University of Massachusetts - Amherst
ScholarWorks@UMass Amherst

Masters Theses | Dissertations and Theses

2007

Whip-poor-will Prey Availability and Foraging Habitat: Implications for Management in Pitch Pine / Scrub Oak Barrens Habitats

Ross M. Garlapow
University of Massachusetts Amherst, rmgarlapow@aol.com

Follow this and additional works at: http://scholarworks.umass.edu/theses

Garlapow, Ross M., "Whip-poor-will Prey Availability and Foraging Habitat: Implications for Management in Pitch Pine / Scrub Oak Barrens Habitats" (2007). *Masters Theses.* Paper 27.
http://scholarworks.umass.edu/theses/27

This Open Access is brought to you for free and open access by the Dissertations and Theses at ScholarWorks@UMass Amherst. It has been accepted for inclusion in Masters Theses by an authorized administrator of ScholarWorks@UMass Amherst. For more information, please contact scholarworks@library.umass.edu.

WHIP-POOR-WILL PREY AVAILABILITY AND FORAGING HABITAT: IMPLICATIONS FOR MANAGEMENT IN PITCH PINE / SCRUB OAK BARRENS HABITATS

A Thesis Presented

by

Ross M. Garlapow

Submitted to the Graduate School of the
University of Massachusetts Amherst in partial fulfillment
of the requirements for the degree of

MASTER OF SCIENCE

September 2007

Wildlife and Fisheries Conservation

© Copyright by Ross M. Garlapow 2007

All Rights Reserved

WHIP-POOR-WILL PREY AVAILABILITY AND FORAGING HABITAT: IMPLICATIONS FOR MANAGEMENT IN PITCH PINE / SCRUB OAK BARRENS HABITATS

A Thesis Presented

by

ROSS M. GARLAPOW

Approved as to content by:

_____
David I. King, Chair

_____
Michael A. Ciaranca, Member

_____
Stephen DeStefano, Member

_____
John P. Kelly, Consultant

_____
Matthew J. Kelty, Department Head
Natural Resources Conservation

ACKNOWLEDGEMENTS

I would like to thank everyone on this thesis committee, and everyone that have influenced my personal growth in this field and made this study possible. The Massachusetts Army National Guard Natural Resources Office personnel at Camp Edwards, specifically Mike Ciaranca and John Kelly for providing funding, field equipment, and mentoring. My advisor, Dave King at the USDA Forest Service Northeast Research Station in Amherst, MA for helping me interpret scientific journals, reviewing many renditions of this thesis, and having the patience to teach me a whole lot about statistics. Rachel Charow for volunteering the entire summer of 2005 during all hours of the day and night, and all of the other staff at Camp Edwards that helped make this study not only possible, but a pleasant experience. Thanks again.

ABSTRACT

WHIP-POOR-WILL PREY AVAILABILITY AND FORAGING HABITAT: IMPLICATIONS FOR MANAGEMENT IN PITCH PINE / SCRUB OAK BARRENS HABITATS

SEPTEMBER 2007

ROSS M. GARLAPOW, B.S., STATE UNIVERSITY OF NEW YORK COLLEGE OF ENVIRONMENTAL SCIENCE AND FORESTRY

M.S., UNIVERSITY OF MASSACHUSETTS AMHERST

Directed by: Dr. David I. King

Recently, the Whip-poor-will (*Caprimulgus vociferous*) has become focus of considerable conservation concerns as the result of evidence indicating significant population declines throughout its breeding range (Veit and Petersen 1993). The lack of quantitative data concerning much of this species natural history has delayed recovery efforts and is a fundamental shortcoming in forming effective conservation strategies.

Current surveys show Pitch Pine (*Pinus rigida*) / Scrub Oak (*Quercus illicifolia*) Barrens (PPSO) as habitat with high numbers of Whip-poor-wills relative to other forest types found throughout the northeastern United States (Cavanaugh in Cink 2002), so we focused our study in these habitats in an attempt to 1) identify habitat selection within PPSO, and 2) determine characteristics of PPSO that make it relatively high quality habitat.

Our Study was conducted during the 2005 and 2006 breeding seasons at the Massachusetts Military Reservation on Cape Cod, Massachusetts, USA. We used mist nets to capture adult Whip-poor-wills and affix radio-transmitters for locating individuals during night hours, using triangulation techniques. A kernel analysis of these locations

was used to estimate the home range of each individual, where structural characteristics of vegetation was measured, for use in habitat selection analyses. Prey availability was estimated using captures from light traps (Leroy Koehn design, Georgetown, KY) with UV bulbs. Light traps were run on 12 different nights in each habitat during both years of the study. We assessed diet from fecal samples collected at day roost locations used by radio-marked individuals on a daily basis. Samples were dissected under a 22x stereoscope with prey fragments identified to the family when possible.

Generalized Linear Mixed Models were used to model habitat selection from structural variables of the habitat collected at used and random locations within the home range, while a compositional analysis of habitat use was also done by comparing the amount of radio-locations in each habitat type to the total amount of that habitat found within the home range. A compositional analysis was also used to test for prey selection.

Data from 15 Whip-poor-wills were used in our analyses. Univariate and multivariate statistics showed that there was no difference in vegetation structure between used and random sites. Ground cover was the best predictor of habitat use identified by the GLMM, but was still inefficient for determining habitat use. However, the compositional analysis of habitat use did show a preference of pitch pine – oak forests over pitch pine – scrub oak communities. The fecal analysis showed Whip-poor-wills preferred moths over scarab beetles, and "other" prey items that consisted mainly of beetles other than scarabs, along with neuropterans. Light trap captures showed prey was distributed equally among habitats at the MMR.

Although our study did not show any strong relationships between vegetation structure and habitat selection, this may not be the case in habitats of lesser quality (i.e.

not PPSO). The habitat preference rank from the compositional analysis directly correlated with the amount of ground cover found in each habitat, which is supporting evidence that ground cover may be an important factor in selecting habitat. Low amounts of ground cover may allow Whip-poor-wills to detect and capture prey more easily, as well as provide open area for an easy escape route from potential predators. Land management techniques such as prescribed burning that reduce understory are recommended treatments to increase habitat quality for Whip-poor-wills.

TABLE OF CONTENTS

Page

ACKNOWLEDGMENTS iv

ABSTRACT v

LIST OF TABLES ix

LIST OF FIGURES x

CHAPTER

I INTRODUCTION 1

II MICROHABITAT SELECTION OF FORAGING WHIP-POOR-WILLS IN PITCH PINE-SCRUB OAK FORESTS OF EASTERN MASSACHUSETTS 5

Introduction 5
Study Site 6
Methods 8
Statistical Analyses 10
Results 12
Discussion 13

III HABITAT SELECTION BY WHIP-POOR-WILLS: THE INFLUENCE OF PREY AVAILABILITY 22

Introduction 22
Study Site 25
Methods 26
Results 31
Discussion 33

LITERATURE CITED 41

LIST OF TABLES

Table Page

1. Comparison of habitat variables between random (n =15) and used (n = 15) sites for Whip-poor-wills studied at the Massachusetts Military Reservation in 2005 and 2006, using the Wilcoxon rank sum test.....18

2. Whip-poor-will habitat selection models constructed from significant univariate variables sampled at the MMR, Cape Cod, Massachusetts, USA, during 2005 and 2006.....19

3. Ranking matrix for Whip-poor-will foraging habitat preference at Camp Edwards, MA, based on t –values comparing the proportion of foraging locations in each habitat with proportions of habitat within an individuals foraging range.....38

4. The ranks and pairwise comparison of prey composig the Whip-poor-will diet at Camp Edwards, MA.....39

LIST OF FIGURES

Figure Page

1. The study was conducted at the Massachusetts Military Reservation, located on Cape Cod, Massachusetts, USA in 2005 and 2006 20

2. Distribution of vegetation community types throughout the study area at the MMR, located on Cape Cod, Massachusetts, USA 21

3. Mean and standard error of lepidoptera (LEP), scarab beetle (SCA), all other taxa, and totals, of light trap captures per night by habitat for 2005 at Camp Edwards, MA 40

4. Mean and standard error of lepidoptera (LEP), scarab beetle (SCA), all other taxa, and totals, of light trap captures per night by habitat for 2006 at Camp Edwards, MA 40

CHAPTER I

INTRODUCTION

The Whip-poor-will (*Caprimulgus vociferous*) is a small (≈ 50 g), nocturnal insectivorous bird with a large geographic range (Cink 2002). Whip-poor-wills breed during the temperate summer from Saskatchewan to Georgia and winter from southern Texas, the Gulf Coast, and east-central South Carolina south to Central America (DeGraaf and Rappole 1995). The Whip-poor-will forages mainly during crepuscular and night hours (Cink 2002). Whip-poor-wills nest on the ground, and will remain at roost on the ground or on a perch close to the ground throughout the daytime hours (Cink 2002).

Recently, the Whip-poor-will has become the focus of considerable conservation concerns as the result of evidence indicating significant population declines over most of its breeding range (Veit and Petersen 1993, Sauer et al. 2005). Although Whip-poor-wills do not have any formal conservation status, such as threatened or endangered, these trends and the general lack of knowledge regarding habitat requirements resulted in their identification by the Northeast Working Group of Partners in Flight as a monitoring priority (Hunt 2006b).

Various hypotheses have been offered to explain these declines. Whip-poor-wills are thought to require forest for nesting adjacent to openings where they forage (Tyler 1940). Thus, this species might be negatively affected by loss of openings through forest maturation (Mills 1987, Eastman 1991), or loss of nesting habitat through deforestation (Stewart 1975, Smith 1966) and urbanization (Santner 1992). The nocturnal behavior and cryptic plumage of the Whip-poor-will makes this species difficult to study and has

led to a lack of quantitative data concerning much of this species natural history that could increase the effectiveness of conservation and management efforts (Cink 2002).

Current surveys show Pitch Pine (*Pinus rigida*) / Scrub Oak (*Quercus illicifolia*) Barrens (PPSO) as habitat with high numbers of Whip-poor-wills relative to other forest types found throughout the northeastern United States (Sibley 1988, Hunt 2006, King and Collins 2007). Furthermore, preliminary results indicate that Whip-poor-wills are associated with particular habitat features within PPSO (Cavanaugh in Cink 2002). Fire has had a profound influence on forming and maintaining PPSO, which is now rare and threatened globally, as suppression of wildfires has allowed the open canopies to succeed into savannas and closed-canopy forests (Swain and Kearsley 2001). This mosaic of seral habitats and associated wildlife are now dependent on active management to prevent vegetation composition and structure from transitioning into homogeneous older seral stages. Current management techniques implemented to create and maintain PPSO habitats include practices that could either increase or decrease habitat quality for Whip-poor-wills by changing the structural and floristic composition or even the relative abundance of favored plant communities. The goal of this study was to identify habitat characteristics associated with Whip-poor-wills to increase the effectiveness of management efforts for this species.

This study fits into a hierarchy of selection studies done at several scales to answer questions about Whip-poor-will populations. The concepts within hierarchy theory show that at least three levels or scales should be considered in any study: at least one above and below the focal level which will provide specific information pertinent to the study objectives (Turner at al. 2001). The higher levels provide context for the focal

level, while the levels below the focus provide explanations for observed behaviors (O'neill et al. 1989). Efforts are currently underway to determine the regional distribution of Whip-poor-wills among habitats in the northeast (Hunt 2006a, King and Collins 2007). This study compliments these more extensive investigations by focusing on the factors affecting habitat selection at the microhabitat scale within the home ranges of individuals. Understanding that characteristics of suitable habitat will help managers create and maintain suitable habitat for Whip-poor-wills.

This project consisted of two parts. In Chapter 2, I compared habitat structure at used and random locations within the foraging range. Used locations were determined from radio-triangulating marked Whip-poor-wills during foraging hours. Habitat was compared between used and random sites using a variety of statistical techniques. Although the results were only marginally significant, they indicated that ground cover and vertical habitat structure 0-2 m were lower at sites used by Whip-poor-wills. These findings are consistent with previous studies (Wilson 1985, Eastman 1991), however, I found no difference in canopy coverage between sites occupied by Whip-poor-wills and unoccupied sites, which contrasts with previous results from this site from call count surveys (Cavanaugh in Cink 2002). I conclude that management practices that maintain open understory structure will benefit Whip-poor-wills.

In Chapter 3, I investigated the influence of prey resources on habitat selection. Cavanaugh (in Cink 2002) hypothesized that Whip-poor-will habitat selection at the Massachusetts Military Reservation (MMR) is influenced by prey availability. Habitat selection by other bird species is influenced by prey availability (Zach and Falls 1976). I used radio marked individuals to establish home ranges. Compositional analysis of

habitat was conducted for locations within the home range to investigate habitat selection at this scale. Invertebrate prey items were sampled at random locations within habitat types throughout the study site using light traps. The light trap capture data were extrapolated to calculate prey abundance per individual based on habitat use. Diet was analyzed using fecal samples collected from dayroosts of marked individuals. Diet was then compared to prey abundance using compositional analysis to investigate prey preferences. I found that Whip-poor-wills preferred pitch pine – oak forests while showing a relative avoidance of pitch pine – scrub oak communities. The prey sampling showed that lepidopterans, scarab beetles, and all other potential prey items were distributed equally throughout the study site. These data combined with the fecal analysis showed that Whip-poor-wills select lepidopterans over other prey types. I conclude that food abundance does not necessarily affect habitat selection by Whip-poor-wills, although availability could be influenced by habitat structure, as open understory likely facilitates successful foraging.

CHAPTER II

MICROHABITAT SELECTION OF FORAGING WHIP-POOR-WILLS IN PITCH PINE-SCRUB OAK FORESTS OF EASTERN MASSACHUSETTS

Introduction

The Whip-poor-will (*Caprimulgus vociferous*) is a small (≈ 50 g), nocturnal insectivorous bird with a large geographic range. Whip-poor-wills breed during the temperate summer from from Saskatchewan to Georgia, and winter from southern Texas, the Gulf Coast, and east-central South Carolina south to Central America (DeGraaf and Rappole 1995). The Whip-poor-will forages mainly during crepuscular and night hours (Cink 2002). Whip-poor-wills nest on the ground, and will remain at roost on the ground or on a perch close to the ground throughout the daytime hours (Cink 2002).

Recently, the Whip-poor-will has become the focus of considerable conservation attention as the result of evidence indicating significant population declines over most of its breeding range. These data include information from state atlas projects reporting the absence of Whip-poor-wills from previously occupied areas (Veit and Petersen 1993, Cink 2000), as well as the North American Breeding Bird Survey, which indicates a significant 2.2% annual rate of decline survey-wide from 1966 to 2005 (Sauer et al. 2005). Various hypotheses have been offered to explain these declines. Whip-poor-wills are thought to require forest for nesting adjacent to openings where they forage (Tyler 1940). Thus, this species might be negatively affected by loss of openings through forest maturation (Mills 1987, Eastman 1991) or loss of nesting habitat through deforestation (Stewart 1975, Smith 1966) and urbanization (Santner 1992). The nocturnal behavior

and cryptic plumage of the Whip-poor-will makes this species difficult to study and has lead to a lack of quantitative data concerning much of this species natural history that could increase the effectiveness of conservation and management efforts (Cink 2002).

Although Whip-poor-wills do not have any formal conservation status, such as threatened or endangered, these trends and the general lack of knowledge on their conservation status and habitat requirements resulted in their identification by the Northeast Working Group of Partners in Flight as a monitoring priority (Hunt 2006a). Preliminary results from these monitoring efforts have identified Pitch Pine (*Pinus rigida*) / Scrub Oak (*Quercus illicifolia*) Barrens (PPSO) as habitat with high numbers of Whip-poor-wills relative to other forest types in New England (Hunt 2006b, King and Collins 2007). The goal of our study was to identify specific attributes of the PPSO that the Whip-poor-wills are exploiting. An understanding of how the Whip-poor-will uses its habitat will permit more comprehensive management practices.

Study Site

The study was conducted on the Massachusetts Military Reservation (MMR), which is a compilation of military installations on Cape Cod that consist primarily of the Massachusetts Army National Guard, Massachusetts Air National Guard, U.S. Coast Guard, and U.S. Air Force (Figure 1). The 9090 hectares that make up the MMR are located approximately between 41°37’30’’ and 41°45’00’’N latitude and 70°30’00’’ to 70°37’30’’W longitude, in the towns of Bourne, Sandwich, and Mashpee (Figure 1).

The MMR is mostly undeveloped, forested land that has a large network of unpaved roads used in military training activities. Average annual temperature is 10°C, and average annual precipitation at the MMR is approximately 122 centimeters. The

proximity to the Atlantic coast moderates the climate for much of the year (Patterson and Ruffner 2003). The Sandwich and Plymouth terminal moraines compose land on the north and west sides of the MMR, which is characterized by hilly terrain, and soils mostly from the Plymouth, Barnstable, and Nantucket series. The land that these moraines surround to the South and East is the outwash plain, which is essentially flat, and covered by soils mostly from the Enfield, Merrimac, and Carver series (Fletcher 1993).

The vegetation on the MMR is characterized as PPSO. This is a disturbance-dependant community type created by historic logging, grazing, agriculture, and wildfires. The PPSO at the MMR consist of a combination of scrub oak, pitch pine, white oak (*Quercus alba*), black oak (*Q. nigra*), and scarlet oak (*Q. coccinea*). The vegetation was sampled and classified by Massachusetts Army National Guard (MARNG) Natural Resources Office personnel in 2003. Classifications were based on the Massachusetts Division of Fisheries and Wildlife's Natural Heritage and Endangered Species Program's Plant Communities of Massachusetts (Swain and Kearsley 2001). Vegetation at the MMR was delineated from digitized, true color aerial photographs taken in the spring of 2002, and ground truthing techniques. The vegetation was classified into the following community types: black oak–scarlet oak forest, cultural grassland, immature pitch pine, pitch pine–oak forest, Scotch pine (*Pinus sylvestris*)–pitch pine–oak forest, pitch pine–scrub oak, Scotch pine–pitch pine–scrub oak, red maple (*Acer rubrum*) swamp, sandplain heathland, and scrub oak shrubland. I studied Whip-poor-wills on a 2,325 hectare portion of the MMR, which comprised a contiguous area in the central portion of the MMR bounded on the south by developed land not used by Whip-poor-wills, and on the east and west by the boundaries of the MMR. The northern section of the MMR was not used

due to military restrictions as well as its inaccessibility. The vegetation in the study area consisted almost entirely of pitch pine–oak forest, pitch pine–scrub oak community, and scrub oak shrubland (Figure 2).

Methods

This study follows a general design for a resource selection study identified by Thomas and Taylor (1990) where individual animals are identified, and the resources that are used and available by each animal are sampled. This type of analysis has been recommended for resource selection studies by White and Garrott (1990) and has been widely used in wildlife resource selection studies (Manly et al. 2002). In the context of this chapter, individuals were captured and marked with radio transmitters, used resources were sampled at sites estimated from radio-locations, and available resources were sampled at randomly chosen sites within an individual's home range. Current survey efforts by other researchers are directed at identifying Whip-poor-will habitat preferences at a regional scale and indicate that Whip-poor-wills are most abundant in PPSO habitats (Hunt 2006a, King and Collins 2007). Because PPSO habitats appear to be important to Whip-poor-wills, and are globally threatened and require active management, I focused our study on habitat selection at the microhabitat level within PPSO in an effort to compliment these more extensive studies.

Whip-poor-wills arrive in southeastern Massachusetts around late April – mid May (Tyler 1940). Nightly visits were made to the study area to listen for the first arrivals of Whip-poor-wills beginning in mid-April in 2005 and 2006, with capture efforts commencing 2 weeks thereafter to avoid catching Whip-poor-wills that would continue to migrate off site. I captured Whip-poor-wills using approximately 10 2-m tall

mistnets with 32-36 mm mesh and varying in length from 6-18 m. I deployed nets in a random-systematic manner to ensure even covereage of the study area by dividing the study area into a grid of 99-25 ha cells (an area corresponding to the average home range of Whip-poor-wills at our site) and selecting cells at random. I listened for Whip-poor-wills at selected cells, and placed an array of nets as close as possible to where the calls originated. Mist nets were set during good weather (i.e., no rain or surface wind >8 mph) between the hours of 1945 and 0100, and checked at 30-40 minute intervals. All captured Whip-poor-wills were fitted with a 1.95 gram radio transmitter, (model BD-2, Holohil Systems Ltd., Carp, Ontario, Canada), using a backpack harness attachment modified from the design described by Rappole and Tipton (1991). Radios had an estimated battery life of 11.5 weeks, and transmitted at a unique frequency between 164-165 Khz.

Foraging locations were collected in July and August of 2005 and 2006, after the majority of courting and breeding had taken place. This was to avoid collecting locations that were associated with these behaviors, as the objective of our study was to describe foraging sites in quantitative terms. At least 20 locations (21.4 ± 2.0) were collected from each Whip-poor-will used in our analyses. I located foraging sites based on simultaneous bearings taken by two researchers and triangulating the locations of Whip-poor-wills. Bearings of the strongest radio signal were recorded from 4 points on surrounding roads and analyzed with Location of a Signal (Ecological Software Solutions 1998) telemetry analysis software. The software was used to estimate locations and associated error ellipses. Error elipses for locations averaged ≈20 m, and locations with error elipses >50m were eliminated from the analyses. Foraging ranges (95% kernel) were calculated from these radio locations using the Animal Movement extension (Hooge et al. 1999) in

ArcView 3.2a (Environmental Systems Research Institute, Inc.1999). A subset of 10 foraging sites per individual was chosen at random for sampling habitat variables. ArcView also chose 10 points in each foraging range, randomly, for comparison to foraging sites.

Handheld GPS units were used to navigate to foraging and random sites. Habitat was sampled on 0.04 ha circular plots (Noon 1981). I recorded tree basal area (estimated using a 10-factor optical prism), as well as the species and DBH of all contributing trees. I established strip transects along the east-west and north-south axes of each plot (22.6 m each) where I recorded the species and presence of woody and herbaceous cover $\leq$ 1.0 m in height at 10 evenly spaced points along each transect. These yielded 20 observations per plot, which I multiplied by five to obtain estimates of percent ground cover and the species composing it. Canopy cover was estimated using a spherical densiometer at the plot center. Vertical cover between 0 and 2 meters was estimated by observing a 2 m pole, graduated into 10 cm increments from 10 m away at each transect end (Harrell and Fuhlendorf 2002). The number of increments covered at least 25% by vegetation was multiplied by 5 to obtain percent vertical cover, and the 4 vertical cover percentages averaged to estimate vertical cover for the site.

Statistical Analyses

The Shapiro-Wilk test was used to evaluate variables for normality. None of the variables followed the normal distribution. Percentage variables were arcsine transformed, while a square root transformation was used on count variables, however normality was not significantly improved through data transformations. Thus, nonparametric tests were used on untransformed variables.

The Wilcoxon rank sum test was used to make univariate comparisons of variables measured at used and random sites were made to see if there were strong differences among variables. Values used for this analysis were variable means from pooled data on all individuals over both years. The comparisons were considered significant at a Bonferroni corrected alpha level of 0.01. Applying univariate models to situations where several variables affect the response can lead to incorrect inferences (Block and Brennan 1993). I therefore chose to test for between-group differences for all variables simultaneously, using Multi-Response Permutation Procedure (MRPP) tests for blocked data (Mielke and Berry 1982). The MRPP provides a test for equivalence of distribution of variables measured at the random and used sites. The BLOSSOM software developed by the United States Geological Survey (Slauson et al. 1991) was used to perform the MRPP test.

The variables were also used to fit the data with a generalized linear mixed model (GLMM) via penalized quasilikelihood (PQL) (Breslow and Clayton 1993), using R software (R Development Core Team 2005). The GLMM includes fixed effects to make inferences on populations as well as random effects to show the variability among individuals. The MRPP will show if the used and random variables are significantly different from a multivariate viewpoint, and the GLMM will determine how efficient the variables are at predicting foraging site location, if they are indeed different. A correlation matrix was created for all variables, and one of each pair of highly correlated variables (Pearson coefficients >0.70) was removed to reduce collinearity (Hosmer and Lemeshow 1989). Univariate regressions were conducted first as a screening procedure for including variables in multivariate models. Univariate models within 5 Akaike

Information Criterion (AIC) values of the best were considered for the multivariate models. Supported multivariate models were considered those with an Akaike Information Criterion value corrected for small sample sizes (AIC_c) < 2 of the best model (Burnham and Anderson 2002). Receiver Operating Characteristic (ROC) curves were used as diagnostics to provide information on how well models predicted habitat selection. The ROC is a plot of the fraction of true positives to the fraction of the false positive predictions resulting from the model (Zweig et al. 1993). The Somers D_{xy} rank correlation between predicted probabilities and observed outcomes was also calculated with

$$D_{xy} = 2(c - 0.5),$$

where c is the area under the ROC curve. When $D_{xy} = 0$, the model is making random predictions. When $D_{xy} = 1$, the model discriminates perfectly. Both models had a D_{xy} value of 0.13.

Results

A total of 18 Whip-poor-wills were captured during the study. Two of these were depredated, and another was unable to be located due to transmitter failure, migration from the study site, or some other unknown factor. In all, 15 individuals (8 females, 7 males) were used for the analyses. There were no statistically significant differences in habitat characteristics at points occupied by Whip-poor-wills between 2005 and 2006, or between males and females, so data were pooled for year and sex.

A total of 6 habitat variables measuring vegetation structure were compared at random and used sites for the 15 individuals. None of these variables were significantly different at used and random sites after a Bonferroni correction was applied (Table 1).

Similarly, the MRPP test for the multivariate assessment of these six variables was also not significant ($P = 0.3017$).

GLMM's indicated that the best predictor of foraging habitat was the univariate model containing only the variable for total ground cover, with vertical structure as the only other univariate or multivariate model considered supported under our selection criteria (Table 2). The AIC_c weights (w_i) describe the likelihood that the model is the best model of the candidates, and shows our criteria for supported models, was appropriate. However, although ground cover and vertical structure were supported models for predicting habitat use, Receiver Operating Characteristic (ROC) curves (Mason and Graham 2002) show that they were not efficient. The slopes of the curves are greater than 1 with roughly 57% of the area falling under the curve of the models.

Discussion

Whip-poor-wills are reported to use a variety of forest types, including open pine forests and pine plantations in Ontario (Mills 1987), low-elevation deciduous and mixed forests in New York (Sibley 1988), West Virginia (Hall 1983), and Illinois (Bjorkland and Bjorkland 1983). However, this species is most abundant in pitch pine-oak habitats in the northeastern part of its range (Sibley 1988, Cavanaugh in Cink 2002, Hunt 2006b, King and Collins 2007). A key element repeatedly referred to in descriptions of Whip-poor-will habitat is openness, either in reference to the canopy (Wilson 1985, James and Neal 1986, Cavanaugh in Cink 2002) or the understory (Eastman 1991, Cink 2002). The patterns of habitat selection I observed were relatively weak, perhaps due to the relatively modest samples size, the relatively homogenous habitat, and the fact that the unoccupied

sites were potentially "contaminated", that is, potentially occupied at a time other than the sampling occaision (Keating and Cherry 2004). Nevertheless, the patterns I observed were consistent with patterns observed from other studies and readily interpreted relative to the biology of the bird (see below).

Our finding that canopy coverage did not differ between areas where Whip-poor-wills were located and nearby unoccupied areas, contrasts with previous studies that suggest that Whip-poor-wills are associated with open canopy conditions in logged areas (Wilson 2003) and PPSO (Cavanaugh in Cink 2002). Sierro et al. (2001) suggested that lack of light due to dense canopy was a factor in explaining the avoidance of pine forests by the closely related European Nightjar (*C. europaeus*). These conclusions contrast with our results that showed pitch pine-oak forests that are characterized by closed canopy conditions (Cavanaugh in Cink 2002), are selected. Conditions throughout the MMR were characterized by relatively open canopy conditions (≈50%), which probably explains why Whip-poor-will habitat use was not associated with this factor. This range of canopy coverage is similar to that measured at sites occupied by Whip-poor-wills in other studies (26.5-83%; Brenner 1993, Prior 1995, Browne and Storer 1995, Hunt 2006b). Thus, the association of Whip-poor-wills with open canopy evident in previous studies might not have been evident in this study because canopy coverage was within the range of suitable conditions throughout the study area. Open canopy is thought to benefit Whip-poor-wills by increasing light availability, which may enhance foraging success (Mills 1986).

Our findings that understory openness was greater at sites occupied by Whip-poor-wills is consistent with the results of other studies. Wilson (1985) studied Whip-

poor-will distribution in Minnesota and concluded these birds preferred habitats with little or no underbrush, and did not consider tree species or canopy closure to be limiting factors. Eastman (1991) also agreed with our findings and stated that sparse underbrush was a fundamental component of Whip-poor-will habitat. Open understory structure might facilitate successful foraging by providing a clear line of sight for Whip-poor-wills to detect prey, either directly or by silhouetting them against the sky (Mills 1986, Cink 2002). European Nightjars also exhibit this behavior (Alexander and Cresswell 1990), and the availability for unobstructed understory conditions has been cited as a reason for avoidance of pine forests by foraging nightjars in Switzerland (Sierro et al. 2001).

Our finding that Whip-poor-wills are associated with open understory structure is consistent with studies of other species of nocturnal birds with similar morphology and natural history. The Common poorwill (*Phalaenoptilus nuttallii*) was found to use roost sites that had less ground cover than at random sites (Wang and Brigham 1997, Green and Griffiths 1994). This species is thought to select these locations primarily for predation avoidance, using the bare ground to match their mottled brown colors, but also for ease of navigating take-offs and landings (Brigham in Wang and Brigham 1997). The results of these two studies supports our findings understory structure plays a significant role in Whip-poor-will habitat selection.

The open canopy and understory conditions suitable for Whip-poor-wills are the result of chronic disturbance, both natural and anthropogenic. Frost kill, insect infestations, salt spray, and wind events have repeatedly disturbed these communities, along with livestock grazing, fuel wood harvesting, silviculture, and fires set continually by humans since they first inhabited the barrens systems following glaciation (Patterson

and Ruffner 2003). Fire has had the most widespread influence on forming and maintaining PPSO, which are now rare and threatened globally, as suppression of wildfires has allowed the open canopies to succeed into savannas and closed-canopy forests (Swain and Kearsley 2001). Mills (1987) cites wildfire suppression as a contributing factor to Whip-poor-will population declines in Ontario, Canada.

This disturbance regime results in a mosaic of forest, shrubland, and grassland habitats, which benefits Whip-poor-wills by providing habitats with reduced ground cover that provides areas of litter within interstitial spaces of dispersed shrubs, and open vertical structure within forested and shrubland habitats, and are now dependent on active management to persist (Swain and Kearsley 2001). Current management techniques implemented to create and maintain the disturbance-dependent mosaic within PPSO habitats include cutting overstory trees to open the canopy, mowing understory growth, and prescribed burning. The timing and frequency to which these management activities take place can have dramatic immediate and long-term effects on the composition and structure of the understories in these habitats. A burn of moderate intensity will immediately eliminate much of the understory, which is composed primarily of scrub oak, huckleberry (*Gaylussacia baccata*), and blueberry (*Vaccinium angustifolium*). However, these species are adapted to frequent fires of this type (Swain and Kearsley 2001) and will resprout vigorously from root sources in the following growing season (Gucker 2006, Carey 1992, Tirmenstein 1991). Additionally, disturbances of this type to tree oaks will initiate coppice growth (Cary 1986). The combination of growth from root sources by shrub and tree species following a prescribed burn can increase the amount of vertical and horizontal vegetative cover after several growing seasons. Therefore, an intermediate

level of burn frequency and intensity that keeps the majority of the tree canopy intact, and only top-kills shrubs, is recommended to maintain a balance of vegetation that does not become over-stressed from fire effects (i.e., is able to re-grow following fire), and understory openness.

Table 1. Comparison of habitat variables between random (n =15) and used (n = 15) sites for Whip-poor-wills studied at the Massachusetts Military Reservation in 2005 and 2006, using the Wilcoxon rank sum test.

Variable Description	**Variable**	**Used**	**se**	**Random**	**se**	***P***
% canopy cover	CAN	52.36	3.65	50.16	3.29	0.46
% vertical structure (0-2 m)	VERT	37.87	5.24	40.93	5.16	0.25
% ground cover (0-1 m)	GC	61.55	2.97	65.26	3.59	0.07
average dbh (inches) of trees	DBH	7.60	0.31	7.28	0.25	0.30
coniferous basal area	CON	31.13	3.00	32.73	4.31	0.53
deciduous basal area	DEC	4.089	0.28	4.21	0.282	0.39

Table 2. Whip-poor-will habitat selection models constructed from significant univariate variables sampled at the MMR, Cape Cod, Massachusetts, USA, during 2005 and 2006. Models within 2 of the lowest AIC_c are considered supported.

Model	**AIC_c**	**Δ AIC_c**	**Wi**
-0.85 GC	415.15	0.0000	0.4641
-0.58 VERT	417.58	2.4300	0.1377
intercept only model	418.05	2.8977	0.1090
-0.16 VERT + -0.74 GC	418.17	3.0218	0.1024
0.08 CAN + -0.83 GC	418.28	3.1318	0.0969
0.37 CAN	419.81	4.6600	0.0452
0.12 CAN + -0.54 VERT	420.67	5.5218	0.0293
0.04 CAN + -0.15 VERT + -0.73 GC	421.97	6.8200	0.0153

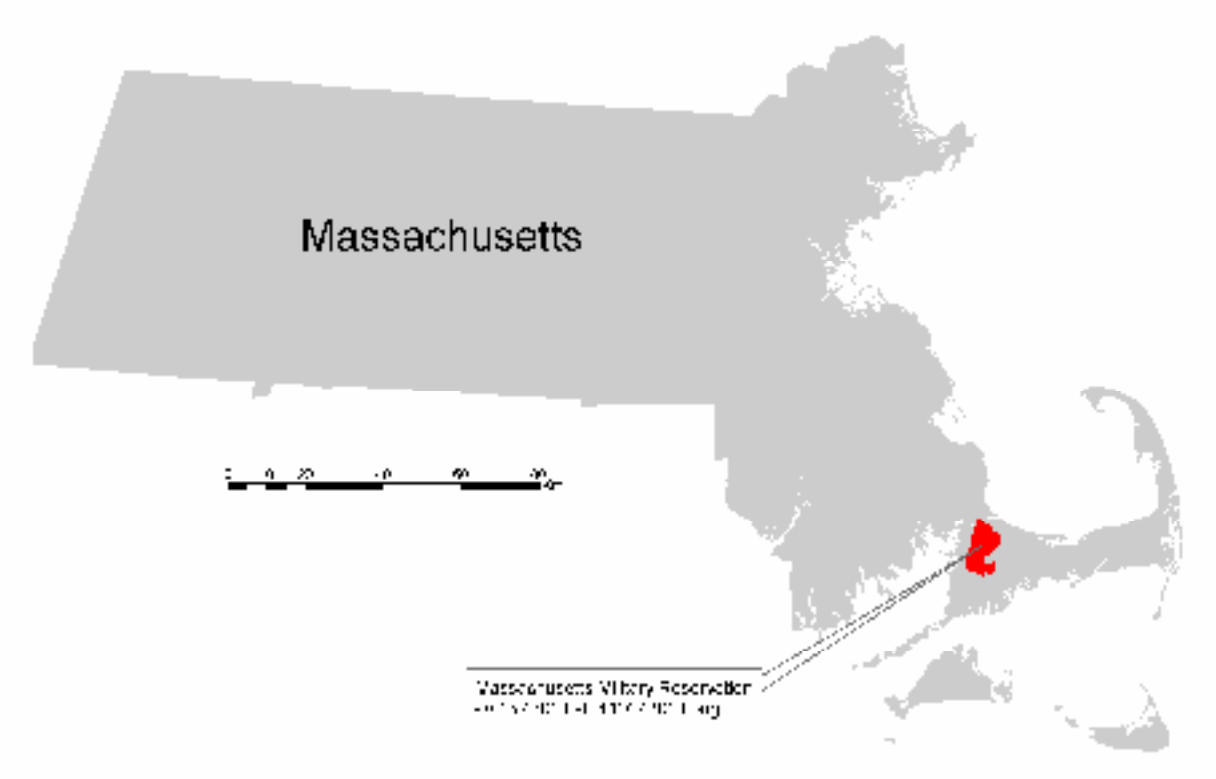


Figure 1. The study was conducted at the Massachusetts Military Reservation, located on Cape Cod, Massachusetts, USA in 2005 and 2006.

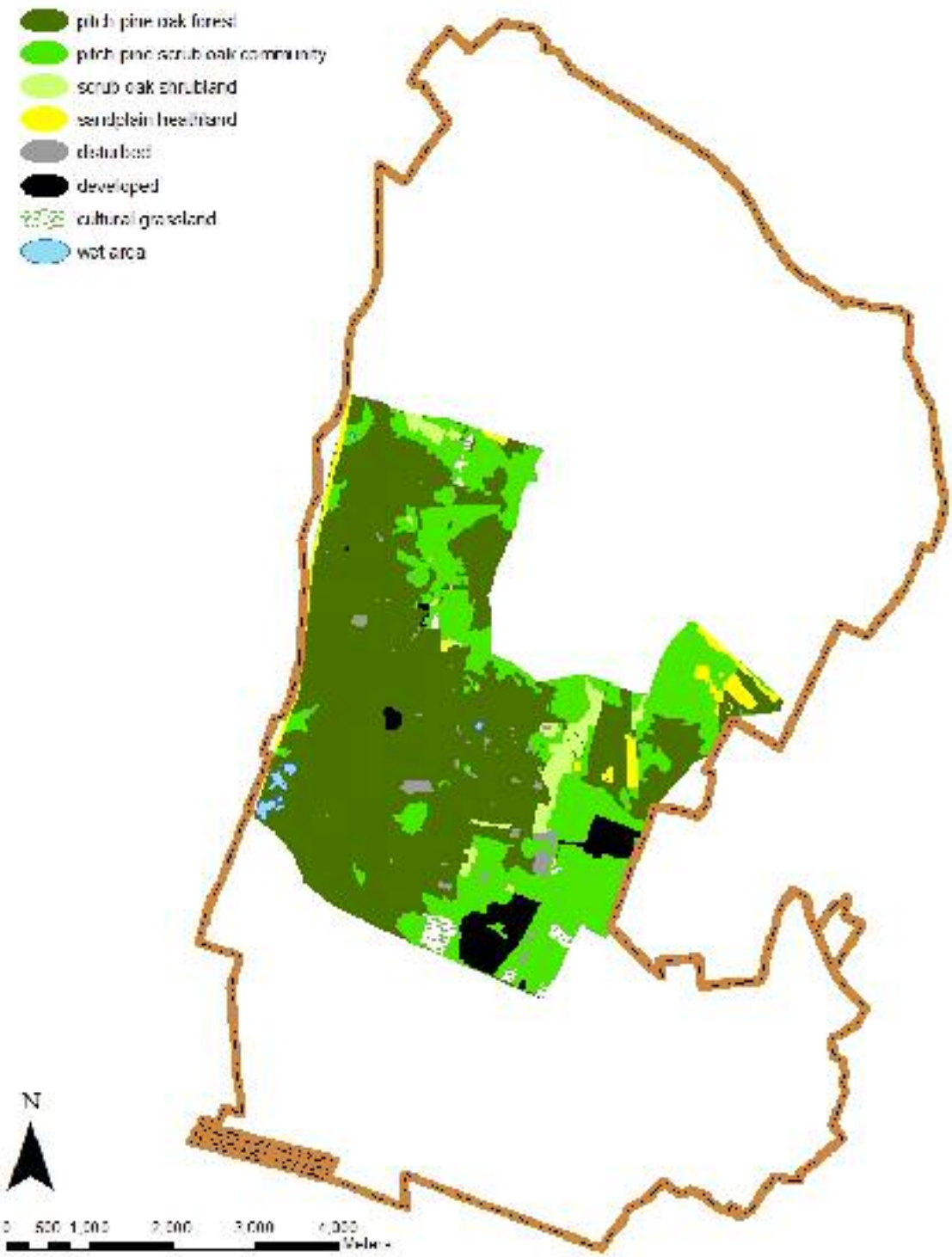


Figure 2. Distribution of vegetation community types throughout the study area at the MMR, located on Cape Cod, Massachusetts, USA.

CHAPTER III

HABITAT SELECTION BY WHIP-POOR-WILLS: THE INFLUENCE OF PREY AVAILABILITY

Introduction

The Whip-poor-will is a neotropical migrant with a large geographic range. The breeding range extends west from the east coast of the US and southern Canada, to Arizona and Texas at its southernmost point, north to the lower portions of Sasketchewan (DeGraaf and Rappole 1995). Seldom seen due to its cryptic plumage and nocturnal behavior, it is most recognized for its unique, charismatic song. Recently, the Whip-poor-will has become the focus of considerable conservation attention as the result of evidence indicating significant population declines over most of its breeding range. These data include information from state atlas projects reporting the absence of Whip-poor-wills from previously occupied areas (Veit and Petersen 1993, Cink 2000), as well as the North American Breeding Bird Survey, which indicates a significant 2.2% annual rate of decline survey-wide from 1966 to 2005 (Sauer et al. 2005). Although Whip-poor-wills do not have any formal conservation status, such as threatened or endangered, these trends and the general lack of knowledge on their conservation status and habitat requirements resulted in their identification by the Northeast Working Group of Partners in Flight as a monitoring priority (Hunt 2006b).

Regional surveys in the northeast have identified Pitch Pine (*Pinus rigida*) / Scrub Oak (*Quercus illicifolia*) barrens (PPSO) as habitats with high numbers of Whip-poor-wills relative to other forest types (Sibley 1988, Hunt 2006, King and Collins 2007). These barrens include a mosaic of forest, shrubland, and grassland habitats with acidic,

dry, sandy, nutrient-poor soils. These habitats have been divided into vegetation communities that differ in habitat structure and composition (Swain and Kearsley 2001). Historically, PPSO have been subject to chronic disturbances, which are responsible for maintaining the mosaic of habitats within barrens systems. Disturbances include both natural and anthropogenic agents, such as frost kill, insect infestations, salt spray, and wind events, have repeatedly disturbed these communities, along with livestock grazing, fuel wood harvesting, silviculture, and fires set continually by humans since they first inhabited the barrens systems following glaciation (Patterson and Ruffner 2003). Fire has had the most widespread influence on forming and maintaining PPSO, which are now rare and threatened globally, as suppression of wildfires has allowed the open canopies to succeed into savannas and closed-canopy forests (Swain and Kearsley 2001). These habitats and associated wildlife are now dependent on active management to persist.

Preliminary surveys within the PPSO community on the MMR indicate that Whip-poor-will abundance differs markedly among habitat types within PPSO (Cavanaugh in Cink 2002). Because different management regimes favor different vegetation types within the PPSO, the type, timing and frequency with which disturbance occurs can have dramatic immediate and long-term effects on the composition and structure of these habitats. For example, prescribed fire of moderate intensity will result in an open understory under closed canopy conditions, whereas frequent intense burns can result in very different conditions of a denser understory structure and open canopy. These conditions may result from fires that kill overstory trees, which open the canopy and allow for vigorous shrub growth (Gucker 2006, Carey 1992, Tirmenstein 1991, Cary

1986). Wildlife responses to habitat management are generally species specific, and therefore require specific knowledge of individual species (White and Harrod 1997).

Ultimately habitat selection reflects availability of resources necessary for successful survival and reproduction. These resources include components such as nesting habitat, cover from predators, or food availability (Hunter 1999). Royama (1970) reported that net energy yields for foraging Great Tits (*Parus major*) were lower where available prey abundance is low, which probably provides a mechanism underlying habitat selection for species such as Ovenbirds (*Seiurus aurocapillus*) that concentrate foraging efforts in habitats where the abundance of available prey is highest (Zach and Falls 1976). Although there are no quantitative data on prey selectivity in Whip-poor-wills (Cink 2002), food availability has been cited as a factor affecting habitat selection in the congeneric European nightjar (*C. europeus*; Alexander and Cresswell 1990, Sierro et al. 2001). Cavanaugh (in Cink 2002) hypothesized that Whip-poor-will habitat selection in Massachusetts PPSO was influenced by prey availability; however, in the absence of quantitative data, the influence of food availability on habitat selection is a matter of conjecture.

Because Massachusetts PPSO communities require management to maintain their distinctive ecological qualities, and these management activities affect their suitability, detailed information is needed on the habitat relationships of for vulnerable fauna such as Whip-poor-wills. To this end, I conducted a study to investigate Whip-poor-will habitat selection within Pitch Pine / Scrub Oak Barrens, which include the systematic study of food resources in PPSO habitats to determine whether habitat preference of Whip-poor-wills is influenced by food availability.

Study Site

The study was conducted on the Massachusetts Military Reservation (MMR), which is a compilation of military installations on Cape Cod that consist primarily of the Massachusetts Army National Guard, Massachusetts Air National Guard, U.S. Coast Guard, and U.S. Air Force (Fig 1). The 9090 hectares that make up the MMR are located approximately between 41°37'30'' and 41°45'00''N latitude and 70°30'00'' to 70°37'30''W longitude, in the towns of Bourne, Sandwich, and Mashpee (Figure 1).

The MMR is mostly undeveloped, forested land that has a large network of unpaved roads used in military training activities. Average annual temperature is 10°C, and average annual precipitation at the MMR is approximately 122 centimeters. The proximity to the Atlantic coast moderates the climate for much of the year (Patterson and Ruffner 2003). The Sandwich and Plymouth terminal moraines compose land on the north and west sides of the MMR, which is characterized by hilly terrain, and soils mostly from the Plymouth, Barnstable, and Nantucket series. The land that these moraines surround to the South and East is the outwash plain, which is essentially flat, and covered by soils mostly from the Enfield, Merrimac, and Carver series (Fletcher 1993).

The vegetation on the MMR is characterized as PPSO. This is a disturbance-dependent community type created by historic logging, grazing, agriculture, and wildfires. The PPSO at the MMR consist of a combination of scrub oak, pitch pine, white oak (*Q. alba*), black oak (*Q. nigra*), and scarlet oak (*Q. coccinea*). The vegetation was sampled and classified by Massachusetts Army National Guard (MARNG) Natural Resources Office personnel in 2003. Classifications were based on the Massachusetts Division of Fisheries and Wildlife, Natural Heritage and Endangered Species Program's Plant

Communities of Massachusetts (Swain and Kearsley 2001). Vegetation at the MMR was delineated from digitized, true color aerial photographs taken in the spring of 2002, and ground truthing techniques. The vegetation was classified into the following community types: black oak–scarlet oak forest, cultural grassland, immature pitch pine, pitch pine–oak forest, Scotch pine (*Pinus sylvestris*)–pitch pine–oak forest, pitch pine–scrub oak community, Scotch pine–pitch pine–scrub oak community, red maple (*Acer rubrum*) swamp, sandplain heathland, and scrub oak shrubland. I studied Whip-poor-wills on a 2,325 hectare portion of the MMR, which comprised a contiguous area in the central portion of the MMR bounded on the south by developed land not used by Whip-poor-wills, on the east and west by the boundaries of the MMR. The northern section of the MMR was not used due to military restrictions as well as its inaccessibility. The vegetation in the study area consisted almost entirely of pitch pine–oak forest, pitch pine–scrub oak, and scrub oak shrubland.

Methods

Whip-poor-wills arrive in southeastern Massachusetts around late April – mid May (Tyler 1940). Nightly visits were made to the study area to listen for the first arrivals of Whip-poor-wills beginning in mid-April in 2005 and 2006, with capture efforts commencing 2 weeks thereafter to avoid catching migrating Whip-poor-wills. . I captured Whip-poor-wills using approximately 10 2-m tall mistnets with 32-36 mm mesh and varying in length from 6-18 m. I deployed nets in a random-systematic manner to ensure even covereage of the study area by dividing the study area into a grid of 99 25 ha cells (an area corresponding to the average home range of Whip-poor-wills at our site) and selecting cells at random. I listened for Whip-poor-wills at selected cells, and placed

an array of nets as close as possible to where the calls originated. Mist nets were set during good weather (i.e., no rain or surface wind >8 mph) between the hours of 1945 and 0100, and checked at 30-40 minute intervals. All captured Whip-poor-wills were fitted with a 1.95 gram radio transmitter, (model BD-2, Holohil Systems Ltd., Carp, Ontario, Canada), using a backpack harness attachment modified from Rappole and Tipton (1991). Radios had an estimated battery life of 11.5 weeks, and transmitted at a unique frequency between 164-165 Khz.

Foraging locations were collected in July and August of 2005 and 2006, after the majority of courting and breeding had taken place. This was to avoid collecting locations that were associated with these behaviors, as the objective of our study was to describe foraging habitat use. At least 20 locations (21.4 ± 2.0) were collected from each Whip-poor-will used in our analyses. I located foraging sites based on simultaneous bearings taken by two researchers and triangulating the locations of Whip-poor-wills. Bearings of the strongest radio signal were recorded from 4 points on surrounding roads and analyzed with Location of a Signal (Ecological Software Solutions 1998) telemetry analysis software. The software was used to estimate locations and associated error ellipses. Error elipses for locations averaged ≈20 m, and locations with error elipses >50m were eliminated from the analyses. Foraging ranges (95% kernel) were calculated from these radio locations using the Animal Movement extension (Hooge et al. 1999) in ArcView 3.2a (Environmental Systems Research Institute, Inc.1999).

I assessed diet by collecting Whip-poor-will fecal samples at day roost locations used by radio-marked individuals on a daily basis during the breeding season (mid June - late August, 2005 and 2006), with the exception of females during incubation and brood

rearing, due to concerns that disturbance associated with collection would negatively affect reproductive success. Whip-poor-wills are territorial and exhibit fidelity to individual day roosts (Massachusetts Army National Guard, unpublished data) so it was possible to assign fecal samples to individual birds with complete certainty.

Samples were stored in a solution of 70% ethanol prior to diet analyses. A 180 μm screen was used to filter out lepidopteran wing scales that would otherwise cloud and cover the sample in the petri dish making identification of the parts difficult. Prey fragments were examined under a 22X binocular microscope and categorized to the lowest taxonomical level possible. The proportion of each prey category was estimated, using a petri dish that was marked with a 6 x 6 – 1 cm^2 grid, based on the surface area covered (Browne and Aebischer 2003). The 36 grid-cell values were averaged to calculate the relative amount of each prey category in the sample. Fecal samples from each individual were averaged for each month, and the averages of the monthly means were used in the analyses.

Browne and Aebischer (2003) used this method to evaluate the diet of Turtle Doves (*Streptopelia turtur*). Although their fecal samples consisted of floral material, their methods lend themselves to insectivorous species as well. In our case, this method was a good fit versus estimating definitive numbers of prey caught and consumed by counting a minimum number of parts found in the fecal sample, as described in Ralph et al. (1985). The minimum number of parts would have been difficult to employ given the high degree of maceration that occurs in the Whip-poor-will digestion process. The soft-bodied lepidopteran prey was particularly susceptible to being fragmented into many unrecognizable parts. The difference in color and texture of the prey fragments found in

Whip-poor-will feces was often a good indicator of what prey was consumed, therefore allowing us to estimate a proportion of prey types consumed based on relatively small prey fragments. The surface area method also considers the size of the prey item that was consumed without doing any further calculations. Csada et al. (1992) used the femur length of coleopterans to estimate prey size in Common Poorwills (*Phalaenoptilus nuttallii*), but notes that this method does not work for soft-bodied prey, such as lepidopterans, that would not yield measurable parts.

Prey availability was estimated using captures from light traps (Leroy Koehn design, Georgetown, KY) with UV bulbs. Light traps were run on 12 different nights in each habitat during both years of the study. Nightjars are known to feed most actively at dusk when prey availability is highest (Jetz et al. 2003), so light traps were run for 2 ½ hours immediately following sunset to coincide with the peak of foraging activity. I assumed that light traps attracted and captured potential prey items in proportion to their abundance; however, the trap effectiveness of light traps for different insect species on the MMR is not known (M. Mello, pers. comm.). Three traps were set out once a week between June – August in 2005 and 2006, one in each of the major habitat types at Camp Edwards (pitch pine-oak forest, pitch pine-scrub oak, and scrub oak shrubland). I used ArcView 3.2a GIS software (Environmental Systems Research Institute, Inc.1999) to randomly choose locations within each of the habitat types, with the constraint that there was at least 300 m between light trap locations. Locations from 2005 were resampled at the same time in 2006. Traps were emptied each night and their contents frozen until analyses. Volumes of prey were calculated for each taxonomic group using the formula for a prolate spheroid (Hofer et al. 2003). Prey volume was used as a measure of

abundance, versus mass, to avoid bias towards heavy prey items such as beetles. Volumes for each habitat were averaged for each month.

To account for the fact that composition of territories of individual Whip-poor-wills differed in the proportion of habitat types, and that prey availability might differ among habitat types, the prey availability for an individual was calculated by multiplying the amount of available prey in each habitat type by the proportion of each habitat within its foraging range.

An analysis of variance was used to test for differences in prey abundances among habitat types. Compositional analysis (Aebischer et al. 1993) was used to test for prey and habitat selection and rank items according to preference. These calculations were performed using R statistical software package (R Development Core Team 2005).

Compositional analysis is a multivariate analysis of variance for determining a selection of a categorical variable. Resource use is measured in terms of proportion of used versus available resources within a defined home range, with individual animals as replicates. The analysis determines which resources are used more or less than expected by chance, while considering the use and availability of all resources. Thus, one resource is not necessarily considered preferred if one is avoided. The categorical nature of the Whip-poor-will foraging dataset, the methods for addressing common problems in resource selection studies, and the straightforward means for computing and reporting results, made compositional analysis an efficient means for using our data to investigate Whip-poor-will prey and habitat preferences.

Whip-poor-wills are known to exhibit territorial behavior. However, this behavior has not been well studied, and it is unknown how this behavior influences habitat selection (Cink 2002). Aebischer et al. (1993) advocate using compositional analysis to investigate habitat selection at several spatial scales. They suggest using the proportion of habitat types within the home range as the used habitat, and the proportion of habitat within the study area as available habitat for a broad-scale analysis. A finer-scale analysis has the proportion of radio-locations in each habitat type as the used habitat, versus proportion of habitat within the home range as available habitat. As the effects of territoriality are unknown, we chose not to do a broad-scale analysis, and instead, concentrated our efforts on a finer-scale, where territorial behavior would not influence habitat selection.

Results

A total of 18 Whip-poor-wills were captured during the study. Two of these were depredated, and another was unable to be located due to transmitter failure, migration from the study site, or some other unknown factor. In all, 15 individuals (8 females, 7 males) were used for the analyses. There were no statistically significant differences in habitat use of Whip-poor-wills between 2005 and 2006, or between males and females, so data were pooled for year and sex. Habitat use was significantly different from random when data on all individuals from 2005 and 2006 was pooled ($n = 15$) ($\Lambda = 0.53$, $p = 0.008$). There was not a detectable difference between the use of pitch pine – oak forests and scrub oak shrublands, or between scrub oak shrublands and pitch pine – scrub oak communities. However, there was a difference between the use of pitch pine – oak

forests and pitch pine – scrub oak communities (Table 3) indicating that pitch pine – oak forests are preferred by Whip-poor-wills.

A total of 70 fecal samples were analyzed from 10 Whip-poor-wills, 5 males and 5 females that were captured and tracked during the 2005 season. The number of samples per individual ranged from 4-11 (6.8 ± 2.3). Because female Whip-poor-wills that were incubating and/or brood rearing were not intentionally flushed, some individuals do not have data for each month of the study.

Nearly 98% of prey items found in feces were lepidoptera and coleoptera (scarabidae), so I focused our analyses on these two groups, plus a third category "other" which consisted mainly of beetles other than scarabs, along with neuropterans. The Whip-poor-will diet consisted of Lepidopterans (60.9±3.4%) followed by Scarab beetles (36.7±3.1%), with the remainder of prey items consisting of "other".

In 2005 the abundance of total prey, lepidopterans, scarab beetles, and "other" prey, measured from light trap captures, did not differ among habitat types or months ($P > 0.05$) (Figure 3). In 2006 the abundance of total prey, lepidopterans, scarab beetles, and "other" prey did not differ among habitat types for all months combined (Figure 4), however there were differences in prey abundances among months for all habitat types combined. Total prey was less in August than in June and July ($F_{[2,23]} = 11.51$, $p < 0.001$), Lepidopterans were more abundant in July than August ($F_{[2,23]} = 5.31$, $p = 0.013$), Scarabs were more abundant in June than July and August ($F_{[2,23]} = 21.2$, $p < 0.001$), and "other" prey was more abundant in July than June and August ($F_{[2,23]} = 3.77$, $p = 0.038$).

A comparison of the diet to the available prey based on prey abundance and habitat use in 2005 indicates Whip-poor-wills did not consume prey in proportion to its

availability ($\Lambda = 0.520$, $p = 0.03$). Prey items were ranked most to least preferred in the following order: lepidopterans, scarab beetles, and other (Table 4). Lepidopterans were preferred significantly more than scarab beetles and "other" prey. Scarab beetles were also preferred significantly more than "other" prey. Although lepidopterans and scarab beetles were the most abundant taxa captured in the light traps (Figures 3 and 4), Whip-poor-wills preyed upon these taxa in proportions that they were greater than the proportions making up the light trap captures, therefore showing preference for these items.

Discussion

Our study has showed that all habitats within the PPSO barrens are not used equally, and that pitch pine – oak forest is preferred over the pitch pine – scrub oak community. This is in contrast to results from a call count survey made at the MMR during the late 1990's (Cavanaugh in Cink 2002). That study showed an apparent avoidance of pitch pine – oak forests and a preference for the habitats with a more open canopy. Other studies have shown that habitat at sites where birds sing are not necessarily characteristic of the entire territory (Collins et al. 1983), which might explain the inconsistency between call count surveys, which count displaying birds, and telemetry, which reflects habitat used for foraging. Alexander and Cresswell (1990) reported that European Nightjars foraged in woodland habitats that differed from the conifer plantations and heathlands in which they nested. Although there is no information indicating that Whip-poor-wills select particular habitat conditions for displaying, based on these other studies, this clearly remains a possible explanation for the contrast between our results based on telemetry of foraging individuals and previous call count surveys.

The preference of foraging Whip-poor-wills for pine-oak forests might be the result of selection by this species for habitats with open understory, conditions that are characteristic of pine-oak habitats (Cavanaugh in Cink 2002). Open understory conditions are repeatedly referred to in descriptions of Whip-poor-will habitat (Wilson 1985, Eastman 1991, Cink 2002, Chapter 2). Whip-poor-wills forage by sallying after prey from perches in trees, shrubs, and the ground with flights up to 5 meters in height (Heresy 1923, van Rossem 1927). Open understory structure might facilitate successful foraging by providing a clear line of sight for Whip-poor-wills to detect prey, either directly or by silhouetting them against the sky (Mills 1986, Cink 2002). European Nightjars also exhibit this behavior (Alexander and Cresswell 1990), and the availability for unobstructed understory conditions has been cited as a reason for avoidance of pine forests by foraging nightjars in Switzerland (Sierro et al. 2001). Sierro et al (2001) suggested that lack of light due to dense canopy was also a factor in explaining the avoidance of pine forests by European Nightjars, which contrast with our results that pine oak forest, that are characterized by closed canopy conditions (Cavanaugh in Cink 2002), are selected. Conditions throughout the MMR were characterized by relatively open canopy conditions (≈50%), which probably explains why Whip-poor-will habitat use was not associated with this factor (Chapter 2).

Whip-poor-wills at the MMR did not consume prey in proportion to their abundance. Lepidopterans were found to be the most abundant prey throughout all habitats and the preferred prey of Whip-poor-wills. Our results are the first quantitative analysis of Whip-poor-will diet, and provide support for conclusions on diet based on anecdotal observations (Hersey 1923, Van Rossem 1937) and more recently, limited

quantitative data from stomach contents (Patuxent Wildlife Research Center, Laurel, Md). All of these accounts state Whip-poor-wills feed mostly on moths and beetles, but none of them were conducted in a systematic fashion to permit the establishment of prey preferences. Sierro et al. (2001) analyzed the diet of European Nightjars and found similar results to ours: nightjars selected moths, which were also the most abundant species at their sites in Switzerland, but nightjars also consumed beetles at a lower proportion to their abundance in light-trap samples.

Selection of lepidoptera by Whip-poor-wills is consistent with optimal foraging strategy of maximizing food intake per unit effort (Krebs 1973). Lepidopterans are more energy rich than coleopterans (Bayne and Brigham 1995), which may explain the prey preference. They also lack much of the chitonous material forming the exoskeleton of coleopterans and other insects, which make them more easily digested (Castro et al. 1989, Barclay et al. 1991, Keeler and Studier 1992). The digestibility and energy content of lepidopterans may be of particular importance when choosing prey items to feed to chicks and juveniles (Sierro et al. 2001, Royama 1970). The diet of the Whip-poor-will was similar to nightjars with similar morphology, energy conservation techniques, and foraging strategies (Brigham 1990, Brigham and Fenton 1994, Sierro et al. 2001). The diet does differ from that of the common poorwill (*Phalaenoptilus nuttallii*) (Bayne and Brigham 1995), which is able to enter a daily torpor to conserve energy (Brigham 1992, Kissner and Brigham 1993). Poorwills preferred beetles versus lepidopterans, possibly for their relatively high amounts of polyunsaturated fats (Fast 1970), which they need to maintain the fluidity of their fat (Geiser and Kenagay 1987). Whip-poor-wills are not

known to enter torpor (Cink 2002), and therefore do not need to obtain these polyunsaturated fats.

Prey abundance did not differ among PPSO habitats, and thus I conclude that prey abundance per se did not influence habitat selection. Holmes and Shultz (1988) suggest prey availability in some habitats may be constrained due to forest structure that inhibits the detection and capture of prey. Robinson and Holmes (1981) also concluded that habitat structure influences the ability of a species to detect and capture prey. Bird morphology largely determines foraging tactics through dictation of mobility, prey detection, and prey capture (Robinson and Holmes 1982, Holmes and Robinson 1988). These constraints resulting from morphologic traits of their plumage, feet, and sensory receptors restricts species to foraging within habitats that are conducive to exploiting their abilities and employing the most efficient foraging tactics (Holmes and Robinson 1988). Thus, although there was no difference in prey availability among habitats, if Whip-poor-will foraging efficiency is affected by habitat structure, food could still be influencing habitat selection (Chapter 2). Data on habitat-specific prey capture rates would be necessary to test this, however.

Proper management implementation can improve Whip-poor-will habitat within PPSO barrens and other community types by shifting vegetation structure of habitats to that of pitch pine – oak forests. The PPSO barrens are a gradient of habitats dependent upon disturbance to maintain its mosaic of seral stages. Management techniques such as cutting overstory trees to open the canopy, mowing understory growth, and prescribed burning can provide disturbances that have dramatic immediate and long-term effects on

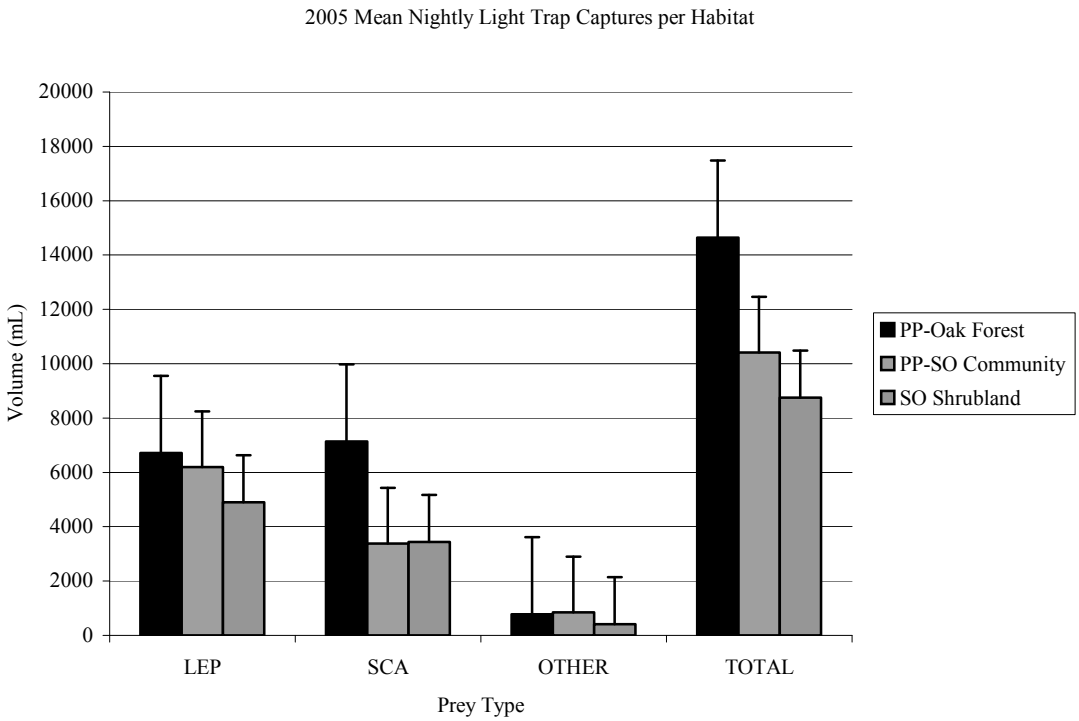
the composition and structure of the understories in these habitats. Mills (1987) cites wildfire suppression as a contributing factor to Whip-poor-will population declines in Ontario, Canada. The regular application of prescribed fire in these habitats would reduce the amount of understory as well as the canopy in some places, providing enhanced foraging opportunities.

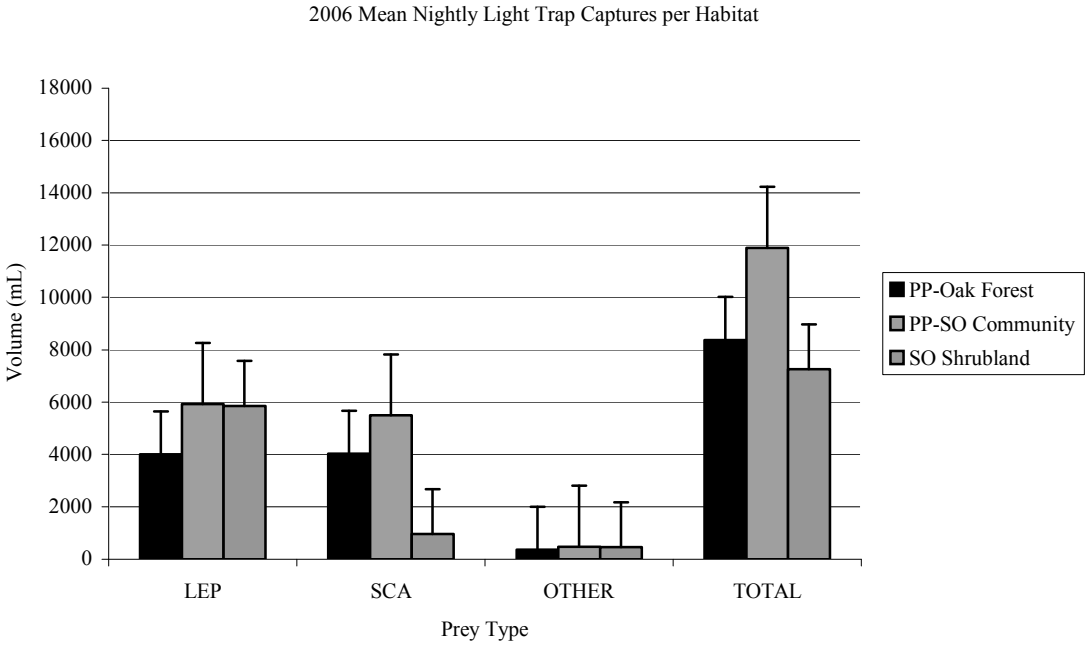
Table 3. Ranking matrix for Whip-poor-will foraging habitat preference at Camp Edwards, MA, based on t –values comparing the proportion of foraging locations in each habitat with proportions of habitat within an individuals foraging range. (+++ and - - - indicate significant values at $P < 0.05$.)

Habitat	PPOF	PPSO	SO	Rank
Pitch Pine-Oak Forest (PPOF)	0	+++	+	2
Pitch Pine-Scrub Oak Community (PPSO)	- - -	0	-	0
Scrub Oak Shrubland (SO)	-	+	0	1

Table 4. The ranks and pairwise comparison of prey composig the Whip-poor-will diet at Camp Edwards, MA. +++ and - - - indicate significant values at $P < 0.05$.

Prey	Lepidoptera	Scarab	Other	Rank
Lepidoptera	0	+ + +	+ + +	2
Scarab	- - -	0	+ + +	1
Other	- - -	- - -	0	0





Figures 3 and 4. Mean and standard error of lepidoptera (LEP), scarab beetle (SCA), all other taxa, and totals, of light trap captures per night by habitat for years 2005 and 2006 at Camp Edwards, MA. In 2005 prey types were distributed equally among habitats and months. In 2006 prey types were distributed equally among habitats, but differed temporally. A indicates a significant ($p < 0.05$) value.

LITERATURE CITED

Aebischer, N. J., P. A. Robertson, and R. E. Kenward. 1993. Compositional analysis of habitat use from animal radio-tracking data. Ecology 74: 1313-1325.

Alexander, I. and B. Cresswell. 1990. Foraging by Nightjars *Caprilmulgus europaeus* away from their nesting areas. Ibis:568-574.

Barclay, R. M., M. A. Dolan, and A. Dyck. 1991. The digestive efficiency of insectivorous bats. Canadian Journal of Zoology 69: 1853-1856.

Bayne, E. M., and R. M. Brigham. 1995. Prey selection and foraging constraints in common poorwills (*Phalaenoptilus nuttallii*). Journal of the Zoological Society of London 235: 1-8.

Block, W. M., and L. A. Brennan. 1993. The habitat concept in ornithology: theory and applications. Current Ornithology 11:35-91.

Breslow, N. E., and D. G. Clayton. 1993. Approximate inference in generalized linear mixed models. Journal of the American Statistical Association 88: 9-25.

Brigham, R. M. 1990. Prey selection by big brown bats (*Eptesicus fuscus*) and common nighthawks (*Chordeiles minor*). American Midland Naturalist 124: 73-80.

Brigham, R. M. 1992. Daily torpor in a free-ranging goatsucker, the common poorwill (*Phalaenoptilus nuttallii*). Journal of Physiological Zoology 65: 457-472.

Brigham, R. M., and M. B. Fenton. 1994. Convergence in foraging strategies by two morphologically and phylogenetically distinct nocturnal aerial insectivores. Journal of the Zoological Society of London 223: 475-489.

Browne, S. J., and N. J. Aebischer. 2003. Habitat use, foraging ecology and diet of Turtle Doves *Streptopelia turtur* in Britain. Ibis 145: 572-582.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. 2nd Edition. Springer-Verlag, New York, New York, USA. 488 pp.

Bushman, E.S., and G.D. Therres. 1988. Habitat management guidelines for forest interior breeding birds of coastal Maryland. Maryland Department of Natural Resources, Wildlife Tech. Publ. 88-1. 50 pp.

Castro, G., N. Stoyan, and J. P. Myers. 1989. Assimilation efficiency in birds: a function of taxon or food type? Comp. Biochem. Physiol. 92: 271-278.

Carey, A. B., and J. D. Gill. 1980. Firewood and wildlife. Res. Note 299. Broomall, PA: U.S. Department of Agriculture, Forest Service, Northeastern Forest Experiment Station. 5 p.

Carey, J. H. 1992. Quercus velutina. In: Fire Effects Information System, [Online]. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fire Sciences Laboratory (Producer). Available: http://www.fs.fed.us/database/feis/ [2007, April 8].

Cink, C. L. 2002. Whip-poor-will. The Birds of North America 620:1-19.

Collins, S. 1981. A comparison of nest-site and perch-site vegetation structure for seven species of warblers. Wilson Bulletin 93(4):542-547.

Csada, R. D., R. M. Brigham, and B. R. Pittendrigh. 1992. Prey selection in relation to insect availability by the common poorwill (*Phalaenoptulis nuttallii*). Canadian Journal of Zoology 70:1299-1303.

DeGraaf, R. M., and J. H. Rappole. 1995. Neotropical migratory birds: natural history, distribution, and population change. Cornell University Press, Ithaca, New York, USA.

Eastman, J. 1991. Whip-poor-will. In: Brewer, R., G. A. McPeek, and R. J. Adams, Jr., eds. The atlas of breeding birds of Michigan. Pp. 252-253. Michigan State University Press, East Lansing, Michigan, USA.

Edwards, T. C., Jr., G. G. Moisen, T. S. Frescino, and J. J. Lawler. In press. Modeling multiple ecological scales to link landscape theory to wildlife conservation. Pages XX in J. A. Bissonette and I. Storch, editors. Landscape ecology and resource management: making the linkages. Island Press, Covelo, California, USA.

Environmental Systems Research Institute, Inc. 1999. ArcView®. Version 3.2 [computer program]. Environmental Systems Research Institute, Inc., Redlands, Calif.

Fast, P. G. 1970. Insect lipids. In: Holman, R. T., editor. Progress in the chemistry of fats and other lipids. pp. 181-242. Pergamon Press, Oxford, England.

Fletcher, P. C. 1993. Soil survey of Barnstable county, Massachusetts. U.S. Department of Agriculture, Soil Conservation Service, Massachusetts Agricultural Experiment Station, Amherst, Massachusetts, USA.

Geiser, F., and G. J. Kenagy. 1987. Polyunsaturated lipid diet lengthens torpor and reduces body temperature in a hibernator. American Journal of Physiology 252: 897-901.

Gill, F. B. 1994. Ornithology. 2nd ed. W. H. Freeman and Company, New York, New York, USA. 766 p.

Green, R. E., and G. H. Griffiths. 1994. Use of preferred nesting habitat b yStone-Curlews (*Burhinus oedicnemus*) in relation to vegetation structure. Journal of Zoology (London) 233:457-471.

Gucker, C. L. 2006. Gaylussacia baccata. In: Fire Effects Information System, [Online]. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fire Sciences Laboratory (Producer). Available: http://www.fs.fed.us/database/feis/ [2007, April 8].

Harrell, W.C., and S.D. Fuhlendorf. 2002. Evaluation of habitat structural measures in a shrubland community. Journal of Range Management 55: 488-493.

Heresy, F. S. 1923. Observations on the habits of the Whip-poor-will (*Antrostomus v. vociferous*). Auk 40:534-536.

Hofer, U., H. Baur, and L. F. Bersier. 2003. Ecology of three sympatric species of the genus *Chamaeleo* in a tropical uplandforest in Cameroon. Journal of Herpetology 37 (1): 203-207.

Holmes, R. T., and J. C. Schultz. 1988. Food availability for forest birds: effects of prey distribution and abundance on bird foraging. Canadian Journal of Zoology. 66: 720-728.

Holmes, R.T., and S. K. Robinson. 1988. Spatial patterns, foraging tactics, and diets of ground-foraging birds in a northern hardwoods forest. Wilson Bulletin 100: 377-394.

Hooge, P. N., W. Eichenlaub, and E. Solomon. 1999. Animal movement extension to ArcView, ver. 2.04. Alaska Science Center – Biological Science Office, US Geological Survey, Anchorage.

Hosmer, D. W., and S. Lemeshow. 1989. Applied Logistic Regression. Wiley, New York, New York, USA. 307p.

Hunt, P. D. 2006a. Northeast Nightjar Survey: 2006 Summary. Report to Northeast Coordinated Bird Monitoring Program. Audubon Society of New Hampshire, Concord.

Hunt, P. D. 2006b. An analysis of Whip-poor-will habitat use in the Piscataquog River watershed: 2003-2005 with notes on statewide comparisons. A report submitted to the Piscataquog Watershed Association and Russell Piscataquog River Watershed Foundation.

Hunter, M. L. 1999. Maintaining biodiversity in forest ecosystems. Cambridge University Press, New York, New York, USA. 714 pp.

Jetz. W., J. Steffen, and K. E. Linsenmair. 2003. Effects of light and prey availability on nocturnal, lunar and seasonal activity of tropical nightjars. Oikos 103: 627–639.

Johnson, D. 1980. The comparison of usage and availability measurements for evaluating resource preference. Ecology 65-71.

Keating, K. A. and S. Cherry. 2004. Use and interpretation of logistic regression in habitat-selection studies. Journal of Wildlife Management 68: 774-789

Keeler, J. O., and E. H. Studier. 1992. Nutrition in big brown bats (*Eptesicus nilssoni*) feeding on June beetles. Journal of Mammology 73: 426-430.

King, D. I., and J. M. Collins. 2007. Crepuscular Birds in Wildlife Openings and Clearcuts in Western Massachusetts. Report to Mass Wildlife

Kissner, K. J., and R. M. Brigham. 1993. Evidence for the use of torpor by incubating and brooding common poorwills (*Phalaenoptilus nuttallii*). Ornis scand. 24: 333-334.

Krebs, J. R. 1973. Behavioural aspects of predation. In: Bateson, P. P. G., and P. H. Klopfer, editors. Perspectives in Ethology. pp.73-111. Plenum Press, New York, New York, USA.

Location of a Signal™ (1999). Ecological Software Solutions. Schwägalpstrasse 2, 9107 Urnäsch, Switzerland. Version 2.09.

Manly, B. F. J., L. L. McDonald, D. L. Thomas, T. L. McDonald, and W. P. Erickson. 2002. Resource selection by animals: statistical design and analysis of field studies. 2nd Edition. Kluwer Acedemic Publishers, Dordrecht, The Netherlands. 221 pp.

Martin, T. E. 1987. Food as a limit on breeding birds: a life history perspective. Annual Review of Ecology and Systematics 18:453-487.

Martin, T. E. 1993. Nest predation and nest sites: new perspectives on old patterns. Bioscience 43:523-532.

Mason, S. J., and N. E. Graham. 2002. Areas beneath the receiver operating characteristics (ROC) and relative operating levels (ROL) curves: Statistical significance and interpretation. Quarterly Journal of the Meteorological Society: 2145-2166.

Mielke, P. W., Jr., and K. J. Berry. 1982. An extended class of permutation techniques for matched pairs. Commun. Stat. 11:1197-1207.

Mills, A. M. 1986. The influence of moonlight on the behavior of goatsuckers (Caprimulgidae). Auk 103:370-378.

Mills, A. M. 1987. Whip-poor-will. In: Cadman, M. D., P. F. J. Eagles, and F. M. Helleiner, eds. Atlas of the breeding birds of Ontario. Pp. 224-225. University of Waterloo Press, Waterloo, Ontario, Canada.

Noon, B. R. 1981. Techniques for sampling avian habitats. In: D. E. Capen, ed. The use of multivariate statistics in studies of wildlife habitat. U.S. Forest Service Technical Report RM-87.

O'Neill, R. V. 1989. Perspectives in hierarchy and scale. Pages 140-156 *in* J. Roughgarden, R. M. May, and S. A. Levin, editors. Perspectives in ecological theory. Princeton University Press, Princeton, New Jersey, USA.

Patterson, W. A. III, and C. H. Ruffner. 2002. Camp Edwards training site fire management plan. Massachusetts Army National Guard, Camp Edwards, Natural Resources Office, Camp Edwards, Massachusetts, USA.

R Development Core Team (2005). R: A language and environment for statistical computing. R Foundation for Statistical Computing,Vienna, Austria. ISBN 3-900051-07-0, URL http://www.R-project.org.

Ralph, C. P., S. E. Nagata, and C. J. Ralph. 1985. Analysis of droppings to describe diets of small birds. Journal of Field Ornithology 56:165-174.

Ricklefs, R. E. 1969. An analysis of nesting mortality in birds. Smithsonian Contributions to Zoology 9:1-48.

Royama, T. 1970. Factors governing the hunting behavior and selection of food by the great tit. Journal of Animal Ecology 39:619-668.

Santner, S. 1992. Whip-poor-will. In: D. W. Brauning, ed. Atlas of breeding birds in Pennsylvania. Pp. 172-173. University of Pittsburgh Press, Pittsburgh, Pennsylvania, USA.

Sauer, J. R., J. E. Hines, and J. Fallon. 2005. *The North American Breeding Bird Survey, Results and Analysis 1966 - 2005. Version 6.2.2006.* USGS Patuxent Wildlife Research Center, La*urel, MD*

Sierro, A., R. Arlettaz, B. Naef-Daenzer, S. Strebel, and N. Zbinden. 2001. Habitat use and foraging ecology of the nightjar (*Caprimulgus europaeus*) in the Swiss Alps: towards a conservation scheme. Biological Conservation 98: 325-331.

Slauson, W. L., B. S. Cade, and J. D. Richards. 1991. User manual for BLOSSOM statistical software. U.S. Fish and Wildlife Service, Fort Collins, CO.

Smith, A. R. 1996. Atlas of Saskatchewan birds. Sask. Nat. Hist. Soc. Spec. Publ no. 22, Regina, Saskatchewan, Canada.

Stewart, R. E. 1975. Breeding birds of North Dakota. Tri-College Center for Environmental Studies, Fargo, North Dakota, USA.

Swain, P. C., and J. B. Kearsley. 2001. Classifications of the natural communities of Massachusetts. Massachusetts Division of Fisheries and Wildlife, Natural Heritage and Endangered Species Program, Westborough, Massachusetts, USA.

Therres, G. D. 1999. Wildlife species of regional concern in the northeastern United States. Northeast Wildlife 54: 93-100.

Thomas, D. and E. Taylor. 1990. Study designs and tests for comparing resource use and availability. Journal of Wildlife Management 54:322-330.

Tirmenstein, D. A. 1991. Quercus alba. In: Fire Effects Information System, [Online]. U. S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fire Sciences (Producer). Available: http://www.fs.fed.us/database/feis/ [2007, April 8].

Turner, M. G., R. H. Gargner, and R. V. O'Neill. 2001. Landscape ecology in theory and practice: pattern and process. Springer, New York, New York, USA. 401 pp.

Tyler, W. M. 1940. Eastern Whip-poor-will. U.S. National Museum Bulletin 176:163-183.

van Rossem, A. J. 1927. Eyeshine in birds, with notes on the feeding habits of some goatsuckers. Condor 29:25-28.

Veit, R.R. and W.R. Petersen. 1993. Birds of Massachusetts. Massachusetts Audubon Society. 514 p.

Wang, K., M. C. Kalcounis, D. J. Bender, D. L. Gummer, and R. M. Brigham. 1995. Predation on free-ranging common poorwills in Saskatchewan. Journal of Field Ornithology 63:400-403.

White, G. and R. Garrott. 1990. Analysis of wildlife radio-tracking data. Acedemic Press, New York, New York, USA.

White, P. S. and Harrod, J. 1997. Disturbance and Diversity in a Landscape context. In: Bissonette, J.A. ed. Wildlife and Landscape Ecology. Springer, New York, New York, USA.

Wiens, J. A. 1989. The ecology of bird communities. Volume 2: processes and variations. Cambridge University Press, Cambridge, Massachusetts, USA. 316 p.

Wilson, M. D. 2003. Distribution, abundance, and home range of the Whip-poor-will (*Caprimulgus vociferus*) in a managed forest landscape. MS Thesis. College of William and Mary, Williamsburg, VA.

Wilson, S. G. 1985. Summer distribution of Whip-poor-wills in Minnesota. Loon 57:6-8.

Zach, R., and J. B. Falls. 1976. Ovenbird hunting behavior in patchy environment: an experimental study. Canadian Journal of Zoology. 54: 1863-1879.