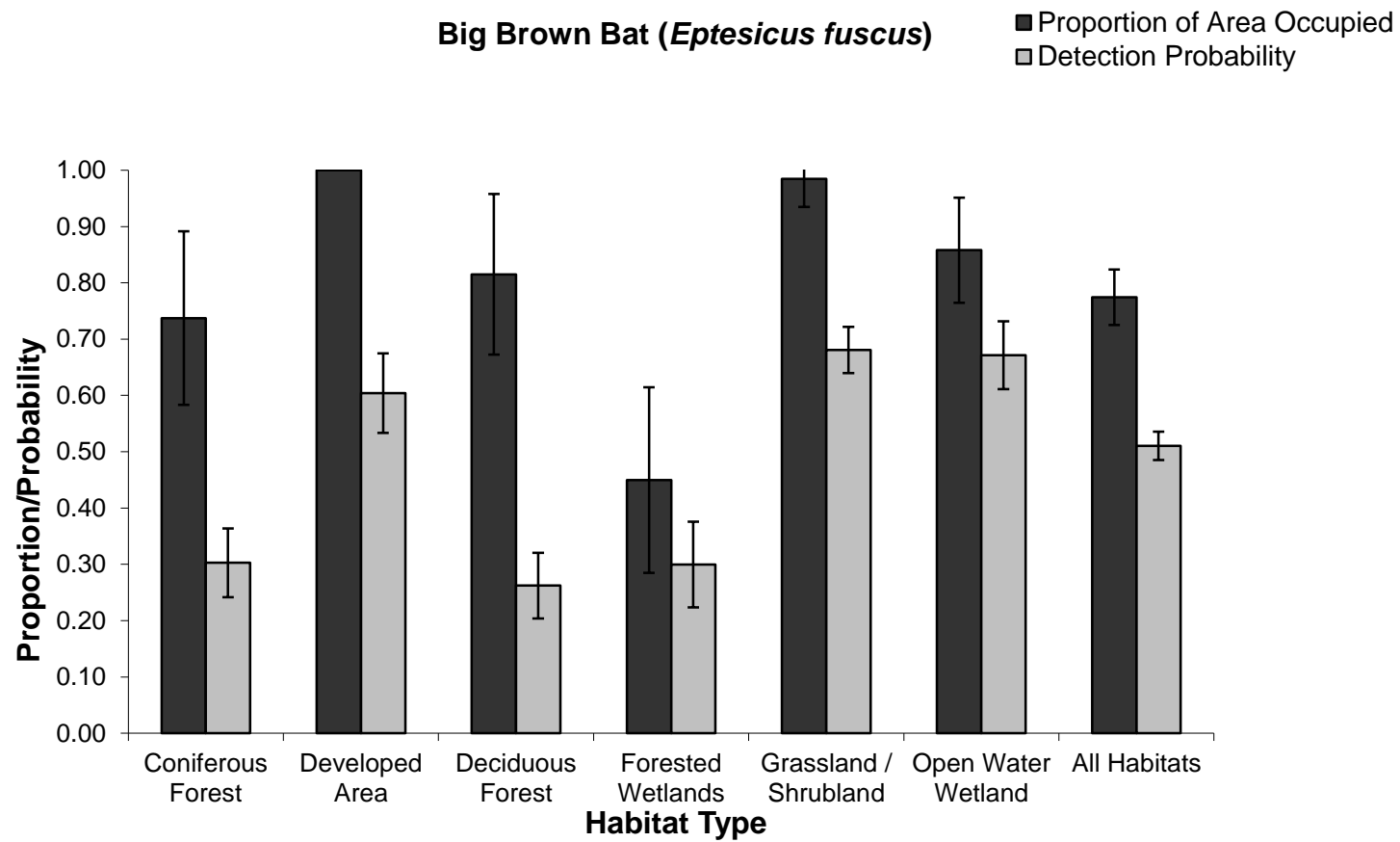


Figure 2.7. Proportion of area occupied (Ψ) and detection probability (p) stratified by habitat types for *Eptesicus fuscus* Big brown bat on ARNG-MTC Ft. Pickett, Blackstone, Virginia in 2007 (St. Germain 2012).

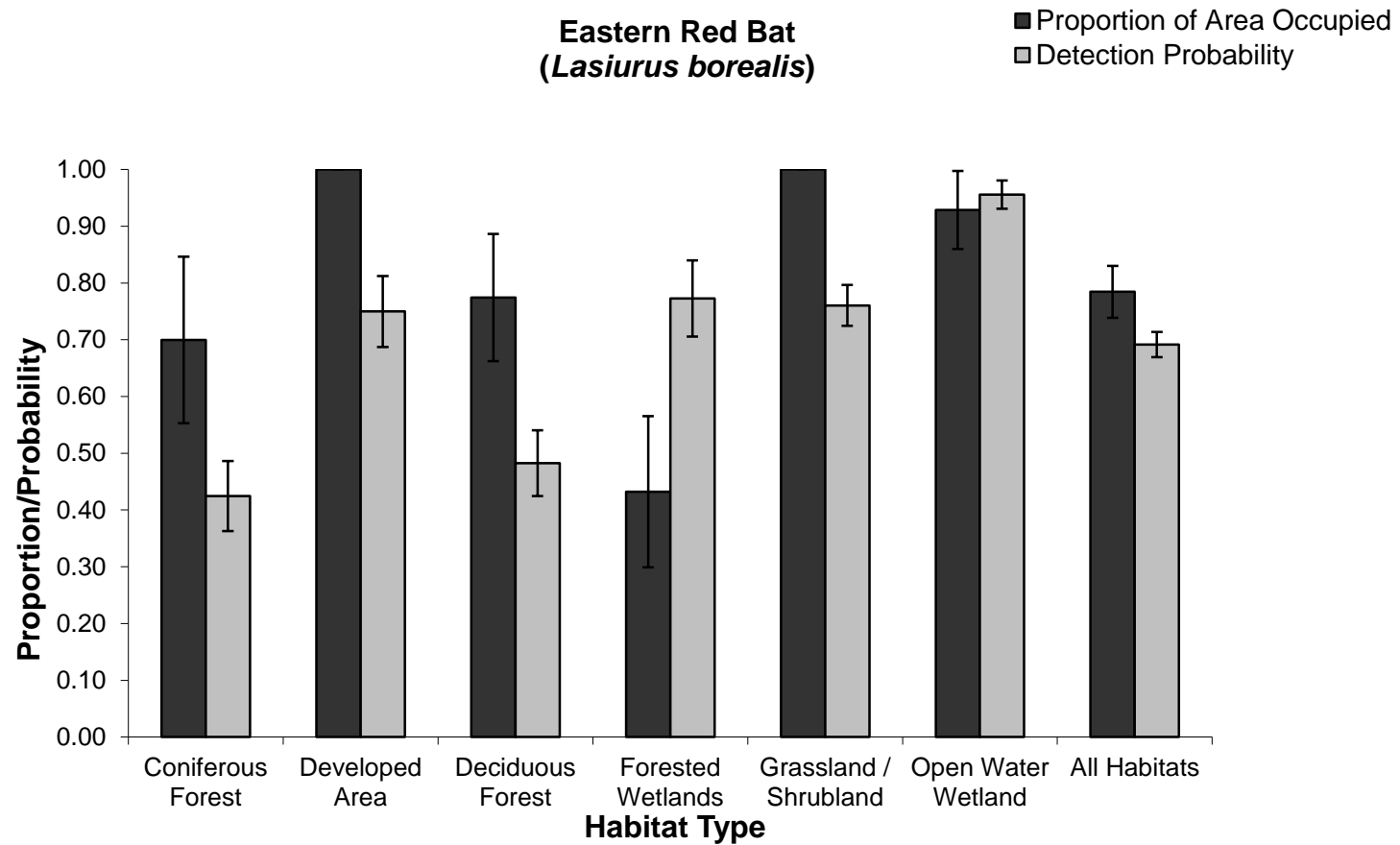


Figure 2.8. Proportion of area occupied (Ψ) and detection probability (p) stratified by habitat types for *Lasiurus borealis* Eastern red bat on ARNG-MTC Ft. Pickett, Blackstone, Virginia in 2007 (St. Germain 2012).

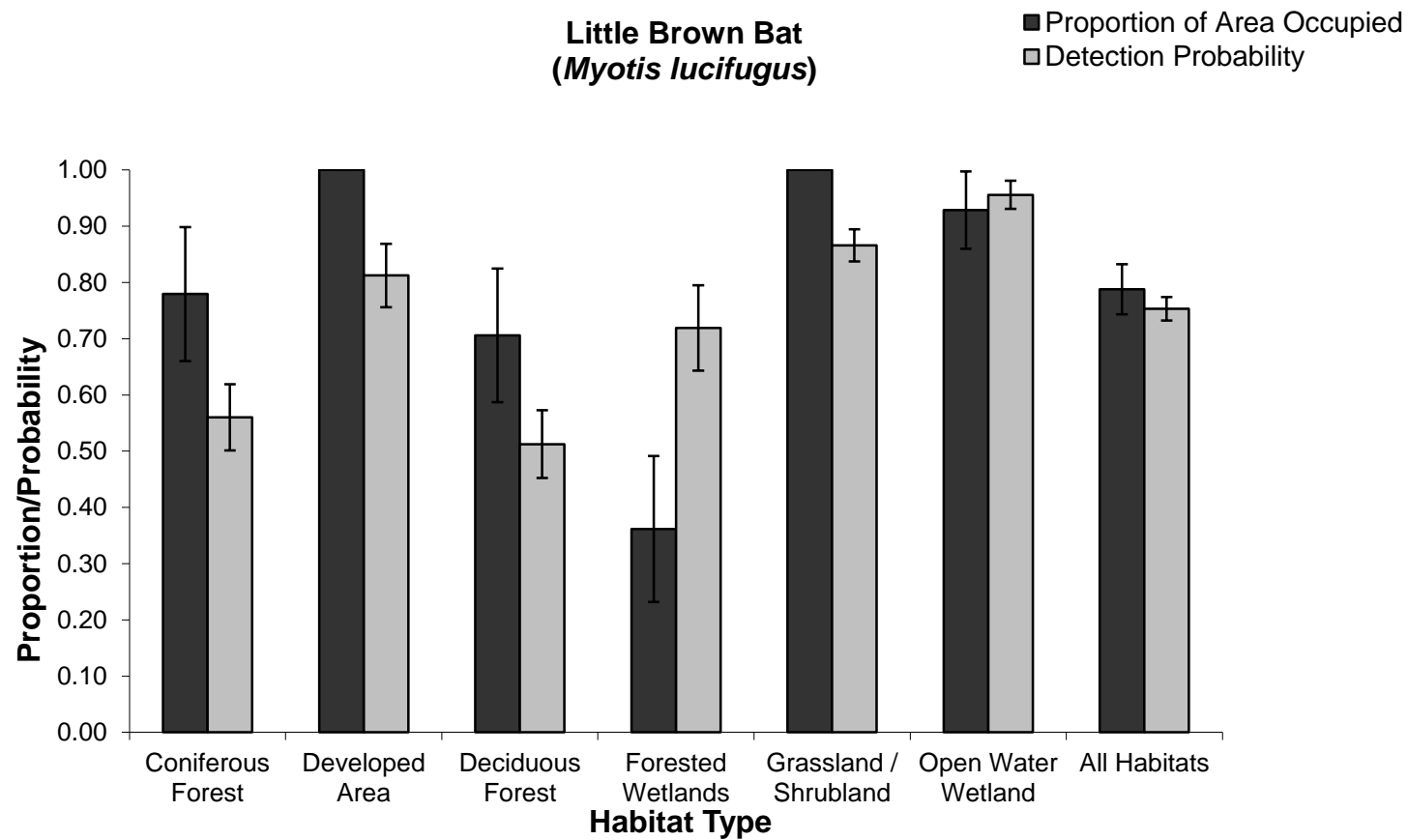


Figure 2.9. Proportion of area occupied (Ψ) and detection probability (p) stratified by habitat types for *Myotis lucifugus*, Little brown bat on ARNG-MTC Ft. Pickett, Blackstone, Virginia in 2007 (St. Germain 2012).

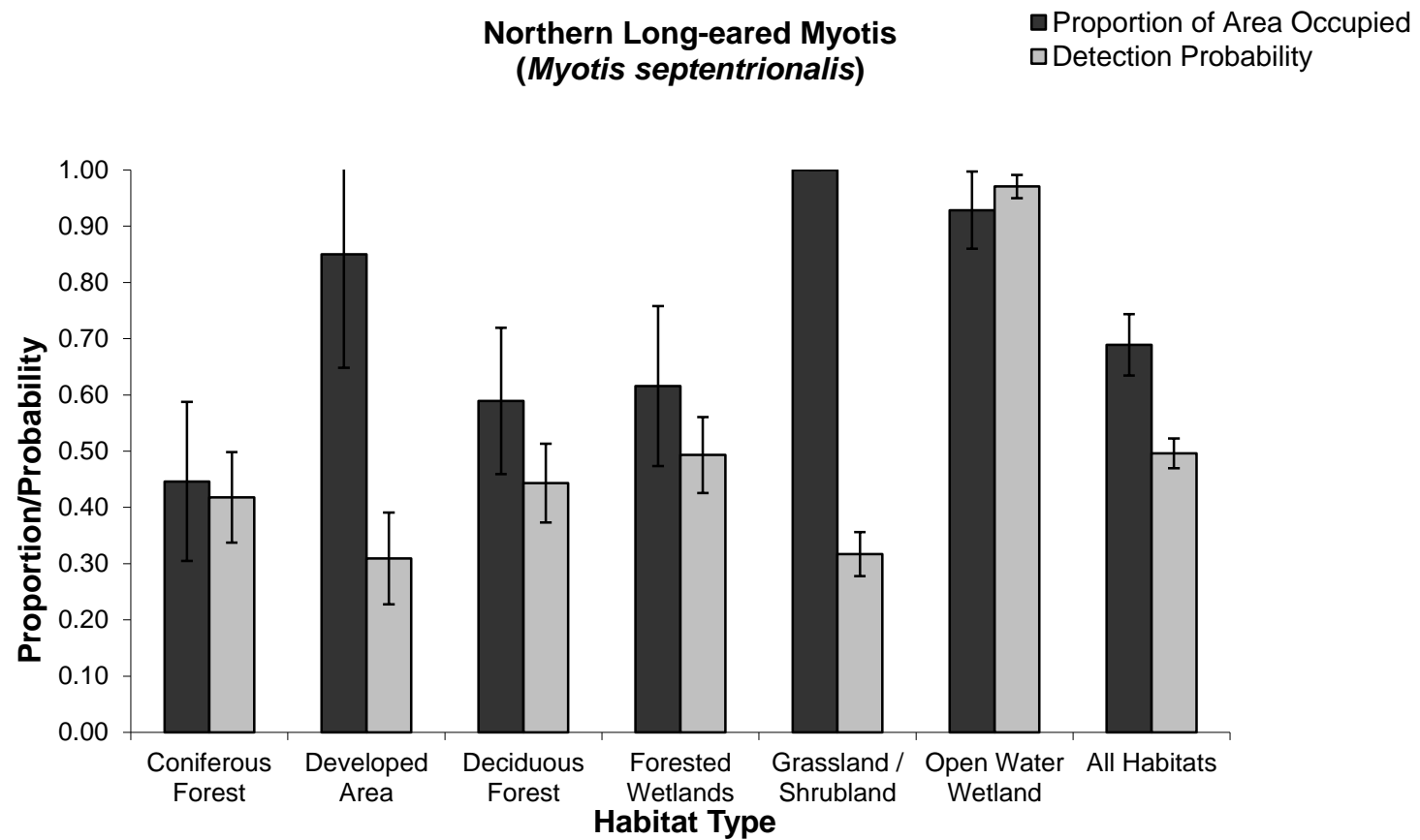


Figure 2.10. Proportion of area occupied (Ψ) and detection probability (p) stratified by habitat types for *Myotis septentrionalis* Northern long-eared myotis on ARNG-MTC Ft. Pickett, Blackstone, Virginia in 2007 (St. Germain 2012).

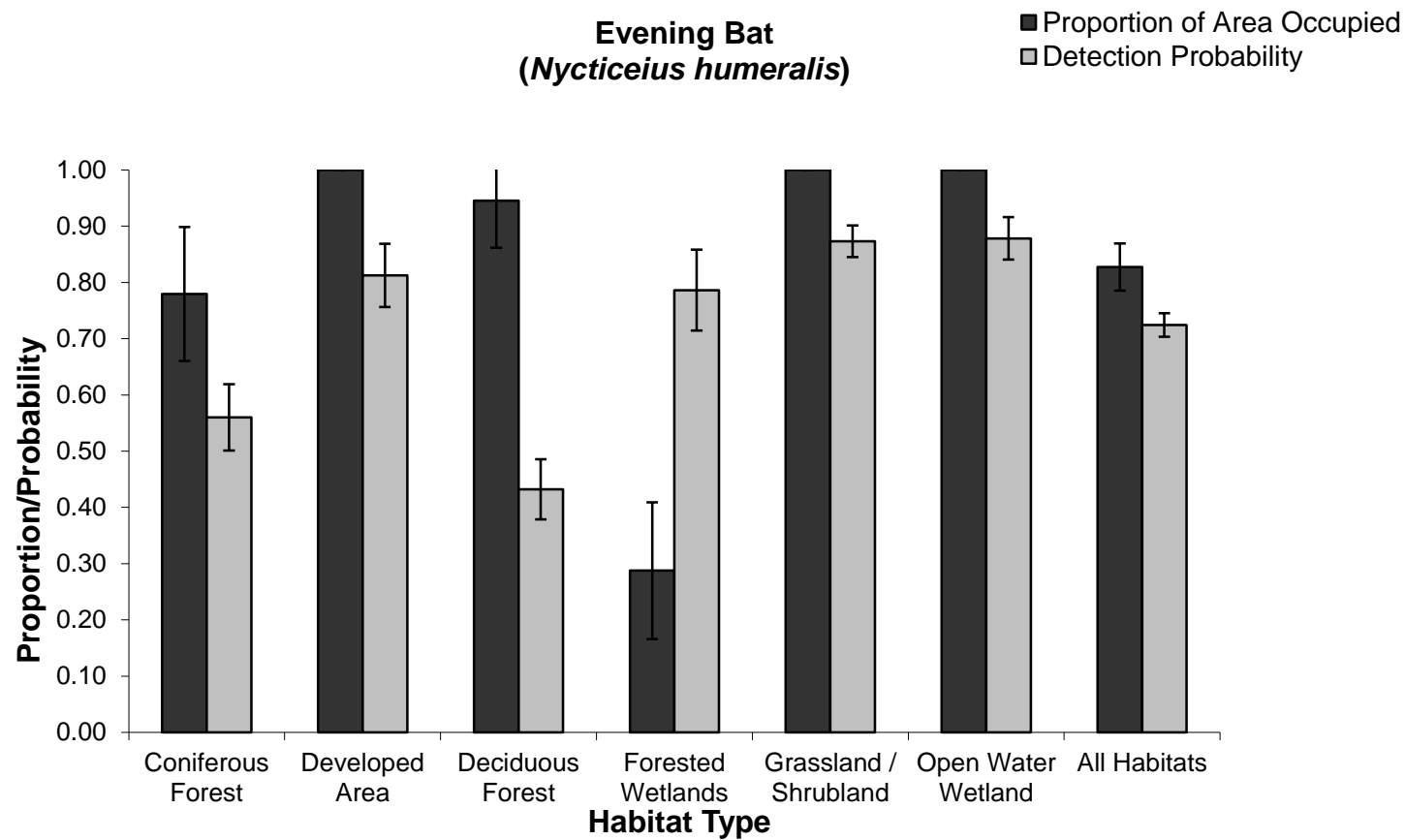


Figure 2.11. Proportion of area occupied (Ψ) and detection probability (p) stratified by habitat types for *Nycticeius humeralis* Evening bat on ARNG-MTC Ft. Pickett, Blackstone, Virginia in 2007 (St. Germain 2012).

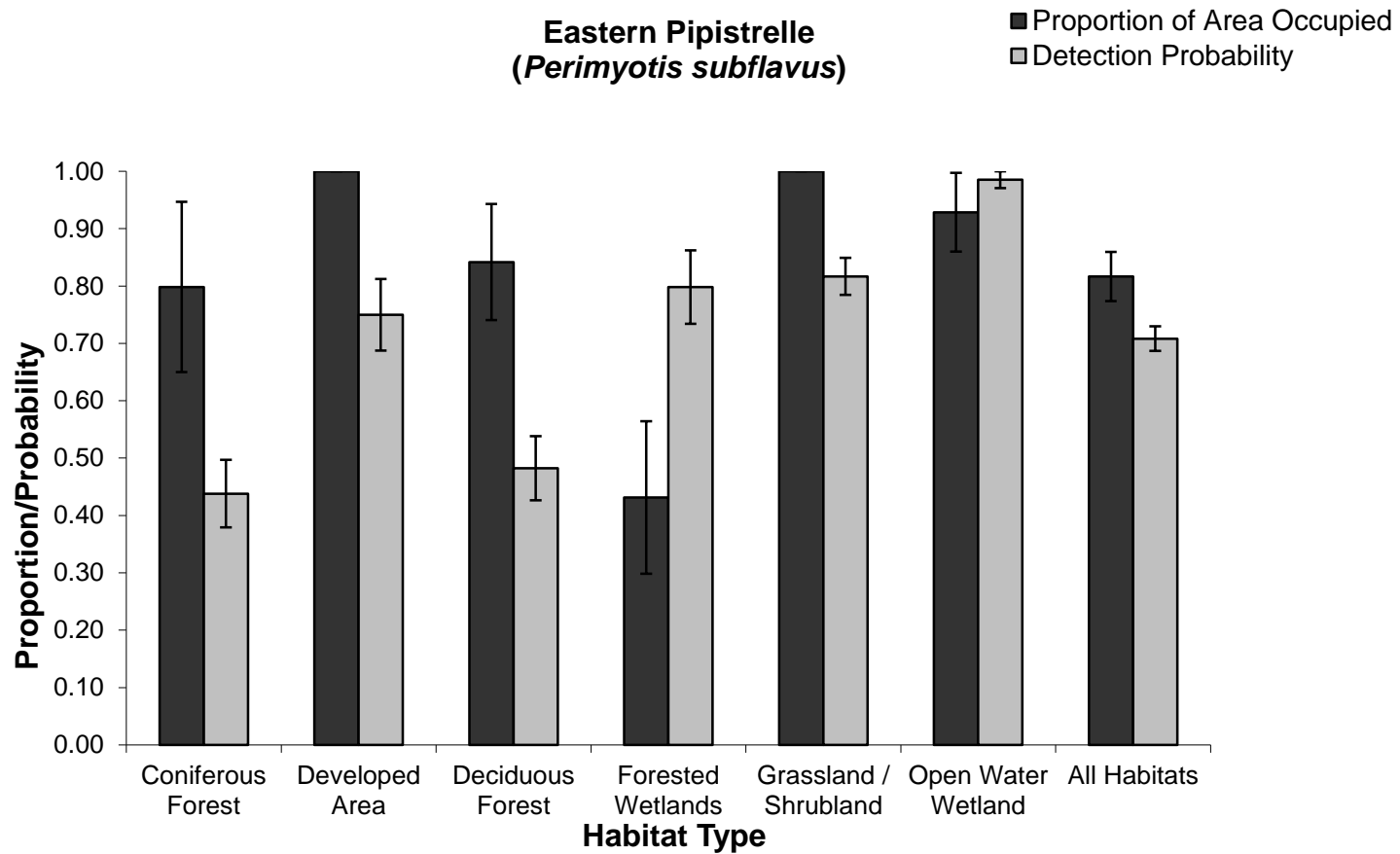


Figure 2.12. Proportion of area occupied (Ψ) and detection probability (p) stratified by habitat types for *Perimyotis subflavus* Eastern pipistrelle on ARNG-MTC Ft. Pickett, Blackstone, Virginia in 2007 (St. Germain 2012).

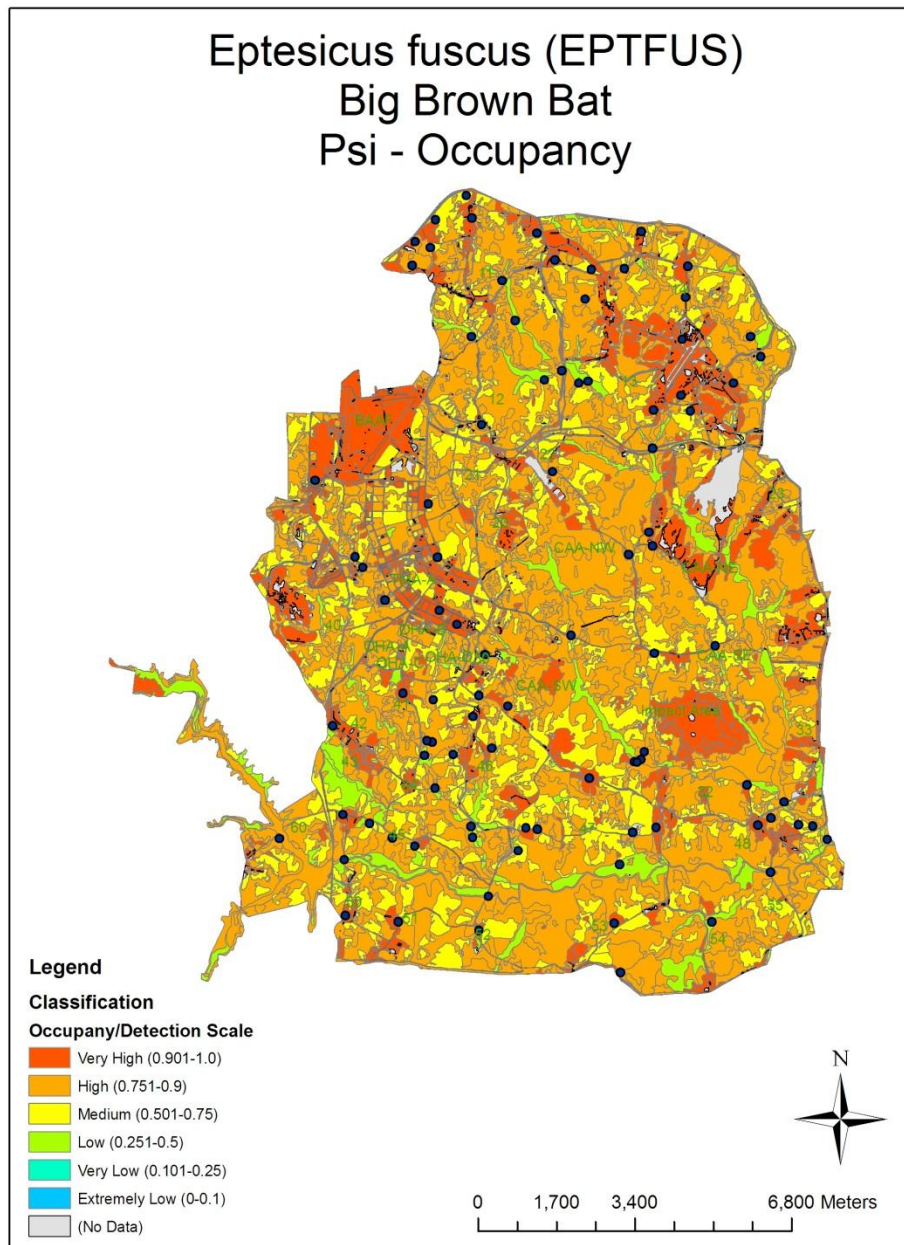


Figure 2.13. Species distribution map for *Eptesicus fuscus* Big brown bat on ARNG-MTC Ft. Pickett, Blackstone, Virginia in 2007. Distributions are represented as the proportion of area occupied (Ψ) based on top species models derived from program PRESENCE (St. Germain 2012).

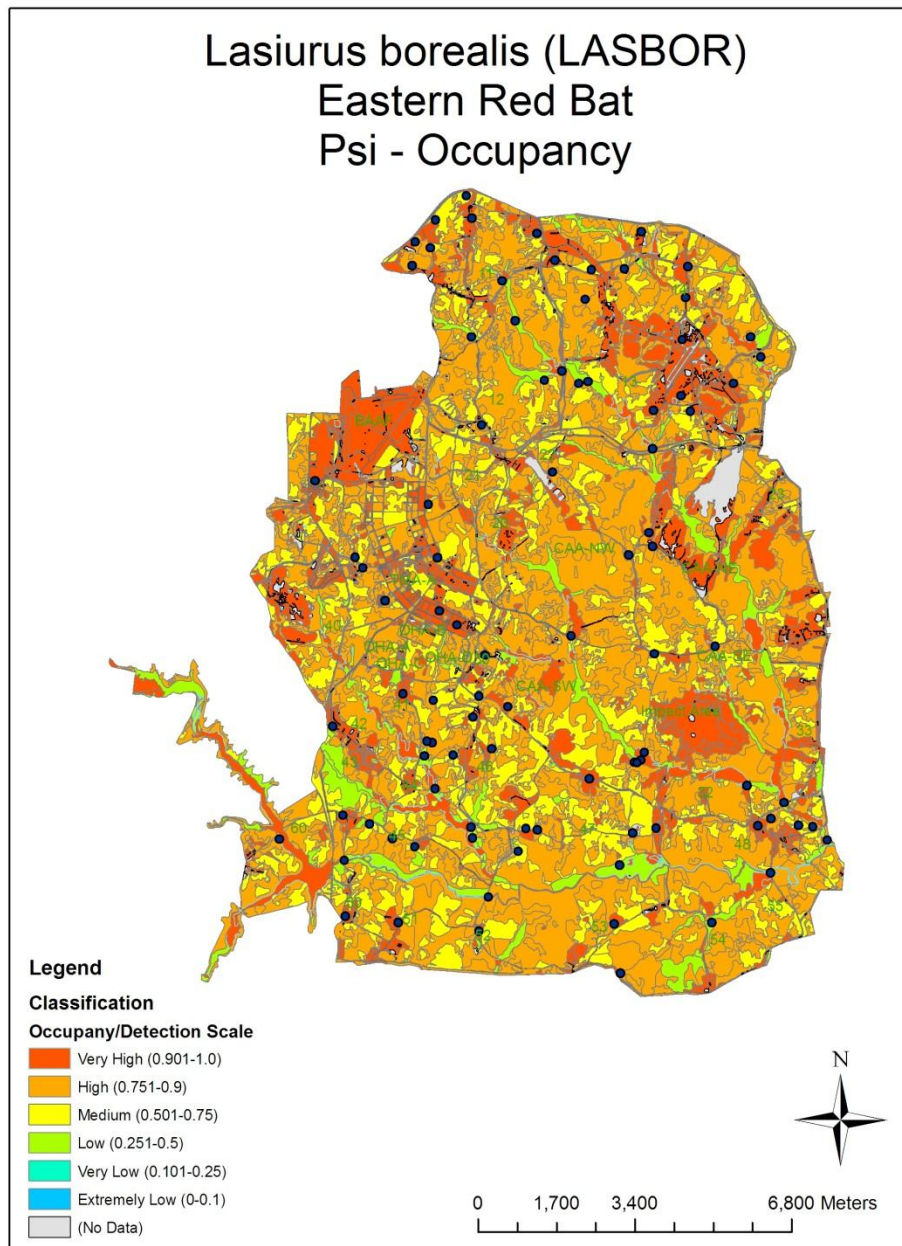


Figure 2.14. Species distribution map for *Lasiurus borealis* Eastern red bat on ARNG-MTC Ft. Pickett, Blackstone, Virginia in 2007. Distributions are represented as the proportion of area occupied (Ψ) based on top species models derived from program PRESENCE (St. Germain 2012).

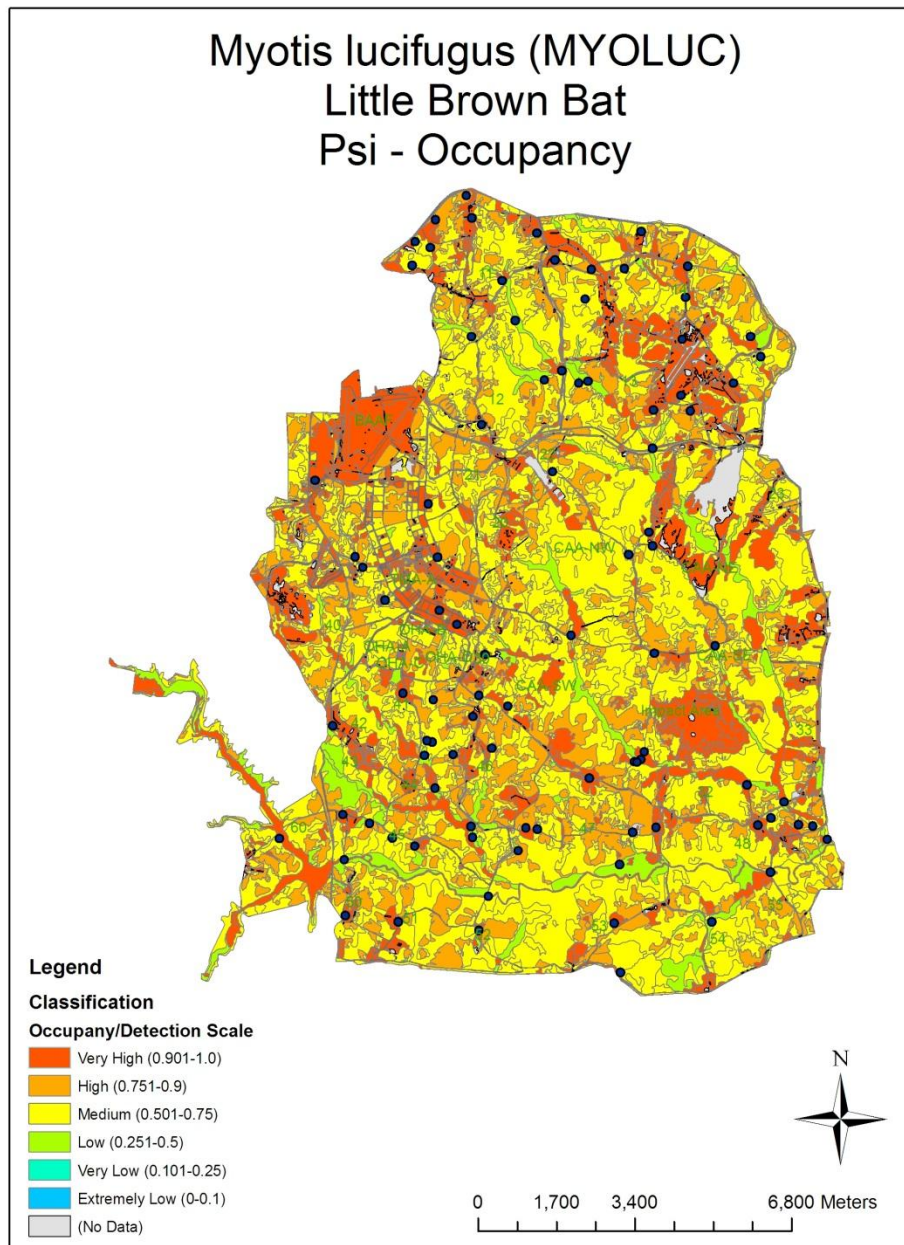


Figure 2.15. Species distribution map for *Myotis lucifugus*, Little brown bat on ARNG-MTC Ft. Pickett, Blackstone, Virginia in 2007. Distributions are represented as the proportion of area occupied (Ψ) based on top species models derived from program PRESENCE (St. Germain 2012).

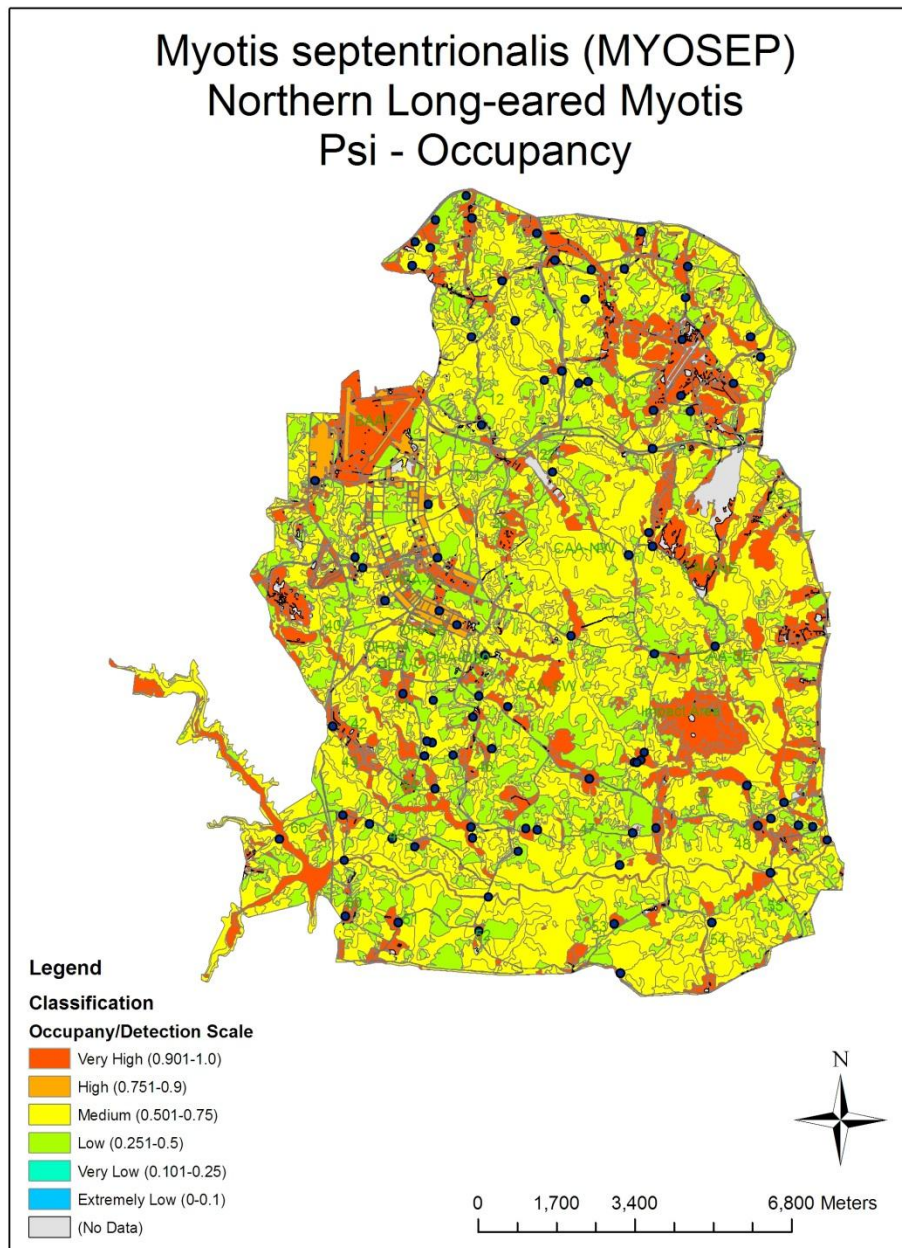


Figure 2.16. Species distribution map for *Myotis septentrionalis* Northern long-eared myotis on ARNG-MTC Ft. Pickett, Blackstone, Virginia in 2007. Distributions are represented as the proportion of area occupied (Ψ) based on top species models derived from program PRESENCE (St. Germain 2012).

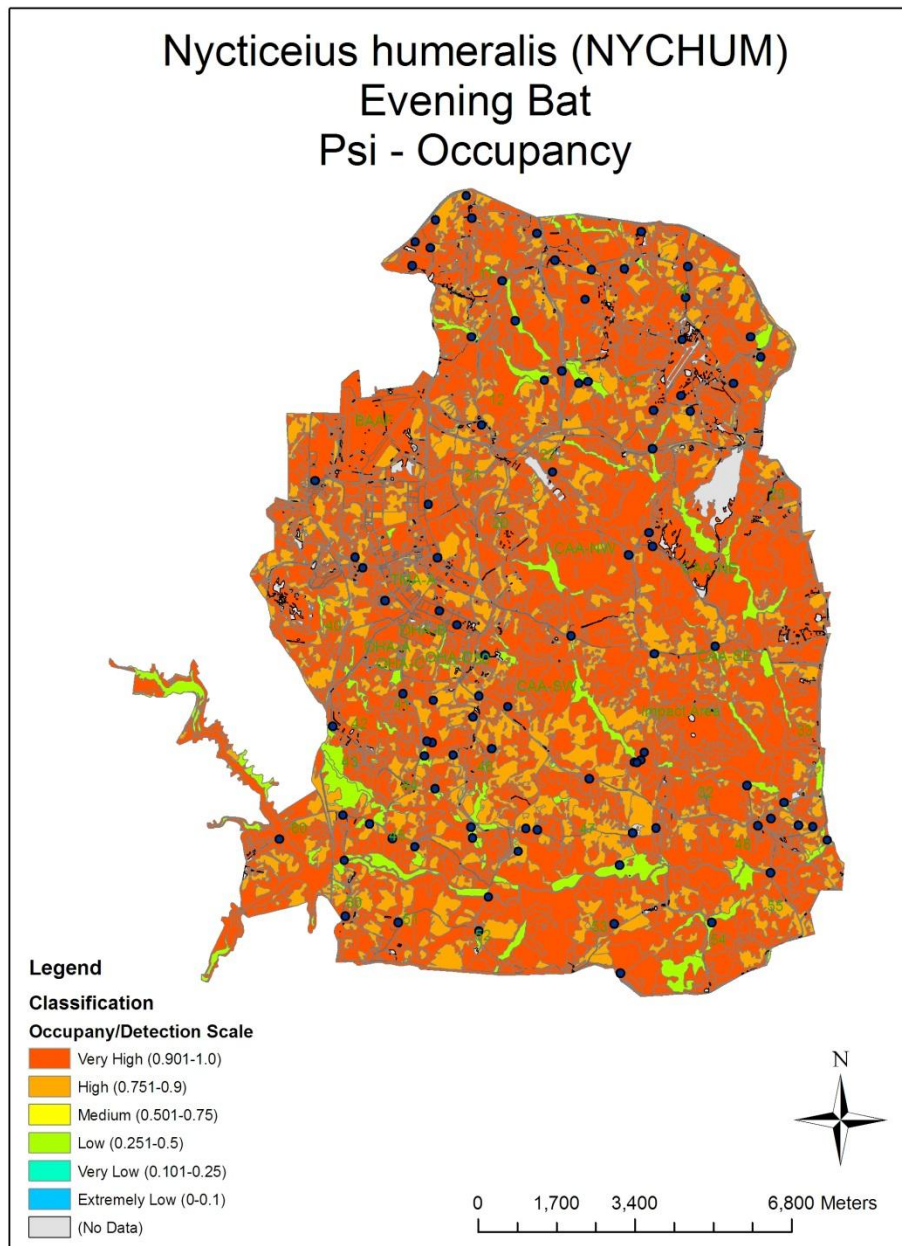


Figure 2.17. Species distribution map for *Nycticeius humeralis* Evening bat dongs on ARNG-MTC Ft. Pickett, Blackstone, Virginia in 2007. Distributions are represented as the proportion of area occupied (Ψ) based on top species models derived from program PRESENCE (St. Germain 2012).

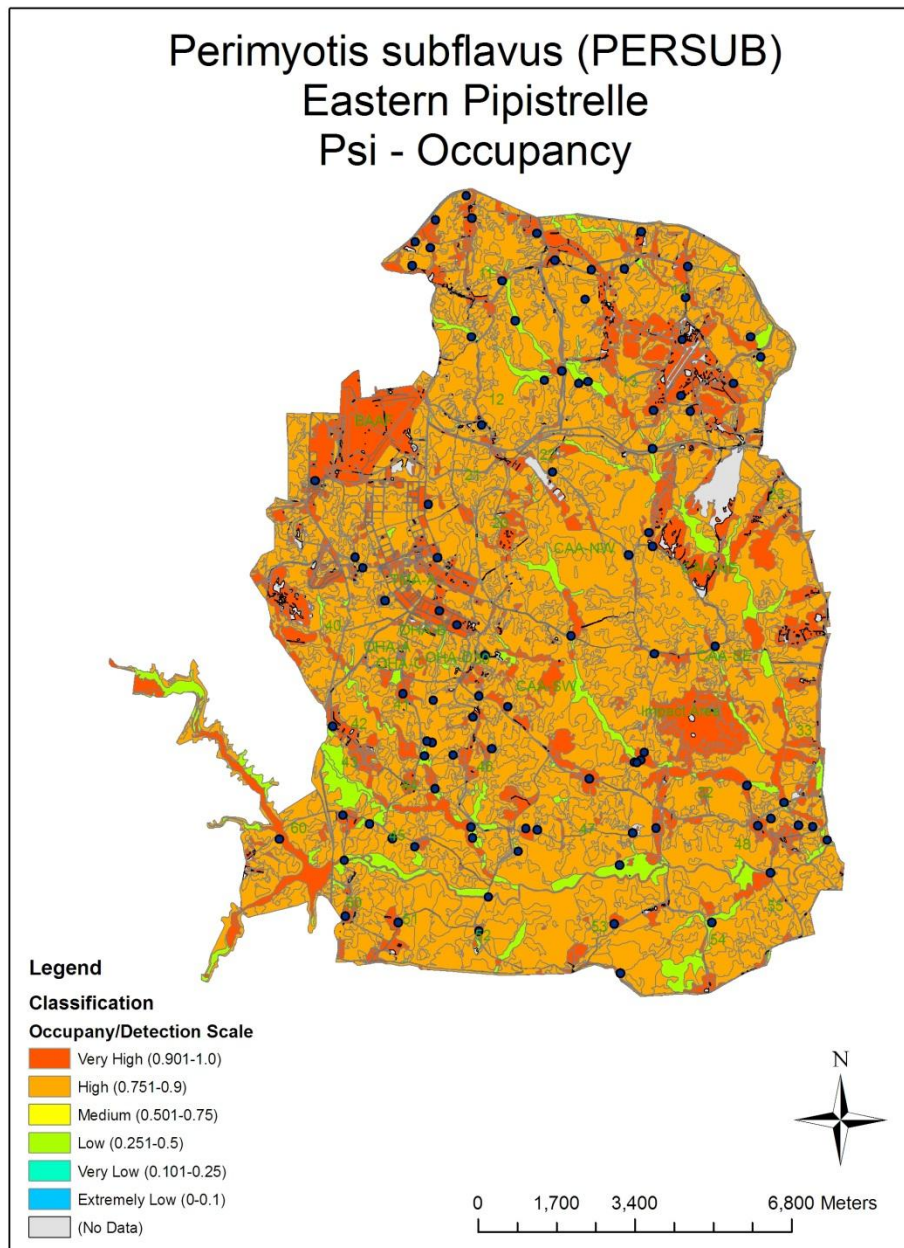


Figure 2.18. Species distribution map for *Perimyotis subflavus* Eastern pipistrelle on ARNG-MTC Ft. Pickett, Blackstone, Virginia in 2007. Distributions are represented as the proportion of area occupied (Ψ) based on top species models derived from program PRESENCE (St. Germain 2012).

Chapter 3

Patterns and Dynamics of Bat Co-occurrence Through Time and Space

“You have to systematically create confusion, it sets creativity free, Everything that is contradictory creates life” -Salvador Dali

ABSTRACT

Understanding species' spatial and temporal activity patterns provides important insight into mechanisms of species coexistence and details of ecological relationships among those species. A species use of time and space can be important in understanding and predicting that species persistence on the landscape. I quantified various scales of spatial and temporal activity patterns for six species of the vespertilionid bat community in a mixed grassland-forested environment of the Virginia piedmont to gain insight on community co-existence ecology. These species include: *Eptesicus fuscus* (Big brown bat), *Lasiurus borealis* (Eastern red bat), *Myotis lucifugus* (Little brown myotis), *Myotis septentrionalis* (Northern long-eared myotis), *Nycticeius humeralis* (Evening bat), and *Perimyotis subflavus* (Eastern pipistrelle). My acoustical sampling array using Anabat acoustical detectors provided an efficient means to sample the entire bat community simultaneously. For the spatial analysis, I used two-species co-occurrence modeling within Program PRESENCE to determine if detection and occupancy were influenced by the presence of co-occurring bats across habitats. For temporal overlap I first used Tukey-Kramer ANOVA of the activity indices to determine if bat activity varied over the 10 hour night. I further examined temporal overlap by creating detection histories at 15 min time intervals and applying kernel density estimation techniques that incorporate utilization distributions to examine bat activity overlap over the 10 hour night. Using

both temporal overlap techniques, I found that bats overlapped extensively in their times of activity. This implies that bats do not use temporal niche partitioning to avoid competition. I also found extensive overlap in spatial habitat use and that bat occurrence was most often positively associated with other bat species at the same location. However, when bats did demonstrate independent occurrence, this occurred primarily when species were morphologically most similar to each other. Therefore, fine scale examination of these bat assemblages revealed that, perhaps when species are very similar the potential for habitat partitioning exists. This study highlights the fact that vespertilinoid bats have extensive overlap in space and time, indicating that perhaps we need to expand our scope of analysis to identify different niche components, such as vertical stratification, that may enable bats to partition resources and thus avoid competition. Conversely, this study site consisted of a mosaic of different habitat types, perhaps allowing bats to co-exist as they switched from one habitat to another. Therefore, maintaining a habitat mosaic could be important component of bat community conservation.

Key words: acoustical detector, activity index, AnaBat, Big brown bat, detection probability, Eastern pipistrelle, Eastern red bat, Evening bat, *Eptesicus fuscus*, *Lasiurus borealis*, military lands, *Myotis lucifugus*, *Myotis septentrionalis*, Northern long-eared myotis, *Nycticeius humeralis*, occupancy, *Perimyotis subflavus*, proportion of area occupied, spatial co-occurrence, species interaction factor, temporal overlapping, two species modeling

INTRODUCTION

Community guild structure has been a long-standing topic of interest among ecologists. A guild, defined as a group of sympatric taxa using similar resources (Root 1967), is characterized by potential interspecific competition (Pianka 1980). This interspecific competition plays an important role in structuring ecological communities (Rosenzweig 1995). Larger species may exclude smaller ones from territories or high value food resources through interference competition (Persson 1985). This interspecific competition may modify a species' choice of resources and lead to niche partitioning (Pimm et al. 1985). These interactions occur both spatially and temporally (Kunz 1973, Rosenzweig 1995).

The observation that local bat faunas are packed, species-rich assemblages usually consisting of morphologically very similar species suggests that competitive niche arrangement might play only a minor role in bat community organization (Arlettaz 1999). These strong morphological similarities in eastern North American bat species is assumed to reflect a similarity of niches, possibly preventing competitive niche partitioning from occurring (Findley and Black 1983, Aldridge and Rautenbach 1987). This view regarding the structure of bat communities (i.e. the lack of niche partitioning) has not been challenged by refined ecological studies (Arlettaz 1999), and in fact, bat community structure has rarely been studied at all. It is also possible that niche partitioning has occurred, but on such a fine scale that is difficult for us to determine the niche dimension. In this respect echolocation studies may well provide insights into the

structure of bat communities (Fenton 1982, Aldridge and Rautenbach 1987, Findley 1993, Arita 1997).

When actively foraging on the landscape bat species are notoriously difficult to study. As result of their small size, nocturnal lifestyle and cryptic nature, direct observation of bats can be problematic. Consequently, these species and their interspecific interactions remain poorly understood. There has been little published information with regard to bat species distribution and activity throughout the night (Thomas and West 1989, Bergallo et al. 2003), and habitat use patterns are poorly understood (Miller et al. 2003, Brooks and Ford 2006). Examination of resource portioning in North American bats has focused primarily on food resources (Kunz 1973, Husar 1976, Hickey et al. 1996) and roost utilization (Swift and Racey 1983). To date, there have not been any published investigations of potential species interactions on free flying bats at the landscape scale.

Acoustic sampling has proven to be an effective means of identifying free flying bat species (O'Farrell 1997, O'Farrell and Miller 1997, O'Farrell et al. 1999a, O'Farrell and Gannon 1999, O'Farrell and Miller 1999, O'Farrell et al. 1999b). The use of ultrasonic detectors is a convenient and efficient method of conducting bat surveys where the main objective is to detect and identify bat species (Thomas 1988, Bettes 1998, Britzke and Murray 2000, Duffy et al. 2000, Larson and Hayes 2000, O'Farrell et al. 2000, Prevett 2002). Although individual identification is not possible with acoustic detection methods, species identification is possible through species-specific call

signatures (see Chapter 1) (Britzke et al. 1999, Britzke 2002, Britzke et al. 2002, Miller 2002). From detection surveys, activity indices for each species can be generated (See Chapter 1) (Miller 2001).

The use of acoustic studies can give insight into species occurrence because the spatial location of the data collected is known. These detector systems typically record the date and time each vocalization is captured, allowing analysis of activity patterns through time. This non-invasive method does not alter the animals' behavior as does the presence of trapping equipment (Rautenbach et al. 1996, Kalko 1997, O'Farrell and Gannon 1999, Duffy et al. 2000) and hence provides an unimpeded assessment of activity of bat species throughout the course of an entire evening.

A simple presence-absence matrix of species occurrence in spatial units has been termed the fundamental unit of analysis of community ecology and biogeography (Gotelli 2000). This information, however, has historically been difficult to interpret because animal detectability is not constant in space or time and previous studies assumed equal and complete detectability ($p = 1$). This potentially results in a negative bias in estimation of species presence especially if detection probabilities ($p < 1$) are not taken into consideration (Vojta 2005). Recent models that incorporate detection probabilities that are < 1.0 have been developed and used to predict occupancy across a landscape. Such models require a determination of detection probabilities by making thorough repeated visits to a site where a species may be detected (MacKenzie et al. 2002) and building a detection-nondetection encounter history for each site.

This occupancy approach has been expanded beyond analysis of single species occurrence across a landscape, to examine co-occurrence of species at a landscape scale. MacKenzie et al. (2004, 2006) developed a flexible, likelihood-based, two-species occupancy model that accounts for imperfect detections while including probabilities that a second species present at a site influences the occupancy of the first species. The model directly estimates a species interaction factor (SIF or ϕ) that is a ratio of how likely the two species are to co-occur compared to what would be expected under a hypothesis of independent occurrence. This two-species occupancy model has been used to examine co-occurrence patterns of terrestrial salamanders (MacKenzie et al. 2004), vipers (Luiselli 2006), owls (Bailey et al. 2009), rails (Richmond et al. 2010), and tigers (Sunarto 2011). To date, such an analysis has never been performed for bats. In addition to providing unbiased estimates of co-occurrence and occupancy, the models also can be used to examine how the presence or detection of one species might affect the detection probability of the other.

Another important component for investigating species interactions is temporal co-occurrence. This niche overlap can be characterized by examining the coefficient of overlap (Δ) through time (Hurlbert 1978). Because acoustical studies provide data on capture times, patterns of temporal overlap can be quantified. Treating the capture times as random samples from underlying continuous distributions, probability density functions can be generated. This coefficient of overlap is produced nonparametrically using a kernel density estimate (Schmid and Schmidt 2006). Precision of the estimator of

overlap is projected by bootstrapping. These measures of temporal co-occurrence and overlap have been used to infer temporal patterns of tropical sympatric felid species (Ridout and Linkie 2009, Sunarto 2011), and Malagasy civets (Gerber 2010).

By using a series of remote acoustical detectors, I set out to examine interspecific spatial and temporal co-occurrence of sympatric vespertilionid bat species found within mixed forest-grassland environment in central Virginia. These species include: *Eptesicus fuscus* (big brown bat), *Lasiurus borealis* (eastern red bat), *Myotis lucifugus* (little brown myotis), *Myotis septentrionalis* (northern long-eared myotis), *Nycticeius humeralis* (evening bat), and *Perimyotis subflavus* (eastern pipistrelle). Understanding the role of inter-specific competition and resource partitioning, which are important processes shaping community structure, will enhance effective management and of this wildlife community.

A Priori Hypothesis

Habitat use by bats often varies among species depending on their body size, wing morphology, foraging mode, and echolocation call structure (Aldridge and Rautenbach 1987, Patterson et al. 2003). I used this natural history information to construct *a priori* hypothesis concerning factors influencing species co-occurrence (Figure 3.1). In general I expect species with morphological characteristics suited to open spaces (e.g. high wing loading, low frequency and low modulation echolocation) to occur in different locations than those more suited to cluttered environments (e.g. low wing loading, steep higher frequency echolocation). I also hypothesize that the more similar the bat species'

morphology, the more likely they will co-occur in space, but also the more likely they are to exhibit temporal partitioning as a means for avoiding competition.

STUDY SITE

Army National Guard Maneuver Training Center (ARNG-MTC) Fort Pickett is located in the Nottoway drainage of lower Piedmont in southeastern Virginia (Figure 1.1). The army base is adjacent to the community of Blackstone, Virginia, within the counties of Brunswick, Dinwiddie, and Nottoway. Fort Pickett is approximately 36 km (22 mi) from the fall line where the Piedmont physiographic region turns into the Coastal Plain physiographic region. It consists of 41,690 acres (16,870 ha) of both open and forested live-fire and maneuver training lands (Figure 1.2). Stratified random sampling locations (n=87) were distributed across the installation (Figures 2.1, 2.2).

METHODS

Acoustic Bat Detection

For ultrasonic acoustic detection, I used a remotely mounted microphone connected to the Anabat II detector and Compact Flash-Zero Crossing Analysis Interface Module (CF-ZCAIM) (Titley Electronics, Ballina, New South Wales, Australia). These units were programmed to turn on 30 min prior to civil twilight and turn off 30 min after civil sunrise. The sampling locations were chosen at random, however the microphone was placed within 30 m of the locations with the objective of capturing as many calls as possible (e.g. Hayes and Hounihan 1994). The microphone placement was ~1.4 meters off the ground, and oriented in the direction of fewest trees (Weller and Zabel 2002) at a

~45° angle (Duffy et al. 2000). The Anabat units were calibrated each season for sensitivity and set at the respective sensitivity level of ~6. All acoustic emissions were recorded to the internal compact flash card with a date and time stamp on each file. All recorded calls were transferred from the CF cards to desktop computer for identification and analysis. The Scan utility function of the AnaLookW (Beta version 3.2h dated 25 August 2005) software (Corben 2005) and constructed filters was used for species identification.

I sampled each of the six major habitat types on Fort Pickett. These types include: Coniferous forest (CF) (n=15), Developed Areas (DA) (n=7), Deciduous Forests (DF) (n=16) Forested Wetlands (FW) (n=14), Grassland / Shrublands (GS) (n=21), and Wetlands with surface water present (WL) (n=14) for a total of n=87 sites (Figure 2.1). Detailed descriptions of habitat types are provided in Appendix A. I used 10 remote detectors for this study. I deployed one detector in each of the habitat types for 3-12 nights per sample. These 3-12 nights were considered the “encounter occasions” in occupancy modeling. Multiple nights of sampling provided an assessment of temporal variation among habitats. To compare differential habitat use, each habitat type was sampled simultaneously to account for temporal variation (Williams et al. 2006). This sampling bout was repeated 2-3 times throughout the season. All acoustical data were summarized into an activity index and detection / non-detection histories were created at various temporal scales. Analysis is derived from data collected between 08 June and 25 August 2007.

Spatial Activity

Bat activity was summarized for each species by an acoustic activity index (AI – see Chapter 1) (Miller 2001). This is the summation of one minute time blocks that a species was detected during a sampling event, standardized to 10 hours. The sampling event is considered one night of survey. The total number of sites examined was 87 over 596 nights for analysis. Analysis of variance (ANOVA) was used to examine activity levels among habitats and species (SYSTAT v13.1). Pairwise comparisons based on the ANOVA using Tukey-Kramer analysis ($\alpha=0.05$ denoting significance) with bonferroni correction indicate where the differences occur.

Flyways were categorized as potential pathways and travel corridors that facilitate movement. These flyway types were classified for each sampling location. The categories are: None (N) typically a forested environment with no apparent flyway, Open (O) open areas such as grassland, shrublands or sparse woodland, Road (R), road, two-track or armor access, Stream (S), stream corridor, Open Water (W) typically a pallustrine or lacustrine system. The same data set used to compare the activity by each habitat type was used for flyway analysis. Each species' acoustic activity index was compared using a analysis of variance comparison for within species flyway use (SYSTAT v13.1). Tukey-Kramer ANOVA ($\alpha=0.05$) was used to examine activity levels for between species comparisons (SYSTAT v13.1). Bonferroni corrected pairwise comparisons based on the ANOVA indicate significant differences.

The spatial activity analyses conducted above for both habitat and flyway use do not consider detection probabilities in their estimations. Rather they are direct summaries of bat presence from the acoustical data, however these data still give us insight into bat activity levels and allow us to compare results to the more in-depth analysis below that incorporates detectability.

Temporal Activity

I summarized temporal activity levels for each species into 1-hour time blocks following the acoustic activity index suggested by (Miller 2001). Time blocks started at 2200 hours and ended at 0600 hours for a total of 10, 1hr blocks per evening. The overall activity was summarized for each species and then further examined by each habitat type for each species. Tukey-Kramer ANOVA was used to examine activity levels between species (SYSTAT v13.1). Pairwise comparisons based on the ANOVA will indicate where significant differences occur.

Similar to the spatial activity, the temporal activity patterns analysis above does not incorporate detection probabilities in the analysis. These data represent summaries of direct observations of acoustical data and allows us to compare results to the more in-depth analysis below that incorporates detectability.

Spatial co-occurrence

I investigated the potential impacts of bat species upon each other or species co-occurrence (termed “co-bats” in the model) following the two-species co-occurrence methods incorporating detection probabilities (p) suggested by (MacKenzie et al. 2004) and implemented in program PRESENCE v4.1 (Hines 2005). This analysis may give evidence of intraspecific competition (i.e. whether one species’ presence has an influence on the presence of another species). These examinations were conducted for every possible combination of the six species. There are three possible biological hypothesis that this model has the capacity of testing (MacKenzie et al. 2006): a) do the two species co-occur more or less frequently than expected by chance alone, b) at locations of co-occurrence, are species detections independent from each other, and c) does the detection of one species depend on the presence of another species.

Using two-species second parameterization models (Richmond et al. 2010), I estimated ϕ , or the Species Interaction Factor (SIF). I considered the two species to be avoiding each other spatially if the value of $\phi < 1$ and the 95% confidence intervals did not overlap 1. I considered that they co-occurred more frequently than expected by chance when $\phi > 1$ and the 95% confidence intervals did not overlap 1. The two species were considered to occur spatially independently if the 95% confidence intervals overlapped $\phi = 1$ (MacKenzie et al. 2006) or if the best model was the once where ϕ was fixed at 1 (see below).

I followed the procedures suggested by MacKenzie (2006) to evaluate the degree of support for these competing hypothesis. This was conducted by developing two different models and formally comparing their performance based on the different AIC values (Burnham and Anderson 1998, Franklin et al. 2001). Models that estimated the species interaction factor (ϕ not fixed to 1) were considered to have strong support and were concluded to perform better than the constant model (ϕ fixed at 1) when the ΔAIC was >2.0 . Models with $\Delta AIC < 2.0$ were considered to be competing with respect to the support for evidence (Burnham and Anderson 2004). The first model was a full model where each of the three parameters, the probability that the site is occupied by species A (Ψ^A), the probability the site is occupied by species B (Ψ^B), and ϕ was estimated. The second model estimated both Ψ^A and Ψ^B while ϕ was set equal to 1 (representing spatial independence). Then for each model above, I evaluated four different potential scenarios that assume detection probability (p) as either: a) equal and independent (E&I), b) equal and non-independent (E&NI), c) non-equal and independent (NE&I), d) non-equal and non-independent (NI&NE). The best model from those scenarios was selected (based on AIC and consideration of any indications of error such as convergence failure or inability to calculate standard errors) and used to estimate the Species Interaction Factor (SIF, ϕ) between pairs of bat species.

To assess the spatial co-occurrence on a finer scale, I treated each acoustic sampling location as the sampling unit or site and created detection/non-detection histories for each sampling unit at 15 minute intervals throughout the night. Then, I selected 1 night at random from each of the 87 sampling units representing a total of 40

sampling events (e.g 40, 15 minute time blocks) per site to analyze all bat species at the night and site. I was unable to break down the species co-occurrence models by habitat type due sample sizes being too small at the within habitat scale.

Temporal co-occurrence

I focused the investigation of temporal co-occurrence interactions between felid species based on their nightly activity patterns. I used a kernel density estimation technique to characterize the activity pattern for each species and calculated the coefficient of overlap (Δ) between species (Ridout and Linkie 2009, Sunarto 2011). I employed the Ridout and Linkie (2009) equation 3.1 kernel estimator and examined three smoothing parameters (c) of 0.25, 1.0, and 1.25 to calculate the coefficient of overlap between species in program R (R-Development-Core-Team 2008). I examined all six species individually for each smoothing factor. A smoothing factor of $c=1.0$ was chosen to examine the kernel density estimate because I had sample sizes ≥ 50 (Gerber 2010, Sunarto 2011). The kernel density estimates were compared for each possible paired combination of bat species to determine the coefficient of overlap (Δ).

To assess this temporal co-occurrence, I used the same data set employed in the spatial co-occurrence models described above partitioned to the 15 minutes intervals. The framework for this analysis required the detection data to be transformed by time of capture at 15 minute intervals and scaled from 0 to 1.

RESULTS

Summary of Effort

From 08 June to 25 August 2007 at 87 sites, I collected 240,189 bat call files with 11,680 hours (1168 nights total) of acoustic monitoring. The 2007 acoustical survey data were used for all data analyses presented herein. Depending on the data structure for the appropriate analysis this represented up to 32,626 unique observations.

Spatial Activity

Bat activity was summarized for within-species comparisons by each habitat and flyway (Table 3.1). Results derived from the Wilcoxon signed rank test showed significant differences for within-species bat activity across habitats ($F = 3.358$, $p = 0.002$). Tukey-Kramer ANOVA revealed a difference in species activity patterns among the habitats types ($F = 3.844$, $p = 0.002$). *Ad hoc* hypothesis tests using nonparametric Tukey-Kramer pairwise comparisons for each species further explained the significance. Overall the developed areas and open water wetlands showed significantly higher levels of bat activity compared to the other habitats sampled. Three of the six species, *Lasiurus borealis*, *Myotis lucifugus*, and *Nycticeius humeralis* had significantly higher activity levels for both of these habitats. Activity levels were higher for *Eptesicus fuscus* in the developed areas, and both *Myotis septentrionalis* and *Perimyotis subflavus* for open water wetlands.

Five species, *Lasiurus borealis*, *Myotis lucifugus*, *Myotis septentrionalis*, *Nycticeius humeralis* and *Perimyotis subflavus* all had significantly higher levels of

activity over open water flyway types ($F = 3.829$ $p = 0.002$). *Eptesicus fuscus* was the exception whose higher levels of activity occurred in open areas and along roads. Both *Myotis lucifugus*, and *Perimyotis subflavus* exhibited significantly lower activity levels where no apparent flyway was available.

Results from ad hoc Tukey-Kramer pairwise comparisons performed between species by habitat and flyway types are described below in the species-specific sections and statistical test results can be found in Table C-1, Appendix C.

Temporal Activity

Using an average activity index for each species summarized into 1 hour intervals indicated when each species was active throughout the night (Figure 3.2). In general, when examining all habitats combined, all species showed higher levels of activity occurring just after dusk (~8:00pm) peaking at 9:00pm. Activity levels remained constant for four of the six species throughout the rest of the evening. The exception to this general pattern was found for *Myotis lucifugus* and *Nycticeius humeralis* where a spike in activity occurred the last hour before sunrise, 5:00 - 6:00 am. Differences in temporal activity began to emerge when investigating each species by habitat type (Figure 3.3). These patterns and results of the post hoc pairwise comparisons (Table C-1, Appendix C) will be described in further detail in the species specific sections below.

Spatial co-occurrence

All 15 combinations of species interactions showed superiority in models that assume detection between species as not equal and non-independent (NE&NI) (Table 3.2). Candidate models for each combination of bat spatial co-occurrence are provided in Tables D-1 to D-15 in Appendix D.

Based on the point estimates of the species interaction factor with a value of $\phi > 1$, and 95% confidence limits not overlapping 1.0, six possible pairs of bat species out of a total of 15 possible combinations co-occurred more frequently than expected from independent distributions (Figure 3.4). Additionally, the comparison of *Myotis septentrionalis* to *Perimyotis subflavus* failed to generate a standard error for ϕ , yet there was evidence supporting co-occurrence between these species in model runs as $\phi = 1.42$, ΔAIC 6.74. Therefore potentially 7 of 15 interactions demonstrated co-occurrence with 5 of these co-occurrences due to *Myotis septentrionalis* spatially co-occurring with all other species. In addition to those co-occurrences, *Eptesicus fuscus* also co-occurred with 2 other species: *Lasiurus borealis* and *Perimyotis subflavus*. The remaining 8 interactions showed independence and no interactions showing avoidance or co-occurrence less frequently than expected by chance. This indicates that all bat species tended to maintain spatial coexistence rather than exhibit spatial exclusion.

Out of the 15 possible pairwise bat species comparisons, excluding the one that failed to generate a standard error, 13 showed strong support for the top model with a $\Delta AIC > 2.0$ for the next best models. Only the *Eptesicus fuscus* to *Nycticeius humeralis*

model of independence $\phi = 1.15$ (0.99-1.33) had a competing $\Delta AIC = 1.8$ as compared to the model where ϕ was fixed to 1. For either model, results indicate spatial independence between the 2 species.

Only 3 combinations of species interactions for the co-occurrence occupancy models had the strongest support when ϕ was fixed at 1.0 (i.e. considered independent (I)) (Table 3.2). These interactions included *Myotis lucifugus* to both *Eptesicus fuscus* and *Nycticeius humeralis*, and *Lasiurus borealis* to *Perimyotis subflavus*. The remaining combinations showed the strongest model to be non-equal detection even if the co-occurrence was considered independent ($\phi=1$).

Temporal co-occurrence

All smoothing parameters ($c = 0.25, 1.0, 1.25$) in KDE analysis produced consistent results (Figure 3.5) and I used $c = 1.0$ for pairwise species analyses. I found that all combinations of species interactions had high levels of overlap (Figure 3.6). The lowest observed value was $\Delta = 0.86$ (SE = 0.03) for *Eptesicus fuscus* and *Nycticeius humeralis* whereas the highest observed value was between *Nycticeius humeralis* and *Myotis lucifugus* at $\Delta=0.97$ (SE=0.02).

Individual species spatial and temporal occurrence relative to other bats

Because of the numerous complex comparisons conducted, I separated each species to highlight the major findings from the spatial and temporal activity and co-

occurrence analyses. A summary of all of the results from pertinent analysis performed is presented in a species comparison matrix in Figure 3.7.

Eptesicus fuscus (Big brown bat)

Eptesicus fuscus had lower activity levels overall ($\bar{x}=6.19 \pm 2.15$) than all other species examined except *Nycticeius humeralis*. *Eptesicus fuscus* also exhibited higher activity levels in the developed areas compared to the other habitats examined. Higher activity levels were also observed in open areas and along roads (Table 3.1). For pairwise comparisons of species within the different habitat types, I found no difference between *Eptesicus fuscus* and all other species in the coniferous forest; significantly higher activity levels compared to *Myotis septentrionalis* ($p=0.014$) in the developed areas; lower levels compared to *Myotis lucifugus* ($p<0.002$) and *Nycticeius humeralis* ($p=0.005$) in the deciduous forests; lower levels compared to *Perimyotis subflavus* ($p=0.001$) in the forested wetlands; lower levels compared to *Myotis lucifugus* ($p=0.005$) but higher levels than *Myotis septentrionalis* ($p=0.004$) in the grassland/shrubland complex; and finally lower levels than *Lasiurus borealis* ($p<0.000$), *Myotis lucifugus* ($p=0.02$), *Myotis septentrionalis* ($p<0.000$), and *Perimyotis subflavus* ($p<0.000$) in the open water wetlands (Appendix D).

The overall temporal activity for *Eptesicus fuscus* showed slightly higher levels around 09:00 pm and then a gradual tapering off until dawn (Figures 3.2, 3.3, & 3.6). When examined at the habitat level (Figure 3.4), temporal activity levels showed an early emergence spike (09:00 pm) in the developed areas then a steady decline with another

small peak just before dawn (04:00 am). A similar, early evening pattern occurred in the grassland shrubland complex with a steady decline as the night progressed.

Each species was compared to the 5 other co-bats. Based on two-species occupancy models (Table 3.2, Figure 3.4, Appendix D) spatial co-occurrence ($\phi > 1$) was shown for *Eptesicus fuscus* more often than expected at random with *Lasiurus borealis* ($\phi = 1.30$ (1.11-1.53)), *Myotis septentrionalis* ($\phi = 1.50$ (1.21-1.88)), and *Perimyotis subflavus* ($\phi = 1.34$ (1.15-1.57)). Spatial independence ($\phi = 1$) was found with *Myotis lucifugus* ($\phi = 1$ (fixed)) and *Nycticeius humeralis* ($\phi = 1.15$ (0.99-1.33)). For all interactions with *Eptesicus fuscus* the detection probability was not equal and non-independent (NE & NI). Based on $\Delta AIC > 2$ there was strong support for all the interactions except with *Myotis lucifugus*, which had a competing model that also indicated spatial independence, with ϕ fixed at 1.

KDEs for temporal overlap (Δ) were similar to the previous, simpler temporal activity analysis and displayed high levels of overlap for all species pairwise comparisons ranging from $\Delta = 0.86$ SE=0.03 to $\Delta = 0.92$ SE=0.02) (Figure 3.6). The lowest overlap for *Eptesicus fuscus* occurred with *Nycticeius humeralis* ($\Delta = 0.86$ SE=0.03) and the highest with *Lasiurus borealis* ($\Delta = 0.92$ SE=0.02).

Lasiurus borealis (Eastern red bat)

Lasiurus borealis exhibited statistically higher activity levels ($\bar{x} = 15.64 \pm 2.64$) than *Eptesicus fuscus* ($p = 0.002$) for all habitats, but no statistical differences were found

for comparisons with the other four species. *Lasiurus borealis* had the highest activity level over open water wetlands followed by the next highest activity levels in the developed areas. Examination of flyway use revealed that most *Lasiurus borealis* activity occurs over open water as compared to streams, roadways, or other potential flight pathways (Table 3.1).

Lasiurus borealis exhibited no differences in activity levels compared to other species in the coniferous forests, developed areas, deciduous forests or forested wetlands. *Lasiurus borealis* did exhibit lower activity levels than *Myotis lucifugus* ($p=0.014$) and higher levels than *Myotis septentrionalis* ($p=0.001$) in the grasslands and shrublands, and higher levels of activity compared to *Eptesicus fuscus* ($p<0.000$) and *Nycticeius humeralis* ($p=0.050$) in the open water wetlands.

The overall temporal activity for *Lasiurus borealis* followed a slight bimodal distribution with a peak taking place around 09:00 pm and then other at 02:00 am however there was no statistical difference through the night (Figures 3.2 & 3.5). Broken down by habitat type however, significantly higher levels for this bimodal distribution occurred only over open water wetlands (Figure 3.3).

Results from the two-species occupancy models (Table 3.2, Figure 3.4, Appendix D) revealed spatial co-occurrence ($\phi>1$) between *Lasiurus borealis* and *Eptesicus fuscus* ($\phi= 1.30$ (1.11-1.53)) and *Myotis septentrionalis* ($\phi= 1.48$ (1.28-1.79)). Spatial independence ($\phi=1$) was demonstrated for *Myotis lucifugus* ($\phi= 1.18$ (0.94-1.49)), and

Nycticeius humeralis ($\phi = 1.19$ (0.89-1.57)), and *Perimyotis subflavus* ($\phi = 1$ (fixed)). For all *Lasiurus borealis* interactions the detection probability was not equal and non-independent (NE & NI). Based on $\Delta AIC > 2$ there was strong support for those top models.

Temporal overlap (Δ) between *Lasiurus borealis* was high in all interactions (Figure 3.6). The lowest overlap occurred with *Eptesicus fuscus* ($\Delta = 0.90$ SE=0.02) and the highest with *Perimyotis subflavus* ($\Delta = 0.95$ SE=0.02).

Myotis lucifugus (Little brown myotis)

Myotis lucifugus had statistically higher activity ($\bar{x} = 15.43 \pm 2.43$) than *Eptesicus fuscus* ($p = 0.002$) for all habitats, but there was no statistical support for activity differences with the other four species. Partitioned down by habitat, higher activity levels were found in the developed areas but only statistically significant higher levels occurred in the open water wetlands (Table 3.1). *Myotis lucifugus* tended to be more active over open water and less active where there was no apparent flyway as compared to open areas, roads or stream corridors. Pairwise comparisons in the different habitat types (Appendix D) revealed no activity differences for *Myotis lucifugus* compared to other species in the coniferous forests and forested wetlands, but higher levels than *Eptesicus fuscus* ($p = 0.002$) and *Myotis septentrionalis* ($p = 0.007$) in the deciduous forests; higher levels than *Eptesicus fuscus* ($p = 0.005$), *Lasiurus borealis* ($p = 0.014$), and *Myotis septentrionalis* ($p = 0.007$) in the grasslands shrublands; higher levels than *Eptesicus fuscus* ($p < 0.000$), but lower levels than *Myotis septentrionalis* ($p = 0.005$) and *Perimyotis subflavus* ($p < 0.000$) in open water wetlands.

The activity pattern for *Myotis lucifugus* followed a bimodal distribution with the first peak arising around 09:00 pm and spiking again just before dawn at 05:00-06:00 am (Figures 3.2 & 3.5). When examining the temporal activity at the habitat level (Figure 3.3), a tri-modal distribution was identified in the open water wetlands where the majority of the activity was taking place. Peaks were at 09:00 pm, 01:00 am, and 05:00 am, although statistical evidence did not support this. The second highest level of activity in the developed area had a peak between 01:00 and 02:00 am. An observation of interest was the significant spike in activity in the grassland shrubland areas from 05:00 to 06:00 am. Where these last 2 significant?

Evidence from two-species occupancy models (Table 3.2, Figure 3.4, Appendix D) revealed spatial co-occurrence ($\phi > 1$) between *Myotis lucifugus* and *Myotis septentrionalis* ($\phi = 1.32$ (1.10-1.58)). The remaining interactions showed spatial independence ($\phi = 1$). For all *Myotis lucifugus* interactions investigated the detection probability was not equal and non-independent (NE & NI). Based on $\Delta AIC > 2$ the top models had strong support.

KDEs for temporal overlap (Δ) exhibited high levels for all species comparisons (Figure 3.6). The lowest overlap for *Myotis lucifugus* occurred with *Eptesicus fuscus* ($\Delta = 0.88$ SE=0.03) and the highest with *Nycticeius humeralis* ($\Delta = 0.97$ SE=0.02).

Myotis septentrionalis (Northern long-eared myotis)

Myotis septentrionalis demonstrated an overall activity level ($\bar{x}= 14.58\pm4.86$) statistically greater than *Eptesicus fuscus* ($p=0.009$) and lower than *Perimyotis subflavus* ($p=0.055$). Significantly higher levels occurred over open water wetlands than any other habitat or flyway (Table 3.1). Pairwise species comparisons in the different habitat types revealed no differences in activity compared to other species in the coniferous forests and forested wetlands. *Myotis septentrionalis* did have higher levels than *Eptesicus fuscus* ($p=0.014$) but lower levels than *Myotis lucifugus* ($p=0.01$) in the developed area: lower levels than *Myotis lucifugus* ($p=0.007$) and *Nycticeius humeralis* ($p=0.015$) in the deciduous forest, lower levels than all species in the grasslands and shrublands; and higher levels than *Eptesicus fuscus* ($p<0.000$), *Myotis lucifugus* ($p=0.005$), and *Nycticeius humeralis* ($p<0.000$) in open water wetlands.

The activity pattern for *Myotis septentrionalis* peaked near 09:00 pm and then tapered off until 12:00 am where it remained constant until the dawn (Figures 3.2& 3.5). This pattern was driven by the open water wetland habitat where the species exhibited significantly higher activity than the other habitats which had minimal activity (Figure 3.3).

The two-species occupancy models (Table 3.2, Figure 3.4, Appendix D) for *Myotis septentrionalis* showed spatial co-occurrence ($\phi>1$) with all species. It should be noted that the interaction between *Myotis septentrionalis* and *Perimyotis subflavus* failed

to generate a standard error ($\phi = 1.42$ (n/a)), however there is some evidence these species also co-occur due to $\phi > 1.0$; ΔAIC 6.74.

KDEs for temporal overlap (Δ) revealed overall high levels of overlap with all other species (Figure 3.6). The lowest overlap for *Myotis septentrionalis* occurred with *Eptesicus fuscus* ($\Delta=0.88$ SE=0.03) and the highest with *Myotis lucifugus* ($\Delta=0.94$ SE=0.02).

Nycticeius humeralis (Evening bat)

Nycticeius humeralis exhibited an overall activity level ($\bar{x} = 12.12 \pm 1.93$) for all habitats that was significantly lower than *Perimyotis subflavus* ($p=0.002$) but not statistically different from all other species. *Nycticeius humeralis* activity levels were statistically higher in developed areas and even higher for open water wetlands compared to other habitats sampled (Table 3.1). The most active flyway type was over open water. Based on pairwise comparisons by habitat type (Appendix D) there were no differences in activity levels in coniferous forests, developed areas, and forested wetlands compared to the other five species. *Nycticeius humeralis* displayed higher activity levels than *Eptesicus fuscus* ($p=0.005$) and *Myotis septentrionalis* ($p=0.015$) in the deciduous forest; higher activity than *Myotis septentrionalis* ($p<0.000$) in the grasslands shrublands, and lower levels than *Lasiurus borealis* ($p=0.05$), *Myotis septentrionalis* ($p<0.000$), and *Perimyotis subflavus* ($p<0.000$) in the open water wetlands.

Nycticeius humeralis followed a strikingly similar pattern to that of *Myotis lucifugus* which followed a bimodal distribution. The first peak of activity occurred around 09:00 pm and the second just before the dawn at 05:00-06:00 am (Figures 3.2 & 3.5). When examining the temporal activity at the habitat level (Figure 3.2), a slightly more pronounced tri-modal distribution was identified in the open water wetlands where the majority of the activity was taking place. Peaks were at 09:00 pm, 01:00 am, and 05:00 am, although statistical tests did not reveal significant differences. The second highest level of activity in the developed area had a peak between 01:00 and 02:00 am. Again an observation of interest was the significant spike in activity in the grassland/shrubland areas from 05:00 to 06:00 am.

The two-species occupancy models for *Nycticeius humeralis* (Table 3.2, Figure 3.4, Appendix D) revealed co-occurrence with *Myotis septentrionalis* ($\phi = 1.33$ (1.12-1.58)). All remaining interactions resulted in spatial independence ($\phi = 1$). Based on ΔAIC there was strong support for the top models and all detection probability comparisons to *Nycticeius humeralis* were not equal and non-independent (NE & NI).

Temporal overlap resulting from kernel density estimates (Δ) was high overall in all species comparisons (Figure 3.6). The lowest overlap for *Nycticeius humeralis* occurred with *Eptesicus fuscus* ($\Delta = 0.86$ SE=0.03) and the highest with *Myotis lucifugus* ($\Delta = 0.97$ SE=0.02).

Perimyotis subflavus (Eastern pipistrelle)

Perimyotis subflavus activity level ($\bar{x}=21.51\pm4.69$) was significantly higher than *Eptesicus fuscus* ($p<0.000$) and *Nycticeius humeralis* ($p=0.002$). *Perimyotis subflavus* was significantly more active in the open water wetlands than in any other habitat (Table 3.1). They utilized the open water flyway type significantly more than open types, roads, or stream corridors, but significantly less than areas where there was no flyway present. Activity levels did not differ from the other species in coniferous forests, developed areas, deciduous forests. But activity levels were significantly higher for *Perimyotis subflavus* compared to *Eptesicus fuscus* ($p=0.001$) in the forested wetlands, *Myotis septentrionalis* ($p<0.000$) in the grasslands/shrublands, and all species in the open water wetlands.

The activity patterns of *Perimyotis subflavus* were similar to *Lasiurus borealis* with generally higher activity levels compared to the other species. The pattern followed a slight bimodal distribution with a peak taking place around 09:00 pm and then other at 02:00 am, however, there was no statistical difference through the night except for the early emergence period (Figures 3.2 & 3.6). Significantly higher levels for this bimodal distribution occurred over open water wetlands compared to other habitats (Figure 3.3). Peaks were shown to occur between 09:00 pm and 10:00 pm and again at 02:00 am and 04:00 am, however again there was no statistical support for these differences within this habitat type. There was a slight but significant increase in activity over the grasslands/shrublands just prior to dawn.

Results from the two-species occupancy models for *Perimyotis subflavus* (Table 3.2, Figure 3.4, Appendix D) revealed spatial co-occurrence ($\phi > 1$) with *Eptesicus fuscus* ($\phi = 1.34$ (1.15-1.57)). The interaction model between *Myotis septentrionalis* and *Perimyotis subflavus* failed to generate a standard error ($\phi = 1.42$ (n/a)), however there is some evidence these species also co-occur compared to the model where ϕ is fixed at 1.0, ΔAIC 6.74. All detection probabilities for *Perimyotis subflavus* species interactions were not equal and non-independent (NE & NI). There was strong model support based on ΔAIC for all the top models, those with $\Delta AIC = 0.00$ and $\phi \neq 1.0$ were competing with those where ϕ was fixed to 1.

Kernel density estimates for temporal overlap for *Perimyotis subflavus* (Δ) revealed overall high levels of overlap with all species (Figure 3.6). The lowest overlap for *Perimyotis subflavus* occurred with *Myotis septentrionalis* ($\Delta = 0.90$ SE=0.03) and the highest with *Lasiurus borealis* ($\Delta = 0.95$ SE=0.02).

DISCUSSION

Understanding species' spatial and temporal activity patterns provides important insight into mechanisms of species coexistence and details of ecological relationships between those species. How animals use time and space also is important in understanding and predicting how species can persist on the landscape. This is particularly important in changing landscapes, especially in light of potential climate change, and for species whose populations levels are threatened by outside factors such as energy production and fungal pathogens (Arnett 2008, Blehert et al. 2009).

Interspecific competition is considered a powerful evolutionary force, selecting for adaptations that result in different resource utilization (Schoener 1982). Species that are very similar in resource use cannot coexist for long without competitive exclusion, and species that do co-occur do so by sufficient differences in ecological niches that they occupy (Schoener 1982). Therefore, I would expect a high degree of overlap in one niche component should be associated with a low degree of overlap in one or more niche dimensions (Schoener 1974). At first glance it appears that there is little evidence of niche partitioning in space or time and instead, I found that these six sympatric bat species appear to have a stable community with species exhibiting high spatial and temporal overlap. However, where species do co-occur there are finer scale and sometimes complex interactions that could indicate niche partitioning in resource selection and habitat use. I will discuss these findings and implications in the individual species sections below.

Eptesicus fuscus (Big brown bat)

Eptesicus fuscus was found to spatially co-occur with *Lasiurus borealis*, *Myotis septentrionalis*, and *Perimyotis subflavus*. *Eptesicus fuscus* and *Lasiurus borealis* share very similar morphological characteristics such as body size, wing shape, and prey size preference, however *Eptesicus fuscus* prefers coleopterans, whereas *Lasiurus borealis* lepidopterans (Schwartz and Schwartz 1981). Where they tend to diverge is in the amount of activity in different habitats. *Eptesicus fuscus* was most active in the developed areas whereas *Lasiurus borealis* over wetlands, but each had similar overlap in the

grassland shrubland complex. This would suggest that they may avoid direct competition by utilizing differential habitat resources for foraging. *Myotis septentrionalis* and *Perimyotis subflavus* more heavily utilize the open water wetlands and are considerably smaller than *Eptesicus fuscus* likely utilizing different size prey items (Schwartz and Schwartz 1981). Therefore where overlap occurs, niche partitioning is likely occurring at the food resource.

Lasiurus borealis (Eastern red bat)

Lasiurus borealis spatially co-occurs with both *Eptesicus fuscus* (as described above) and *Myotis septentrionalis*, more often than random. *Myotis septentrionalis* also heavily uses open water wetlands. While we could not demonstrate spatial or temporal partitioning, *Myotis septentrionalis* is significantly smaller in body size compared to the larger *Lasiurus borealis*. I suggest they avoid direct competition by feeding on different sized prey even though they occupy similar space and time dimensions

Myotis lucifugus (Little brown myotis)

Myotis lucifugus exhibited spatial co-occurrence with *Myotis septentrionalis*. While morphologically and behaviorally similar due to similar size, wing morphology, echolocation call structure and within genus taxonomic relations, *Myotis lucifugus* had greater activity levels in a wider variety of habitats including developed areas, deciduous forests, and grassland shrubland complex, but lower levels over open water wetlands. Evidence suggests that this species is more of a habitat generalist and the ability to utilize

a wider range of resources would reduce competition between these morphologically similar species.

Myotis septentrionalis (Northern long-eared myotis)

Myotis septentrionalis spatially co-occurred with the other five species examined. However, I found that they are active over the wetlands more than any other habitat or species except *Perimyotis subflavus*. Interestingly, this is contrary to the literature where they have been found to forage mostly around dense vegetation (Schwartz and Schwartz 1981). These two species are morphologically similar in size and shape however their echolocation call structure is markedly different. Visual observations during this study suggests that despite habitat and temporal overlap, vertical partitioning may be the mechanism reducing direct competition. *Myotis septentrionalis* was typically observed foraging just above the waters' surface while *Perimyotis subflavus* typically foraged at higher altitudes, however this study was not designed to test this hypothesis. A similar vertical partitioning pattern was found with regards to two similar western North American vespertilionid species, *Myotis velifer* and *Perimyotis hesperus* (Vaughn 1959). Also *Myotis septentrionalis* tends to forage as a gleaner and *Perimyotis subflavus* as ahawker. This partitioning will also lead to competition avoidance.

Nycticeius humeralis (Evening bat)

Nycticeius humeralis spatially co-occurred with *Myotis septentrionalis*. These two species, however, are different in size, shape, echolocation call structure, and habitat use. *Nycticeius humeralis* appears to be a more generalist species seemingly utilizing a wide

variety of habitats and *Myotis septentrionalis* focuses most of its activity over open water. Even though spatial co-occurrence was documented these different behavioral and morphological characteristics indicate that different resources likely are being utilized thus minimizing direct competition. There was a striking similarity in temporal overlap between *Nycticeius humeralis* and *Myotis lucifugus*. These two species had the highest coefficient of overlap of any other combination. Their temporal patterns were almost identical using both the KDE and the activity index approaches even at the within habitat level. They are morphologically somewhat similar except in their echolocation call structure. However, these species were found to be spatially independent suggesting that spatial separation is potentially the mechanism for niche partitioning.

Perimyotis subflavus (Eastern pipistrelle)

Perimyotis subflavus co-occurs spatially with *Eptesicus fuscus* greater than random chance would suggest. As noted above, their size differences likely indicate different prey resources as a mechanism to avoid direct competition between these two species. Circumstantial evidence suggests that vertical partitioning is promoting niche partitioning (see *Myotis septentrionalis* discussion above). Capture evidence from mist-netting from other portions of this study not discussed here, lead me to hypothesis that *Perimyotis subflavus* and *Lasiurus borealis* would spatially co-occur. Each location I captured one species I would invariably capture the other, however, analysis showed that these two species exhibit spatial independence across the landscape. They do have a high degree of acoustic temporal overlap as revealed by both the temporal estimators. Because

mist nets are usually placed over flight corridors and it was likely this temporal overlap in physical capture was what I was witnessing in my nets.

My ability to fully explore the spatial co-occurrence of sympatric bats species efficiently using two-species occupancy models was limited by the study design. I followed the general strategy in sampling more sites with fewer surveys for a rare species versus fewer sites for more common species with similar detection probability (MacKenzie et al. 2006). However what I had perceived as adequate number of sampling locations effective for single species modeling was limited in two-species co-occurrence modeling. A better approach with the same equipment and logistical constraints would have been to at least triple the number of sampling locations, survey each location for a maximum of 5-7 nights, and then not revisit that location again during the survey season. This would likely be sufficient to cover the objectives for both single species and two-species modeling. Because the 15 minute time intervals expanded out to 40 sampling occasions per night, an ideal approach for two species modeling might be to only survey a sampling location one time (night) and increase the number of sampling locations until sufficient power is obtained (e.g. following (Bailey et al. 2007)). Even with this limitation I was able to gain new information on bat ecology and draw meaningful conclusions derived from both the species co-occurrence models and the summary of the activity index by the habitat types.

Using the acoustic activity index for temporal distribution throughout the night resulted in similar patterns as those derived from the kernel density estimate for each

species (Figures 3.2, 3.5). Using the KDE approach allowed for quantitative comparisons of species overlap without the need to interpret complex pairwise comparison outputs. My findings regarding the temporal activities patterns within both analysis frameworks are fairly consistent with other studies. Bat activity is not uniformly distributed through the night. For most species, several distinct periods of activity occur (Thomas and West 1989). Activity is highest during the first ca. 60 minutes that correspond with dispersal away from roosts and the first feeding period (Anthony and Kunz 1977, Swift 1980). Activity often declines after this, but marked peaks may occur around midnight and again towards dawn (Thomas and West, 1989).

This study is one of the first to examine bat community distributional patterns by means of acoustic identification at the landscape scale and for varying habitat types. I quantified spatial and temporal activity patterns of six species belonging to the bat community in a mixed grassland forested environment in central Virginia to gain insight into species interactions and coexistence ecology. My acoustical sampling array provided an efficient means to sample the entire bat community simultaneously in contrast to physical trapping which has some inherent capture biases and is logistically more difficult time consuming and inefficient of large geographic scales (Thomas and LaVal 1988, Thomas and West 1989, Ministry of Environment 1998). This sampling strategy and analysis framework was effective to meet the intended objectives for Chapter 2 but could be further refined and streamlined for co-occurrence modeling especially by conducting a more thorough analysis of the number of sites versus repeat surveys needed to meet study objectives. Nonetheless acoustic monitoring provides a relatively new and

novel approach to examine bat community dynamics from acoustically derived detection-nondetection data.

CONCLUSION

Eastern North American bat species have shared this geographic region across a long evolutionary time scale, suggesting that competitive partitioning in the community may have occurred long ago. Because of strong overall morphological resemblances in these insectivorous bat species, I assumed there were similar niches but that spatial and temporal partitioning prevented direct competition and allowed species co-existence. However, I found high levels of overlap especially temporally, among all species suggesting that temporal partitioning does not appear to be the driving force in preventing competition among these species. But, when broken down into different habitat types, I did find evidence of habitat partitioning for nearly all species, especially when species were more similar in morphology. Those that did not differ by habitat and time, tended to have extreme size differences and anecdotally notable differences in feeding heights.

Another possibility is niches that appear so similar to us may have differences that we have difficulty in distinguishing on such a fine scale (Findley and Black 1983, Aldridge and Rautenbach 1987). It has also been suggested that perhaps competitive niche arrangement plays only a minor role in bat community organization (Arlettaz 1999) perhaps because food for insectivorous bats is so abundant. Finally, it is possible that the mosaic of habitat types distributed across this landscape promotes species diversity and allows species to switch habitats quickly through the night to avoid potential competition

with other species. Protecting or preserving landscapes containing such habitat mosaics could be key to bat community-level conservation.

My study can be seen as a first step in building more complex species interaction models that could include other variables such as feeding heights, prey species and size, hunting success, etc; thereby building on our knowledge of co-existence ecology and providing much needed ecological information useful for bat conservation.

LITERATURE CITED

- Aldridge, H. D. J. N. and I. L. Rautenbach. 1987. Morphology, echolocation, and resource partitioning in insectivorous bats. *Journal of Animal Ecology* **56**.
- Altringham, J., D. and M. B. Fenton. 2003. Sensory ecology and the communication in the Chiroptera. Pages 90-127 *in* T. H. Kunz and M. B. Fenton, editors. *Bat Ecology*. University of Chicago Press, Chicago.
- ANHC. 2005. Mammals of Special Concern (dated 16 March 2005)
<http://www.naturalheritage.com/pdf/ANIMALS-Mammals-2005.pdf>. Arkansas Natural Heritage Commission, Little Rock, AR.
- Animal Care and Use Committee. 1998. Guidelines for the capture, handling, and care of mammals as approved by the American Society of Mammalogists. *Journal of Mammalogy* **79**:1416-1431.
- Anthony, E. L. P. 1988. Age Determination in Bats. Pages 47-58 *in* T. H. Kunz, editor. *Ecological and behavioral methods for the study of bats*. Smithsonian Institution Press, Washington, DC.
- Anthony, E. L. P. and T. H. Kunz. 1977. Feeding strategies of the little brown bat (*Myotis lucifugus*) in southern New Hampshire. *Ecology* **58**:775-786.
- Arita, E. 1997. Species composition and morphological structure of the bat fauna of Yucatan, Mexico. *Journal of Animal Ecology* **66**:83-97.
- Arlettaz, R. 1999. Habitat selection as a major resource partitioning mechanism between the two sympatric sibling bat species *Myotis myotis* and *Myotis blythii*. *Journal of Animal Ecology* **68**:460-471.

- Arnett, E., B. 2003. Advancing science and partnerships for the conservation of bats and thier habitats. *Wildlife Society Bulletin* **31**:2-5.
- Arnett, E., B. 2008. Patterns of bat fatalities at wind energy facilities in North America. *Journal of Wildlife Management* **72**:61-78.
- Bailey, L., L., J. Hines, E., J. Nichols, D., and D. MacKenzie, I. 2007. Sampling design trade-offs in occupancy studies with imperfect detection: Examples and software. *Ecological Applications* **17**:281-290.
- Bailey, L., L., J. Reid, A., E. Forsman, D., and J. Nichols, D. 2009. Modeling co-occurrence of northern spotted and barred owls: Accounting for detection probaility differences. *Biological Conservation* **142**:2983-2989.
- Barbour, R. W. and W. H. Davis. 1969. *Bats of America*, Lexington, KY.
- Barclay, R. M. R. 1985. Long- versus short- range foraging strategies of hoary (*Lasivirus cinereus*) and silver-haired (*Lasionycteris noctivigans*) bats and the consequence of prey selection. *Canadian Journal of Zoology* **63**:2507-2515.
- Barclay, R. M. R. 1991. Population structure of temperate zone insectivorous bats in relation to foraging behaviour and energy demand. *Journal of Animal Ecology* **60**:165-178.
- Bergallo, H. G., C. E. L. Esberard, M. A. R. Mello, V. Lins, R. Mangolin, G. G. S. Melo, and M. Baptista. 2003. Bat species richness in Atlantic Forest: What is the minimum sampling effort? *Biotropica* **35**:278-288.
- Berry, N., W. O'Connor, M. W. Holderied, and G. Jones. 2004. Detection and avoidance of harp traps by echolocating bats. *Acta Chiropterologica* **6**:335-346.

- Bettes, B., J. 1998. Effects of Interindividual Variation in Echolocation Calls on Identification of Big Brown and Silver-haired Bats. *Journal of Wildlife Management* **62**:1003-1010.
- Blehert, D., S., A. Hicks, C., M. Behr, C. Meteyer, U., B. Berlowski-Zier, M., E. L. Buckles, T. Coleman, H., S. Darling, R., A. Gargas, R. Niver, J. Okoniewski, C., R. Rudd, J., and W. Stone, B. 2009. Bat White-nosed syndrome: an emerging fungal pathogen? *Science* **323**:227.
- Boyles, J., G., P. Cryan, M., G. McCracken, F., and T. H. Kunz. 2011. Economic importance of bats in agriculture. *Science* **332**:41-42.
- Britzke, E. R. 2002. Designing monitoring programs using frequency-division bat detectors: active versus passive sampling. Pages 79-83 *in* R. Brigham, Mark, E. K. V. Kalko, C. Jones, S. Parsons, and H. J. G. A. Limpens, editors. *Bat Echolocation Research: tools, techniques, and analysis*. Bat Conservation International, Austin, Texas.
- Britzke, E. R. and K. L. Murray. 2000. A quantitative method for selection of identifiable search-phase calls using the Anabat System. *Bat Research News* **41**:33-36.
- Britzke, E. R., K. L. Murray, B. M. Hadley, and L. W. Robins. 1999. Bat activity as measured with the Anabat system. *Bat Research News* **40**:89.
- Britzke, E. R., K. L. Murray, J. S. Heywood, and L. W. Robbins. 2002. Acoustic Identification. Pages 221-227 *in* A. Kurta and J. Kennedy, editors. *The Indiana Bat: Biology and Management of an Endangered Species*. Bat Conservation International, Austin, Texas.

- Broders, H. G., G. M. Quinn, and G. J. Forbes. 2003. Species status, and the spatial and temporal patterns of activity of bats in southwest Nova Scotia, Canada. *Northeastern Naturalist* **10**:383-398.
- Brooks, R., T. and W. M. Ford. 2006. Introduction to the special section - Bat habitat use in eastern North American temperate forests: stand, site, and landscape effects. *Journal of Wildlife Management* **70**:1171-1173.
- Burnham, K. P. and D. R. Anderson. 1998. Model selection and inference: a practical information-theoretic approach. Springer-Verlag, New York, New York.
- Burnham, K. P. and D. R. Anderson. 2004. Multimodel inference: understanding AIC and BIC in model selection. *Sociological Methods & Research* **33**:261-304.
- Carter, T. C. 2006. Indiana bats in the midwest: The importance of Hydric Habitats. *Journal of Wildlife Management* **70**:1185-1190.
- Carter, T. C., M. A. Menzel, S. F. Owen, J. W. Edwards, J. M. Menzel, and W. M. Ford. 2003. Food habits of seven species of bats in the Allegheny Plateau and Ridge and Valley of West Virginia. *Northeastern Naturalist* **10**:83-88.
- Choate, J. R., J. K. Knox Jr., and C. Jones. 1994. Handbook of Mammals of the Southcentral States. Louisiana State University Press, Baton Rouge, LA.
- Cleveland, C., J., M. Betke, P. Federico, J. Frank, D., T. Hallman, G., J. Horn, J. Lopez Jr, D., G. McCracken, F, R. Medellin, A., A. Moreno-Valdez, Sansone, Chris, G., J. Westbrook, K, and T. H. Kunz. 2006. Economic value of the pest control service provided by Brazilian free-tailed bats in south-central Texas. *Frontiers in Ecology and the Environment* **4**:238-243.

- Constantine, D. G. 1958. An automatic bat collecting device. *Journal of Wildlife Management* **22**:17-22.
- Cooper, R. J. and R. C. Whitmore. 1990. Arthropod sampling in ornithology. *Studies in Avian Biology* **12**:29-37.
- Corben, C. 2002. Zero-crossings analysis for bat identification: an overview. Pages 95-107 *in* R. Brigham, Mark, E. K. V. Kalko, C. Jones, S. Parsons, and H. J. G. A. Limpens, editors. *Bat Echolocation Research: tools, techniques and analysis*. Bat Conservation International, Austin, Texas.
- Corben, C. 2005. AnalookW (Beta version 3.2h dated 25 August 2005). URL http://users.lmi.net/corben/WinAnalook.htm#AnaLookW_Contents.
- Davis-Klopfer, M. 2008. AnaMichelle. Virginia Tech, Blacksburg, Virginia.
- Dorr, J., L. V. R. Emrick, P. Swint, and E. Pokorski. 2007. Army National Guard - Maneuver Training Center Fort Pickett vegetative communities map and vegetation classification system. CMI-MLD R-46 Conservation Management Institute - Military Lands Division, College of Natural Resources, Virginia Polytechnic Institute and State University, Blacksburg, Virginia.
- Duffy, A. M., L. F. Lumsden, C. R. Caddle, R. R. Chick, and G. R. Newell. 2000. The efficacy of Anabat ultrasonic detectors and harp traps for surveying microchiropterans in south-eastern Australia. *Acta Chiropterologica* **2**:127-144.
- Dwyer, P. D. 1966. The population pattern of *Miniopterus schreibersii* (Chiroptera) in north-eastern New South Wales. *Australian Journal of Zoology* **14**:1073-1137.
- Ellison, L. E., T. J. O'Shea, M. A. Bogan, A. L. Everette, and D. Schneider, M. 2003. Existing data on colonies of bats in the United States: Summary and analysis of

- the U.S. Geological Survey's bat population database. Pages 127-237 in T. J. O'Shea and M. A. Bogan, editors. Monitoring trends in bat populations of the United States and Territories: problems and prospects. U.S. Geological Survey, Biological Resources Discipline, Information and Technology Report, USGS/BRD/ITR--2003-0003.
- Emrick, V. R. and R. L. Murray, editors. 2001. Integrated Natural Resource Management Plan Fort Pickett Maneuver Training Center, Blackstone, Virginia. Conservation Management Institute- Military Lands Division at Virginia Polytechnic Institute and State University, Blacksburg, Virginia.
- Evans, D., E., W. Mitchel, A., and R. Fischer, A. 1998. Species Profile: Indiana bat (*Myotis sodalis*) on military installations in the Southeastern United States. Technical Report SERDP 98-3,. U. S. Army Engineer Waterways Experiment Station, Vicksburg, MS.
- Feldhamer, G. A., B. C. Thompson, and C. J. A. 2003. Wild Mammals of North America: biology, management, and conservation. The Johns Hopkins University Press, Baltimore, Maryland.
- Fenton, M. B. 1982. Echolocation calls and patterns of hunting bats and habitat use of bats (Microchiroptera) from Chillagoe, North Queensland. Australian Journal of Zoology **30**:417-425.
- Fenton, M. B. 1997. Science and the conservation of of bats. Journal of Mammalogy **78**:1-14.
- Fenton, M. B. and G. P. Bell. 1979. Echolocation and feeding behaviour in four species of myotis (Chiroptera). Canadian Journal of Zoology **57**:1271-1277.

- Findley, J. S. 1993. Bats, a community perspective. Cambridge University Press, Cambridge, UK.
- Findley, J. S. and H. Black. 1983. Morphological and dietary structuring of a Zambian insectivorous bat community. *Ecology* **64**:625-630.
- Ford, W. M., J. M. Menzel, M. Menzel, A., J. W. Edwards, and J. C. Kilgo. 2006. Presence and absence of bats across habitat scales in the upper coastal plain of South Carolina. *Journal of Wildlife Management* **70**:1200-1209.
- Ford, W. M., M. A. Menzel, J. L. Rodrigue, J. M. Menzel, and J. B. Johnson. 2005. Relating bat species presence to simple habitat measures in a central Appalachian forest. *Biological Conservation* **126**:528-539.
- Franklin, A., B., T. M. Shenk, D. R. Anderson, and K. P. Burnham. 2001. Statistical model selection: an alternative to null hypothesis testing. *in* T. M. Shenk and A. Franklin, B., editors. Modeling in natural resource management: development interpretation and application. Island Press, Washington, DC.
- Gehrt, S. D. and J. E. Chelsvig. 2004. Species-specific patterns of bat activity in an urban landscape. *Ecological Applications* **14**:625-635.
- Gerber, B., D. 2010. Comparing density analysis and carnivore ecology in Madagascar's southeastern rainforest. Virginia Polytechnic Institute and State University.
- Gorrensens, P. M., A. C. Miles, C. M. Todd, F. J. Bonaccorso, and T. J. Weller. 2008. Assessing bat detectability and occupancy with multiple automated echolocation detectors. *Journal of Mammology* **89**:11-17.
- Gotelli, N., J. 2000. Null model analysis of species co-occurrence patterns. *Ecology* **81**:2606-2621.

- Gressitt, J. L. and M. K. Gressitt. 1962. An improved malaise trap. *Pacific Insects* **4**:87-90.
- Griffin, D. R. 1958. *Listening in the dark*. Yale University Press, New Haven, Connecticut.
- Grindal, S. D., T. S. Collard, R. M. Brigham, and R. M. R. Barclay. 1992. The influence of precipitation on the design of ecolocation-monitoring studies. *Journal of Mammalogy* **78**:514-524.
- Hall, L. S. 1981. *The Biogeography of Australian Bats*. 41 edition.
- Harvey, M. J. 1986. *Arkansas Bats: A Valuable Resource*. Arkansas Game and Fish Commission.
- Harvey, M. J., J. S. Altenbach, and T. L. Best. 1999. *Bats of the United States*. Arkansas Game and Fish Commission, Little Rock, Arkansas.
- Harvey, M. J. and R. K. Redman. 2001. *Endangered bats of Arkansas: distribution, status, and ecology (2000 - 2001)* W-56-R. Tennessee Technological University, Cookeville, TN.
- Hayes, J. P. 1997. Temporal variation in activity of bats and the design of echolocation-monitoring studies. *Journal of Mammalogy* **78**:514-524.
- Hayes, J. P., editor. 2000. Assumptions and practical considerations in the design and interpretation of echolocation-monitoring studies. *Acta Chiropterologica*.
- Hayes, J. P. and M. D. Adam. 1996. The influence of logging riparian areas on habitat use by bats in western Oregon. Pages 185-198 *in* R. M. R. Barclay and R. M. Brigham, editors. *Bats and Forest symposium*. Ministry of Forestry, Victoria, British Columbia.

- Hayes, J. P. and P. Hounihan. 1994. Field use of the Anabat II bat-detector system to monitor activity. *Bat Research News* **35**:1-3.
- Henry, M., P. Barriere, A. Gautier-Hion, and M. Colyn. 2004. Species composition, abundance and vertical stratification of a bat community (Megachiroptera : Pteropodidae) in a West African rain forest. *Journal of Tropical Ecology* **20**:21-29.
- Hickey, M., Brian, C., L. Acharya, and S. Pennington. 1996. Resource partitioning by two species of vespertilionid bats (*Lasiurus cinereus* and *Lasiurus borealis*) feeding around street lights. *Journal of Mammalogy* **77**:325-334.
- Hines, J., E. 2005. Program PRESENCE. USGS Patuxent Wildlife Research Center, Laurel, Maryland.
- Hurlbert, S., H. 1978. The measurement of niche overlap. *Ecology* **59**:67-77.
- Husar, S., L. 1976. Behavioural character displacement: Evidence of food partitioning in insectivorous bats. *Journal of Mammalogy* **57**:331-338.
- Hutson, A. M., S. P. Mickleburgh, and P. A. Racey. 2001. Microchiropteran bats: global status survey and conservation action plan. Gland, Switzerland and Cambridge: IUCN/SSC Chiroptera Specialist Group. IUCN:258.
- Hutto, R. L. 1990. Measuring the availability of food resources. *Studies in Avian Biology*:20-28.
- IUCN. 2007. International Union for the Conservation of Nature and Natural Resources: Redlist 2006. <http://www.iucnredlist.org/>.
- Johnson, J. B., M. A. Menzel, J. W. Edwards, and W. M. Ford. 2002. A comparison of 2 acoustical bat survey techniques. *Wildlife Society Bulletin* **30**:931-936.

- Jung, T. S., I. D. Thompson, R. D. Titman, and A. P. Applejohn. 1999. Habitat selection by forest bats in relation to mixed-wood stand types and structure in central Ontario. *Journal of Wildlife Management* **63**:1306-1319.
- Kalko, E. K. V. 1997. Diversity in tropical bats. Pages 13-43 *in* Proceedings from the International Symposium on Biodiversity and Systematics in Tropical Ecosystems. Zoologisches Forschungsinstitut und Museum Alexander Koenig, Bonn, 357 pp.
- Kalko, E. K. V., C. O. Hnadle Jr., and D. Hnadle, editors. 1996. Organization, diversity, and long-term dynamics of a Neotropical bat community. Academic Press, New York.
- Kuenzi, A. J. and M. L. Morrison. 1998. Detection of bats by mist-nets and ultrasonic Sensors. *Wildlife Society Bulletin* **26**:307-311.
- Kunz, T. H. 1973. Resource utilization: temporal and spatial components of bat activity in central Iowa. *Journal of Mammalogy* **54**:14-31.
- Kunz, T. H. and C. E. Brock. 1975. A COMPARISON OF MIST NETS AND ULTRASONIC DETECTORS FOR MONITORING FLIGHT ACTIVITY OF BATS. *Journal of Mammalogy* **56**:907-911.
- Kunz, T. H. and M. B. Fenton. 2003. Preface. Pages xiii-xix *in* T. H. Kunz and M. B. Fenton, editors. *Bat Ecology*. University of Chicago Press, Chicago.
- Kunz, T. H. and A. Kurta. 1988. Capture Methods and Holding Devices. Pages 1-29 *in* T. H. Kunz, editor. *Ecological and Behavioral methods for the study of bats*. Smithsonian Institution Press, Washington, DC.

- Kunz, T. H. and L. F. Lumsden. 2003. Ecology of cavity and foliage roosting bats. Pages 3-89 in T. H. Kunz and M. B. Fenton, editors. *Bat Ecology*. University of Chicago Press, Chicago.
- Kurta, A., J. Kath, E. L. Smith, R. Foster, M. W. Orick, and R. Ross. 1993a. A maternity roost of the endangered Indiana bat (*Myotis sodalis*) in an unshaded hollow sycamore tree (*Plantanus occidentalis*). *American Midland Naturalist* **130**:405-407.
- Kurta, A., D. King, J. A. Teramino, J. M. Stribley, and K. F. Williams. 1993b. Summer roosts of the endangered Indiana bat (*Myotis sodalis*) on the northern edge of its range. *American Midland Naturalist* **129**:132-138.
- Larson, D. J. and J. P. Hayes. 2000. Variability in sensitivity of AnaBat II bat detectors and a method of calibration. *Acta Chiropterologica* **2**:209-213.
- LaVal, R. K. and M. L. LaVal. 1977. Reproduction and behavior of the African banana bat (*Pipistrellus nanus*). *Journal of Mammalogy* **58**:403-410.
- Law, B., J. Anderson, and M. Chidel. 1998. A bat survey in state forests on the south-west slopes region of New South Wales with suggestions of improvements for future surveys. *Australian Zoologist* **30**:467-479.
- Livengood, K., R. Drobney, and C. Corben. 2002. The evaluation of call parameters for three Missouri *Myotis* species. Report to Missouri Department of Conservation - Research Unit, Columbia, Missouri.
- Loeb, S., C. and J. O'Keefe, M. 2006. Habitat use by forest bats in South Carolina in relation to local, stand, and landscape characteristics. *Journal of Wildlife Management* **70**:1210-1218.

- Luiselli, L. 2006. Site occupancy and density of sympatric Gaboon viper (*Bitis gabonica*) and nose-horned viper (*Bitis nasicornis*). *Journal of Tropical Ecology* **22**:555-564.
- Lumsden, L. F. and A. F. Bennett. 1995. Bats of a semi-arid environment in south-eastern Australia: biogeography, ecology and conservation. *Wildlife Research* **22**:217-240.
- MacKenzie, D., I. 2005. What are the issues with presence - absence data for wildlife managers? *Journal of Wildlife Management* **69**:849-860.
- MacKenzie, D., I., L. Bailey, L., and J. Nichols, D. 2004. Investigating species co-occurrence patterns when species are detected imperfectly. *Journal of Animal Ecology* **73**.
- MacKenzie, D., I., J. Nichols, D., J. Hines, E., M. Knutson, G., and A. Franklin, B. 2003. Estimating site occupancy, colonization, and local extinction when a species is detected imperfectly. *Ecology* **84**:2200-2207.
- MacKenzie, D., I., J. Nichols, D., G. Lachman, B., S. Droege, J. A. Royle, and C. Langtimm, A. 2002. Estimating site occupancy rates when detection probabilities are less than one. *Ecology* **83**:2248-2255.
- MacKenzie, D., I., J. Nichols, D., J. A. Royle, K. Pollock, H., L. Bailey, L., and J. Hines, E. 2006. *Occupancy Estimation and Modeling, Inferring Patterns and Dynamics of Species Occurrence*. Elsevier Academic Press, New York.
- MacKenzie, D., I. and J. A. Royle. 2005. Designing occupancy studies: general advice and allocating survey effort. *Journal of Applied Ecology* **42**.
- Marcot, B. G. 1996. An ecosystem context for bat management : a case study of the interior Columbia River Basin. *in* R. M. R. Barclay and R. M. Bringham, editors.

- Bats and forest symposium. British Colombian Ministry of Forestry, Victoria, Canada.
- Menzel, J. M., W. M. Ford, M. A. Menzel, T. C. Carter, J. E. Gardner, J. D. Garner, and J. E. Hofmann. 2005a. Summer habitat use and home-range analysis of the endangered Indiana bat. *Journal of Wildlife Management* **69**:430-436.
- Menzel, J. M., M. A. Menzel, J. C. Kilgo, W. M. Ford, J. W. Edwards, and G. F. McCracken. 2005b. Effect of habitat and foraging height on bat activity in the Coastal Plain of South Carolina. *Journal of Wildlife Management* **69**:235-245.
- Miller, B. W. 2001. A method for determining relative activity of free flying bats using a new activity index for acoustic monitoring. *Acta Chiropterologica* **3**:93-105.
- Miller, B. W. 2002. Acoustic surveys and Non-phylostomid neotropical bats: How effective are they? Pages 58-63 *in* R. Brigham, Mark, E. K. V. Kalko, C. Jones, S. Parsons, and H. J. G. A. Limpens, editors. *Bat Echolocation Research: tools, techniques, and analysis*. Bat Conservation International, Austin Texas.
- Miller, D., A., E. Arnett, B., and M. J. Lacki. 2003. Habitat management for forest-roosting bats of North America: a critical review of habitat studies. *Wildlife Society Bulletin* **31**:30-44.
- Mills, D. J., T. W. Norton, H. E. Parnaby, R. B. Cunningham, and H. A. Nix. 1996. Designing surveys for microchiropteran bats in complex forested landscapes - a pilot study from south-eastern Australia. *Forest Ecology and Management* **85**:149-161.

- Ministry of Environment. 1998. Inventory Methods for Bats No. 20. Standards for Components of British Columbia's Biodiversity. Ministry of Environment, Victoria, British Columbia.
- Morena, C., E. and G. Halfetter. 2000. Assessing the completeness of bat biodiversity inventories using species accumulation curves. *Journal of Applied Ecology* **37**:149-151.
- Murray, K. L., E. R. Britzke, B. M. Hadley, and L. W. Robbins. 1999a. A comparison of acoustic sampling and mist netting in assessing bat species presence. *Bat Research News* **40**:96.
- Murray, K. L., E. R. Britzke, B. M. Hadley, and L. W. Robbins. 1999b. Surveying bat communities: a comparison between mist nets and the Anabat II bat detector system. *Acta Chiropterologica* **1**:105-112.
- Nagorsen, D. W. and R. M. Brigham. 1993. Royal British Columbia Museum Handbook: Bats of British Columbia.
- Nichols, J., D. and K. U. Karanth. 2002. Statistical concepts: assessing spatial distributions. Pages 29-38 *in* K. U. Karanth and J. Nichols, D., editors. *Monitoring Tigers and Their Prey: A Manual for Wildlife Managers, Researchers, and Conservationists*. Center for Wildlife Studies, Bangalore, India.
- Nowak, R., M. 1994. *Walker's Bats of the World*. Johns Hopkins University Press, Baltimore, Maryland.
- O'Farrell, M. J. 1997. Use of echolocation calls for the identification of free-flying bats. *Transactions of the western section of the wildlife society* **33**:1-8.

- O'Farrell, M. J. 1998. A Passive monitoring system for Anabat II using a laptop computer. *Bat Research News* **39**:147-150.
- O'Farrell, M. J., C. Corben, W. L. Gannon, and B. W. Miller. 1999a. Confronting the Dogma: A Reply. *Journal of Mammalogy* **80**:297-302.
- O'Farrell, M. J., C. J. Corben, and W. L. Gannon. 2000. Geographic variation in the echolocation calls of the Hoary Bat (*Lasiurus cinereus*). *Acta Chiropterologica* **2**:185-195.
- O'Farrell, M. J. and W. L. Gannon. 1999. A comparison of acoustic versus capture techniques for the inventory of bats. *Journal of Mammalogy* **80**:24-30.
- O'Farrell, M. J. and B. W. Miller. 1997. A new examination of echolocation calls of some Neotropical bats (Emballonuridae and Mormoopidae). *Journal of Mammalogy* **78**:954-963.
- O'Farrell, M. J. and B. W. Miller. 1999. Use of vocal signatures for the inventory of free-flying neotropical bats. *Biotropica* **31**:507-516.
- O'Farrell, M. J., B. W. Miller, and W. L. Gannon. 1999b. Qualitative identification of free-flying bats using the Anabat detector. *Journal of Mammalogy* **80**:11-23.
- O'Shea, T. J. and M. A. Bogan. 2003. Monitoring trends in bat populations of the United States and Territories: problems and prospects. Page 274 in T. J. O'Shea and M. A. Bogan, editors. U.S. Geological Survey, Biological Resources Discipline, Information and Technology Report, USGS/BRD/ITR--2003-0003.
- O'Shea, T. J., M. A. Bogan, and L. E. Ellison. 2003. Monitoring trends in bat populations of the United States and territories: status of the science and recommendations for the future. *Wildlife Society Bulletin* **31**:16-29.

- Ochoa, G. J., M. J. O'Farrell, and B. W. Miller. 2000. Contribution to acoustic methods to the study of insectivorous bat diversity in protected areas from northern Venezuela. Pages 171-183 *in* W. L. Gannon and W. Bogdanowicz, editors. Contributions to the study of Bats: field use of acoustic detectors. Acta Chiropterologica.
- Padgett, T., M. and R. Rose, k. 1991. Bats (Chiroptera: Vespertilionidae) of the Great Dismal Swamp of Virginia and North Carolina. *Brimleyana* **17**:17-25.
- Patriquin, K., L. Hogberg, B. Chruszcz, and R. Barclay. 2000. The influence of habitat type on the ability to detect bats with anabat II detectors. *Bat Research News* **41**:133.
- Patterson, B., D., M. Willig, R., and R. Stevens, D. 2003. Trophic strategies, niche partitioning, and patterns of ecological organization. Pages 536-579 *in* T. H. Kunz and M. B. Fenton, editors. *Bat Ecology*. University of Chicago Press, Chicago.
- Persson, L. 1985. Asymmetrical competition: Are larger animal competitively superior? *American Naturalist* **126**:261-266.
- Pettersson, L. 2002. The properties of sound and bat detectors. Pages 9-12 *in* R. Brigham, Mark, E. K. V. Kalko, C. Jones, S. Parsons, and H. J. G. A. Limpens, editors. *Bat Echolocation Research: tools, techniques, and analysis*. Bat Conservation International, Austin, Texas.
- Phillips, W. R. and S. J. Inwards. 1985. The annual activity and breeding cycles of Gould's Long-eared Bat. *Australian Journal of Zoology* **33**:111-126.
- Pianka, E., R. 1980. Guild structure in desert lizards. *Oikos* **35**:194-201.

- Pierson, E. D. 1998. Tall trees, deep holes, and scarred landscapes: conservation biology of North American bats. Pages 309-325 *in* T. H. Kunz and P. A. Racey, editors. Bat Biology and Conservation. Smithsonian Institution Press, Washington DC.
- Pimm, S. L., M. Rosenzweig, L., and W. A. Mitchell. 1985. Competition and food selection: field-tests of a theory. *Ecology* **66**:798-807.
- Prevett, P. 2002. Anabat-computer survey for microbats: sampling considerations, call identification and analysis. *Bat Research News* **43**:21.
- R-Development-Core-Team. 2008. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- Racey, P. A. 1988. Reproductive assessment in bats. Pages 31-43 *in* T. H. Kunz, editor. Ecological and Behavioural Methods for the Study of Bats. Smithsonian Institution Press, 533pp., Washington DC.
- Rautenbach, I. L., M. B. Fenton, and M. J. Whiting. 1996. Bats in riverine forest and woodlands; a latitudinal transect in southern Africa. *Canadian Journal of Zoology* **74**:312-322.
- Richmond, O., M., J. Hines, E., and S. Beissinger, R. 2010. Two-species occupancy models: an new parameterization applied to co-occurrence of secretive rails. *Ecological Applications* **20**:2036-2046.
- Ridout, M., S. and M. Linkie. 2009. Estimating overlap of daily activity patterns from camera trap data. *Journal of Agricultural, Biological, and Environmental Statistics* **14**:322-337.

- Roble, S. M. 2003. Natural Heritage Resources of Virginia: Rare Animal Species. Natural Heritage Technical Report 03-04, Virginia Department of Conservation and Recreation, Division of Natural Heritage, Richmond, Virginia.
- Root, R., B. 1967. Niche exploitation pattern of the blue-gray gnatcatcher. *Ecological Monographs* **37**:317-350.
- Rosenzweig, M., L. 1995. Species diversity in space and time. Cambridge University Press, Cambridge, UK.
- Schmid, F. and A. Schmidt. 2006. Nonparametric estimation of the coefficient of overlapping - theory and empirical application. *Computational Statistics and Data Analysis* **50**:1583-1596.
- Schoener, T., W. 1974. Resource partitioning in ecological communities. *Science* **185**:27-39.
- Schoener, T., W. 1982. The controversy over interspecific competition. *American Scientist* **70**:586-595.
- Schwartz, C. W. and E. R. Schwartz. 1981. Flying Mammals, Order *Chiroptera*. The Wild Mammals of Missouri. University of Missouri Press and Missouri Department of Conservation, Columbia, MO.
- Sealander, J. A. and G. A. Heidt. 1990. Arkansas Mammals: Their natural history, classification, and distribution. University of Arkansas Press.
- Siemers, B., M. 2002. Bats in the field and in a flight cage: recording and analysis of thier echolocation calls and behavior. Pages 107-120 *in* R. Brigham, Mark, E. K. V. Kalko, C. Jones, S. Parsons, and H. J. G. A. Limpens, editors. Bat Echolocation

- Research: tools, techniques, and analysis. Bat Conservation International, Austin, Texas.
- Simmons, N., B. and T. Conway, M. 2003. Evolution of ecological diversity in bats. Pages 493-535 *in* T. H. Kunz and M. B. Fenton, editors. Bat Ecology. University of Chicago Press, Chicago.
- Smith, W. J. 1977. The behavior of communicating. Harvard University Press, Cambridge, Massachusetts.
- St Germain, M. J. and R. M. Murray-Schneider. 2012. Grassland bird diversity and density on ARNG-MTC Ft. Pickett, Blackstone, Virginia. Conservation Management Institute, College of Natural Resources and Environment, Virginia Polytechnic Institute and State University, Blacksburg, Virginia. **Technical Report**:1-24.
- St. Germain, M., J. 2005. Pilot Planning Level Survey of Bat Species at ARNG-MTC Fort Pickett, Blackstone, Virginia. CMI-MLD R-30a, Conservation Management Institute - Military Lands Division, College of Natural Resources, Virginia Polytechnic Institute and State University., Blacksburg, Virginia.
- St. Germain, M., J. 2008a. Bats of Fort Pickett, Blackstone, Virginia. Conservation Management Institute-Virginia Tech College of Natural Resources and Environment. CMI-MLD R-67. 21p.
- St. Germain, M., J. and B. W. Miller. 2005. Bat survey for Fort Chaffee MTC, Fort Smith, Arkansas. CMI-MLD R-38, Conservation Management Institute - Military Lands Division, College of Natural Resources, Virginia Polytechnic Institute and State University., Blacksburg, Virginia.

- St. Germain, M., J. and B. W. Miller. 2007. Bat species assemblage at Army National Guard Maneuver Training Center Fort Pickett, Blackstone, Virginia. CMI-MLD R-59 20070718
- St. Germain, M. J. 2008b. Bat Species Assemblage on ARNG-MTC fort Pickett, Blackstone, Virginia. Technical Report CMI-MLD R 39.
- Sunarto. 2011. Ecology and restoration of Sumartan tigers in forest and plantation landscapes. Virginia Polytechnic Institute and State University.
- Swift, S. M. 1980. Activity patterns of pipistrelle bats (*Pipistrellus pipistrellus*) in northeast Scotland. *Journal of Zoology of London* **190**:285-295.
- Swift, S. M. and P. A. Racey. 1983. Resource partitioning in two species of vespertilionid bats (chiroptera) occupying the same roost. *Journal of Zoology of London* **200**:249-259.
- Szewczak, J., M. 2002. Advanced analysis techniques for identifying bat species. Pages 121-127 in R. Brigham, Mark, E. K. V. Kalko, C. Jones, S. Parsons, and H. J. G. A. Limpens, editors. *Bat Echolocation Research: tools, techniques, and analysis*. Bat Conservation International, Austin, Texas.
- Thomas, D. W. 1988. The distribution of bats in different ages of Douglas-fir forests. *Journal of Wildlife Management* **52**:619-628.
- Thomas, D. W. and R. K. LaVal. 1988. Survey and Census Methods. Pages 77-89 in T. H. Kunz, editor. *Ecological and Behavioral Methods for the Study of Bats*. Smithsonian Institution Press, 533 pp, Washington DC.

- Thomas, D. W. and S. West, D. 1989. Wildlife-habitat relationships: sampling procedures for Pacific Northwest vertebrates. PNW-GTR-243, USDA Forest Service, Portland, OR.
- Thompson, M. J. A. 1987. Longevity and Survival of female pipistrelle bats (*Pipistrellus pipistrellus*) on the Vale of York, England. Journal of Zoology of London **211**:209-214.
- Townes, H. 1962. Design for a malaise trap. Proceeding of the Entomological Society Washington **64**:253-262.
- Townes, H. 1972. A light-weight malaise trap. Entomological News **83**:239-247.
- Tuttle, M. D. 1974. An improved trap for bats. Journal of Mammalogy **55**:475-477.
- VAFWIS. 2005. Virginia Fish and Wildlife Information Service. Virginia Department of Game and Inland Fisheries, Richmond, VA
<http://vafwis.org/WIS/ASP/home.asp?sID=64394&ln=I>.
- Vaughn, T. A. 1959. Functional morphology of three bats: Eumops, Myotis, Macrotus. University of Kansas Publishing, Museum of Natural History, 12:1-153.
- Vaughn, T. A. 1986. Mammals. Saunders College Publishing, Orlando, FL.
- Vojta, C., D. 2005. Old dog, new tricks: innovations with presence - absence information. Journal of Wildlife Management **69**:845-848.
- Weller, T. J. 2008. Using occupancy estimation to assess the effectiveness of a regional multiple-species conservation plan: bats in the Pacific Northwest. Biological Conservation **141**:2279-2289.
- Weller, T. J. and C. J. Zabel. 2002. Variation in bat detections due to detector orientation in a forest. Wildlife Society Bulletin **30**:922-930.

- Whitaker, J. O. J. and W. J. J. Hamilton. 1998. Order Chiroptera. Mammals of the Eastern United States. Comstock Publishing Associates of Cornell University Press, Ithaca, NY.
- Williams, J., A., M. J. O'Farrell, and B. Riddle, R. 2006. Habitat use by bats in a riparian corridor of the mojave desert in southern Nevada. *Journal of Mammalogy* **87**:1145-1153.
- Wilson, D. E. and D. M. Reeder. 1993. *Mammal Species of the World*. Smithsonian Institution Press, Washington DC.
- Wilson, D. E. and D. M. Reeder, editors. 2003. *Mammal species of the world: a taxonomic and geographic reference*. 2nd edition. Smithsonian Institution Press, Washington, D.C.
- Wolda, H. 1990. Food availability for an insectivore and how to measure it. *Studies in Avian Biology* **13**:38-43.
- Yates, M. D. and R. M. Muzika. 2006. Effect of forest structure and fragmentation on site occupancy of bat species in Missouri Ozark forests. *Journal of Wildlife Management* **70**:1238-1248.
- Youngston, W. K. and N. L. McKenzie. 1977. An improved bat collecting technique. *Bulletin of the Australian Mammalian Society* **3**:20-21.

Table 3.1. Mean acoustic activity levels (number of 1 minute time blocks) per hour over 10 hour night (95% confidence intervals) by species, physiognomic cover type, and flyway presence on ARNG-MTC Ft. Pickett, Blackstone, Virginia in 2007. The sample size (n) equals the number of sites that include the physiognomic habitat/cover and flyway type. ANOVA's were conducted on the samples for among type comparisons. Ranks with the same letters were not significantly different ($p < 0.05$, Tukey Kramer's pairwise comparisons)

Physiognomic Cover	n	<i>Eptesicus</i> <i>fuscus</i>			<i>Lasiurus</i> <i>borealis</i>			<i>Myotis</i> <i>lucifugus</i>			<i>Myotis</i> <i>septentrionalis</i>			<i>Nycticius</i> <i>humeralis</i>			<i>Perimyotis</i> <i>subflavus</i>		
		\bar{X}	SE		\bar{X}	SE		\bar{X}	SE		\bar{X}	SE		\bar{X}	SE		\bar{X}	SE	
All Habitats	87	6.2	1.1		15.6	1.7		15.4	1.2		14.5	2.4		12.0	1.0		21.4	2.4	
Coniferous Forest	15	4.0	3.0	A	2.4	0.8	A	3.1	0.9	A	0.8	0.4	A	2.7	0.7	A	2.4	0.9	A
Deciduous Forest	7	0.8	0.3	A	5.3	1.0	A	6.3	1.5	A	1.3	0.4	A	6.0	1.3	A	5.3	1.1	A
Developed Area	16	25.2	8.3	B	10.6	2.2	A	25.4	6.3	C	2.8	1.4	A	20.3	4.8	B	8.7	1.9	A
Forested Wetland	14	0.4	0.1	A	4.5	1.1	A	3.2	0.8	A	3.8	1.4	A	2.5	0.6	A	6.8	2.1	A
Grassland / Shrubland	21	9.7	2.2	A	10.3	1.6	A	17.6	1.7	B	1.7	0.3	A	14.1	1.5	B	11.7	1.4	B
Open Water Wetland	14	4.0	1.0	A	71.7	9.2	B	45.9	5.4	D	93.6	15.1	B	33.8	4.5	C	109.9	13.1	B
<i>df=5, F=8.23, p=0.000 df=5, F=54.11, p=0.000 df=5, F=34.01, p=0.000 df=5, F=45.54, p=0.000 df=5, F=27.82, p=0.000 df=5, F=70.37, p=0.000</i>																			
Flyway	n	AI			SE			AI			SE			AI			SE		
		AI	SE		AI	SE		AI	SE		AI	SE		AI	SE		AI	SE	
None	26	0.4	0.1	A	4.2	0.8	A	2.9	0.6	A	0.8	0.2	A	2.8	0.6	A	3.6	0.7	A
Open	27	12.2	2.4	B	11.8	1.6	A	18.1	1.6	B	3.0	0.7	A	14.8	1.4	B	13.4	1.7	A
Road	11	8.3	5.4	B	5.7	1.8	A	15.7	5.9	B	2.4	1.3	A	12.0	4.4	B	5.4	1.7	A
Stream	12	0.9	0.3	A	11.5	2.5	A	14.2	2.4	B	13.6	2.3	A	11.2	1.9	B	22.3	4.1	A
Water	11	5.6	1.7	A	98.9	14.1	B	53.2	8.4	C	142.5	24.6	B	36.7	6.9	C	149.0	20.5	B
<i>df=4, F=6.143, p=0.000 df=4, F=84.527, p=0.000 df=4, F=31.79, p=0.000 df=4, F=93.03, p=0.000 df=4, F=22.94, p=0.000 df=4, F=105.43, p=0.000</i>																			

Table 3.2. Top two-species spatial co-occurrence models for each paired combination of species interactions on ARNG-MTC, Ft. Pickett, Blackstone, Virginia in 2007. The Δ AIC in this case represents the difference between the top model and the next closest model.

Model	Species A	Species B	ϕ	ϕ 95% lcl	ϕ 95% ucl	Δ AIC	Outcome
psiA(.),psiB(.),phi(.),{NE-NI}pA(.),pB(.),rA(.),rB(.),delta(.)	<i>Eptesicus fuscus</i>	<i>Lasiurus borealis</i>	1.30	1.11	1.53	2.78	co-occurrence
psiA(.),psiB(.),phi(1),{NE-NI}pA(.),pB(.),rA(.),rB(.),delta(.)	<i>Eptesicus fuscus</i>	<i>Myotis lucifugus</i> <i>Myotis</i>	1.00	1.00	1.00	4.31	independent
psiA(.),psiB(.),phi(.),{NE-NI}pA(.),pB(.),rA(.),rB(.),delta(.)	<i>Eptesicus fuscus</i>	<i>septentrionalis</i>	1.50	1.21	1.88	6.74	co-occurrence
psiA(.),psiB(.),phi(.),{NE-NI}pA(.),pB(.),rA(.),rB(.),delta(.)	<i>Eptesicus fuscus</i>	<i>Nycticeius humeralis</i>	1.15	0.99	1.33	1.08	independent
psiA(.),psiB(.),phi(.),{NE-NI}pA(.),pB(.),rA(.),rB(.),delta(.)	<i>Eptesicus fuscus</i>	<i>Perimyotis subflavus</i>	1.34	1.15	1.57	2.13	co-occurrence
psiA(.),psiB(.),phi(.),{NE-NI}pA(.),pB(.),rA(.),rB(.),delta(.)	<i>Lasiurus borealis</i>	<i>Myotis lucifugus</i> <i>Myotis</i>	1.18	0.94	1.49	334.96	independent
psiA(.),psiB(.),phi(.),{NE-NI}pA(.),pB(.),rA(.),rB(.),delta(.)	<i>Lasiurus borealis</i>	<i>septentrionalis</i>	1.48	1.28	1.79	7.30	co-occurrence
psiA(.),psiB(.),phi(.),{NE-NI}pA(.),pB(.),rA(.),rB(.),delta(.)	<i>Lasiurus borealis</i>	<i>Nycticeius humeralis</i>	1.19	0.89	1.57	267.87	independent
psiA(.),psiB(.),phi(1),{NE-NI}pA(.),pB(.),rA(.),rB(.),delta(.)	<i>Lasiurus borealis</i>	<i>Perimyotis subflavus</i>	1.00	1.00	1.00	2.45	independent
psiA(.),psiB(.),phi(.),{NE-NI}pA(.),pB(.),rA(.),rB(.),delta(.)	<i>Myotis lucifugus</i>	<i>Myotis septentrionalis</i>	1.32	1.10	1.58	2.95	co-occurrence
psiA(.),psiB(.),phi(.),{NE-NI}pA(.),pB(.),rA(.),rB(.),delta(.)	<i>Myotis lucifugus</i>	<i>Nycticeius humeralis</i>	1.00	1.00	1.00	65.65	independent
psiA(.),psiB(.),phi(.),{NE-NI}pA(.),pB(.),rA(.),rB(.),delta(.)	<i>Myotis lucifugus</i>	<i>Perimyotis subflavus</i>	1.12	0.85	1.47	370.37	independent
psiA(.),psiB(.),phi(.),{NE-NI}pA(.),pB(.),rA(.),rB(.),delta(.)	<i>Myotis septentrionalis</i>	<i>Nycticeius humeralis</i>	1.33	1.12	1.58	6.05	co-occurrence
psiA(.),psiB(.),phi(.),{NE-NI}pA(.),pB(.),rA(.),rB(.),delta(.)	<i>Myotis septentrionalis</i>	<i>Perimyotis subflavus</i>	1.42	1.42	1.42	6.74	uncertain*
psiA(.),psiB(.),phi(.),{NE-NI}pA(.),pB(.),rA(.),rB(.),delta(.)	<i>Nycticeius humeralis</i>	<i>Perimyotis subflavus</i>	1.22	0.96	1.55	281.64	independent

*uncertain designation is due to the failure of the models' ability to generate standard errors for ϕ

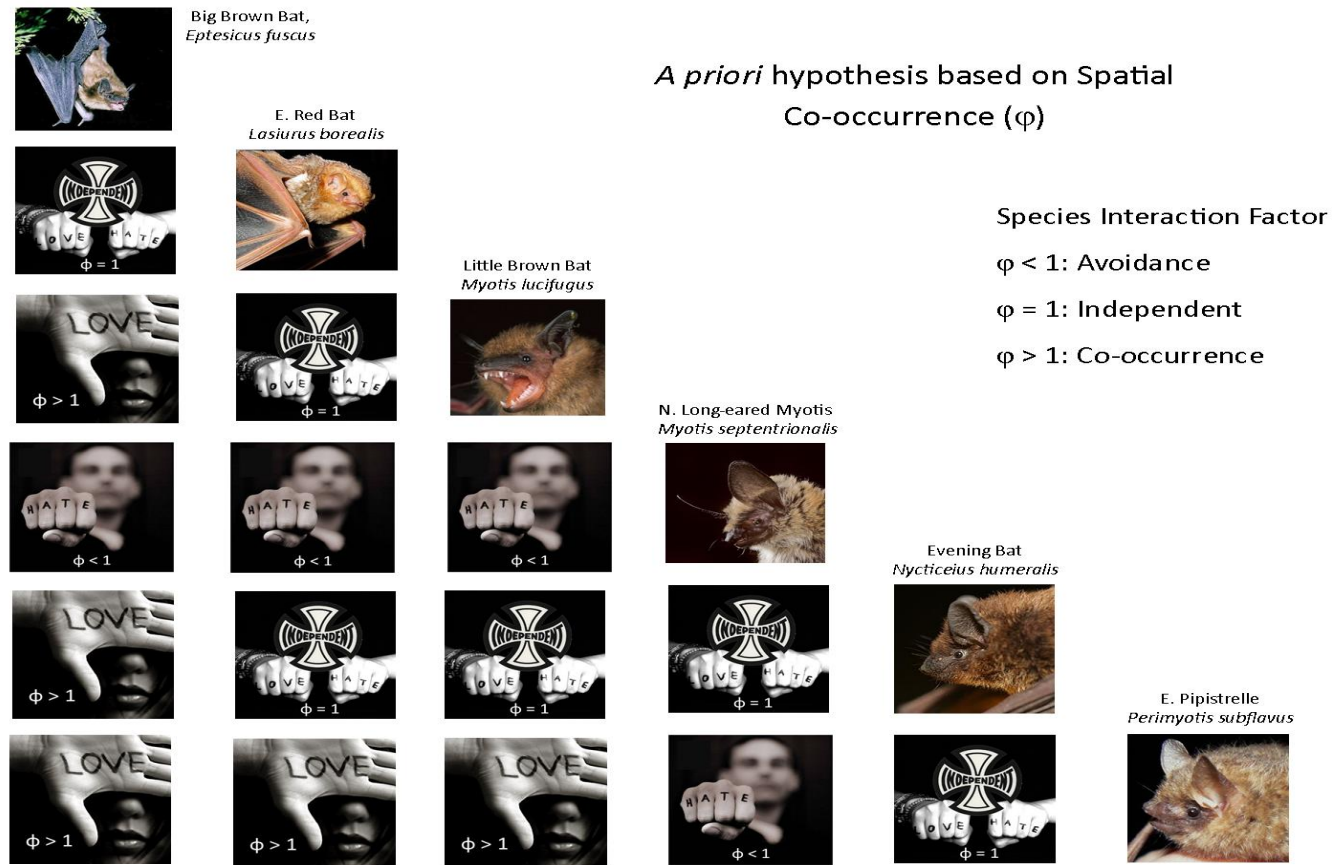


Figure 3.1. *A priori* hypothesis regarding spatial co-occurrence based on morphology, natural history, echolocation call structure and habitat use among six vespertilionid species on ARNG-MTC Ft. Pickett, Blackstone, Virginia in 2007 (St. Germain 2012).

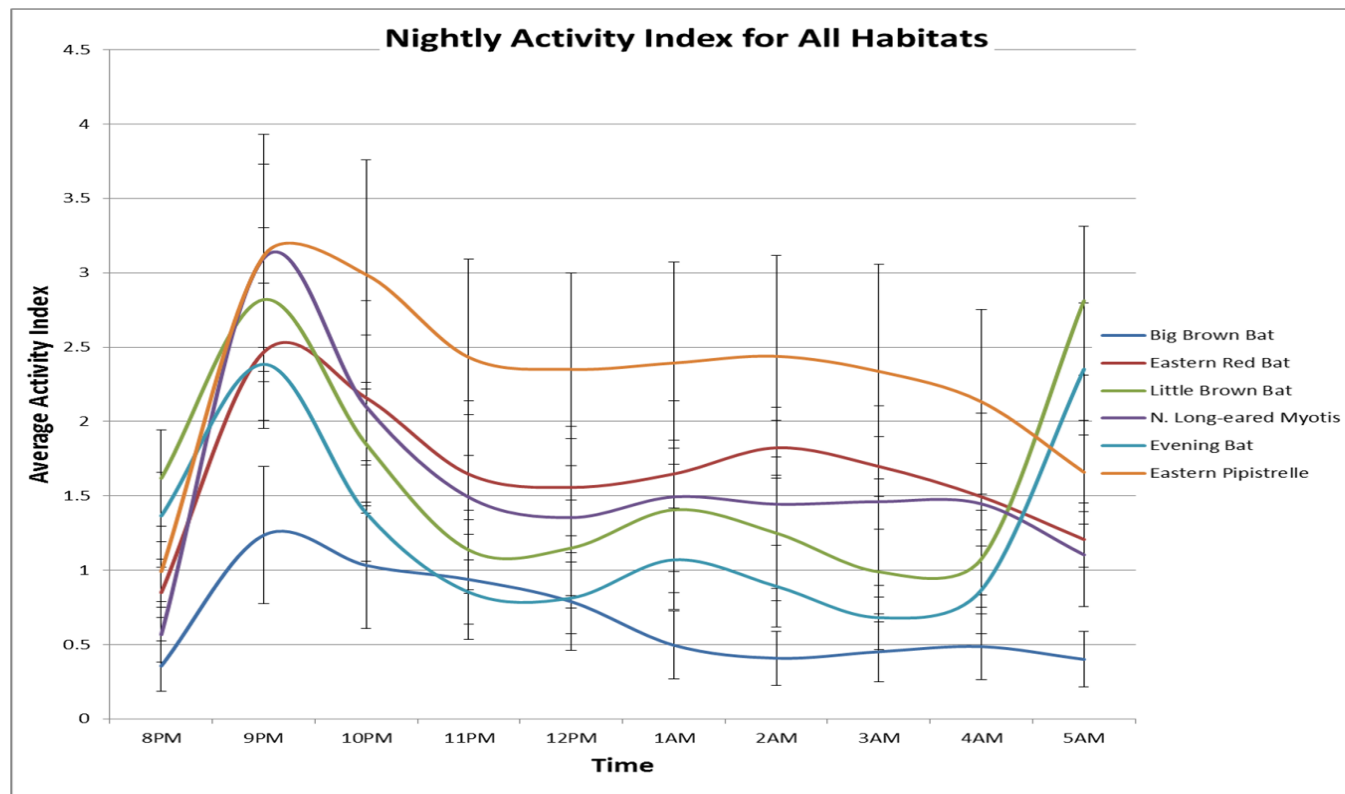


Figure 3.2. Temporal activity patterns for six sympatric bat species based on average activity index on ARNG-MTC Ft. Pickett, Blackstone, Virginia in 2007 (St. Germain 2012).

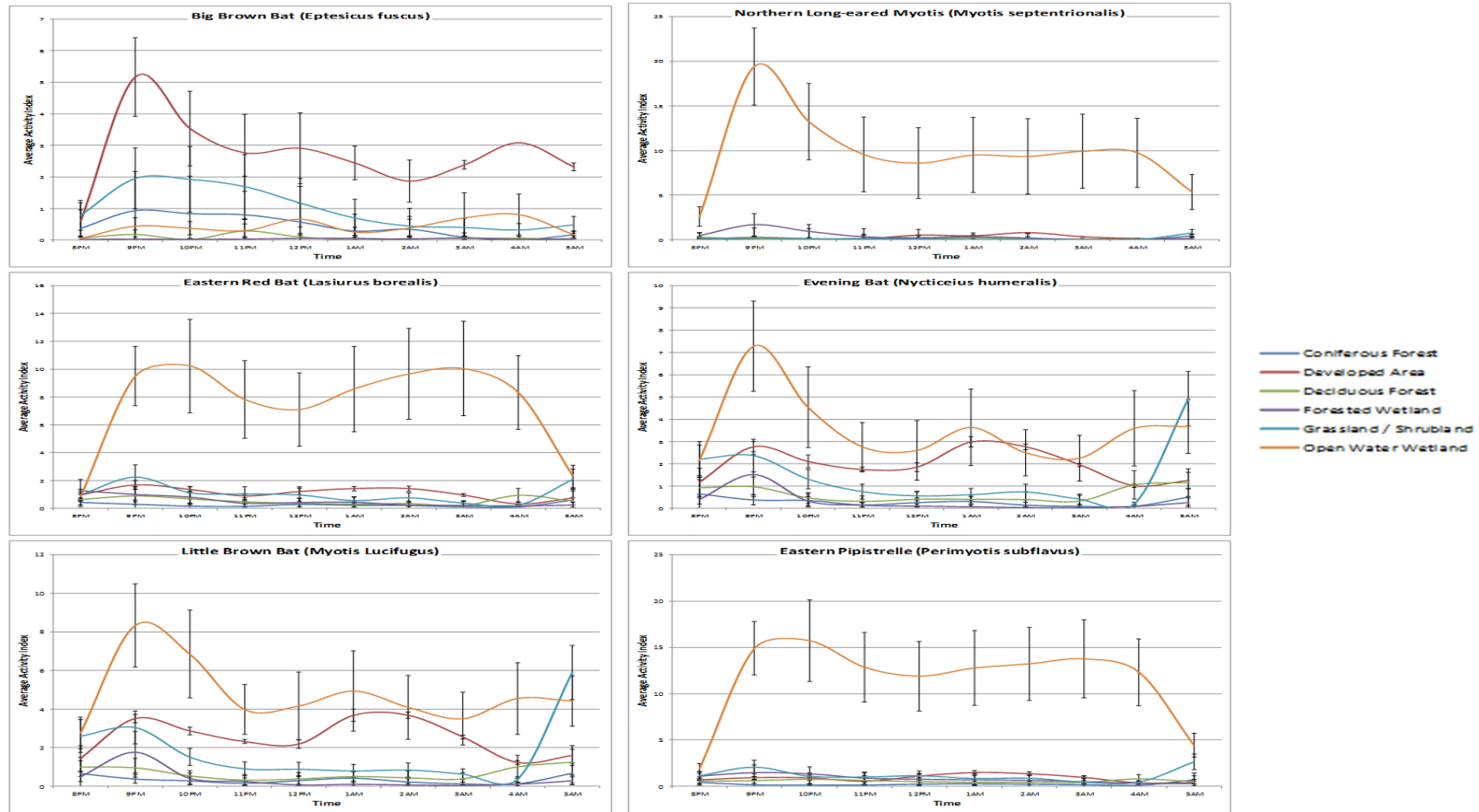


Figure 3.3. Average nightly activity index for six sympatric bat species by major physiognomic habitat type on ARNG-MTC Ft. Pickett, Blackstone, Virginia in 2007 (St. Germain 2012).

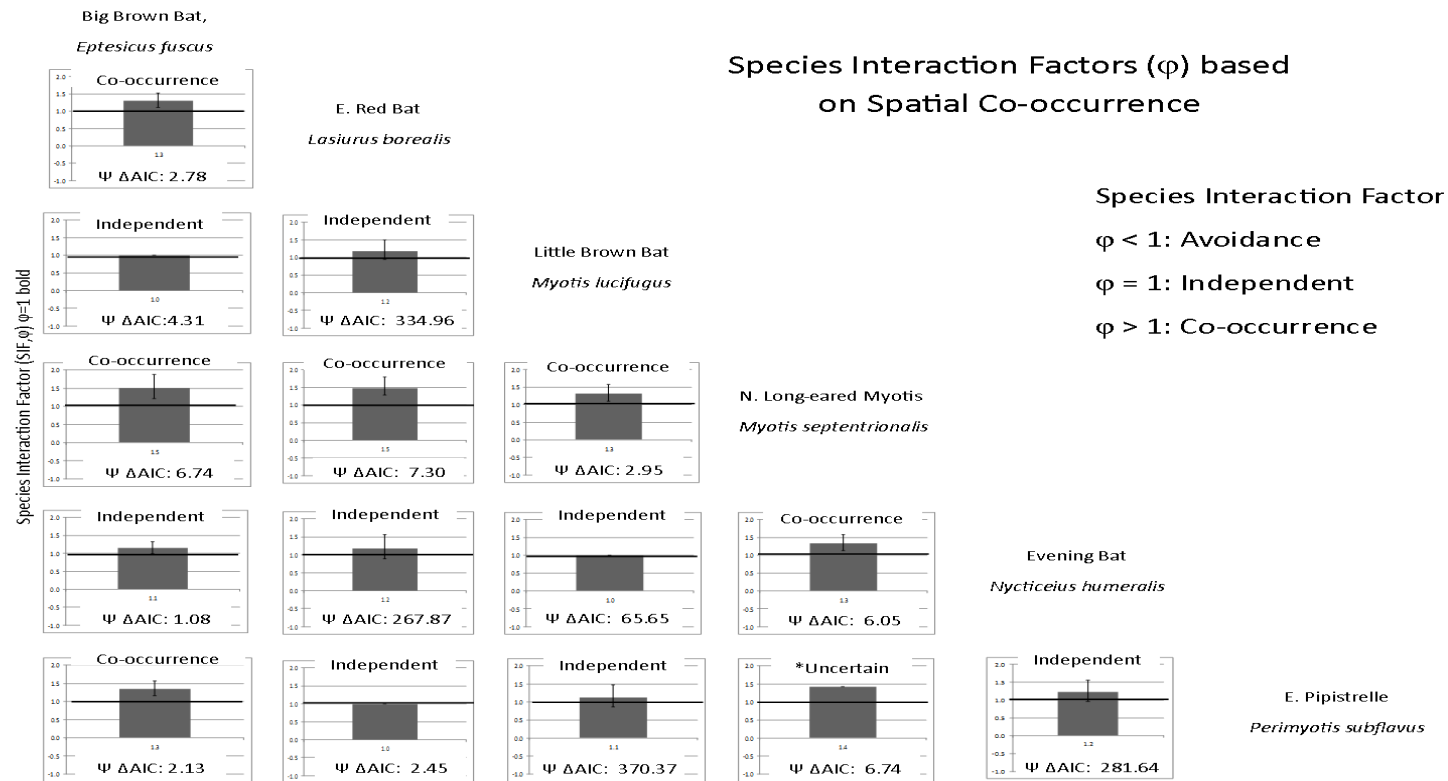


Figure 3.4. Spatial co-occurrence based on two-species occupancy models among six vespertilionid species on ARNG-MTC Ft. Pickett, Blackstone, Virginia in 2007. ΔAIC represents the difference between the top model and the next best model (St. Germain 2012).

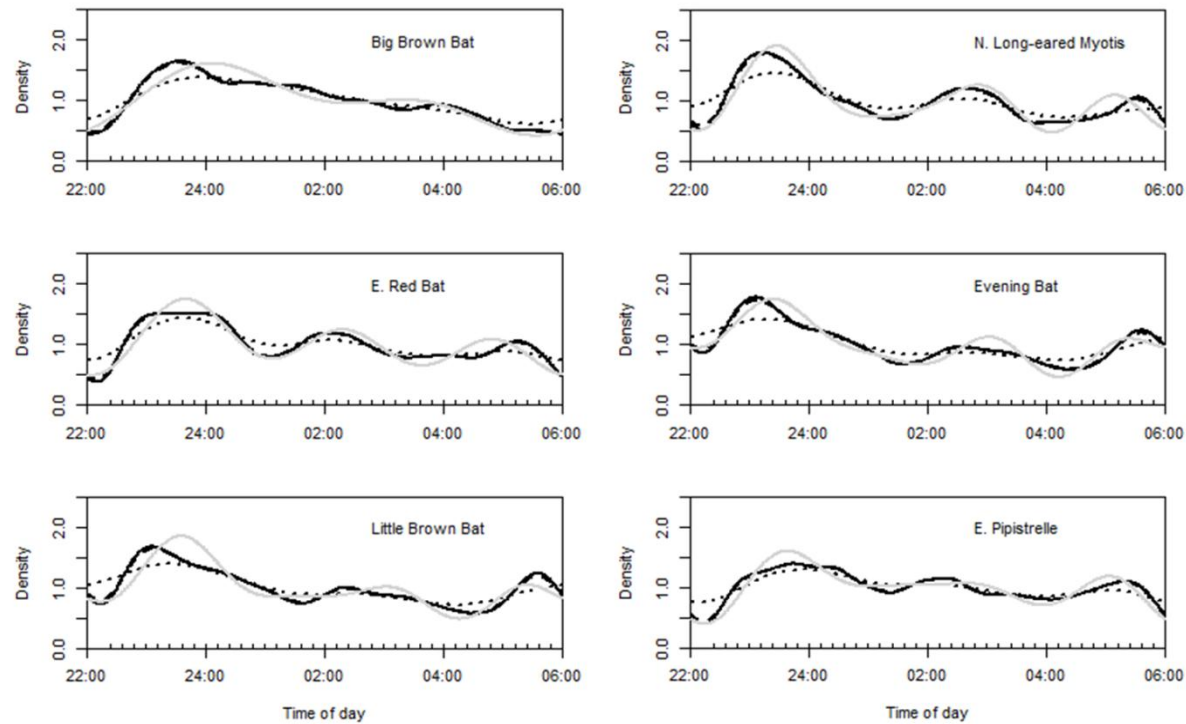


Figure 3.5. Temporal activity based on kernel density estimates among six vespertilionid species on ARNG-MTC Ft. Pickett, Blackstone, Virginia in 2007. Various smoothing factors are represented, Light grey $c=0.25$, Solid line $c=1.0$, dotted line $c=1.25$ (St. Germain 2012).

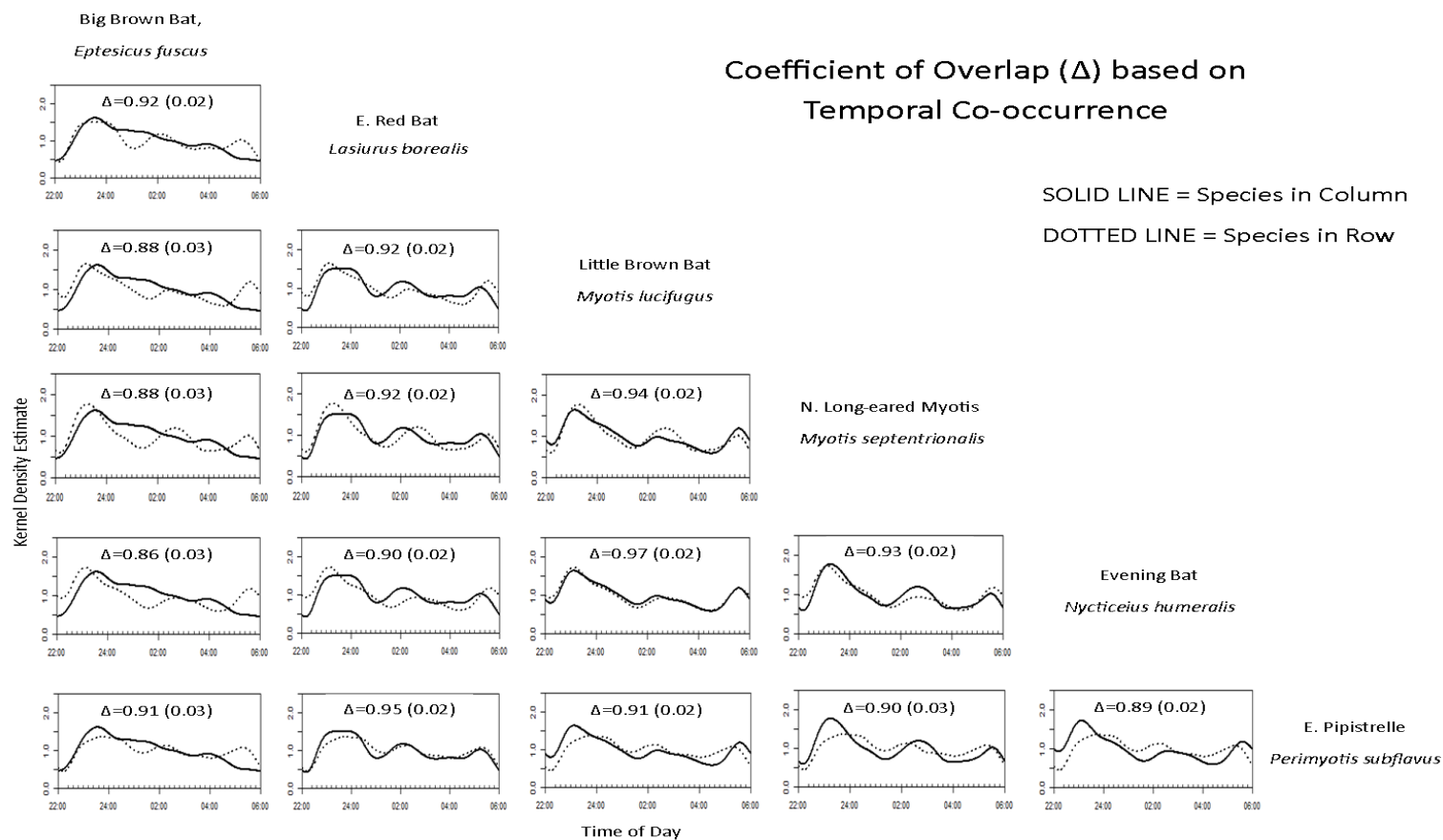


Figure 3.6. Two-species temporal overlap (Δ) based on kernel density estimates among six vespertilionid species on ARNG-MTC Ft. Pickett, Blackstone, Virginia in 2007. The solid line represents species in column, dotted line denotes species in row (St. Germain 2012).

<p>Big Brown Bat, <i>Eptesicus fuscus</i></p>				<p>Species Co-occurrence</p> <p>Ψ = Co-bat occupancy model difference from the null model</p> <p>ϕ = Species Interaction Factor (95% CI)</p> <p>Δ = Temporal Coefficient of Overlapping (SE)</p> <p>Ω = Habitats of strong activity overlap $p > 0.95$</p> <p>ξ = Habitats of strong activity non-overlap $p < 0.05$</p>	
<p>Co-occurrence Ψ ΔAIC: 7.46 ϕ = 1.30 (1.11-1.53) Δ = 0.92 (0.02) Ω = CF GS ξ = WL</p>	<p>E. Red Bat <i>Lasiurus borealis</i></p>				
<p>Independent Ψ ΔAIC: 62.24 ϕ = 1.00 (1) Δ = 0.88 (0.03) Ω = CF DA ξ = DF GS WL</p>	<p>Independent Ψ ΔAIC: 0.00 ϕ = 1.18 (0.94-1.49) Δ = 0.92 (0.02) Ω = CF DF FW ξ = GS</p>	<p>Little Brown Bat <i>Myotis lucifugus</i></p>			
<p>Co-occurrence Ψ ΔAIC: 8.73 ϕ = 1.50 (1.21-1.88) Δ = 0.88 (0.03) Ω = DF ξ = DA GS WL</p>	<p>Co-occurrence Ψ ΔAIC: 7.30 ϕ = 1.48 (1.28-1.79) Δ = 0.92 (0.02) Ω = CF FW ξ = GS</p>	<p>Co-occurrence Ψ ΔAIC: 2.95 ϕ = 1.32 (1.10-1.58) Δ = 0.94 (0.02) Ω = FW ξ = DF GS WL</p>	<p>N. Long-eared Myotis <i>Myotis septentrionalis</i></p>	<p>Habitats</p> <p>CF Coniferous forest</p> <p>DA Developed area</p> <p>DF Deciduous forest</p> <p>FW Forested wetland</p> <p>GS Grassland / shrubland</p> <p>WL Open water wetland</p>	
<p>Independent Ψ ΔAIC: 1.08 ϕ = 1.15 (0.99-1.33) Δ = 0.86 (0.03) Ω = CF DA ξ = DF</p>	<p>Independent Ψ ΔAIC: 0.00 ϕ = 1.19 (0.89-1.57) Δ = 0.90 (0.02) Ω = CF DF ξ = WL</p>	<p>Independent Ψ ΔAIC: 65.65 ϕ = 1.00 (1) Δ = 0.97 (0.02) Ω = CF DF FW ξ = n/a</p>	<p>Co-occurrence Ψ ΔAIC: 6.05 ϕ = 1.33 (1.12-1.58) Δ = 0.93 (0.02) Ω = FW ξ = DF GS WL</p>	<p>Evening Bat <i>Nycticeius humeralis</i></p>	
<p>Co-occurrence Ψ ΔAIC: 15.29 ϕ = 1.34 (1.15-1.57) Δ = 0.91 (0.03) Ω = CF ξ = FW WL</p>	<p>Independent Ψ ΔAIC: 2.45 ϕ = 1.00 (1) Δ = 0.95 (0.02) Ω = CF DA DF GS ξ = n/a</p>	<p>Independent Ψ ΔAIC: 0.00 ϕ = 1.12 (0.85-1.47) Δ = 0.91 (0.02) Ω = CF DF ξ = WL</p>	<p>*Uncertain Ψ ΔAIC: 6.74 ϕ = 1.42 (*1.42-1.42) Δ = 0.90 (0.03) Ω = CF DA ξ = GS</p>	<p>Independent Ψ ΔAIC: 0.00 ϕ = 1.22 (0.96-1.55) Δ = 0.89 (0.02) Ω = CF DF ξ = WL</p>	<p>E. Pipistrelle <i>Perimyotis subflavus</i></p>

Figure 3.7. Overall results of spatial, temporal and activity co-occurrence for six sympatric bat species on ARNG-MTC Ft. Pickett, Blackstone, Virginia in 2007 (St. Germain 2012).

APPENDIX A - Dominant Vegetation Classifications on ARNG-MTC Fort Pickett

Refers to Chapter 1

Coniferous Forests (CF):

This cover type is very common at Fort Pickett-MTC and is almost exclusively dominated by loblolly pine (*Pinus taeda*). Loblolly pine comprises over 80% of the basal area in this cover type.

Developed / Cantonment Areas (DA):

The cantonment area encompasses most of the buildings (barracks, dining halls, maintenance areas, warehouses, etc.) at ARNG-MTC Fort Pickett. Blackstone army airfield (BAAF), helicopter landing zones and the ammunition supply point (ASP) are all also located within the cantonment area. Within the cantonment area there are also several buildings that are abandoned and in various states of decay.

Deciduous Forests (DF):

The Deciduous Forest class is an upland hardwoods cover type. This classification is the most variable of all the cover types at ARNG-MTC Fort Pickett. This type occurs on a variety of sites with black oak being more prevalent on the drier more exposed sites and northern red oak more common on the less exposed wetter sites. As with many oak dominated cover types, fire appears to be necessary for the stand to perpetuate itself. The dominant vegetation is comprised of: white oak (*Quercus alba*), black oak (*Quercus velutina*), northern red oak (*Quercus rubra*) southern red oak (*Quercus falcata*), chestnut

oak (*Quercus montana*), sweetgum (*Liquidambar styraciflua*), loblolly pine (*Pinus taeda*), tulip poplar (*Liriodendron tulipifera*) pignut hickory (*Carya glabra*), and mockernut hickory (*Carya tomentosa*).

Forested Wetlands / Bottomland Hardwood Forests (FW):

This cover type occurs on frequently flooded bottomlands and alluvial plains of major rivers. It is especially common along the Nottoway River floodplain at ARNG-MTC Fort Pickett in deep coarse textured soils. Dominant vegetation indicative of this cover type include: sweetgum (*Liquidambar styraciflua*), willow oak (*Quercus phellos*) American beech (*Fagus grandifolia*), river birch (*Betula nigra*), American sycamore (*Plantanus occidentalis*), loblolly pine (*Pinus taeda*), red maple (*Acer rubra*), tulip poplar (*Liriodendron tulipifera*) and American Elm (*Ulmus americana*).

Grassland / Shrublands / Open Areas (GS):

The open areas at Fort Pickett-MTC exist because of the training requirements of the military and are maintained in an early successional status by training activities, prescribed fire, drum-chopping and mowing. The plant communities resemble abandoned agricultural fields in their species composition (Keever 1950 and Odum 1971). Typically they comprise a mosaic of warm and cold season grasslands (Emrick and Murray 2001). Species composition at any one site will vary depending upon disturbance and maintenance regimes. The dominant woody species in these communities are loblolly pine, oak species, and sweetgum. Broomsedge (*Andropogon virginicus*), little bluestem (*Schizachyrium scoparuim*) and panicums (*Dicanthelium spp*

and *Panicum spp*) dominate the grass component of the herbaceous strata. Whereas, various goldenrods (*Solidago spp*) and asters (*Aster spp*) dominate the forb component of the herbaceous strata.

Open Water Wetlands (WL):

The dominant vegetation along the shorelines of open water wetlands on Ft. Pickett are comprised of red maple (*Acer rubrum*), willow oak (*Quercus phellos*), American hornbeam (*Carpinus carolinensis*) American elm (*Ulmus Americana*) and sweetgum (*Liquidamber styraciflua*). Tag alder (*Alnus serrulata*) buttonbush (*Cephalanthus occidentalis*) and swamp rose (*Rosa palustris*) comprise the shrub layer.

Rare communities within the Controlled Access Area

These communities occur with some frequency in the Controlled Access Area (CAA). The CAA serves as buffer zone for various live fire ranges, resulting in frequent training-caused wildfires, which in turn maintain these communities. They are comprised of fire maintained oak (*Quercus sp*)- hickory (*Carya sp.*) -little bluestem (*Schizachyrium scoparium*) woodlands, and loblolly pine (*Pinus teada*)- little bluestem savannas.

APPENDIX B- Natural History of Bats on ARNG-MTC Fort Pickett

Refers to Chapter 1

Corynorhinus rafinesquii macrotis (CORRAF), formerly (*Plecotus rafinesquii*):

The eastern big-eared bat, also known as Rafinesque's big-eared bat, is found from Florida to North Carolina, West Virginia, and the southern parts of the southern Great Lakes states, westward to southeastern Oklahoma and eastern Texas (Schwartz and Schwartz 1981, Choate et al. 1994). Nowhere is this species abundant (Schwartz and Schwartz 1981). This species is one of the least known North American bats (Sealander and Heidt 1990) and carries a designation of state endangered, a global rank of very rare to common, and a state rank of very rare (Roble 2003, VAFWIS 2005). In the northern portion of its range, hibernation occurs from November to March (Whitaker and Hamilton 1998). This species hibernates in caves and mines, either singly or in small groups (Choate et al. 1994). It prefers hibernacula that are more open and lighted than those of most other bat species (Choate et al. 1994). It is a colonial species, with groups formed from a few to 100 or more (Choate et al. 1994). Nursery colonies have been reported in buildings, but only rarely in caves. In summer, males tend to roost in buildings or under loose bark of trees and in hollow trees (Schwartz and Schwartz 1981). These bats forage after dark; they are not crepuscular (Choate et al. 1994). Eastern big-eared bats prey on moths (Whitaker and Hamilton 1998). The estimated life span is 8 – 10 years (VDGIF 2005). Currently there is no reliable acoustic information available to identify *Corynorhinus rafinesquii* to the species level. Due to life history and

morphological traits it is assumed that the vocal signature is similar to *Corynorhinus townsendii virginianus*.

Corynorhinus townsendii virginianus (CORTOW), formerly (*Plecotus townsendii virginianus*):

The Virginia subspecies of the western big-eared bat, or Townsend's big-eared bat, occurs in isolated areas of mountainous regions of western Virginia (VAFWIS 2005). This subspecies, including the populations in Virginia, is listed as federally endangered by the US Fish and Wildlife Service (Harvey 1986). It also has a state status of endangered, a sub-specific global rank of critically imperiled, and a state rank as vulnerable to extirpation (Roble 2003, VAFWIS 2005). It has been suggested that this species occurred throughout the continental United States during the Wisconsin glaciation, but has been unable to adjust to climatic changes (Schwartz and Schwartz 1981).

From October to April, this species almost exclusively hibernates in cold portions of caves and rocky crevices. When hibernating in caves, this species tends to occur near the entrance. These bats hang in clusters from a few to as many as 50, with mixed sexes and ages. In summer they live in caves, rocky crevices, old buildings, tunnels or in abandon mines (Schwartz and Schwartz 1981, Ellison et al. 2003). Nursery colonies are formed in summer in warmer portions of caves and may contain from 12 to 200 individuals. During the maternity period males are apparently solitary and it is unknown where most males spend the summer (Harvey et al. 1999). No long distance migrations are known and this species does not move around much, although most individuals

change caves seasonally (Whitaker and Hamilton 1998). However recorded movements of about 64 km (40 miles) have been reported (Barbour and Davis 1969). Like many other bat species they return to the same roost sites year after year (Harvey et al. 1999). These bats are very wary and take alarm at the least disturbance (Whitaker and Hamilton 1998).

Relatively little is known about the behavior of this species. It is an extremely agile late flier and usually begins to forage well after dark. They are believed to forage entirely on moths but may take other insects as well (Schwartz and Schwartz 1981, Sealander and Heidt 1990, Harvey et al. 1999). Based on banding records the lifespan for this species may be 16 or more years (Sealander and Heidt 1990, Harvey et al. 1999). The call signature is characterized as a steep signature with a maximum frequency of 60 kHz to minimum frequency of 30 kHz, with durations of ~5 milliseconds (see Figure 1.3).

Eptesicus fuscus (EPTFUS):

The big brown bat ranges from southern Canada to northern South America, and is found on many islands of the Antilles (Choate et al. 1994). They have relatively short seasonal movements, with most occupying the same site in both winter and summer (Schwartz and Schwartz 1981, Choate et al. 1994). They hibernate from late-November to February or March, preferring drier, cooler parts of caves (Sealander and Heidt 1990). Big brown bats hibernate in caves and mines, hollow trees, deep crevices in rocky cliffs, buildings, storm sewers, road culverts, and burial vaults (Schwartz and Schwartz 1981). They are rarely found in large numbers (Whitaker and Hamilton 1998). They hang by

their feet or lie horizontally when hibernating, depending on the site (Schwartz and Schwartz 1981). In late-spring and early-summer, females establish nursery colonies in hollow trees, attics, chimneys, lofts, or caves (Schwartz and Schwartz 1981, Whitaker and Hamilton 1998). These colonies may consist of 30 to 2,000 or so individuals. In the summer, males roost in man-made structures or in trees. These bats forage at sunset, flying along watercourses at the forest edge. They generally fly below or within the tree canopy. They feed on May beetles, click beetles, flying ants, and houseflies (Schwartz and Schwartz 1981). Big brown bats have a maximum life span around 14 years (VAFWIS 2005). This species has midrange minimum frequency echolocation calls from 35 to 25 kHz, with durations of 4 to 10 milliseconds (Feldhamer et al. 2003) (see Figure 1.3). Some audible chattering can be heard when the bats are in flight (Choate et al. 1994). *Eptesicus fuscus* has no special federal or state designation and is not of management concern for ARNG-MTC Fort Pickett.

Lasionycteris noctivagans (LASNOC):

The silver-haired bat occurs from southwestern Alaska to northeastern Mexico and is found in all but the southernmost portions of the United States (Choate et al. 1994). The Virginia Gap analysis shows the wintering range of *L. noctivagans* throughout Virginia and predictive habitat models shows potential occurrence on the ARNG-MTC Fort Pickett. This species migrates in large numbers, wintering in the southern portion of its range and summering in the northern portion (Schwartz and Schwartz 1981). During the summer, females are gregarious, but males live singly and apart from the females. The silver-haired bat lives in the forest and along wooded waterways and can swim for

short distances (Schwartz and Schwartz 1981). It roosts in dense tree foliage, but may also roost under bark or in tree hollows, caves, rock crevices, or buildings (Schwartz and Schwartz 1981). The preservation of dead snags in clear-cuts will provide roosting sites (Sealander and Heidt 1990). They feed at dusk, foraging along waterways or the borders of hardwood groves. Flight patterns are slow and erratic, with twists and glides up to 40 feet or more above ground. They feed on beetles and other flying insects (Schwartz and Schwartz 1981). They have an estimated maximum life span of 12 years (VAFWIS 2005). *Lasionycteris noctivagans* has no special federal or state designation and is not of management concern for ARNG-MTC Fort Pickett.

Lasiurus borealis (LASBOR):

The eastern red bat occurs in the eastern United States and southeastern Canada, west to Wyoming, Colorado, and Texas, and south to eastern Mexico (Choate et al. 1994). The sexes are segregated prior to migratory movements (Sealander and Heidt 1990). In the north, red bats migrate southward, beginning in September, over several hundred miles (Schwartz and Schwartz 1981). In the south-central region of their range, they are active all year in the same areas (Choate et al. 1994). This bat is a tree-inhabiting species. In summer, they frequent forests and shade trees around cities and farms. In spring and fall, they often hang on shrubs or tall weeds during the day (Schwartz and Schwartz 1981). In the south, they prefer clumps of Spanish moss (Choate et al. 1994). They roost in places with thick, leafy ‘ceilings’ and open ‘floors’ (Whitaker and Hamilton 1998). In summer, these bats are solitary and females do not form nursery colonies. They start to feed before dusk and continue into the night. They

often forage in great concentrations, along the edges of forests, flood plain timber, and fence rows. They can also be seen over corncribs, meadows, and around street lights. They consume moths, beetles, crickets, flies, and cicadas (Schwartz and Schwartz 1981). The life span of the eastern red bat is estimated not to exceed 12 years (VAFWIS 2005). Echolocation calls have maximum frequency of about 50 kHz, with minimum frequency alternating in an undulating pattern between 38 and 42 kHz ranging for 10 milliseconds (Feldhamer et al. 2003) (see Figure 1.3). *Lasiurus borealis* has no special federal or state designation and is not of management concern for ARNG-MTC Fort Pickett. Add call signature info.

Lasiurus cinereus (LASCIN):

The hoary bat occurs from Canada, southward to Guatemala. Isolated subspecies occur in South America and on the Hawaiian Islands (Choate et al. 1994). It is considered uncommon throughout its vast range and little is known of its populations or home range (Whitaker and Hamilton 1998). *Lasiurus cinereus* is strongly migratory, moving southward in October and November and returning northward in the spring (Schwartz and Schwartz 1981, Choate et al. 1994). Bats travel individually or in small groups (Schwartz and Schwartz 1981). Nursery colonies are not formed. This is a tree-inhabiting bat whereby solitary individuals roost on tree branches, well-covered above and open below (Schwartz and Schwartz 1981, Choate et al. 1994). They forage in the late evening, flying above watercourses and meadows (Schwartz and Schwartz 1981). Individuals do not share foraging areas and the sexes are largely separated during summer (Schwartz and Schwartz 1981, Sealander and Heidt 1990). They feed on moths,

but will also consume wasps, mosquitoes, dragonflies, and beetles (Schwartz and Schwartz 1981). There are reports of these bats preying on smaller species of bats (Sealander and Heidt 1990). Their life span is estimated to range from 6-7 years. Hoary bats emit a chattering in flight that can be heard by humans (Choate et al. 1994). Echolocation calls have maximum frequency of about 50 kHz, with minimum frequency alternating between 25 and 20 kHz (Feldhamer et al. 2003) (see Figure 1.3). *Lasiurus cinereus* does not have any special federal or state designation and is not of management concern for ARNG-MTC Fort Pickett.

Lasiurus seminolus (LASSEM):

The Seminole bat is distributed from Florida to Virginia, westward to southeastern Oklahoma and eastern Texas (Choate et al. 1994). This is the most abundant and commonly seen bat in much of the south-central region of the United States (Choate et al. 1994) but there is very little known about its biology or population behavior (Whitaker and Hamilton 1998). This bat is active all year round, with small seasonal movements in autumn and winter from only those areas of its northernmost breeding range (Sealander and Heidt 1990). This bat inhabits wooded areas, both deciduous and coniferous (Choate et al. 1994). It roosts in Spanish moss, individually or in pairs. Clumps of moss with a southwestern exposure are preferred. This species begins foraging in early evening (Sealander and Heidt 1990). They forage mostly at tree-top level, but also fly over watercourses and forest clearings, and along forest edges. Seminole bats feed on insects caught in flight, preferring dipterans, beetles, dragonflies,

and hymenopterans (Choate et al. 1994). *Lasiurus seminolus* does not have any special federal or state designation and is not of management concern for ARNG-MTC Fort Pickett. However, *Lasiurus seminolus* in the northwestern portions of its range is considered rare and a species of concern (ANHC 2005, St. Germain and Miller 2005). Currently there is no reliable information on the call structure of the seminole bat.

Myotis leibii (MYOLEI):

The eastern small-footed myotis is considered rare in scattered locations throughout Missouri and in the remainder of its range in the eastern United States and Canada (Schwartz and Schwartz 1981). It carries a global rank of very rare, and a state rank of extremely rare (Roble 2003, VAFWIS 2005). The western form, now considered a separate species, *Myotis ciliolabrum* (Harvey and Redman 2001), is common throughout its wide range in western North America. *M. leibii* ranges in mountainous regions from the Ozarks of Arkansas, Missouri, and Oklahoma eastward to the Appalachian region, and northward to the New England states and adjacent southeastern Canada (Choate et al. 1994). It is the smallest of the North American bats and considered one of the rarest bats in the eastern United States (Choate et al. 1994). This bat hibernates in caves or mine tunnels in winter, and roosts and forms nursery sites in caves, buildings, and cavities in the ground or beneath rocks (Schwartz and Schwartz 1981). It roosts singly or in small groups (Choate et al. 1994). This species does not move into caves until late November or early December and exits earlier than most species, usually in March (Sealander and Heidt 1990). Small-footed bats forage low over streams and ponds and along cliffs, ledges, and wooded areas, rarely more than 20

feet above ground (Choate et al. 1994) Beetles are a predominant food source (Schwartz and Schwartz 1981). Currently there is no reliable information for acoustic signatures at the species level for the eastern small-footed myotis.

Myotis lucifugus (MYOLUC):

The little brown myotis has the broadest range of any North American myotis, ranging between the Atlantic and Pacific coasts, and from Alaska to Mexico. This species is common in the northern states but is considered uncommon in Arkansas (Sealander and Heidt 1990). *M. lucifugus* hibernates colonially in small clusters in caves or abandoned mines in the winter (October to late March or April), and in summer inhabits hot attics, church steeples, hollow trees, and behind loose bark or other sheltered spots (Sealander and Heidt 1990). Migration of this species is typically local but they may fly as far as 160-320 km (100-200 miles) to find suitable hibernacula (Whitaker and Hamilton 1998). Females form maternity colonies, whereas the males tend to roost individually. These bats begin to forage at late dusk, frequenting the same areas night after night. The usual flight pattern is over water (lakes, ponds, streams, and rivers), and along woodland borders (Choate et al. 1994). *M. lucifugus* eats a variety of insects, including flies, moths, and small beetles. Small prey are typically eaten on the wing, but landing occurs to consume larger prey. They have a documented life span of 10 years with records up to 32 years, however survival rates are estimated at 2.15 years (VAFWIS 2005). Echolocation calls last from about 1 to 5 milliseconds and range from about 40 to 80 kHz, with most of the energy being produced at 45 kHz (Fenton and Bell 1979) (see

Figure 1.3) A bat in free flight may produce about 20 pulses per second with “feeding buzz” of over 50 pulses per second (Whitaker and Hamilton 1998).

Myotis septentrionalis (MYOSEP), formerly lumped with (*Myotis keenii*):

The northern myotis was formerly grouped with *Myotis keenii* (Keen’s myotis) but now represents its own species (Whitaker and Hamilton 1998). It is irregularly distributed within its range (Schwartz and Schwartz 1981). In the east, it is found in the Florida panhandle, Alabama, Georgia, Arkansas, Kentucky, Tennessee, and northeastern Mississippi. In the north, it ranges across southern Canada and the northern United States east of the Rockies (Choate et al. 1994). This species is primarily a cave dweller, but females seem to prefer trees or barns. They hibernate from October to March and tend to return to the same caves each year. Individuals roost in deep crevices, either alone or with one or two others (Schwartz and Schwartz 1981). Northern myotis may disperse 160 km (100 miles) from hibernacula (Choate et al. 1994). Small maternity colonies form in spring (Choate et al. 1994). Foraging begins just after dark and continues to just before dawn, with a bimodal peak at 1-2 hours and 7-8 hours after sunset (Sealander and Heidt 1990, Choate et al. 1994). Bats forage among trees on hillsides and ridges, feeding primarily below the crowns of trees (Schwartz and Schwartz 1981). Prey includes reduviids, cicadellids, ichneumons, lepidopterans, caddisflies, mayflies, dipterans, and spiders (Whitaker and Hamilton 1998). They have an estimated life span of 14 years (VAFWIS 2005). Echolocation calls last from about 8-10 milliseconds and range from about 40 to 60 kHz, with most of the energy being produced at and flattening out 42 kHz

(Fenton and Bell 1979) (see Figure 1.3). There is no management concern for *M. septentrionalis* on ARNG-MTC Fort Pickett. Add call signature info.

Myotis sodalis (MYOSOD):

The Indiana bat (or Social myotis), is classified as federally endangered by the US Fish and Wildlife Service (Harvey 1986). It is also state endangered, carries a global rank of critically imperiled, and a state rank of susceptible to extirpation (Roble 2003, VAFWIS 2005). It is distributed from central New England westward to Iowa, Missouri, and Oklahoma, and southward to northern Florida (Schwartz and Schwartz 1981, Choate et al. 1994). It hibernates in great masses from mid-October through late March or April. Hundreds or thousands of bats hibernate in a single cave. Possibly 95% or more of these bats winter in 15 caves- six in Missouri and nine in the eastern United States (Whitaker and Hamilton 1998). This bat winters in large, cool caves or abandoned mine tunnels with high humidity. They swarm at the caves prior to entering hibernation and after emergence (Whitaker and Hamilton 1998). These bats generally migrate southward up to several hundred kilometers to occupy their summer range (Whitaker and Hamilton 1998).

During the summer females form small maternity colonies and bear young in hollow trees or beneath the bark of trees (Schwartz and Schwartz 1981, Choate et al. 1994). Indiana bats require closed canopy, riparian forests for foraging and hardwood stands with open to partially closed canopies for roosting (Evans et al. 1998). They gather in small colonies, usually under the loose bark of trees in semi-wooded areas, upland and bottomland forests, or even completely in the open (Kurta et al. 1993a, Kurta et al.

1993b) The trees used as roosts, in order of preference (the numbers are small), are slippery elm, northern red oak, shagbark hickory, silver maple, cottonwood, bitternut hickory, sassafras, sugar maple, white and shingle oak, and American elm (Kurta et al. 1993b). They primarily feed on moths though they will also consume beetles, caddis flies, and other flies (Schwartz and Schwartz 1981). Their average life span is 5 – 10 years (VAFWIS 2005). *Myotis sodalis* has high minimum-frequency calls of near 40 kHz, with very steep slopes (120 octaves/sec). Calls are curvilinear, with a short, flat terminal segment (Feldhamer et al. 2003)

Nycticeius humeralis (NYCHUM):

The evening bat ranges from New Jersey and the southern part of the Great Lakes region, westward to Nebraska, Kansas, Oklahoma, and Texas, and southward in eastern Mexico to Vera Cruz (Choate et al. 1994). The species is uncommon throughout the northern part of its range, but is abundant in Texas and the southeastern United States (Schwartz and Schwartz 1981). In the southern portion of its range, this species is active year-round, but migrates southward in winter from northern portions of its range. This is primarily a tree-inhabiting species, though bats have been found in attics and other building spaces. In summer, large nursery colonies are formed under the bark of dead trees or in houses (Schwartz and Schwartz 1981). Males of this species are solitary (Whitaker and Hamilton 1998). Evening bats begin foraging during the last half hour of daylight, hunting over clearings, farm ponds, and other open water, or along forest edge (Schwartz and Schwartz 1981, Choate et al. 1994). They feed on flying insects, including

moths, beetles, flies, true bugs, and flying ants (Schwartz and Schwartz 1981, Choate et al. 1994). Echolocation calls have maximum frequency of about 48 kHz, with minimum frequency alternating in a heavily undulating pattern between 34 and 36 kHz lasting for 10 - 14 milliseconds (Feldhamer et al. 2003) (see Figure 1.3). Currently there are not any special state or federal designations for *Nycticeius humeralis* and they are not of management concern at ARNG-MTC Fort Pickett.

Perimyotis subflavus (PERSUB) formerly *Pipistrellus subflavus* ([Hooper, 2006 #179]):

The eastern pipistrelle is distributed across eastern North America, west to Nebraska and Texas, and from southeastern Canada southward to Honduras (Choate et al. 1994). This species hibernates from mid-October to mid-April, and is often found in the same site in a cave year after year (Schwartz and Schwartz 1981, Sealander and Heidt 1990). They are 'profound' hibernators and do not awaken and fly about as much as other species do (Schwartz and Schwartz 1981). They hibernate individually or in small groups and seem to prefer warm, humid areas, and vertical walls and flat ceilings rather than crevices (Schwartz and Schwartz 1981, Sealander and Heidt 1990). In summer, they roost in trees, crevices in cliffs or buildings, and in barns (Schwartz and Schwartz 1981). Females establish nursery colonies in high domes of caves or under eaves of barns and other buildings (Schwartz and Schwartz 1981). Swarming near hibernacula has been observed in late summer and early autumn (Choate et al. 1994). Eastern pipistrelles appear to be weak fliers, fluttering about on undulating courses. They feed primarily at dusk and dawn, high over watercourses at the forest edge. This species feeds on tiny

insects such as flies, moths, wasps, leafhoppers, and beetles, many of which are aquatic forms (Schwartz and Schwartz 1981). They have a life span ranging from 4-8 years (VAFWIS 2005). The call signature ranges from 50 to 41 kHz and lasts for 5 - 10 milliseconds. It exhibits a well defined horizontal structure at 41 – 43 kHz with a slight increase in frequency at the terminus (see Figure 1.3). *Perimyotis subflavus* carries no special federal or state designation and is not of management concern for ARNG-MTC Fort Pickett.

LITERATURE CITED

- ANHC. 2005. Mammals of Special Concern (dated 16 March 2005)
<http://www.naturalheritage.com/pdf/ANIMALS-Mammals-2005.pdf>. Arkansas
Natural Heritage Commission, Little Rock, AR.
- Barbour, R. W. and W. H. Davis. 1969. Bats of America, Lexington, KY.
- Choate, J. R., J. K. Knox Jr., and C. Jones. 1994. Handbook of Mammals of the
Southcentral States. Louisiana State University Press, Baton Rouge, LA.
- Ellison, L. E., T. J. O'Shea, M. A. Bogan, A. L. Everette, and D. Schneider, M. 2003.
Existing data on colonies of bats in the United States: Summary and analysis of
the U.S. Geological Survey's bat population database. Pages 127-237 in T. J.
O'Shea and M. A. Bogan, editors. Monitoring trends in bat populations of the
United States and Territories: problems and prospects. U.S. Geological Survey,
Biological Resources Discipline, Information and Technology Report,
USGS/BRD/ITR--2003-0003.
- Emrick, V. R. and R. L. Murray, editors. 2001. Integrated Natural Resource Management
Plan Fort Pickett Maneuver Training Center, Blackstone, Virginia. Conservation

- Management Institute- Military Lands Division at Virginia Polytechnic Institute and State University, Blacksburg, Virginia.
- Evans, D., E., W. Mitchel, A., and R. Fischer, A. 1998. Species Profile: Indiana bat (*Myotis sodalis*) on military installations in the Southeastern United States. Technical Report SERDP 98-3,. U. S. Army Engineer Waterways Experiment Station, Vicksburg, MS.
- Feldhamer, G. A., B. C. Thompson, and C. J. A. 2003. Wild Mammals of North America: biology, management, and conservation. The Johns Hopkins University Press, Baltimore, Maryland.
- Fenton, M. B. and G. P. Bell. 1979. Echolocation and feeding behaviour in four species of myotis (Chiroptera). Canadian Journal of Zoology **57**:1271-1277.
- Harvey, M. J. 1986. Arkansas Bats: A Valuable Resource. Arkansas Game and Fish Commission.
- Harvey, M. J., J. S. Altenbach, and T. L. Best. 1999. Bats of the United States. Arkansas Game and Fish Commission, Little Rock, Arkansas.
- Harvey, M. J. and R. K. Redman. 2001. Endangered bats of Arkansas: distribution, status, and ecology (2000 - 2001) W-56-R. Tennessee Technological University, Cookeville, TN.
- Kurta, A., J. Kath, E. L. Smith, R. Foster, M. W. Orick, and R. Ross. 1993a. A maternity roost of the endangered Indiana bat (*Myotis sodalis*) in an unshaded hollow sycamore tree (*Plantanus occidentalis*). American Midland Naturalist **130**:405-407.

- Kurta, A., D. King, J. A. Teramino, J. M. Stribley, and K. F. Williams. 1993b. Summer roosts of the endangered Indiana bat (*Myotis sodalis*) on the northern edge of its range. *American Midland Naturalist* **129**:132-138.
- Roble, S. M. 2003. Natural Heritage Resources of Virginia: Rare Animal Species. Natural Heritage Technical Report 03-04, Virginia Department of Conservation and Recreation, Division of Natural Heritage, Richmond, Virginia.
- Schwartz, C. W. and E. R. Schwartz. 1981. Flying Mammals, Order *Chiroptera*. The Wild Mammals of Missouri. University of Missouri Press and Missouri Department of Conservation, Columbia, MO.
- Sealander, J. A. and G. A. Heidt. 1990. Arkansas Mammals: Their natural history, classification, and distribution. University of Arkansas Press.
- St. Germain, M., J. and B. W. Miller. 2005. Bat survey for Fort Chaffee MTC, Fort Smith, Arkansas. CMI-MLD R-38, Conservation Management Institute - Military Lands Division, College of Natural Resources, Virginia Polytechnic Institute and State University., Blacksburg, Virginia.
- VAFWIS. 2005. Virginia Fish and Wildlife Information Service. Virginia Department of Game and Inland Fisheries, Richmond, VA
<http://vafwis.org/WIS/ASP/home.asp?sID=64394&ln=I>.
- Whitaker, J. O. J. and W. J. J. Hamilton. 1998. Order Chiroptera. Mammals of the Eastern United States. Comstock Publishing Associates of Cornell University Press, Ithaca, NY.

Table B-1. Natural history summary for all 13 species with the potential to occur on ARNG-MTC Ft. Pickett, Blackstone, Virginia.

Common Name	Genus	Species	Residency	Summer habitat	Winter habitat	Hibernation	Sociality	Life span estimates
Eastern big-eared bat	<i>Corynorhinus</i>	<i>rafinesquii</i>	year round	forests	forests	complete	small - medium groups	8 - 10 years
Virginia big-eared bat	<i>Corynorhinus</i>	<i>townsendii</i>	year round	caves	caves	complete	small groups	16 years
* Big brown bat	<i>Eptesicus</i>	<i>fuscus</i>	year round	structures	caves / structures	complete	small - medium groups	14 years
Silver-haired bat	<i>Lasionycteris</i>	<i>noctivagans</i>	winter migrant	forests	forests	partial	solitary	12 years
* Eastern red bat	<i>Lasiurus</i>	<i>borealis</i>	migrational shift	forests	forests	partial	solitary	12 years
Hoary bat	<i>Lasiurus</i>	<i>cinereus</i>	migrational shift	forests	forests	partial	solitary	6 - 7 years
Seminole bat	<i>Lasiurus</i>	<i>seminolus</i>	migrational shift	forests	forests	partial	solitary	unknown
Small-footed myotis	<i>Myotis</i>	<i>leibii</i>	year round	structures / caves	caves	complete	small groups	12 years
* Little brown bat	<i>Myotis</i>	<i>lucifugus</i>	year round	structures / forests	caves / structures	complete	small - medium groups	10 years
* Northern long-eared myotis	<i>Myotis</i>	<i>septentrionalis</i>	year round	forests	caves	complete	small - medium groups	12 years
Indiana bat	<i>Myotis</i>	<i>sodalis</i>	migrational shift	forests	caves	complete	small - large groups	5 - 10 years
* Evening bat	<i>Nycticeius</i>	<i>humeralis</i>	migrational shift	forests / structures	unknown	partial	small - large groups	5 years
* Eastern pipistrelle	<i>Perimyotis</i>	<i>subflavus</i>	year round	forests / structures	caves / structures	complete	small - medium groups	4- 8 years

* Species included for detailed analysis

APPENDIX C – Pairwise comparisons for species activity for each habitat type
Refers to Chapter 3

Table C-1. Results of the Tukey-Kramer ANOVA pairwise comparisons of species activity to each physiognomic habitat type on ARNG-MTC Ft. Pickett, Virginia in 2007

Coniferous forest						Developed area					
Source	Type III SS	df	Mean Squ	F-Ratio	p-Value	Source	Type III SS	df	Mean Squ	F-Ratio	p-Value
SPECIES	574.88	5	114.976	0.561	0.73	SPECIES	23294.1	5	4658.819	3.844	0.002
Error	121703	594	204.887			Error	363580.2	300	1211.934		

Species A	Species B	Difference	p value	95% LCL	95% UCL	Species A	Species B	Difference	p value	95% LCL	95% UCL
Eptfus	Lasbor	1.67	0.963	-4.099	7.439	Eptfus	Lasbor	14.569	0.28	-5.077	34.214
Eptfus	Myoluc	0.95	0.997	-4.819	6.719	Eptfus	Myoluc	-0.725	1	-20.371	18.92
Eptfus	Myosep	3.26	0.592	-2.509	9.029	Eptfus	Myosep	22.431	0.014	2.786	42.077
Eptfus	Nychum	1.31	0.987	-4.459	7.079	Eptfus	Nychum	4.941	0.98	-14.705	24.587
Eptfus	Persub	1.69	0.961	-4.079	7.459	Eptfus	Persub	16.451	0.161	-3.195	36.097
Lasbor	Myoluc	-0.72	0.999	-6.489	5.049	Lasbor	Myoluc	-15.294	0.229	-34.94	4.352
Lasbor	Myosep	1.59	0.97	-4.179	7.359	Lasbor	Myosep	7.863	0.864	-11.783	27.509
Lasbor	Nychum	-0.36	1	-6.129	5.409	Lasbor	Nychum	-9.627	0.729	-29.273	10.018
Lasbor	Persub	0.02	1	-5.749	5.789	Lasbor	Persub	1.882	1	-17.763	21.528
Myoluc	Myosep	2.31	0.864	-3.459	8.079	Myoluc	Myosep	23.157	0.01	3.511	42.803
Myoluc	Nychum	0.36	1	-5.409	6.129	Myoluc	Nychum	5.667	0.964	-13.979	25.312
Myoluc	Persub	0.74	0.999	-5.029	6.509	Myoluc	Persub	17.176	0.126	-2.469	36.822
Myosep	Nychum	-1.95	0.929	-7.719	3.819	Myosep	Nychum	-17.49	0.113	-37.136	2.156
Myosep	Persub	-1.57	0.972	-7.339	4.199	Myosep	Persub	-5.98	0.954	-25.626	13.665
Nychum	Persub	0.38	1	-5.389	6.149	Nychum	Persub	11.51	0.552	-8.136	31.156

Table C-1 continued. Results of the Tukey-Kramer ANOVA pairwise comparisons of species activity to each physiognomic habitat type on ARNG-MTC Ft. Pickett, Virginia, in 2007.

Deciduous forest						Forested wetland					
Source	Type III SS	df	Mean Squ	F-Ratio	p-Value	Source	Type III SS	df	Mean Squ	F-Ratio	p-Value
SPECIES	3226.05	5	645.21	5.66	0	SPECIES	2361.847	5	472.369	3.348	0.005
Error	72500.19	636	113.994			Error	80426.13	570	141.098		

Species A	Species B	Difference	p value	95% LCL	95% UCL	Species A	Species B	Difference	p value	95% LCL	95% UCL
Eptfus	Lasbor	-4.486	0.026	-8.646	-0.326	Eptfus	Lasbor	-4.125	0.154	-9.011	0.761
Eptfus	Myoluc	-5.505	0.002	-9.664	-1.345	Eptfus	Myoluc	-2.823	0.567	-7.709	2.063
Eptfus	Myosep	-0.458	1	-4.618	3.702	Eptfus	Myosep	-3.583	0.292	-8.469	1.303
Eptfus	Nychum	-5.178	0.005	-9.337	-1.018	Eptfus	Nychum	-2.24	0.782	-7.125	2.646
Eptfus	Persub	-4.486	0.026	-8.646	-0.326	Eptfus	Persub	-6.708	0.001	-11.594	-1.822
Lasbor	Myoluc	-1.019	0.982	-5.178	3.141	Lasbor	Myoluc	1.302	0.974	-3.584	6.188
Lasbor	Myosep	4.028	0.064	-0.132	8.188	Lasbor	Myosep	0.542	1	-4.344	5.428
Lasbor	Nychum	-0.692	0.997	-4.851	3.468	Lasbor	Nychum	1.885	0.882	-3	6.771
Lasbor	Persub	0	1	-4.16	4.16	Lasbor	Persub	-2.583	0.66	-7.469	2.303
Myoluc	Myosep	5.047	0.007	0.887	9.206	Myoluc	Myosep	-0.76	0.998	-5.646	4.125
Myoluc	Nychum	0.327	1	-3.833	4.487	Myoluc	Nychum	0.583	0.999	-4.303	5.469
Myoluc	Persub	1.019	0.982	-3.141	5.178	Myoluc	Persub	-3.885	0.208	-8.771	1
Myosep	Nychum	-4.72	0.015	-8.879	-0.56	Myosep	Nychum	1.344	0.97	-3.542	6.23
Myosep	Persub	-4.028	0.064	-8.188	0.132	Myosep	Persub	-3.125	0.451	-8.011	1.761
Nychum	Persub	0.692	0.997	-3.468	4.851	Nychum	Persub	-4.469	0.096	-9.355	0.417

Table C-1 continued. Results of the Tukey-Kramer ANOVA pairwise comparisons of species activity to each physiognomic habitat type on ARNG-MTC Ft. Pickett, Virginia, in 2007.

Grassland Shrubland						Open water wetland					
Source	Type III SS	df	Mean Squ	F-Ratio	p-Value	Source	Type III SS	df	Mean Squ	F-Ratio	p-Value
SPECIES	22738.88	5	4547.775	11.586	0	SPECIES	645431.2	5	129086.2	17.556	0
Error	372126.7	948	392.539			Error	3529412	480	7352.943		

Species A	Species B	Difference	p value	95% LCL	95% UCL	Species A	Species B	Difference	p value	95% LCL	95% UCL
Eptfus	Lasbor	-0.616	1	-6.949	5.716	Eptfus	Lasbor	-68.58	0	-106.978	-30.183
Eptfus	Myoluc	-7.881	0.005	-14.213	-1.548	Eptfus	Myoluc	-42.494	0.02	-80.891	-4.096
Eptfus	Myosep	8.063	0.004	1.731	14.395	Eptfus	Myosep	-90.741	0	-129.138	-52.343
Eptfus	Nychum	-4.396	0.355	-10.728	1.936	Eptfus	Nychum	-30.16	0.22	-68.558	8.237
Eptfus	Persub	-1.981	0.949	-8.313	4.351	Eptfus	Persub	-107.173	0	-145.57	-68.775
Lasbor	Myoluc	-7.264	0.014	-13.596	-0.932	Lasbor	Myoluc	26.086	0.38	-12.311	64.484
Lasbor	Myosep	8.679	0.001	2.347	15.011	Lasbor	Myosep	-22.16	0.569	-60.558	16.237
Lasbor	Nychum	-3.78	0.531	-10.112	2.552	Lasbor	Nychum	38.42	0.05	0.022	76.817
Lasbor	Persub	-1.365	0.99	-7.697	4.967	Lasbor	Persub	-38.593	0.048	-76.99	-0.195
Myoluc	Myosep	15.943	0	9.611	22.276	Myoluc	Myosep	-48.247	0.005	-86.644	-9.849
Myoluc	Nychum	3.484	0.62	-2.848	9.817	Myoluc	Nychum	12.333	0.943	-26.064	50.731
Myoluc	Persub	5.899	0.085	-0.433	12.232	Myoluc	Persub	-64.679	0	-103.077	-26.281
Myosep	Nychum	-12.459	0	-18.791	-6.127	Myosep	Nychum	60.58	0	22.183	98.978
Myosep	Persub	-10.044	0	-16.376	-3.712	Myosep	Persub	-16.432	0.827	-54.83	21.965
Nychum	Persub	2.415	0.887	-3.917	8.747	Nychum	Persub	-77.012	0	-115.41	-38.615

APPENDIX D-Two-species models to examine species spatial co-occurrence
Refers to Chapter 3

Table D-1. Two-species co-occurrence models among vespertilionid species on ARNG-MTC Ft. Pickett, Blackstone, Virginia in 2007. Species A= *Eptesicus fuscus*, B= *Lasiurus borealis*

Model: Species A= <i>Eptesicus fuscus</i> , B= <i>Lasiurus borealis</i>	AIC	Δ AIC	ω	Model Likelihood	k	-2l	ϕ	ϕ 95% lcl	ϕ 95% ucl
psiA(.),psiB(.),phi(.),{NE-NI}pA(.),pB(.),rA(.),rB(.),delta(.)	3450.52	0	0.7823	1	8	3434.52	1.3	1.1072	1.5264
psiA(.),psiB(.),phi(.),{NE-I}pA(.),pB(.),rA(.),rB(.),delta(1)	3453.3	2.78	0.1949	0.2491	7	3439.3			
psiA(.),psiB(.),phi(1),{NE-NI}pA(.),pB(.),rA(.),rB(.),delta(.)	3457.98	7.46	0.0188	0.024	7	3443.98			
psiA(.),psiB(.),phi(1),{NE-I}pA(.),pB(.),rA(.),rB(.),delta(1)	3461.04	10.52	0.0041	0.0052	6	3449.04			
psiA(.),psiB(.),phi(.),{E-I}pA(.)=pB(.),rA(.)=rB(.),delta(1)	3584.96	134.44	0	0	5	3574.96			
psiA(.),psiB(.),phi(.),{E-NI}pA(.)=pB(.),rA(.)=rB(.),delta(.)	3586.96	136.44	0	0	6	3574.96			
psiA(.),psiB(.),phi(1),{E-NI}pA(.)=pB(.),rA(.)=rB(.),delta(.)	3599.16	148.64	0	0	5	3589.16			
psiA(.),psiB(.),phi(1),{E-I}pA(.)=pB(.),rA(.)=rB(.),delta(1)	3600.87	150.35	0	0	4	3592.87			

Table D-2. Two-species co-occurrence models among vespertilionid species on ARNG-MTC Ft. Pickett, Blackstone, Virginia in 2007. Species A= *Eptesicus fuscus*, B= *Myotis lucifugus*

Model Species A= <i>Eptesicus fuscus</i> , B= <i>Myotis lucifugus</i>	AIC	Δ AIC	ω	Model Likelihood	k	-2l	ϕ	ϕ 95% lcl	ϕ 95% ucl
psiA(.),psiB(.),phi(1),{NE-NI}pA(.),pB(.),rA(.),rB(.),delta(.)	3626.02	0	0.8622	1	7	3612.02	1.00	1.00	1.00
psiA(.),psiB(.),phi(1),{NE-I}pA(.),pB(.),rA(.),rB(.),delta(1)	3630.33	4.31	0.0999	0.1159	6	3618.33			
psiA(.),psiB(.),phi(.),{NE-I}pA(.),pB(.),rA(.),rB(.),delta(1)	3632.27	6.25	0.0379	0.0439	7	3618.27			
psiA(.),psiB(.),phi(.),{NE-NI}pA(.),pB(.),rA(.),rB(.),delta(.)	3688.26	62.24	0	0	8	3672.26			
psiA(.),psiB(.),phi(.),{E-NI}pA(.)=pB(.),rA(.)=rB(.),delta(.)	3790.4	164.38	0	0	6	3778.4			
psiA(.),psiB(.),phi(.),{E-I}pA(.)=pB(.),rA(.)=rB(.),delta(1)	3791.05	165.03	0	0	5	3781.05			
psiA(.),psiB(.),phi(1),{E-NI}pA(.)=pB(.),rA(.)=rB(.),delta(.)	3814.8	188.78	0	0	5	3804.8			
psiA(.),psiB(.),phi(1),{E-I}pA(.)=pB(.),rA(.)=rB(.),delta(1)	3815.48	189.46	0	0	4	3807.48			

Table D-3. Two-species co-occurrence models among vespertilionid species on ARNG-MTC Ft. Pickett, Blackstone, Virginia in 2007. Species A= *Eptesicus fuscus*, B= *Myotis septentrionalis*

Model Species A= <i>Eptesicus fuscus</i> , B= <i>Myotis septentrionalis</i>	AIC	Δ AIC	ω	Model Likelihood	k	-2l	ϕ	ϕ 95% lcl	ϕ 95% ucl
psiA(.),psiB(.),phi(.),{NE-NI}pA(.),pB(.),rA(.),rB(.),delta(.)	2556.18	0	0.955	1	8	2540.18	1.5049	1.2064	1.8772
psiA(.),psiB(.),phi(1),{NE-I}pA(.),pB(.),rA(.),rB(.),delta(1)	2562.92	6.74	0.0328	0.0344	6	2550.92			
psiA(.),psiB(.),phi(1),{NE-NI}pA(.),pB(.),rA(.),rB(.),delta(.)	2564.91	8.73	0.0121	0.0127	7	2550.91			
psiA(.),psiB(.),phi(.),{NE-I}pA(.),pB(.),rA(.),rB(.),delta(1)	2584.58	28.4	0	0	7	2570.58			
psiA(.),psiB(.),phi(.),{E-I}pA(.)=pB(.),rA(.)=rB(.),delta(1)	2613.74	57.56	0	0	5	2603.74			
psiA(.),psiB(.),phi(.),{E-NI}pA(.)=pB(.),rA(.)=rB(.),delta(.)	2615.5	59.32	0	0	6	2603.5			
psiA(.),psiB(.),phi(1),{E-I}pA(.)=pB(.),rA(.)=rB(.),delta(1)	2617.4	61.22	0	0	4	2609.4			
psiA(.),psiB(.),phi(1),{E-NI}pA(.)=pB(.),rA(.)=rB(.),delta(.)	2619.16	62.98	0	0	5	2609.16			

Table D-4. Two-species co-occurrence models among vespertilionid species on ARNG-MTC Ft. Pickett, Blackstone, Virginia in 2007. Species A= *Eptesicus fuscus*, B= *Nycticeius humeralis*

Model Species A= <i>Eptesicus fuscus</i> , B= <i>Nycticeius humeralis</i>	AIC	Δ AIC	ω	Model Likelihood	k	-2l	ϕ	ϕ 95% lcl	ϕ 95% ucl
psiA(.),psiB(.),phi(.),{NE-NI}pA(.),pB(.),rA(.),rB(.),delta(.)	3446.84	0	0.4877	1	8	3430.84	1.1481	0.9893	1.3323
psiA(.),psiB(.),phi(1),{NE-NI}pA(.),pB(.),rA(.),rB(.),delta(.)	3447.92	1.08	0.2842	0.5827	7	3433.92			
psiA(.),psiB(.),phi(.),{NE-I}pA(.),pB(.),rA(.),rB(.),delta(1)	3448.36	1.52	0.2281	0.4677	7	3434.36			
psiA(.),psiB(.),phi(1),{E-I}pA(.)=pB(.),rA(.)=rB(.),delta(1)	3591.79	144.95	0	0	4	3583.79			
psiA(.),psiB(.),phi(.),{E-NI}pA(.)=pB(.),rA(.)=rB(.),delta(.)	3592.26	145.42	0	0	6	3580.26			
psiA(.),psiB(.),phi(.),{E-I}pA(.)=pB(.),rA(.)=rB(.),delta(1)	3592.88	146.04	0	0	5	3582.88			
psiA(.),psiB(.),phi(1),{E-NI}pA(.)=pB(.),rA(.)=rB(.),delta(.)	3597.57	150.73	0	0	5	3587.57			
psiA(.),psiB(.),phi(1),{NE-I}pA(.),pB(.),rA(.),rB(.),delta(1)	3676.91	230.07	0	0	6	3664.91			

Table D-5. Two-species co-occurrence models among vespertilionid species on ARNG-MTC Ft. Pickett, Blackstone, Virginia in 2007. Species A= *Eptesicus fuscus*, B= *Perimyotis subflavus*

Model Species A= <i>Eptesicus fuscus</i> , B= <i>Perimyotis subflavus</i>	AIC	Δ AIC	ω	Model Likelihood	k	-2l	ϕ	ϕ 95% lcl	ϕ 95% ucl
psiA(.),psiB(.),phi(.),{NE-NI}pA(.),pB(.),rA(.),rB(.),delta(.)	3714.43	0	0.7433	1	8	3698.43	1.3435	1.1518	1.5672
psiA(.),psiB(.),phi(.),{NE-I}pA(.),pB(.),rA(.),rB(.),delta(1)	3716.56	2.13	0.2562	0.3447	7	3702.56			
psiA(.),psiB(.),phi(1),{NE-NI}pA(.),pB(.),rA(.),rB(.),delta(.)	3729.72	15.29	0.0004	0.0005	7	3715.72			
psiA(.),psiB(.),phi(1),{NE-I}pA(.),pB(.),rA(.),rB(.),delta(1)	3731.84	17.41	0.0001	0.0002	6	3719.84			
psiA(.),psiB(.),phi(.),{E-I}pA(.)=pB(.),rA(.)=rB(.),delta(1)	3905.91	191.48	0	0	5	3895.91			
psiA(.),psiB(.),phi(.),{E-NI}pA(.)=pB(.),rA(.)=rB(.),delta(.)	3907.78	193.35	0	0	6	3895.78			
psiA(.),psiB(.),phi(1),{E-I}pA(.)=pB(.),rA(.)=rB(.),delta(1)	3923.35	208.92	0	0	4	3915.35			
psiA(.),psiB(.),phi(1),{E-NI}pA(.)=pB(.),rA(.)=rB(.),delta(.)	3925.24	210.81	0	0	5	3915.24			

Table D-6. Two-species co-occurrence models among vespertilionid species on ARNG-MTC Ft. Pickett, Blackstone, Virginia in 2007. Species A= *Lasiurus borealis*, B= *Myotis lucifugus*

Model Species A= <i>Lasiurus borealis</i> , B= <i>Myotis lucifugus</i>	AIC	Δ AIC	ω	Model Likelihood	k	-2l	ϕ	ϕ 95% lcl	ϕ 95% ucl
psiA(.),psiB(.),phi(.),{NE-NI}pA(.),pB(.),rA(.),rB(.),delta(.)	4286.32	0	1	1	8	4270.32	1.1831	0.9381	1.492
psiA(.),psiB(.),phi(.),{E-NI}pA(.)=pB(.),rA(.)=rB(.),delta(.)	4621.28	334.96	0	0	6	4609.28			
psiA(.),psiB(.),phi(.),{NE-I}pA(.),pB(.),rA(.),rB(.),delta(1)	4646.38	360.06	0	0	7	4632.38			
psiA(.),psiB(.),phi(.),{E-I}pA(.)=pB(.),rA(.)=rB(.),delta(1)	4650.38	364.06	0	0	5	4640.38			

Table D-7. Two-species co-occurrence models among vespertillionid species on ARNG-MTC Ft. Pickett, Blackstone, Virginia in 2007. Species A= *Lasiurus borealis*, B= *Myotis septentrionalis*

Model Species A= <i>Lasiurus borealis</i> , B= <i>Myotis septentrionalis</i>	AIC	Δ AIC	ω	Model Likelihood	k	-2l	ϕ	ϕ 95% lcl	ϕ 95% ucl
psiA(.),psiB(.),phi(.),{NE-NI}pA(.),pB(.),rA(.),rB(.),delta(.)	3301.56	0	0.9747	1	8	3285.56	1.4778	1.28183	1.7926
psiA(.),psiB(.),phi(1),{NE-NI}pA(.),pB(.),rA(.),rB(.),delta(.)	3308.86	7.3	0.0253	0.026	7	3294.86			
psiA(.),psiB(.),phi(.),{E-NI}pA(=)pB(.),rA(=)rB(.),delta(.)	3371.9	70.34	0	0	6	3359.9			
psiA(.),psiB(.),phi(.),{NE-I}pA(.),pB(.),rA(.),rB(.),delta(1)	3506.65	205.09	0	0	7	3492.65			
psiA(.),psiB(.),phi(.),{E-I}pA(=)pB(.),rA(=)rB(.),delta(1)	3546.29	244.73	0	0	5	3536.29			

Table D-8. Two-species co-occurrence models among vespertillionid species on ARNG-MTC Ft. Pickett, Blackstone, Virginia in 2007. Species A= *Lasiurus borealis*, B= *Nycticeius humeralis*

Model Species A= <i>Lasiurus borealis</i> , B= <i>Nycticeius humeralis</i>	AIC	Δ AIC	ω	Model Likelihood	k	-2l	ϕ	ϕ 95% lcl	ϕ 95% ucl
psiA(.),psiB(.),phi(.),{NE-NI}pA(.),pB(.),rA(.),rB(.),delta(.)	4214.31	0	1	1	8	4198.31	1.185	0.8931	1.5724
psiA(.),psiB(.),phi(.),{E-I}pA(=)pB(.),rA(=)rB(.),delta(1)	4482.18	267.87	0	0	5	4472.18			
psiA(.),psiB(.),phi(.),{NE-I}pA(.),pB(.),rA(.),rB(.),delta(1)	4490.28	275.97	0	0	7	4476.28			

Table D-9. Two-species co-occurrence models among vespertillionid species on ARNG-MTC Ft. Pickett, Blackstone, Virginia in 2007. Species A= *Lasiurus borealis*, B= *Perimyotis subflavus*

Model Species A= <i>Lasiurus borealis</i> , B= <i>Perimyotis subflavus</i>	AIC	Δ AIC	ω	Model Likelihood	k	-2l	φ	φ 95% lcl	φ 95% ucl
psiA(.),psiB(.),phi(1),{NE-NI}pA(.),pB(.),rA(.),rB(.),delta(.)	3741.64	0	0.7729	1	7	3727.64	1	1	1
psiA(.),psiB(.),phi(.),{NE-NI}pA(.),pB(.),rA(.),rB(.),delta(.)	3744.09	2.45	0.2271	0.2938	8	3728.09			
psiA(.),psiB(.),phi(.),{E-NI}pA(=)pB(.),rA(=)rB(.),delta(.)	3881.88	140.24	0	0	6	3869.88			
psiA(.),psiB(.),phi(.),{NE-NI}pA(.),pB(.),rA(.),rB(.),delta(1)	4932.89	1191.25	0	0	7	4918.89			
psiA(.),psiB(.),phi(.),{E-I}pA(=)pB(.),rA(=)rB(.),delta(1)	5070.62	1328.98	0	0	5	5060.62			

Table D-10. Two-species co-occurrence models among vespertillionid species on ARNG-MTC Ft. Pickett, Blackstone, Virginia in 2007. Species A= *Myotis lucifugus*, B= *Myotis septentrionalis*

Model Species A= <i>Myotis lucifugus</i> , B= <i>Myotis septentrionalis</i>	AIC	Δ AIC	ω	Model Likelihood	k	-2l	ϕ	ϕ 95% lcl	ϕ 95% ucl	
psiA(.),psiB(.),phi(.),{NE-NI}pA(.),pB(.),rA(.),rB(.),delta(.)	3515.4	0	0.8138		1	8	3499.4	1.3209	1.1027	1.5822
psiA(.),psiB(.),phi(1),{NE-NI}pA(.),pB(.),rA(.),rB(.),delta(.)	3518.35	2.95	0.1862	0.2288	7	3504.35				
psiA(.),psiB(.),phi(.),{NE-I}pA(.),pB(.),rA(.),rB(.),delta(1)	3612.01	96.61	0	0	7	3598.01				
psiA(.),psiB(.),phi(.),{E-NI}pA(=pB(.),rA(=rB(.),delta(.)	3628.13	112.73	0	0	6	3616.13				
psiA(.),psiB(.),phi(.),{E-I}pA(=pB(.),rA(=rB(.),delta(1)	3695.08	179.68	0	0	5	3685.08				

Table D-11. Two-species co-occurrence models among vespertillionid species on ARNG-MTC Ft. Pickett, Blackstone, Virginia in 2007. Species A= *Myotis lucifugus*, B= *Nycticeius humeralis*

Model Species A= <i>Myotis lucifugus</i> , B= <i>Nycticeius humeralis</i>	AIC	Δ AIC	ω	Model Likelihood	k	-2l	ϕ	ϕ 95% lcl	ϕ 95% ucl
psiA(.),psiB(.),phi(1),{NE-NI}pA(.),pB(.),rA(.),rB(.),delta(.)	3371.3	0	1	1	7	3357.3	1	1	1
psiA(.),psiB(.),phi(.),{NE-NI}pA(.),pB(.),rA(.),rB(.),delta(.)	3436.95	65.65	0	0	8	3420.95			
psiA(.),psiB(.),phi(.),{NE-I}pA(.),pB(.),rA(.),rB(.),delta(1)	4936.53	1565.23	0	0	7	4922.53			
psiA(.),psiB(.),phi(.),{E-I}pA(.)=pB(.),rA(.)=rB(.),delta(1)	4943.81	1572.51	0	0	5	4933.81			

Table D-12. Two-species co-occurrence models among vespertillionid species on ARNG-MTC Ft. Pickett, Blackstone, Virginia in 2007. Species A= *Myotis lucifugus*, B= *Perimyotis subflavus*

Model Species A= <i>Myotis lucifugus</i> , B= <i>Perimyotis subflavus</i>	AIC	Δ AIC	ω	Model						
				Likelihood	k	-2l	ϕ	ϕ 95% lcl	ϕ 95% ucl	
psiA(.),psiB(.),phi(.),{NE-NI}pA(.),pB(.),rA(.),rB(.),delta(.)	4562.32	0	1	1	8	4546.32	1.1188	0.8542	1.4654	
psiA(.),psiB(.),phi(.),{E-I}pA(.)=pB(.),rA(.)=rB(.),delta(1)	4932.69	370.37	0	0	5	4922.69				
psiA(.),psiB(.),phi(.),{E-NI}pA(.)=pB(.),rA(.)=rB(.),delta(.)	5034.97	472.65	0	0	6	5022.97				
psiA(.),psiB(.),phi(.),{NE-I}pA(.),pB(.),rA(.),rB(.),delta(1)	5396.66	834.34	0	0	7	5382.66				

Table D-13. Two-species co-occurrence models among vespertilionid species on ARNG-MTC Ft. Pickett, Blackstone, Virginia in 2007. Species A= *Myotis septentrionalis*, B= *Nycticeius humeralis*

Model Species A= <i>Myotis septentrionalis</i> , B= <i>Nycticeius humeralis</i>	AIC	Δ AIC	ω	Model Likelihood	k	-2l	ϕ	ϕ 95% lcl	ϕ 95% ucl
psiA(.),psiB(.),phi(.),{NE-NI}pA(.),pB(.),rA(.),rB(.),delta(.)	3382.66	0	0.9537	1	8	3366.66	1.3332	1.1247	1.5802
psiA(.),psiB(.),phi(1),{NE-NI}pA(.),pB(.),rA(.),rB(.),delta(.)	3388.71	6.05	0.0463	0.0486	7	3374.71			
psiA(.),psiB(.),phi(.),{E-NI}pA(=)pB(.),rA(=)rB(.),delta(.)	3425.5	42.84	0	0	6	3413.5			
psiA(.),psiB(.),phi(.),{NE-I}pA(.),pB(.),rA(.),rB(.),delta(1)	3472.77	90.11	0	0	7	3458.77			
psiA(.),psiB(.),phi(.),{E-I}pA(=)pB(.),rA(=)rB(.),delta(1)	3502.78	120.12	0	0	5	3492.78			

Table D-14. Two-species co-occurrence models among vespertilionid species on ARNG-MTC Ft. Pickett, Blackstone, Virginia in 2007. Species A= *Myotis septentrionalis*, B= *Perimyotis subflavus*

Model Species A= <i>Myotis septentrionalis</i> , B= <i>Perimyotis subflavus</i>	AIC	Δ AIC	ω	Model Likelihood	k	-2l	ϕ	ϕ 95% lcl	ϕ 95% ucl
psiA(.),psiB(.),phi(.),{NE-NI}pA(.),pB(.),rA(.),rB(.),delta(.)	3473.13	0	0.9668	1	8	3457.13	1.4184	1.4184	1.4184
psiA(.),psiB(.),phi(1),{NE-NI}pA(.),pB(.),rA(.),rB(.),delta(.)	3479.87	6.74	0.0332	0.0344	7	3465.87			
psiA(.),psiB(.),phi(.),{E-NI}pA(=)pB(.),rA(=)rB(.),delta(.)	3643.05	169.92	0	0	6	3631.05			
psiA(.),psiB(.),phi(.),{NE-I}pA(.),pB(.),rA(.),rB(.),delta(1)	3708.34	235.21	0	0	7	3694.34			
psiA(.),psiB(.),phi(.),{E-I}pA(=)pB(.),rA(=)rB(.),delta(1)	3803.73	330.6	0	0	5	3793.73			

Table D-15. Two-species co-occurrence models among vespertilionid species on ARNG-MTC Ft. Pickett, Blackstone, Virginia in 2007. Species A= *Nycticeius humeralis*, B= *Perimyotis subflavus*

Model Species A= <i>Nycticeius humeralis</i> , B= <i>Perimyotis subflavus</i>	AIC	Δ AIC	ω	Model		-2l	ϕ	ϕ 95% lcl	ϕ 95% ucl
				Likelihood	k				
psiA(.),psiB(.),phi(.),{NE-NI}pA(.),pB(.),rA(.),rB(.),delta(.)	4513.38	0	1	1	8	4497.38	1.2181	0.9599	1.5458
psiA(.),psiB(.),phi(.),{E-I}pA(.)=pB(.),rA(.)=rB(.),delta(1)	4795.02	281.64	0	0	5	4785.02			
psiA(.),psiB(.),phi(.),{E-NI}pA(.)=pB(.),rA(.)=rB(.),delta(.)	5050.34	536.96	0	0	6	5038.34			
psiA(.),psiB(.),phi(.),{NE-I}pA(.),pB(.),rA(.),rB(.),delta(1)	5584.04	1070.66	0	0	7	5570.04			