DISPERSAL BEHAVIOR AND CONNECTIVITY OF RED-COCKADED WOODPECKERS IN THE NORTH CAROLINA SANDHILLS

Anne Maura Trainor

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Approved by:

Dr. Aaron Moody

Dr. Conghe Song

Dr. Larry Band

Dr. Dean Urban

Dr. Jeffery Walters

ABSTRACT

Anne Maura Trainor: Dispersal Behavior and Connectivity of Red-cockaded
Woodpeckers in the North Carolina Sandhills
(Under the direction of Aaron Moody)

Human activities are degrading natural ecosystems globally, thus eroding biological diversity and reducing wildlife populations. One prominent example is the Red-cockaded woodpecker (*Picoides borealis*) which is a federally endangered, cooperative breeding species endemic to highly-fragmented longleaf pine (*Pinus palustris*) forests in the southeastern United States. The persistence of *P. borealis* is dependent upon managing longleaf pine forests to facilitate prospecting and dispersal movements and thus connecting populations.

My overall research objective was to interrelate spatial environmental data and animal movement behaviors in order to evaluate *P. borealis* habitat connectivity. First, I developed a novel method to empirically estimate and validate landscape resistance surfaces using mark-recapture and radio-telemetry data. I then applied this method to determine how prospecting movements were influenced by both environmental and conspecific cues during forays. The detail prospecting and dispersal data was then combined with detailed data on forest structure to estimate habitat connectivity across the landscape. Finally, I evaluate if *P. borealis* connectivity is positively impacted by private landowners involvement in a voluntary incentive-based agreement.

My results illustrated with an empirically-derived resistance surface that *P. borealis* are influenced by subtle changes in vegetation structure and land-use activities. The resistance surface successfully predicted most of the short-distance dispersal events. In addition, prospecting individuals' are cueing into environmental characteristics between breeding sites and complex social dynamics at potential breeding sites. When the network model was correlated with observed dispersal events, the abrupt transition from highly connected to disconnected territories provides insight into habitat connectivity within and between habitat patches. This approach showed that highly connected territories reside within managed areas of continuous forest but territories on private properties are isolated from managed lands and each other by agriculture or development. However, voluntary incentive-based conservation programs on private land are increasing the connectivity of *P. borealis* populations by managing and restoring habitat on private property.

DEDICATION

This work is dedicated to Zackary I. Cleveland, with his love and support he supported me during many years as a graduate student while sharing the journey and all of its ups and downs.

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CHAPTER 1

INTRODUCTION

Human activities are reducing and degrading natural ecosystems globally (Hoekstra et al. 2005). As a result, extensive contiguous natural habitats have become fragmented and interspersed by human land-uses, such as urban development and agriculture. This spatial arrangement restricts the movement of animals between habitat patches, thus reducing genetic diversity within populations and increasing extinction risk for local populations (Fahrig and Merriam 1994, Goodwin and Fahrig 2002). Natal dispersal, an animal's movement from its natal site to the first site where it obtains breeding status, is arguably the most essential behavior responsible for demographically and genetically connecting populations (Greenwood and Harvey 1982, Wiens 2001). Despite its importance for wildlife management and conservation, natal dispersal behavior is poorly understood for most animal species. This is partially due to the brevity and complexity of the phenomenon which varies among species and individual. For many organisms, a common trend is that natal dispersal occurs once in a lifetime but consists of three components: 1) a decision to leave the natal site, 2) an intermediate transient phase in which individuals search for and evaluate potential breeding sites, and 3) the selection of a breeding site (Clobert et al. 2001).

To better understand natal dispersal behavior, data are typically gathered by capturing and marking juveniles at their birth sites and then attempt to recapture them at a breeding site (Bowler and Benton 2005). Mark-recapture data provides information about the straight line distance between the natal site and the selected breeding site. However, some individuals engage in extensive exploratory forays when prospecting for potential breeding sites prior to the final dispersal event (Waser 1985, Reed et al. 1999, Norris and Stutchbury 2001). During this transient phase of dispersal, prospecting individuals are likely assessing the surrounding environments and social cues to evaluate breeding sites for potential reproductive success (Ward 2005). Mark-recapture data do not capture prospecting movements or how organisms react to spatially complex landscape mosaics between resources.

There are numerous techniques, including direct observations, radio or satellite tracking, and florescent powder tracking, that can be used to record more geographically detailed information on the route taken by animals as they disperse through the landscape. Radio telemetry is perhaps the most powerful of these methods because it allows animals to be located and observed during the animals elusive movements. Although noted drawbacks, especially for tracking small mammals and bird species, include creating transistors and batteries compact and light enough to allow continuous transmission over long ranges without harming the animal or altering their movement behavior (Kenward 2001). Movement data obtained with radio telemetry combined with spatial environmental data can provide greater insight about how landscape characteristics influence prospecting and dispersal behaviors. For example, it is possible in this framework to estimate how landscape characteristics (e.g., vegetation type and structure) affect the probability that a dispersing individual will move through a given area. This information can then be used to map what is often called "resistance" (or its converse "permeability") which represents the degree to which a given land-cover type facilitates or impedes dispersal (Adriaensen et al. 2003).

In the absence of such information, it is typically assumed that landscape characteristics do not matter for dispersal, and Euclidean distance is used as a measure of the degree to which any two habitat patches are connected demographically. Using a well designed resistance surface, one can replace the simple Euclidean distance model with a friction-weighted distance model derived from a least-cost algorithm. The most challenging part of using a resistance surface is estimating biologically relevant values depicting how a species' movements are impeded by landscape features, known as friction values (Adriaensen et al. 2003). Due to the lack of dispersal behavior information, friction values on a resistance surface are usually created with subjectively based expert opinion (Beier et al. 2009). By incorporating environmental characteristics with a resistance surface and movement data via radio telemetry, it is possible to increase the explanatory power when estimated the connectivity between species' habitat patches in fragmented landscape and thus improve effectiveness of conservation actions.

Over 60% of the land area in the United States is privately owned (GAO 1994). Collectively, these private properties contain high wildlife diversity and provide habitat for more than 90% of the federally-protected species (Hoppe and Wiebe 2002). To ensure the persistence and recovery of federally-protected species, habitat restoration and conservation effort must focus heavily on habitat located on private property (Beatley 1996), where there is currently no legal mandate for landowners to manage habitat for wildlife protection (Bingham and Noon 1998, U.S. Fish and Wildlife Service 2003, Wilcove 2004)**.** To benefit federally-protected species on private land, incentive-based conservation program is known as Safe Harbor Program (SHP) was developed by U.S. Fish and Wildlife Service (USFWS). The USFWS strives to increase individuals' ability and willingness to move between relatively isolated and remnant habitat patches with SHP (U. S. Fish and Wildlife Service 2004). However, the USFWS has yet to verify that this approach of enhancing habitat quality with SHP sponsored conservation actions improve connectivity.

This dissertation aims to increase the effectiveness of conservation planning by evaluating how the prospecting and natal dispersal behavior of a federally-protected species, Red-cockaded woodpecker (*Picoides borealis*), is influenced by the juxtaposition of natural and human-modified land-cover characteristics. Specifically, my research addresses the following objectives:

1. To empirically estimate and validate landscape resistance surfaces for *P. borealis* dispersal using mark-recapture and radio-telemetry data (Chapter 2)
2. To determine if and how prospecting movements are guided by environmental and conspecific (i.e., social) cues during natal dispersal. (Chapter 3)
3. To combine *P. borealis* dispersal behavior with detailed data on landscape structure to estimate habitat connectivity. (Chapter 4)
4. To evaluate if *P. borealis* connectivity is positively impacted by private landowners involvement in SHP. (Chapter 5)

For this research I focused on the longleaf pine (*Pinus palustris*) forests. There are several advantages using this ecosystem to study natal dispersal behavior, connectivity, and conservation programs. First longleaf pine forests, one of the most species-rich plant communities outside the tropics, is an extremely fragmented system with less than 3% of its original extent remaining (Frost 2006, Peet 2006). Loss and degradation of this old-growth forest has caused drastic declines many longleaf pine forest endemic species, such as the *P. borealis* which lead to its designation as a federally endangered species in 1970 (U.S. Department of the Interior 1970). Since its initial listing as a federally endangered species, *P. borealis* has been intensely studied throughout its geographic range, with several long-term monitoring projects evaluating their habitat requirements, demography, group composition, and dispersal behavior (Costa and Daniels 2004). With the available mark-recapture data and technological advances in radio-telemetry technology, it is now possible to closely examine population-level and territory-level *P. borealis* connectivity. Many federally mandated conservation and management actions have since focused on increasing the persistence of *P. borealis* populations by restoring patches of longleaf pine ecosystem throughout the southeastern United States. Most of these actions have been implemented at small spatial scales within forest patches without considering how the juxtaposition of longleaf pine forests and surrounding landscape features influence the long-term persistence of *P. borealis* populations. Understanding how *P. borealis* movement behaviors interact with natural and anthropogenic land-cover types will help inform and improve the design and implementation of future *P. borealis* conservation actions.

Chapter Summaries

Chapter 2: Beyond expert opinion: Empirical estimation and validation of dispersal resistance surfaces for Red-cockaded Woodpecker.

P. borealis dispersal behavior has been extensively studied with mark-recapture data. Little is known, however, about how natural and human-modified landscape features influence *P. borealis* prospecting and dispersal movements. In Chapter 2, I examined the interaction of dispersal behavior and landscape structure. *P. borealis* prospecting data obtained with radio-telemetry was used to assess how land-cover type and structure affects movements. This information was used to estimate resistance surface. The optimal resistance surface reflecting prospecting behavior was compared with independent mark-recapture dispersal data to determine if it enhanced our ability to predict dispersal behavior.

Chapter 3: Environmental and conspecific cues influencing Red-cockaded Woodpecker prospecting behavior.

Radio-telemetry data collected for Chapter 2 revealed that juvenile female *P. borealis* are guided by forest structure during prospecting forays. It still remains unclear if prospecting individuals rely upon social cues to evaluate the quality of potential breeding sites. In chapter 3, I examined if prospecting birds visiting territories are using not only environmental cues to guide their movements but also conspecific cues at destination territories to evaluate a territory's breeding potential. The resistance surface generated in Chapter 2 was used to represent environmental cues expected to guide prospecting movements. To evaluate if social factors influence prospecting, I assembled conspecific information, such as group composition, from banding data collected at all territories.

Chapter 4: Calibrating connectivity estimates for Red-cockaded woodpecker populations

The purpose of Chapter 4 was to estimate the connectivity of *P. borealis*. I used detailed prospecting and dispersal behavior knowledge obtained in Chapter 2 to develop an empirical estimated resistance surface. This surface was used to estimate the least-cost effective, or friction-weighted, distances between territories, which were incorporated into a graph-theory-based habitat connectivity model. The network models constructed at varying friction-weighted distances was then correlated with an extensive set of observed dispersal events, which allowed me to examine the patterns in *P. borealis* dispersal in terms of network topology. Finally, this biologically calibrated connectivity model, created by incorporating detailed dispersal ability data for the entire dispersing portion of the population, was used to identify which territories are necessary to maintain well connectivity and those where occupancy might be limited due to environmental barriers to dispersal.

Chapter 5: Evaluation of Safe Harbor Program influence on current and future connectivity: Case study of the Red-cockaded Woodpecker

The SHP is an incentive-based program initiated by the USFWS in 1995 to promote voluntary conservation actions on private property for *P. borealis* (Bonnie 1997, U. S. Fish and Wildlife Service 2004). The program has since grown to include over 20 endangered species of various taxa with habitat restoration projects covering nearly 2 million acres nationwide (Wilcove 2004). One of the goals of the SHP is to preserve habitat connectivity. In chapter 5, I used the connectivity model created in Chapter 4 to examine whether breeding territories on properties enrolled in SHP have a greater impact on connectivity than private properties not enrolled in the SHP during current environmental conditions and with predicted urban growth. I also prioritized private properties based on their value for improving *P. borealis* connectivity.

Overall Synthesis

I synthesize the results from each chapter and discuss how my research combined animal behavior, landscape ecology, and wildlife management disciplines to enhance the effectiveness of conservation biology. I then suggested future directions for integrating organisms' dispersal behavior in relation to environments to improve our understanding of habitat connectivity.

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CHAPTER 2

BEYOND EXPERT OPINION: EMPIRICAL ESTIMATION AND VALIDATION OF DISPERSAL RESISTANCE SURFACES FOR RED-COCKADED WOODPECKER

Abstract

Anthropogenic activities have drastically altered the spatial configuration of ecosystems, often with negative consequences to biological diversity and wildlife populations. For instance, populations of federally endangered Red-cockaded woodpecker (*Picoides borealis*) are dependent upon mature longleaf pine woodland, an ecosystem type that has been diminished to small scattered forest patches covering only 3% of its historical extent. The persistence of *P. borealis* populations depends upon the degree to which landscape features facilitate or impede prospecting and dispersal movements between territories in the remaining habitat patches. Relative resistance surfaces, a common method to model and predict movement in heterogeneous environments, are usually defined subjectively by expert opinion. To improve the rigor of these analyses, we introduce an empirical approach to estimate extensive large-scale resistance surfaces with species occurrence locations (territory centers and radio telemetry data) and remotely sensed data. The optimal resistance surface predicting juvenile female *P. borealis* prospecting behavior beyond territories was selected with a discrete-choice modeling approach, which allows for differences in surrounding environments and available breeding territories for each radio-tagged bird. *P. borealis* visited territories that were effectively closer based on forest structure than territories not visited within their prospecting range. The preferred forest structure contained stands with a tall canopy, minimal midstory vegetation, and a slightly positively skewed distribution of vegetation heights. Our data also suggests that a non-linear relationship between habitat preference and friction values was a better predictor of prospecting behavior than a linear transformation. The top-ranked resistance surface 25% least-cost corridors also closely corresponded to over 70% of an independent set of short-distance dispersal events. This increased knowledge of *P. borealis* prospecting behavior will help to identify areas necessary for maintaining habitat connectivity and to implement effective *P. borealis* management strategies. Further, our approach provides a framework to estimate and evaluate resistance surfaces based on species-specific responses to intervening landscape features.

Key words: Discrete-choice Models, Maxent, Natal dispersal, North Carolina, *Picoides borealis*, Prospecting, Radio-telemetry, Red-cockaded Woodpecker, Remote Sensing

Introduction

Fragmentation of natural areas has restricted many wildlife species to small, isolated patches with limited exchange of individuals between patches, thus reducing genetic diversity and increasing the extinction probability of local populations (Fahrig and Merriam 1994). An essential behavior for maintaining gene flow, population persistence, and recolonizing geographically distinct populations is an organism’s movement from its natal site to the first site where it obtains breeding status, known as natal dispersal (Greenwood and Harvey 1982). Natal dispersal consists of three components: a decision to leave the natal site, an intermediate transient phase, and the selection of a breeding site (Clobert et al. 2001). Despite the importance of natal dispersal to population ecology and ecosystem management, it remains one of the least understood animal behaviors. The dearth of knowledge on natal dispersal behavior is partially due to the brevity and complexity of the phenomenon.

Natal dispersal data are typically gathered by capturing and marking juveniles at their birth sites and then attempting to recapture them at a breeding site, known as the capture-mark-recapture (CMR) method (Bowler and Benton 2005). CMR provides information about the outcome (i.e., extent and destination) of natal dispersal events, but does not capture the transient phase when the individual is searching for and evaluating potential breeding sites. CMR study areas' finite extents and shapes also affect the accuracy of dispersal distance distribution estimates (Lahaye et al. 2001, Cooper et al. 2008). Studies only employing CMR methods to understand natal dispersal may be misleading because natal dispersal is represented as a single abrupt movement from the natal area directly to the new breeding site and neglects the distance and route an organism actually travels (Howard 1960, Nathan et al. 2003).

Greater insight into the elusive transient phase of a species' natal dispersal can be acquired through studies using radio telemetry (Nathan et al. 2003). Such studies have demonstrated that some species perform exploratory forays to potential breeding sites prior to the final dispersal event (Norris and Stutchbury 2001, Forsman et al. 2002, Gillies and St. Clair 2008). Exploratory forays, or prospecting events are potentially influenced by environmental cues guiding or impeding movements. For example, young individuals searching for breeding sites may be attracted by environmental cues similar to their natal territories (Stamps and Davis 2006) or repelled by features not associated with breeding sites (e.g., clear cuts, agricultural fields, or developments). It is important to understand how species movement behavior responds to natural and human-modified land-cover types in order to increase the effectiveness of conservation planning designed to increase population persistence and biodiversity in human dominated landscape.

Accounting for the affects of landscape structure on dispersal begins with developing ways to depict the relative resistance of different land-cover types or land uses encountered during species' movements. Each land-use type throughout a continuous gridded surface of the study area is assigned a friction value, which approximates how much that feature impedes or facilitates movement (Adriaensen et al. 2003). With this approach, the most important step when evaluating species dispersal behavior is the estimation of biologically relevant friction values (Adriaensen et al. 2003). However, due to the lack of detailed information about dispersal and movement behavior, friction values are usually defined subjectively based on expert opinion, or are converted from species habitat preferences during common daily activities, and therefore not representative of dispersal behavior (Schultz and Crone 2001, Schadt et al. 2002). Friction values derived from these routine movements may not accurately depict an individual's reaction to landscape features outside their habitat because behavior may differ during dispersal through non-habitat (Palomares et al. 2000). Moreover, only a few studies, such as Driezen and collogues (2007) and Rabinowitz and Zeller (2010), have validated friction values derived from expert opinion or daily activities with independent dispersal data.

Resistance surfaces require continuous maps of natural and human-modified land-cover types spanning large spatial extents. This obstacle can be overcome by creating regional maps of habitat and landscape features with remote sensing technology. Passive, optical sensors such as those aboard the Landsat series of satellites have been used to map various types of vegetation and anthropogenic objects (Hudak et al. 2002). Many wildlife species are also influenced by three-dimensional vegetation structure (MacArthur and Horn 1969, Erdelen 1984) which can be inferred and mapped using active sensors, such as LiDAR (Light Detection And Range). By combining spectral and LiDAR data, detailed maps can be created depicting spatial arrangement of land-use and land-cover types along with vertical forest structure at spatial extents suitable for modeling dispersal of many wildlife species (Lefsky et al. 1999, Hudak et al. 2002, Hyde et al. 2006). Thus, combining various remote sensing data can help parameterize landscape resistance to support models depicting dispersal through spatially heterogeneous landscapes.

We studied the prospecting strategies of the federally endangered red-cockaded woodpecker (*Picoides borealis*). *P. borealis* is endemic to mature longleaf pine (*Pinus palustris*) forests in the southeastern US coastal plain. The longleaf pine ecosystem has been reduced to less than 3% of its original extent, due to clearing, logging, and fire suppression (Frost 2006). High quality *P. borealis* habitat is characterized as containing a moderate density of mature longleaf pine trees, low density of small and medium sized pines, little or no hardwood midstory, and abundant diverse herbaceous groundcover (Conner et al. 2002, Rudolph et al. 2002, Walters et al. 2002). The dispersal behavior of *P. borealis* has been extensively studied with CMR methods (Daniels and Walters 2000, Kesler et al. 2010). Based on previous banding studies, it is known that *P. borealis* is a cooperative breeder that exhibits territorial behavior. Juvenile males often remain in their home territory as helpers for several years, assisting and caring for their parents' subsequent offspring (Walters et al. 1988, Walters 1990, Haig et al. 1994). In contrast, juvenile females usually disperse to new territories to obtain breeder status. Dispersal distances of *P. borealis* exhibit a right-skewed distribution, with most juvenile females dispersing less than 3.5 km and a small proportion dispersing distances as high as 31 km (Walters 1990, Kesler et al. 2010). Previous CMR research suggested that *P. borealis* acquire information about surrounding territories using extra-territorial forays before the final dispersal event (Pasinelli and Walters 2002). Radio telemetry data has confirmed juvenile female *P. borealis* conduct prospecting behavior with extensive forays from their natal territory before settling on a single breeding site (Kesler et al. 2010).

Despite the extensive *P. borealis* studies, little is still known about how natural and human-modified landscape features influence *P. borealis* prospecting and dispersal movements. Recently, remote sensing technology has been used to identify and evaluate *P. borealis* habitat characteristics (Smart 2009, Santos et al. 2010). However, this is the first study to use remote sensing data to evaluate *P. borealis* prospecting movements and dispersal behavior in relation to surrounding land-cover characteristics. The objective of this study was to empirically evaluate which environmental characteristics, estimated with remote sensing data, create the most biologically relevant resistance surface explaining juvenile female *P. borealis* prospecting behavior. We then validated the best resistance surface model by examining if the resistance surface with the same environmental characteristics explaining prospecting movement can also increase our ability to predict dispersal behavior.

Methods

Study Site

This study was conducted in the Sandhills ecoregion of North Carolina (Griffith et al. 2007), within a 2,388 km^2 area centered on two military installations, Fort Bragg and Camp Mackall (79°12'12"W 35°7'31"N). This region contains rolling topography and deep fluvial sandy soil interdigitated with alluvial clays in bottomlands (Peet 2006). The average elevation in the study area is 89 m. Historically, the prevailing vegetation type throughout the Sandhills ecoregion was the fire-dependent longleaf pine forest, characterized by an open canopy with minimal hardwood midstory and dense herbaceous understory vegetation (Frost 2006, Peet 2006). Currently, the dominant vegetation types are comprised of cropland, pasture, and woodland (Griffith et al. 2007). The remaining evergreen forests are primarily composed of mixed-pine species (longleaf pine, loblolly [*P. taeda*], shortleaf [*P. echinata*], and pond pine [*P. serotina*]) in second-growth forest (Griffith et al. 2007). The largest tracts of federally owned longleaf pine ecosystem in North Carolina are located on Fort Bragg and Camp Mackall (Britcher and Patten 2004). These federal properties also include over 70% (n = 437) of the 604 established *P. borealis* territories located in the study area.

Overall Approach

We captured the varying land-cover characteristics expected to influence *P. borealis* prospecting and dispersal movements by combining known *P. borealis* locations with several types of land-cover and remote sensing data (Figure 2.1). We iteratively increased the complexity of land-cover to evaluate which remote sensing data provided the most biologically relevant resistance surface to explain juvenile female *P. borealis* prospecting behavior. The simplest landscape model contains four general land-cover classes while the most complex model has additional variables depicting horizontal vegetation patterns and vertical forest structure.

Since *P. borealis* location data should reflect land-cover characteristics that facilitate movements, we can assume that resistance surface is inversely related to habitat suitability. Therefore, we generated a habitat suitability models with a maximum entropy modeling approach using a machine-learning algorithm that predicts a species' geographic distribution based on locations of known occurrences and layers of environmental data (Elith et al. 2006, Phillips et al. 2006).

For many species habitat suitability grids are converted into resistance surface with a single function, such as linear or inverse functions (Ferreras 2001, Singleton et al. 2004, Richard and Armstrong 2010). However, there is no overwhelming reason to assume that friction values for dispersal are linearly or inversely related to habitat preferences. Therefore, we tested the sensitivity of the relationship between habitat suitability and friction values for the prospecting *P. borealis*.

The maximum entropy model with the most variables tend to have the most accurate habitat suitability map, we used an information criterion approach based on maximum likelihood modeling to determine the most parsimonious habitat suitability model that best explains *P. borealis* prospecting movements to nearby territories. In addition, this approach allows us to evaluate which occupancy data and which relationship between habitat suitability and resistance surface best fits observed movements (Figure 2.1).

Within likelihood modeling family we also selected discrete-choice modeling framework to account for individual variation in available territories. Studies that evaluate a species search behavior in relation to resource availability, such as food and nesting sites, usually assume that all resources in the study area are equally available to all individuals in the population regardless of the species' dispersal ability (Manly et al. 2002, Selonen and Hanski 2006). Since the maximum distance between territories in our study area is over 70 km and most female *P. borealis* disperse less than 3.5 km (Kesler et al. 2010), all breeding territories in our study area are not easily accessible to each of the prospecting females. In addition, each fledgling emerging from its natal territory is surrounded by a unique set of environmental features that potentially influencing prospecting behavior.

Finally, we evaluated the performances of the resistance surface with independent dispersal data by assessing whether a birds' final dispersal destination was more often within the least-cost corridor than were other territories not chosen at similar geographic distances from the natal territory (Figure 2.1).

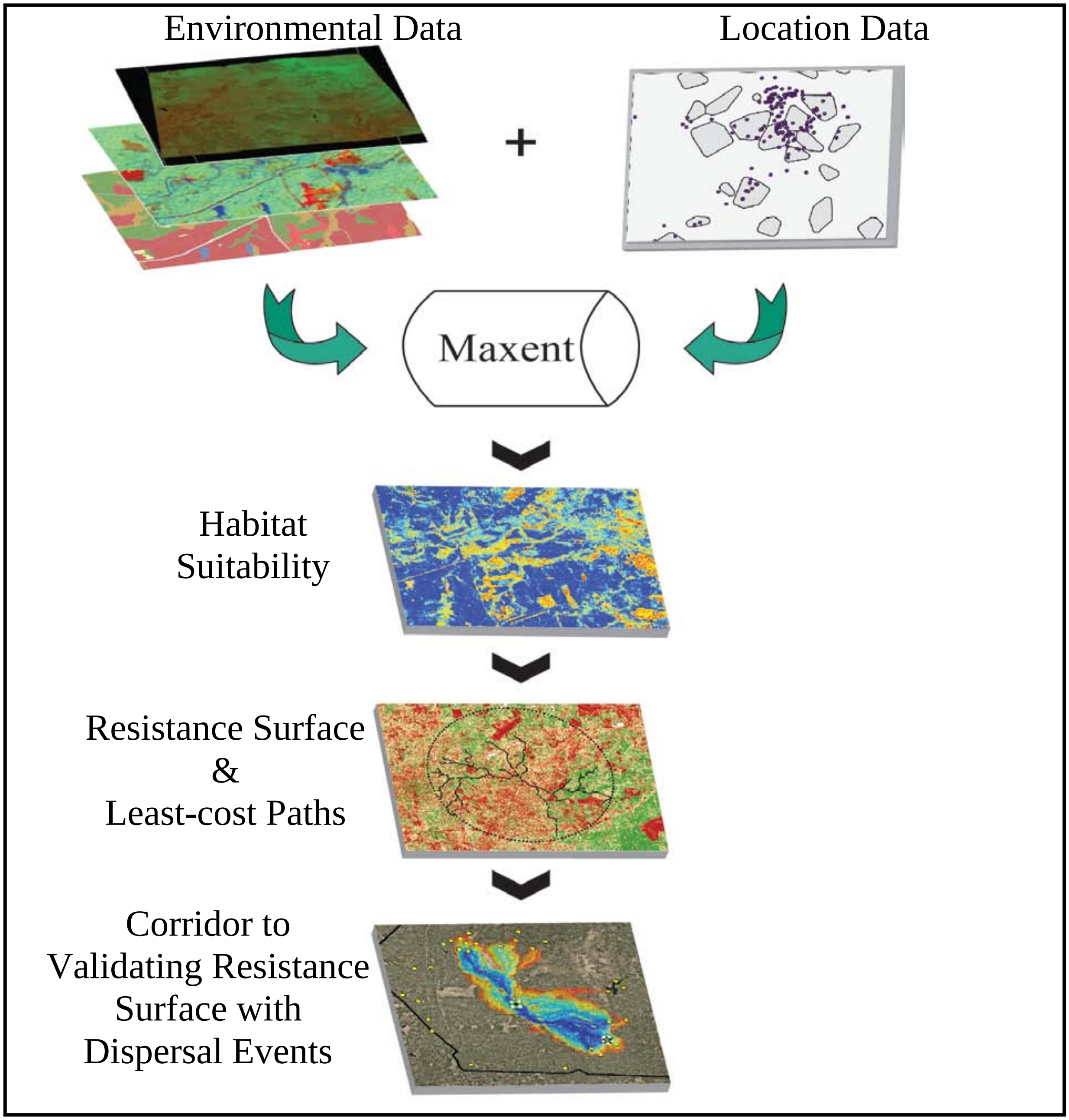

Figure 2.1 Flow chart describing the methods used to evaluate varying environmental data expected to influence Red-cockaded woodpeckers (*Picoides borealis*) prospecting and dispersal movements.

DATA

Radio Telemetry – In spring (March – May) 2006, 18 juvenile female *P. borealis* that had not yet dispersed from their natal territories were captured in their roosting cavities and fitted with a 1.4 g transmitter glued to the base of 2 tail feathers (BD-2, Holohil Systems Ltd., Ontario, Canada). Theses birds were tracked for the life of their radio transmitters (~ 9 wks) on the western portion of Fort Bragg, which contains the largest unfragemented tracts of longleaf pine forest on the property. In order to evaluate how *P. borealis* movements are affected by human-modified landscape features, we radio tagged and tracked an additional 16 individuals during 2007 in the eastern section of Fort Bragg, which consists of highly fragmented forest surrounded by urban and agricultural land use.

We attempted to locate radio-tagged woodpeckers daily. Radio-tagged birds were ordered in a list by geographic location, and then a single individual was randomly selected to be the first daily observation. Animals were located using signal strength and direction with a receiver (R-1000, Communication Specialist, Inc. Orange, CA, USA) and a 3-element Yagi directional antenna (Wildlife Materials, Inc., Carbondale, IL, USA) When an individual was located outside its home territory we recorded a Universal Transverse Mercator (UTM) coordinate using a hand-held Garmin® global positioning system unit (GPS; Olathe, KS, USA). Based on the telemetry data, we calculated the number of days a bird visited a territory (Frequency of Territory Visits). When possible the territory visited for each foray was defined based on intra-species interactions during extra-territorial movements. In the absence of intra-species interactions, the visiting territory was defined as the closest territory within 500 m of the GPS location. Foray distances were approximated using the linear distance between the roosting site and the visited territory, and we defined each individual's prospecting range as the maximum foray distance traveled from the roosting site.

Environmental Data

Categorical Land-Cover Classification – Fort Bragg and Camp Mackall were classified into four land-cover classes (longleaf pine, other non-longleaf pine evergreens (predominately loblolly pine [*P. taeda*], hardwood, and non-forested [herbaceous, developed, and water]) derived from stand-based Forest Inventory Analysis Data collected in 2001. The same land-cover classes were used off the military installations, but for these areas we used the U.S. Geological Survey GAP Analysis Program land-cover database (Gap, Jennings 2000).

Landsat –Two Landsat-5 Thematic Mapper (TM) images (WRS2 Path16, Row 36) collected 12 December 2006 and 5 May 2007 were chosen to represent leaf-off and leaf-on conditions, respectively, which will allow differentiation of evergreen and deciduous canopies. The images were georeferenced to < 1-pixel root mean square error (RMSE) and atmospherically corrected to estimates of surface reflectance (Sexton 2009). These reflectance values were used to compute three variables to determine if *P. borealis* responds to environmental cues related to vegetation composition.

The first variable mapped was mature evergreen forest by using the ratio of near-infrared (0.75 to 0.90 μm, TM band 4) to middle infrared radiance (1.55 to 1.75 μm, TM band 5) of the December image. This ratio, known as the Structural Index (SI, Kushla and Ripple 1998), is a good predictor of stand age and an indicator of forest succession characteristics (e.g., differentiating between mature and old-growth) for conifer forests (Fiorella and Ripple 1993).Young forest stand ages are positively correlated with the infrared reflectance (TM band 4) due to increased amounts of greenleaf biomass with forest age (Fiorella and Ripple 1993) while the middle infrared reflectance (TM band 5) has a strong negative relationship with stand age due to increased shadows produced by variable heights in developing stands (Wulder et al. 2004). Strong reflectance values for TM bands 4 and 5 correspond to young forest stands with low SI values. Mature longleaf pine forest stands containing minimal understory hardwood vegetation and sparse forest canopy will have higher SI values.

We created two additional variables from the Landsat image bands by transforming the reflectance values into composite bands with the Tasseled-Cap transformation (Crist and Cicone 1984). The Tasseled-Cap transformation is a linear data rotation designed to capture brightness, greenness, and wetness of plant canopies in the first composite band (Crist and Cicone 1984). We used the greenness band (Band 2) which is correlated with the amount of photosynthetically active canopy present. The difference in greenness between the two dates (May minus December) was used to map hardwood forest. Since *P. borealis* avoid hardwood forest for nesting habitat (Wood et al. 2008), we hypothesized that the presence of hardwood forest would impede dispersal behavior. We also evaluated if the spatial heterogeneity of summer greenness values influenced *P. borealis* movements by calculating the standard deviation within a 3 x 3 pixel window (8,100 m^2 area) centered on each pixel. Low standard deviation of greenness indicates cells situated in large homogenous patches far from forest edges. In contrast, high standard deviation values denote cells in small segments of forest surrounded by non-forested land-cover features (i.e., agricultural fields). We expected that cells with low spatial variation in the 3 x 3 pixel window would facilitate dispersal movements.

LiDAR – The LiDAR data were collected during leaf-off canopy conditions from 31 December 2000 to 18 February 2001 by engineering and surveying firms subcontracted by the state of North Carolina. The flight paths of two subcontractors overlapped our study area with varying sample density and flight altitude. The average ground spacing between LiDAR postings ranged from 2 - 2.25 m, flight altitude ranged from 914 - 1676 m, and the elevation calibration ranged from 9 - 12 cm elevation RMSE. The raw LiDAR data containing three-dimensional coordinates of laser hits were converted to raster format with Fusion software (McGaughey 2008). In Fusion, the height from the LiDAR points to the ground was calculated with digital elevation models from the North Carolina floodplain mapping program. The LiDAR points referenced with the elevation model were used to estimate seven forest structure variables at a 30 x 30 m resolution to correspond with the Landsat raster. Within the 30 m cells, the average number of LiDAR points was the 289 (SE = 0.13, range = 4 – 10,324).

Ideally, *P. borealis* prefer old (> 100 years) longleaf pine trees for nesting and foraging (Conner et al. 1994, Wood et al. 2008). When longleaf pine trees greater than 100 years old are not available, *P. borealis* will nest and forage on longleaf pine trees greater than 60 years old and over 20 m tall while avoiding trees less than 60 years old (U. S. Fish and Wildlife Service 2003). However, if longleaf pine trees greater than 60 years old are not present, *P. borealis* may use longleaf pine trees between 30 and 60 years old which usually range from 13 to 20 m tall, (Platt et al. 1988, U. S. Fish and Wildlife Service 2003). *P. borealis* also tend to avoid forested areas with dense hardwood understory and midstory vegetation (Walters et al. 2002, Wood et al. 2008).

The first four variables estimated with LiDAR data were percent cover in each of these four biologically relevant distinct height classes (1-8 m, 8-13 m, 13-20 m, and greater than 20 m). In addition, we estimated maximum and median vegetation heights at a 30 m resolution. In order to represent the overall forest structure in a single variable, we calculated skewness of vegetation heights. Recently, Smart (2009) applied skewness of vegetation height distribution to correlated vertical forest structure with high quality *P. borealis* habitat. A negatively skewed distribution of vegetation heights should indicate dense forest, such as plantations or dense hardwood forests, with few canopy gaps since the greatest densities of returns come from the canopy. A forest with an open canopy and minimal midstory vegetation, such as mature longleaf pine forest (Peet 2006), should represent as a positively skewed distribution of vegetation heights with a small but consistent density of returns depicting the canopy with the majority of the returns reaching the herbaceous vegetation in the understory.

MODELS

Maxent –Habitat suitability maps were derived from remotely sensed environmental variables based on *P. borealis* prospecting movements with a maximum entropy modeling approach via Maxent software (Version 3.3.1, Phillips et al. 2006). Maxent requires two types of input data, grids with environmental variables and the coordinates of species occurrences. Two separate sets of Maxent models were created to differentiate the environmental cues associated with breeding sites versus prospecting movements (Figure 2.1). To characterize environmental conditions at breeding sites we used territory centers as occurrence data (n = 604). In contrast, environmental conditions associated with prospecting movements were identified by creating habitat suitability models using all non-natal telemetry locations (n = 1710). For each type of occurrence data, we compiled five different sets of remote sensing derived environmental data with increasing in complexity from simple discrete land-cover maps to the land-cover class combined with all ten remotely sensed environmental variables. The simplest representation of the environment employed a land-cover map of four classes (longleaf pine, non-longleaf pine evergreen species, hardwood, and non-forested). To determine if vegetation composition influenced prospecting movements we created a habitat suitability map using the three Landsat-derived variables (SI, winter greenness, and standard deviation of greenness). Three-dimensional forest structure was represented with seven variables derived from the LiDAR data. We then combined the Landsat and LiDAR data to produce a habitat suitability model. The final and most complex habitat suitability model included the four discrete land-cover classes and all ten remotely sensed environmental variables.

Each set of occurrence data was randomly divided into training (75%) and testing (25%) points. To account for variation in training and testing data sets, we used bootstrapping with 10 replicate samples with replacement for all of the Maxent models. We used jackknifing to estimate the relative contribution of the predictor variables in each model. The model's performance was evaluated with Area Under the Curve (AUC) of a Receiver Operating Characteristic (ROC) plot. The AUC in Maxent evaluates the performance of the model based on true-positive accuracy assessment, which is the ratio of cells correctly classified to the total number of cells classified. The AUC values range from 0 (habitat predictions worse than random) to 1 (perfect prediction of habitat), with 0.5 indicating random classification. Maxent produces a raster estimating logistic probability of habitat suitability for each cell (Phillips and Dudik 2008). Probability values near one indicate the most suitable habitat conditions while unsuitable habitat is indicated by values close to zero.

Friction-weighted Distance – Friction-weighted distance is defined as the minimum cumulative cost from a source to a given site in the landscape (Adriaensen et al. 2003). In this study, the source locations are the radio-tagged *P. borealis* roosting territories. Destination points are defined as all territories within prospecting range of 6 km, the 95th percentile of the observed foray distance from roosting sites (Kesler et al. 2010). To test various functions between habitat suitability and friction values we slightly adjusting the relationship between friction values and habitat suitability with a wide spectrum of possible non-linear relationships (Figure 2.2). For each resistance surface, we converting Maxent's habitat suitability values (h) into friction values (f) with the function:

$$f = 100 - 99\frac{1-\exp(-ch)}{1-\exp(-c)}.$$

A rescaling constant, c, was included in the above function to vary the relationship between habitat suitability (h) and friction values (f). We selected seven rescaling values (c), ranging from 0.25 to 16 (Figure 2.2), to produce a broad range of curves to evaluate which relationship between habitat suitability and friction values best predicts *P. borealis* reaction to landscape features. A range of friction values from 1 to 100 was used, where the lowest value (1) is assigned to the most suitable habitat (Maxent suitable habitat $h = 1$) and the highest value (100) is assigned to the least suitable habitat (Maxent suitable habitat $h = 0$). By selecting a minimal value of 1 for the resistance surface, the friction-weighted distance in the highest quality habitat has minimal cost of movement and is equivalent to Euclidean distance. For each of the ten habitat suitability models and seven rescaling constants (Figure 2.2), we generated 70 resistance surfaces. For each resistance surface, a cost distance model was used to calculate the friction-weighted distance of the least-cost path from each of the radio-tagged *P. borealis* roosting territories to all possible destination territories within each individual's prospecting range.

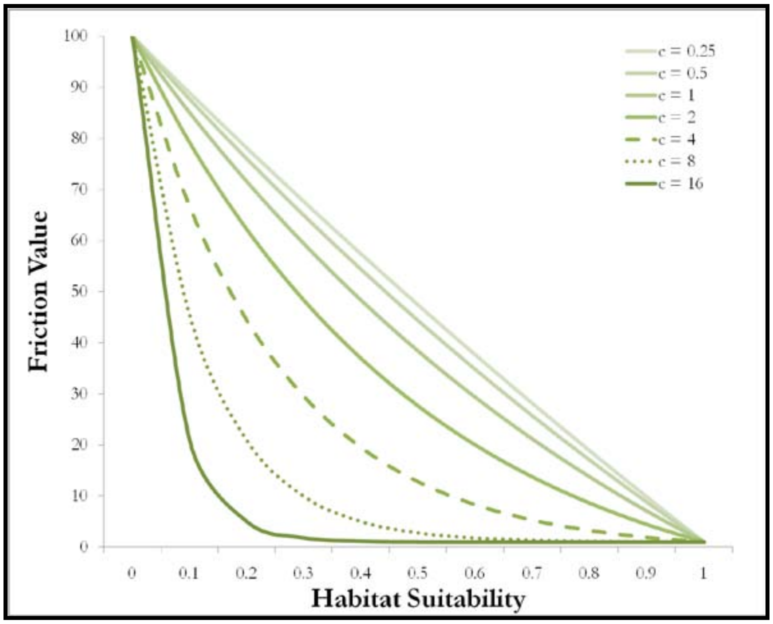

Figure 2.2 The seven curves used to rescale habitat suitability values into friction values. The dash and dotted curves produced the top-ranked and second-ranked predictive rescaling for prospecting behavior, respectively.

ANALYSIS

Discrete-Choice – Discrete-choice analysis was used to determine the best set of remote sensing variables for representing *P. borealis* prospecting movements, while accounting for variation in available territories and surrounding environmental features. The choice set for each individual was defined as all territories within its 6 km prospecting range. Our discrete-choice analysis evaluated *P. borealis* response to landscape features during prospecting by comparing friction-weighted distance from the natal territory to all territories in the choice set for each of the 70 resistance surfaces. In addition, these models were tested against Euclidean distance in a featureless landscape. The response variable in the discrete-choice models was the frequency of territory visits during observed prospecting movements. The likelihood of a bird visiting a territory within its prospecting range for each model was computed and the best predictive model was selected based on Akaike's Information Criterion adjusted for small sample sizes (AICc, Burnham and Anderson 2002). We also computed the AICc weight (ω), which represents the weight of evidence in favor of a model in relation to all the models in the set (Burnham and Anderson 2002). All discrete-choice modeling was conducted with the R package Survival (Version 2.11.0, R Development Core Team 2010).

Model Validation – We evaluated the best resistance surface using an independent dataset of observed juvenile female dispersal events born in 2005 (*n* = 57) and 2006 (*n* = 39). We created corridors using the model derived from each dispersing individual. The corridor function adds the accumulated cost from all least-cost paths between the natal territory and all available territories. For each dispersal event, available territories were defined as all territories with similar geographic distance (within the 25th percentile) from the individuals' natal territory to the observed dispersal destination territory (Figure 2.3). The threshold distance for natal territory was set as maximum distance any juvenile female was observed dispersing from the natal territory during all the years of banding data. Within this analysis we assessed if *P. borealis* short-distance dispersers interact with the environment differently than long-distance dispersers. We defined the long-distance threshold at 6 km, the 95th percentile of the observed foray distances from roosting sites (Kesler et al. 2010). The overall performance of the resistance model was evaluated for short and long-distance dispersers by calculating the percentage of individuals that dispersed to territories within the 25% least-cost corridor for each resistance surface (Figure 2.3).

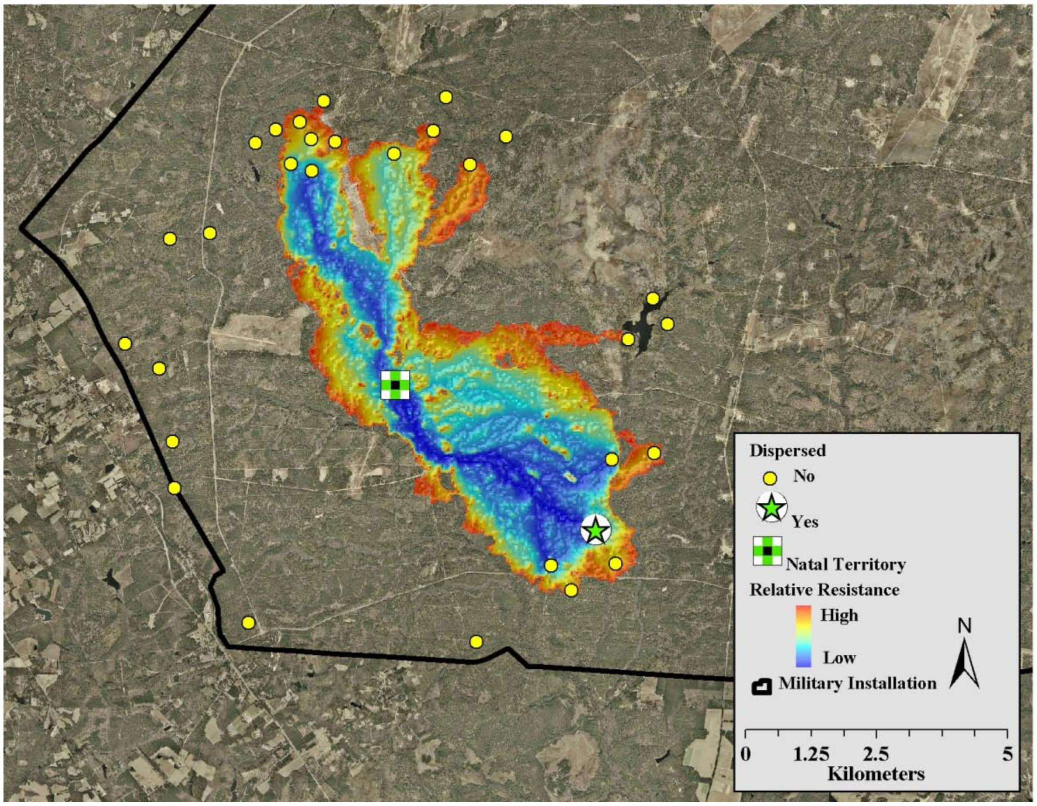

Figure 2.3 An example of a juvenile female Red-cockaded woodpecker (*Picoides borealis*) that dispersed to a breeding territory within the 25% least-cost corridor derived from the top-ranked resistance surface.

Results

Radio telemetry – Radio tracking effort in 2006 and 2007 produced an average of 40 (SE = 4.88) and 121 (SE = 25) locations per individual, respectively. The majority of these locations (68.1% for 2006 and 78.2% for 2007) were defined as prospecting movements (i.e., away from the roosting territory). We observed prospecting individuals conducting 282 and 533 territory visits in 2006 and 2007, respectively. The number of visits ranged from 1 to 23 territories per female, and 49% of the individuals visited a non-natal territory multiple times. The maximum prospecting range from a roosting site was 8.9 km ($\overline{X}$ = 3.54, SE = 0.28).

Maxent Models – The simplest habitat suitability model based on four land-cover classes did not reach an AUC value > 0.75 (Figure 2.4), which is considered an basic threshold for useful Maxent models (Elith et al. 2006) All other habitat suitability models reached AUC values > 0.85, with AUC increasing with complexity of remote sensing data (Figure 2.4). The combination of Landsat and LiDAR data increased the Maxent model's AUC by 5% relative to either data source alone. The most complex habitat suitability model (discrete land-cover data, Landsat and LiDAR data) contained a slightly higher AUC (Figure 2.4). Maxent models trained with environmental data at breeding sites had slightly greater AUC values than models trained with environmental variables at prospecting locations (Figure 2.4).

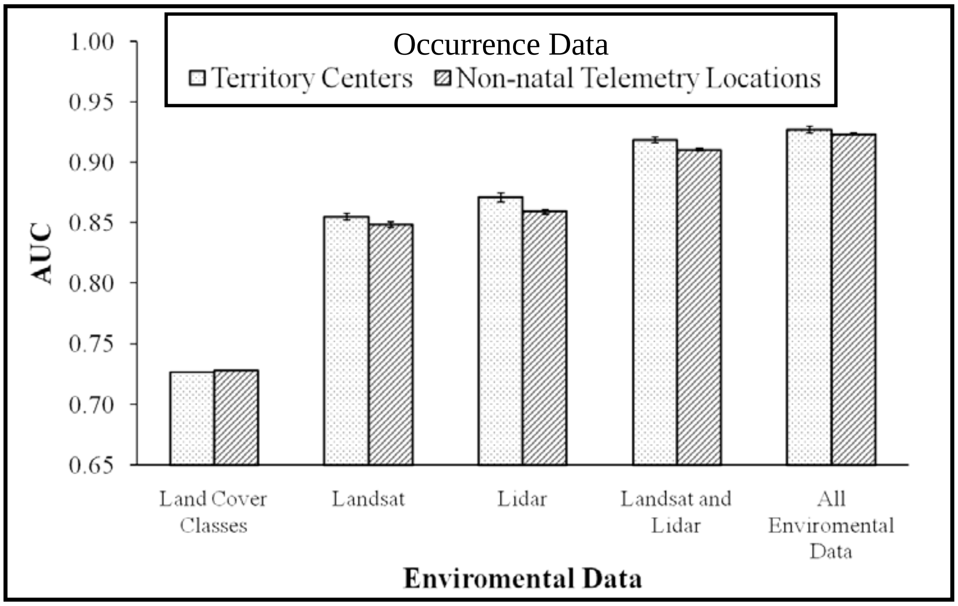

Figure 2.4 The Area Under the Curve (AUC; +/- SE bars) for each Maxent model.

Discrete-choice Analysis – Euclidean distance was a very poor predictor of prospecting behavior (Table 2.1). The resistance surfaces derived from the four categorical land-cover classes slightly increased our ability to predict prospecting behavior (model ranked 48 out of 71, Table 2.1). The top 17 models, according to AICc, explained prospecting behavior with environmental data recognized from non-natal telemetry locations.

The four top-ranked models relating prospecting behavior to environmental variables included only forest structure parameters from LiDAR data (cumulative AICc weight > 0.999, Table 2.1). The top-ranked discrete-choice model had a moderate rescaling constant (*c* = 4, Table 2.1). This rescaling constant suggests that the relationship between forest structure and the friction values on a resistance surface's is best represented with a non-linear function. This model also suggested a negative relationship between probability of visiting a territory and friction-weighted distance ($\beta = -7.44 \times 10^{-5}$, SE = 1.347×10^{-5}, $p < 0.001$). That is, within the prospecting range, territories with greater friction-weighted distances from the roosting site were less likely to be visited during forays.

Table 2.1 The ranking of discrete-choice models describing juvenile female Red-cockaded woodpecker (*Picoides borealis*) prospecting behavior in relation to habitat suitability models constructed with environmental and occurrence data (in Maxent) along with varying friction values converted with rescaling constants (*c*) in the Sandhills region of North Carolina.

	Maxent Model					
Rank[a]	**Occurrence Data**	**Environmental Data**	**Rescaling Constant**	**AICc[b]**	**ΔAICc[c]**	**ω[d]**
1	Telemetry	LiDAR	4	5478.58	0.00	0.70
2		LiDAR	8	5480.34	1.76	0.29
3		LiDAR	2	5488.05	9.47	0.01
4		LiDAR	1	5499.41	20.83	0.00
5		LiDAR + Landsat	2	5509.09	30.51	0.00
6		LiDAR	0.25	5509.69	31.12	0.00
7		LiDAR	0.5	5512.35	33.76	0.00
8		LiDAR + Landsat	1	5513.83	35.25	0.00
9		LiDAR	16	5519.42	40.84	0.00
10		LiDAR + Landsat	4	5520.48	41.89	0.00
15	Telemetry	All Environmental data	0.25	5554.00	75.42	0.00
18	Territory	Landsat	16	5563.02	84.44	0.00
48	Telemetry	Land-cover Classes	0.5	5607.29	128.71	0.00
56	Euclidean Distance (m)			5620.01	141.43	0.000

[a] Rank is out of the 71 models, other models in the shaded box with lower rank are identified for purpose of discussion

[b] Akaike's Information Criterion adjusted for small sample size.

[c] Difference in the value between AICc of the current model and the value for the most parsimonious model.

[d] Relative likelihood of the model given the data and set of candidate models (model weights sum to 1.0).

Resistance Surface – By combining the maximum entropy and discrete-choice modeling approaches we were able to evaluate how specific vegetation structure influences movement behavior. For example, forest structure parameters with the greatest contribution in the top-ranked resistance surface were percent cover of the midstory vegetation (1 – 8 m), maximum vegetation height, and the skewness of the vegetation height distribution for both LiDAR sensors (Figure 2.5). While LiDAR-derived median vegetation heights and percent cover classes greater than 8 m contribute less than 15% to the forest structure habitat suitability model. Prospecting individuals tend to avoid areas containing even small percentages of midstory cover (Figure 2.6). The forested areas with the least resistance for *P. borealis* prospecting movements contained maximum tree heights ranging from 13 to 25 m (Figure 2.5). The probability of an individual prospecting through a forest also increased when the distribution of vegetation heights had a slight positively skewed distribution.

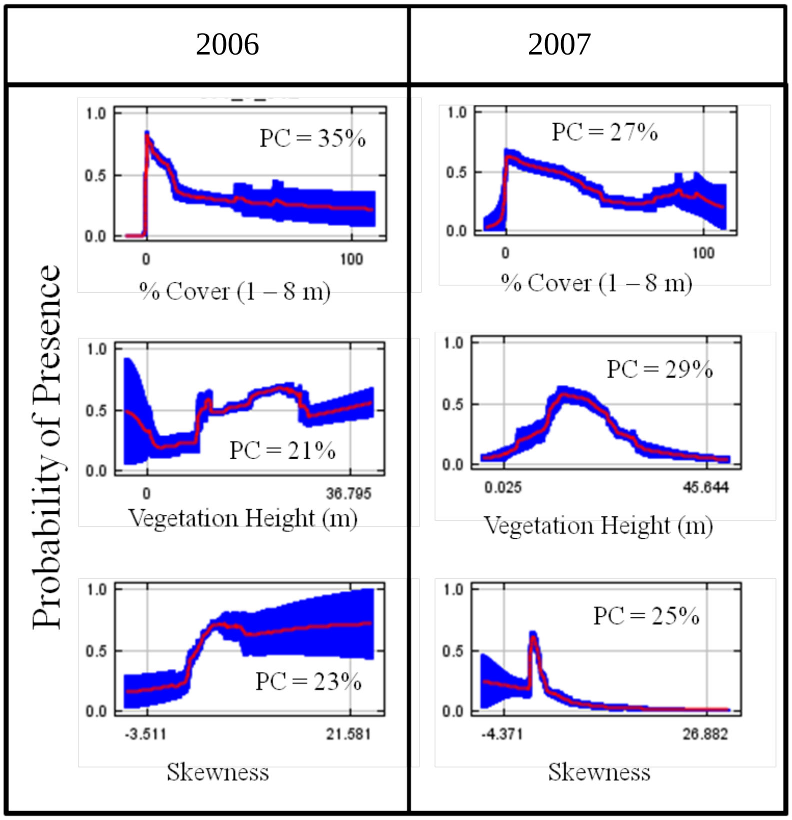

Figure 2.5 The probability of Red-cockaded woodpeckers (*Picoides borealis*) presence based on average habitat suitability (red line) and a standard error (blue shading) based on forest structure variables located at non-natal telemetry locations during 2006 and 2002007 in the Sandhills of North Carolina. The percent contribution (PC) is also provided for each variable in the top-ranked habitat suitably model.

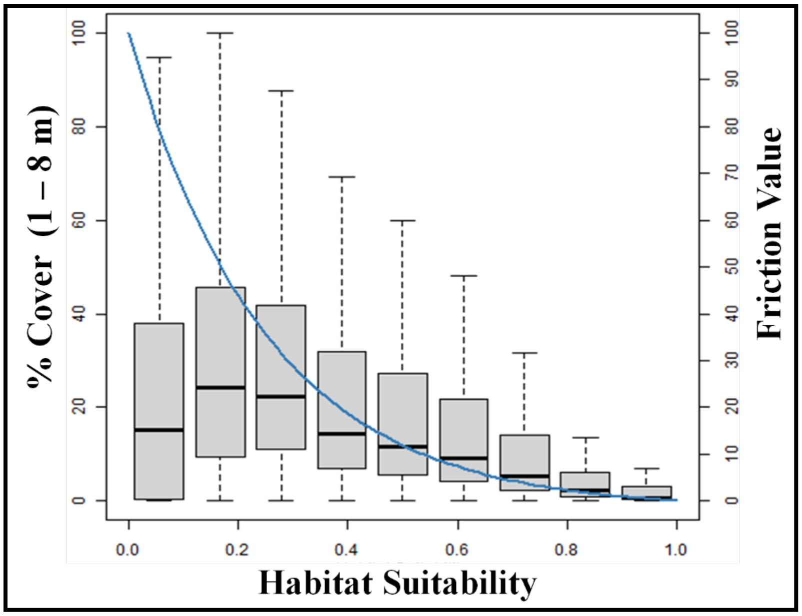

Figure 2.6 Box plot of percent midstory cover (1 to 8 m) in relation to habitat suitability and the friction value in the top-ranked model predicting Red-cockaded woodpecker (*Picoides borealis*) prospecting movements. The line indicates the top-ranked rescaling constant explaining the relationship between friction values and habitat suitability.

Model Validation –Very few individuals in our independent validation dataset dispersed to territories located in corridors with high (> 50th percentile) cumulative cost distances, even when they were at similar straight-line distances from the natal territory as territories with lower cost-distance (Table 2.2). For both years of independent dispersal data, over 60% of the individuals selected territories within the 25th percentile least-cost corridor (Table 2.2). There was a sharp decline in the number of dispersals to territories at greater friction-weighted distances from the natal territory even though the territories were located on wider corridors. Greater than 75% short-distance dispersal events for both years fell within the 25% least-cost corridor (Table 2.2). Long-distance dispersal prediction accuracy was lower with less than 50% of dispersal events fell within the 25% least-cost corridor.

Table 2.2 The percentage of short-distance (SDD) and long-distance (LDD) dispersers that settled into territories within four corridor widths, determined by least-cost percentiles from a resistance surface based on non-natal telemetry locations, forest structure and a moderate rescaling constant ($c = 4$).

Percentile Corridor	**SDD**	**LDD**	**Total**
0 – 25	76 %	47 %	65 %
25 – 50	21 %	39 %	28 %
50 – 75	3 %	11 %	6 %
75 – 100	0 %	3 %	1 %

Discussion

Juveniles prospecting for breeding sites may have limited or no experience with environmental features located outside their natal area (Ward 2005, Stamps 2006). Thus, we expected that individuals searching for suitable breeding habitat would seek out environments similar to their natal habitat to quickly and efficiently locate and evaluate reproductive potential of breeding sites (Davis and Stamps 2004). However, environmental characteristics at the center of active territories (in contrast to data from telemetry locations) did not strongly predict *P. borealis* prospecting movements (Table 2.1). Instead, *P. borealis* prospecting movements were strongly influenced by forest structure encountered away from the home territory. *P. borealis* preferred to pass through forests stands with an average canopy height of approximately 20 m, and less than 20% midstory cover (Figure 2.5). Movements were moderately reduced through forested areas with abundant midstory cover and strongly inhibited by open or developed areas (Figure 2.5).

The minimal explanatory power of environmental characteristics at breeding territories may be partially due to the limited ability of LiDAR data to resolve very specific breeding habitat characteristics, such as nesting trees ranging from 80 to 120 years old

(Hooper et al. 1991, Rudolph et al. 2002, Walters et al. 2002, Jackson and Jackson 2004). For many tree species, age is strongly correlated with heights derived from LiDAR data (Lefsky et al. 2002, Hyde et al. 2005, Goetz et al. 2010). However, longleaf pine age is a better predictor of *P. borealis* breeding habitat than height because the correlation between age and height rapidly diminishes when longleaf pine trees reach 60 years old (Platt et al. 1988, Zwicker and Walters 1999). A habitat specialist breeding sites may not be adequate to model a species reaction to a wide variety of landscape characteristics located away from the breeding site. The resistance surface could become similar to a binary map where all of the specific breeding habitat landscape features are assigned very low friction values and any landscape feature not similar to breeding sites would be assigned very high friction values. Therefore, a resistance surface models derived from breeding sites would not capture the subtle variation between high quality breeding habitats and environments unsuitable for breeding but nonetheless traversable by dispersing individuals.

Prospecting *P. borealis* movement behavior did correspond to habitat characteristics associated with non-natal telemetry location. These habitat characteristics matched preferences for foraging habitat. When foraging *P. borealis* prefer open forest with canopy trees at least 20 m tall and greater than 60 years old (Rudolph et al. 2002, Walters et al. 2002). In addition, *P. borealis* tend to avoid longleaf pine trees less than 30 years old and under 10 m tall (Platt et al. 1988, Hooper et al. 1991). According to the top-ranked Maxent model, prospecting individuals used areas with an average canopy height of 20 m and avoided forested areas with canopy less than 10 m high (Figure 2.5). Foraging *P. borealis* also avoid dense hardwood midstory (Walters et al. 2002, Wood et al. 2008). The positively skewed distribution matches open, mature longleaf pine forest characteristics with a low density of points consistently hitting the tall sparse canopy of longleaf pine trees while majority of the points reaching the herbaceous understory. This finding supports previous research reporting that *P. borealis* habitat quality is related to multiple forest structure characteristics and is difficult to represent with a single variable (Walters et al. 2002).

Similar to most federally listed species, limited information about *P. borealis* biology and habitat requirements was available upon listing. Over time *P. borealis* has become extensively researched throughout its geographic range with several long-term monitoring projects (Costa and Daniels 2004), resulting in intensive management practices based on this research, usually conducted in breeding territories and adjacent foraging areas (Conner et al. 2001, U. S. Fish and Wildlife Service 2003). Our results suggest that persistence of healthy *P. borealis* populations also requires management to extend beyond territories. Specifically, environments between established populations and between territories within populations should encourage *P. borealis* movements by managing evergreen forest with reduction and removal of dense midstory vegetation. These extra-territorial conservation actions will encourage the exchange of individuals between habitat patches necessary to sustain populations.

Animal movement predictions can be improved by replacing uniform landscapes with resistance surfaces (Verbeylen et al. 2003, Magle et al. 2009, Richard and Armstrong 2010). However, the choice of land-cover classes in a resistance surface can strongly influence predicted movement behavior and suggested conservation actions (Minor and Urban 2008). The choice of land-cover features represented on a resistance surface and how they impede movements are usually subjectively defined by expert opinion (Beier et al. 2009), but greater insight can be gained by evaluating observed movement data in relation to environmental features using multiple resistance surfaces with varying complexity of environmental features and a range of friction values (Ricketts 2001, Adriaensen et al. 2003, Beier et al. 2008). When we applied this approach the simplest models based on Euclidian distance or general land-cover classes performed poorly relative to more complex models created with remotely sensed data. The best resistance surface explaining *P. borealis* prospecting behavior focused only on forest structure and adding further environmental complexity to this model did not improve performance (Table 2.1). Verbeylen and colleagues (2003) reported a similar trend in data complexity when explaining red squirrel (*Sciurus vulgaris*) movements across a resistance surface with a similar parsimony approach (AIC model selection). The moderately complex landscape predicted red squirrels' dispersal better than the most complex resistance surface.

The friction values on a resistance surface are usually converted from habitat suitability values with a single (typically linear) function (Ferreras 2001, Singleton et al. 2004, Richard and Armstrong 2010). However, Magle and colleagues (2009) obtained a better estimate of connectivity by adjusting the relationship between friction values and habitat suitability with an exponential term. Our data also suggests that a non-linear relationship between habitat preference and friction values was a better predictor of prospecting behavior than a linear transformation. We obtained greater insight into how *P. borealis* react to landscape features during prospecting movements by comparing multiple transformations between habitat suitability and resistance surface. According to the best function between habitat quality and friction values, dispersal habitat greater than 0.7 does not strongly influence prospecting movements because the friction values vary slightly (< 4,

Figure 2.2). In contrast, habitat suitability between 0.3 and 0.6 contain a wider range of friction values (over 20 friction units).

This is the first study to estimated resistance surfaces via a maximum entropy approach. Maxent's maximum entropy algorithm estimates the species distribution by finding the maximum entropy (i.e., closest to uniform) distribution, constrained by the environmental data associated with known locations of the species (Phillips et al. 2006). There are many advantages to using this approach when creating resistance surfaces to evaluate species movements in heterogeneous landscapes. Maximum entropy is a non-parametric approach that requires presence-only data (Phillips et al. 2006, Phillips et al. 2006). In addition, Maxent software provides a logistic output model estimating the probability of presence or habitat suitability (Phillips and Dudik 2008) that can be easily converted into many different resistance surfaces. This flexibility allows researchers to evaluate small changes in movement behavior due to fine detailed landscape features within varying quality of habitat patches. In addition, the habitat suitability models are easily extrapolated beyond the observed occurrences to the extent of available environmental data.

Historically, complex suites of habitat characteristics were described and mapped using expensive, labor intensive *in situ* measurements at small spatial scales (<1 ha). Advances in remote sensing data and techniques, specifically LiDAR, have vastly improved our ability to delineate habitat at regional scales. This research expands the utility of remote sensing with animal movements to empirically estimate continuous resistance surfaces at regional scales. The empirically estimated resistance surfaces will increases our understanding of how environmental factors influencing species movement patterns and improve our ability to design management strategies, and do so in a more rigorous way than relying solely on expert opinion.

Because of the historical banding data collected in our study area, we were able to validate our top-ranked resistance surface model against an independent dataset of capture-mark-recapture dispersal events. In one of the few recent studies to validate resistance surfaces with empirical data, Driezen and colleagues (2007) correctly predicted approximately one third of hedgehogs' (*Erinaceus europaeus*) dispersal routes based on the best resistance surface, a result similar to our long-distance dispersal results. However, most of the short-distance dispersing *P. borealis* selected breeding sites within the lowest 25% least-cost path created from the resistance surface. This result suggests that short-distance dispersers are strongly affected by forest structure represented in the resistance surface. Long-distance dispersers were much less consistently associated with the 25% least cost path, suggesting that they are not as strongly influenced by environmental features during dispersal, or the environmental cues affecting long-distance movements are not represented in our resistance surfaces. This is also consistent with recent empirical results showing that long-distance dispersal involves behavior (i.e., jumping) distinct from that of short-distance dispersers or forays (Kesler et al. 2010). The limited ability for the Driezen and colleagues (2007) study or our study to predict long-distance dispersal events could be due to unexamined conspecific interactions. However, explanatory power when predicting *P. borealis* long-distance dispersal events did not increase when conspecific cues were combined with resistance surface (Chapter 3). Thus, further research is required to fully understand how individual movements in fragmented landscapes connect populations (Woodroffe 2003). Improvements in landscape-level habitat information will be particularly vital for *P. borealis* management because the remaining longleaf pine forest patches are usually too small to sustain viable *P. borealis* populations.

Conclusion

A common approach to predict how natural and human-modified land covers affect animal movements is to rank land-use types according to expert opinion and published literature (Beier et al. 2009). Resistance surfaces generated from expert opinion usually assign habitat patches the smallest friction values without considering varying habitat quality. For *P. borealis*, most information available through expert opinion and published literature focuses primarily on forest characteristics within and near territories, and our study shows that movement behaviors are strongly influenced by subtle environmental changes encountered away from their natal sites. A species' reaction to landscape characteristics outside natal and breeding sites may be important when estimating friction values for a resistance surface. As a result, resistance surfaces derived solely from expert opinion may not adequately represent prospecting and dispersal behavior. Our results suggest that short-distance dispersing individuals were strongly influenced by vegetation structure and land-use activities while long-distance dispersing individuals were less affected by the surrounding environments.

This paper also provides new rigorous method to determine how habitat features influence dispersal between breeding habitats. We integrated a wide range of variables expected to influence species movement behavior derived from remote sensing data to estimate the suitability of dispersal habitat in varying environments. We then used the observed *P. borealis* movement behavior, not expert opinion, to identify which remote sensing data and resistance surface best represented the species reaction to landscape features. Resistance surfaces, like all models, are a simplified representation of part of the real world. Therefore, we validated the performance of the best resistance surface with independent dispersal data. This validation provides additional confidence in the resistance surface to represent movement behavior for future conservation efforts in fragmented landscapes.

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CHAPTER 3

ENVIRONMENTAL AND CONSPECIFIC CUES INFLUENCING RED-COCKADED WOODPECKER PROSPECTING BEHAVIOR

Abstract

The Red-cockaded woodpecker (*Picoides borealis*), is a federally endangered, cooperative breeding species endemic to the highly-fragmented longleaf pine forests in the southeastern United States. For over 30 years, *P. borealis* dispersal behavior has been extensively researched throughout its geographic range with mark-recapture monitoring projects. Only recently, radio-telemetry movement data revealed that juvenile female *P. borealis* perform complex prospecting movements, leaving and returning to their natal area many times before the final dispersal event to assess the relative quality of adjacent breeding sites. In this study we further the investigation by examining how juvenile female *P. borealis* prospecting behavior is influenced by environmental cues beyond territories along with conspecific cues at destination territories. This was accomplished with a discrete-choice modeling approach that estimated the probability of *P. borealis* visiting territories within their prospecting range. The top-ranked model showed that both environmental and conspecific cues influence *P. borealis* prospecting behavior. *P. borealis* visited territories that were effectively closer based on forest structure and that contained more fledglings and younger breeding males than territories not visited within their prospecting range. Our results suggest that persistence of healthy populations requires habitat management and conservationactions to extend beyond breeding sites and should consider complex conspecific interactions at potential breeding sites.

Key words: Discrete-choice models, LiDAR, North Carolina, *Picoides borealis,* Prospecting, Radio-telemetry, Red-cockaded woodpecker

Introduction

Knowledge of animal movement behavior is fundamental to several biological disciplines; including evolution, population ecology, and wildlife management (Andreassen et al. 2002). Yet, despite the breadth of interest in animal movement, it remains one of the most poorly understood behaviors (Sutherland et al. 2000, Clobert et al. 2001). In particular, natal dispersal behavior, when individuals leave their original home area to establish a new area (Golley et al. 1975, Greenwood and Harvey 1982), is poorly understood due to its infrequency and brevity in an individual's lifetime (Buechner 1987, Sutherland et al. 2000, Kernohan et al. 2001). Natal dispersal is also a complex behavior comprising of a decision to leave the natal site, an intermediate transient phase, and the selection of a new breeding site (Clobert et al. 2001). It is especially challenging to examine dispersal behavior for rare and federally-protected species since they can be difficult to locate within their natural environments and are subject to greater research restrictions regarding handling and direct experimentation (Thompson 2004).

Thus, natal dispersal studies rely on capturing and marking juveniles at their birth sites and then attempt to recapture them at subsequent breeding sites (Bowler and Benton 2005). More accurate insights into dispersal behavior are being obtained by attaching radio transmitters to individuals to observe their transient movements. One of the recurring findings from radio telemetry studies examining dispersal behavior is extensive exploratory forays when individuals prospect for potential breeding sites before the final dispersal event (Waser 1985, Reed et al. 1999, Norris and Stutchbury 2001). Young individuals prospecting for breeding sites may be either attracted by environmental cues similar to their natal territories (Stamps and Davis 2006) or repelled by features not associated with breeding sites (e.g., clear cuts, agricultural fields, or developments).Thus, prospecting movements can be guiding or impeding by natural and human-modified land cover characteristics within and between potential breeding sites.

Along with environmental cues, prospecting individuals may be assessing the quality of a breeding site by monitoring behaviors of conspecifics (Valone and Templeton 2002). For instance, the presence and number of conspecifics can provide information on the quality of a breeding site (Danchin and Wagner 1997, Valone and Templeton 2002, Ward 2005). A more direct index of a site's potential breeding success is the previous year's reproductive success, such as the number of young (Doligez et al. 2002, Part and Doligez 2003, Boulinier et al. 2008). Other less studied conspecific factors include characteristics of potential breeding partners (Danchin and Wagner 1997) or the likelihood of displacing a current breeder. Together, the environmental and conspecific cues acquired during prospecting movements provide public information about the quality of breeding sites (Valone and Templeton 2002). The public information obtained with prospecting movements can increase the probability of encountering and selecting highly suitable breeding sites, which enhances an individual's overall fitness (Stamps 2006). Individuals' prospecting movements may be restricted within small fragments of natural ecosystems surrounded by human-dominated land-cover types which can also limit intra-species interactions. Therefore, environmental and conspecific cues need to be examined concurrently to further advance our understanding of dispersal behavior, especially for federally-protected species.

Loss and degradation of old-growth longleaf pine (*Pinus palustris*) forests has caused drastic declines in the endemic Red-cockaded woodpecker (*Picoides borealis*), leading to its listing as a federally endangered species (U. S. Fish and Wildlife Service 2003). High quality *P. borealis* habitat is characterized as containing a moderate density of mature longleaf pine trees, low density of small and medium sized pines, little or no hardwood midstory, and abundant diverse herbaceous groundcover (Conner et al. 2002, Rudolph et al. 2002, Walters et al. 2002). *P. borealis* is a cooperative breeder that exhibits territorial behavior. Juvenile males often remain in their home territory as helpers for several years, assisting and caring for subsequent offspring (Walters et al. 1988, Walters 1990, Haig et al. 1994). In contrast, juvenile females usually disperse to new territories to obtain breeder status. Previous mark-recapture data suggested that *P. borealis* carry out extra-territorial forays (Pasinelli and Walters 2002). Recently, radio telemetry data confirmed juvenile female *P. borealis* frequently prospect from their natal territory to potential breeding territories with extensive forays before settling on a single breeding site (Kesler et al. 2010).

However, it remains unclear how individuals searching for breeding territories use available public information to guide prospecting movements and evaluate the quality of potential breeding sites. Thus, the purpose of this study was to examine how juvenile female *P. borealis* prospecting behavior is influenced by environmental and conspecific cues. Specifically, we asked if environmental cues between territories and conspecific characteristics (e.g., total group size, number of fledglings, age of breeding female, etc.) at destination territories influence prospecting movements.

Methods

Study Site

This study was conducted in the Sandhills ecoregion of North Carolina (Griffith et al. 2007) , within a 2,388 km^2 area centered on two military installations, Fort Bragg and Camp Mackall (79°12'12"W 35°7'31"N; Figure 3.1). This region contains rolling topography and deep fluvial sandy soil intermixed with clay soil (Skeen et al. 1993, Peet 2006). The average elevation in the study area is 89 m. Historically the prevailing vegetation type throughout the Sandhills ecoregion was the fire-dependent longleaf pine forest, characterized by an open canopy with minimal hardwood midstory and dense herbaceous understory vegetation (Provencher et al. 2001, Frost 2006). Currently, the dominant vegetation types are comprised of cropland, pasture, and mixed woodland (Griffith et al. 2007). The remaining evergreen forests are primarily composed of mixed-pine species (longleaf, loblolly [*P. taeda*], shortleaf [*P. echinata*], and pond pine [*P. serotina*]) in second-growth forest (Griffith et al. 2007). The largest tracts of federally owned longleaf pine ecosystem in North Carolina are located on Fort Bragg and Camp Mackall (Britcher and Patten 2004). These federal properties also include over 70% (n = 437) of the 604 established *P. borealis* territories located in the study area.

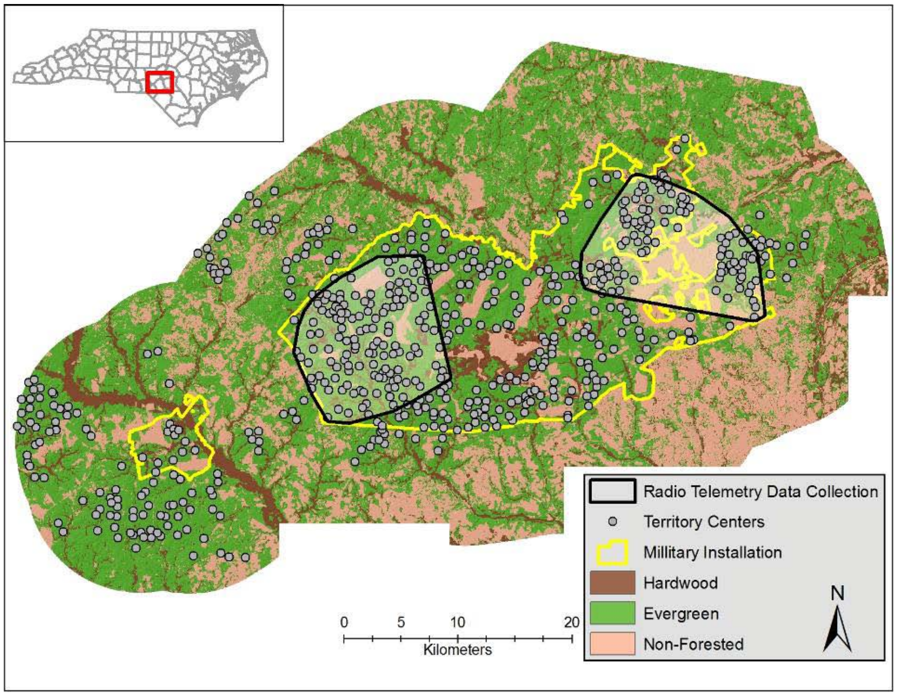


Figure 3.1 The study area extent with the center of Red-cockaded woodpeckers (*Picoides borealis*) territories and military installation boundaries. The two shaded polygons illustrate the spatial coverage of radio telemetry data collection (2006 = west, 2007 = east).

DATA

Radio Telemetry – To parameterize models that predict how public information (environmental and conspecific cues) influence prospecting behavior, we collected movement data on prospecting birds using radio telemetry. In spring (March – May) 2006, 18 juvenile female *P. borealis* that had not yet dispersed were captured in their roosting cavities and fitted with a 1.4 g transmitter glued to the base of 2 tail feathers (BD-2, Holohil Systems Ltd., Ontario, Canada). These birds were tracked for the life of their radio transmitters (~ 9 wks) on the western portion of Fort Bragg, which contains the largest unfragemented tracts of longleaf pine forest on the property. In order to evaluate how *P. borealis* movements are affected by human-modified landscape features, we radio tagged and tracked an additional 16 individuals during 2007 in the eastern section of Fort Bragg, which consists of highly fragmented forest surrounded by urban and agriculture land use (Fig.1).

Animals were located daily via homing by using signal strength and direction with a receiver (R-1000, Communication Specialist, Inc. Orange, CA, USA) and a 3-element Yagi directional antenna (Wildlife Materials, Inc., Carbondale, IL). When an individual was located outside its home territory we recorded a Universal Transverse Mercator (UTM) coordinate using a hand-held Garmin® global positioning system unit (GPS; Olathe, KS, USA). Based on the telemetry data, we calculated the number of days a bird visited a territory (Frequency of Territory Visits). When possible the territory visited for each foray was defined based on intra-species interactions during extra-territorial movements. In the absence of intra-species interactions, the visiting territory was defined as the closest territory within 500 m of the GPS location. Foray distances were approximated using the linear distance between the roosting site and the visited territory, and we defined each individual's prospecting range as the maximum foray distance traveled from the roosting site.

Conspecific Data – To evaluate if social factors influence a prospecting bird's choice of destination territories, we assembled conspecific variables from Fort Bragg Endangered Species Branch and Sandhills Ecological Institute banding data. These banding data have been collected since 1981 for *P. borealis* territories in the study area to determine dispersal events, population dynamics, and group composition (Walters et al. 1988). From the group composition data, we extracted six conspecifics variables that birds are likely to monitor when assessing potential breeding territories: 1) total group size (the number of adults and fledglings residing at the territory during the previous breeding year); 2) the number of male helpers observed during the previous breeding season; 3) the number of male helpers during the current breeding season; 4) the number of fledglings banded the previous year (a measure of reproductive success); 5) age of the breeding male during the previous breeding season (to indicate the quality of potential breeding partners); and 6) the age of the breeding female during the previous breeding season, to account for the likelihood of obtaining a breeding site by filling a vacancy after the death of a female or displacing the current breeding female. Most of the group composition and fitness variables focus on the previous year's monitoring efforts to closely correspond with information available by prospecting individuals.

Environmental Data – Light Detection And Ranging (LiDAR) data was collected during leaf-off canopy conditions from 31 December 2000 to 18 February 2001 by engineering and surveying firms subcontracted by the state of North Carolina. The flight paths of two subcontractors overlapped our study area with varying sample density and flight altitude. The average spacing between LiDAR posting ranged from 2 - 2.25 m, flight altitude ranged from 914 - 1676 m, and the elevation calibration ranged from 9 - 12 cm elevation RMSE. The raw LiDAR data containing three-dimensional coordinates of laser hits were converted to raster format with Fusion software (McGaughey 2008). In Fusion, the height from the LiDAR points to the ground was calculated with digital elevation models from the North Carolina floodplain mapping program.

The elevation referenced LiDAR points were used to estimate seven forest structure variables at a 30 x 30 m resolution which contains an average of 289 (SE = 0.13, range = 4 – 10,324) number of LiDAR points per cell. The first four LiDAR derived forest structured variables were percent cover in each of the four distinct biologically relevant height classes (1-8 m, 8-13 m, 13-20 m, and greater than 20 m, Chapter 2). In addition, maximum and median vegetation heights were estimated at a 30 m resolution. In order to represent the overall forest structure in a single variable, we calculated skewness of vegetation heights. A negatively skewed distribution of vegetation heights should indicate dense forest, such as plantations or dense hardwood forests, with few canopy gaps since the greatest densities of returns come from the canopy. A forest with an open canopy and minimal midstory vegetation, such as mature longleaf pine forest (Peet 2006), should represent as a positively skewed distribution of vegetation heights with a small but consistent density of returns depicting the canopy with the majority of the returns reaching the herbaceous vegetation in the understory.

MODELS

Resistance surface – We approximated how the LiDAR-estimated vegetation structure influenced *P. borealis* prospecting movements with a resistance surface generated from a habitat suitability model. The habitat suitability model was created with a maximum entropy modeling approach. This is a machine-learning algorithm that estimates habitat suitability based on known species locations (e.g., museum records or breeding sites) and layers of environmental data. The algorithm finds the maximum entropy (i.e., closest to uniform) distribution constrained by the environmental data associated with species occurrences (Elith et al. 2006, Phillips et al. 2006). The habitat suitability model was constructed with Maxent software (Version 3.3.1, Phillips et al. 2006).

The Maxent software requires two types of input data, coordinates of species occurrences and grids with environmental variables. The occurrence locations input into Maxent were all non-natal telemetry locations (n = 1710) and randomly divided into training (75%) and testing (25%) points. To account for variation in training and testing data sets, we used bootstrapping with 10 replicate samples (with replacement). The environmental variables used to create the habitat suitability model were the seven forest-structure variables created from LiDAR data. Maxent software outputs a raster with the probability of habitat suitability for the entire study area (Phillips and Dudik 2008). Habitat suitability values near one indicate the most suitable habitat conditions for the species while unsuitable habitat is indicated by values close to zero.

Assuming that habitat suitability is inversely related resistance values during dispersal events, Maxent's habitat suitability values (h) were converted into friction values (v) with the function,

$$v = 100 - 99 \times \frac{(1 - e^{(-4h)})}{(1 - e^{(-4)})}.$$

This non-linear relationship between habitat suitability and friction values has been shown to be a better predictor of *P. borealis* movement behavior than a linear transformation (Chapter 2). We chose a range of friction values from 1 to 100, where the lowest value (1) is assigned to the highest suitable habitat (Maxent suitable habitat = 1) and the highest value (100) is assigned to the most avoided habitat (Maxent suitable habitat = 0). The resistance surface was then processed using the Cost Distance model to calculate the minimum cumulative cost, known as friction-weighted distance (f_{ij}) (Adriaensen et al. 2003), from a the radio-tagged *P. borealis* roosting territories (i) to all territories (j) within a 6 km prospecting range.

ANALYSIS

***Discrete-Choice* –** A maximum likelihood discrete-choice modeling method was used to investigate whether environmental and/or conspecific cues influence *P. borealis* prospecting movements. This discrete-choice modeling approach was selected because it accounts for variation in available territories and surrounding environmental features. This is important for our study because all territories are not accessible to each of the prospecting females. The maximum distance between territories in our study area is over 70 km and most female *P. borealis* disperse less than 3.3 km (Kesler et al. 2010). In addition, each fledgling emerging from its natal territory is surrounded by a unique set of conspecific interactions, possibly influencing prospecting behavior. All territories within its 6 km prospecting range were defined as the choice set for each individual (Figure 3.2). Within each choice set, the friction-weighted distance was calculated from natal territory to possible destination territories and the six conspecific variables were compiled for all destination territories.

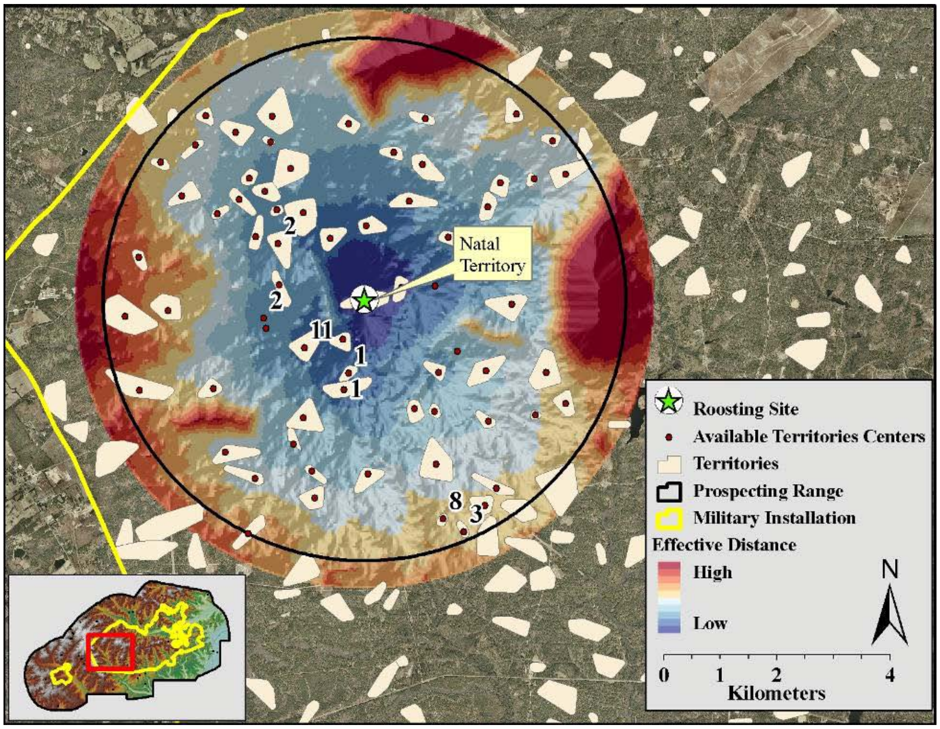


Figure 3.2 An example of a radio-tagged juvenile female Red-cockaded woodpecker (*Picoides borealis*) prospecting movements in relation to effective distance surface. A number to the upper right of a territory indicates the frequency the bird was observed visiting that territory. Territories without numbers were never visited.

The six independent variables describing conspecific interactions at the destination territories along with the effective distance depicting *P. borealis* reaction to environmental cues between territories were incorporated into a suite of 51 *a priori* models. The response variable in the discrete-choice models was the frequency of territory visits during observed prospecting movements. All models were ranked using Akaike's Information Criterion adjusted for small sample sizes (AICc, Burnham and Anderson 2002) with the smallest AICc values indicating with more likely models explaining prospecting behavior based on the radio telemetry data. We also computed the AICc weight (ω), which represents the weight of evidence in favor of a model in relation to all the models in the set (Burnham and Anderson 2002). All discrete-choice modeling was conducted with the R package Survival (Version 2.11.0, R Development Core Team 2010).

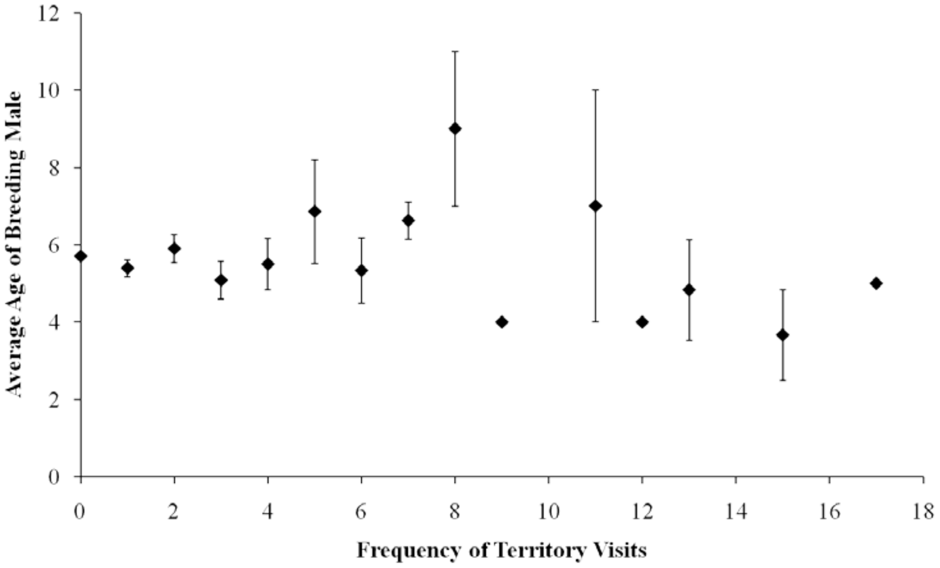
Validation – The LiDAR-derived resistance surface was validated with independent dispersal data (Chapter 2). In this study, we evaluated the performance of the top-ranked model's conspecific cues by comparing the group composition at destination territories with independent dispersal data of observed juvenile female born in 2005 (n = 57) and 2006 (n = 39). We assessed if *P. borealis* short-distance dispersers behave differently than long-distance dispersers. The long-distance threshold was defined at 6 km, the 95th percentile of the observed foray distance from roosting sites (Kesler et al. 2010). Unfortunately, conspecific information was not available for all dispersing individuals' final destination territory. Therefore, we only evaluated dispersal events when the conspecific information was available at the destination territory (84% and 97% of the dispersers for 2005 and 2006 cohorts, respectively). The conspecific parameters at the selected breeding territory were compared to the average of each conspecific parameter for all the territories within a 2-km neighborhood around the dispersed territory. If the trend observed in the destination territory matched the relationship of the estimated conspecific parameters in the top-ranked prospecting model better than the conspecific characteristics of the surrounding territories then the model accurately predicted conspecific behavior for dispersal events.

Results

Radio telemetry –We observed 282 and 533 territory visits during prospecting in 2006 and 2007, respectively. The number of visits ranged from 1 to 23 territories per female. Almost half (49%) of the prospecting events included an individual visiting a territory multiple times. Individuals revisited a single territory an average of 4 times (SE = 0.25) and a maximum of 17 times. The maximum prospecting range from a roosting site was 8.9 km ($\overline{X}$ = 3.54, SE = 0.28). The average age of breeding males at destination territories is relatively constant for territories visited less than eight occasions and greater than 12 visits with a spike in age of breeding males for moderately visited territories (Figure 3.3). The average number of fledglings in territories visited (1.68, SE = 0.07) was greater than territories not visited (1.47, SE = 0.03). In addition, the average number of fledglings increased with the number of occasions an individual revisited a territory (Figure 3.3).

Discrete-choice Analysis – Discrete-choice models explaining *P. borealis* prospecting behavior with conspecific or environmental cues alone were outranked by models combining both conspecific and environmental cues. The best discrete-choice model (ω_i = 0.61) included friction-weighted distance, age of the breeding male, and number of fledglings in destination territories (Table 3.1). According to the top-ranked model, *P. borealis* were more likely to visit territories with lower friction-weighted distance between natal and destination territories and that contained more fledglings (β = 0.214, 95%CI = 0.02

to 0.4, *p* = 0.0283) compared to territories not visited within their prospecting range (Table 3.2). This model also suggests that prospecting birds were selecting territories with younger breeding males (β = - 0.051, 95% CI = -0.1 to 0.00, p = 0.0607). The second-best model with a relative likelihood (ω_i) of 38.2% (ΔAICc = 0.93; Table 3.1) contained the same parameters as the first model, along with Age of Breeding Female. The second-best model suggests that prospecting birds were frequently visit territories that contained older breeding females. However, the 95% coefficient for Age of Breeding Female overlapped zero (β = 0.022, 95% CI = -0.017 to 0.06, Table 3.2).



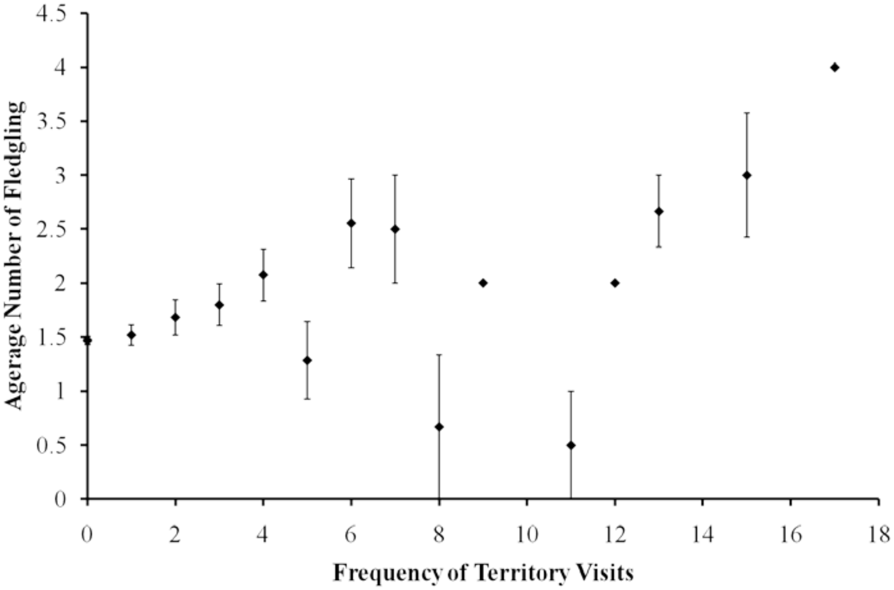


Figure 3.3 Average (+/- SE) age of breeding male (top) and number of fledglings (bottom) by the number of observed territory visits of dispersing juvenile female Red-cockaded woodpecker (*Picoides borealis*).

Table 3.1The ranking of discrete-choice models predicting Red-cockaded woodpecker (*Picoides borealis*) prospecting behavior within the Sandhills ecoregion of North Carolin a in 2006 and 2007. Friction-weighted distance was based on forest structure estimated with LiDAR data.

Rank[a]	**Parameters**	**k**[b]	**AICc**[c]	**ΔAICc**[d]	ω_i[e]
1	Friction-weighted Distance + Age of Breeding Male + # Fledglings	3	4152.04	0.00	0.61
2	Friction-weighted Distance + Age of Breeding Male + # Fledglings + Age of Breeding Female	4	4152.97	0.93	0.38
3	Friction-weighted Distance + Age of Breeding Male + # Male Helpers (Year After) + Age of Breeding Female	4	4160.78	8.74	0.01
4	Friction-weighted Distance + Age of Breeding Male + # Male Helpers (Year After)	3	4163.42	11.38	0.00
5	Friction-weighted Distance + Age of Breeding Male + Total Group Size	3	4176.63	24.59	0.00
6	Friction-weighted Distance + Age of Breeding Male + Age of Breeding Female + Total Group Size	4	4176.94	24.90	0.00
7	Friction-weighted Distance + Age of Breeding Male + # Male Helpers (Year After) + Age of Breeding Female	4	4178.22	26.24	0.00
8	Friction-weighted Distance + Age of Breeding Male + Age of Breeding Female	3	4178.52	26.48	0.00
9	Friction-weighted Distance + Age of Breeding Male	2	4180.42	28.38	0.00
10	Friction-weighted Distance + Age of Breeding Male + # Male Helpers (Year Before)	3	4181.44	29.40	0.00
24	Friction-weighted Distance Only	1	4242.03	89.99	0.00
27	Age of Breeding Male + Age of Breeding Female + # Male Helpers (Year After)	3	4578.09	426.05	0.00

[a] Rank is out of the 51 models, other models in the shaded box with lower rank are identified for purpose of discussion.

[b] Number of estimated parameters in the model.

[c] Akaike's Information Criterion adjusted for small sample size.

[d] Difference in the value between AICc of the current model and the value for the most parsimonious model.

[e] Relative likelihood of the model given the data and set of candidate models (model weights sum to 1.0).

Table 3.2 The predicted estimates, standard errors, and 95% confidence intervals of environmental and conspecific cues influencing Red-cockaded woodpecker (*Picoides borealis*) prospecting behavior from the top-ranked discrete-choice models within the Sandhills ecoregion of North Carolina in 2006 and 2007.

Model Rank	**Parameter**	**β**	**SE**	**LCL**	**UCL**	**p-value**
1	Friction-weighted Distance	-7.08E-05	1.30E-05	-9.62E-05	-4.53E-05	< 0.0001
	Number of Fledglings	0.214	0.097	0.02	0.40	0.0283
	Age of Breeding Male	-0.051	0.027	-0.10	0.00	0.0607
2	Friction-weighted Distance	-7.06E-05	1.29E-05	-9.60E-05	-4.525E-05	< 0.0001
	Number of Fledglings	0.206	0.094	0.022	0.39	0.0281
	Age of Breeding Male	-0.053	0.028	-0.108	0.00	0.0538
	Age of Breeding Female	0.022	0.020	-0.017	0.06	0.2697

Model Validation –Conspecific cues within the 2-km neighborhood of the dispersed territory were not strong predictors of short or long distance dispersal behavior. According to the top-ranked prospecting model, individuals revisited territories with more fledglings and younger breeding males. Only 37% (12 out of 32) long-distance dispersers and 39% (21 out of 54) short-distance dispersers selected destination territories that contained more fledglings than the average number of fledglings observed at territories within a 2-km neighborhood. Half of the short-distance dispersers settled in territories with younger breeding males and 40% of the long-distance dispersers selected territories with younger breeding males.

Discussion

While prospecting behavior can increase an individual's fitness by selecting highly suitable breeding sites (Schjorring et al. 1999, Stamps 2006), the extra-territorial movements can be energetically expensive and results in greater exposure to predators (Conradt et al. 2003, Stamps et al. 2005). For example, *P. borealis'* greatest mortality rate occurs when fledglings attempts to obtain breeding status (Walters et al. 1988, Daniels and Walters 2000). To mitigate predation risks during dispersal, many species, including *P. borealis*, have developed effective systematic search strategies to located and evaluate potential breeding sites (Zollner and Lima 1999, Conradt et al. 2003).

Two types of prospecting strategies include sequential and comparative searching (Stamps et al. 2005, Selonen and Hanski 2006, Stamps and Davis 2006). During a sequential search, individuals consecutively visit multiple breeding sites without deliberately revisiting the same site before selecting the highest quality site from their sample. In contrast, the comparative search strategy entails individuals visiting and revisiting sites multiple times before selecting the site perceived to have the highest quality. According to our radio-telemetry data, most birds used the comparative search strategy. Prospecting individuals were observed revisiting and interacting with individuals at potential breeding sites an average of four times (SE = 0.25). However, seven juvenile female *P. borealis* followed both comparative and sequential strategies by first exploring territories near their natal site, then making a long-distance movement to a new area, and continue visiting and revisiting sites in the new area before settling into a single territory. These complex search strategies may be necessary for cooperative breeding *P. borealis* to collect adequate information about a territories future reproductive potential (Kappes Jr and Walters In Preparation).

Our results suggest that juvenile female *P. borealis* are guided by environmental cues between territories. The environmental cues influencing birds prospecting movements match forest structure characteristics similar to foraging habitat requirements (Chapter 2)**.** When visiting territories, *P. borealis* appear to use not only environmental cues, but also social cues. Each of the conspecific cues varied in their relative importance associated with territory visits. The conspecific cues at potential breeding sites correspond to the reproductive potential and characteristics of potential breeding partners. Compared to territories not visited within their prospecting range, juvenile female *P. borealis* preferred to visit territories with more of fledglings, younger breeding males, and older breeding females (Table 3.2).

A breeding site's reproductive potential can be quickly and reliably assessed by observing the presence or quantity of conspecifics (Stamps 1988, Smith and Peacock 1990, Danchin and Wagner 1997). Our results suggest that neither total group size nor number of male helpers were important conspecific cues associated with *P. borealis* prospecting behavior. This was surprising outcome because group size has been positively associated with breeding site quality and reproductive success for *P. borealis* and other avian species

(Zack and Ligon 1985, Lennartz et al. 1987, Walters et al. 1992, Yaber and Rabenold 2002). Since *P. borealis* is a cooperative breeder, with helpers who incubate eggs, feed nestlings, maintain cavities, and provide additional territorial defense; habitat quality and breeding success are also strongly correlated with number of helpers (Walters 1990, James et al. 1997, Daniels and Walters 2000). The lack of explanatory power with amount of conspecifics observed at destination territories could be related to *P. borealis* aggressive territorial behavior. All group members, including helpers, display aggression to intruders (Ligon 1970, Walters 1990). A young prospecting individual intruding into an unfamiliar territory may need to expend extra energy when fighting a large group with many experienced helpers. Therefore, inexperienced prospecting juveniles with limited fighting ability may quickly leave and not revisit territories with large groups composed of male helpers.

P. borealis prospecting behavior was a strongly related to the conspecific cue directly associated with a territory's reproductive success (number of fledglings). Similar results were observed in a study in which brood size and quality were experimentally manipulated for sea birds (Doligez et al. 2002). Doligez and colleagues (2002) showed that prospecting birds visited nests more frequently that contained more fledglings and fledglings in better physical condition while individuals abandoned sites with reduced brood size and lower quality of fledglings. Similar to these sea birds, prospecting *P. borealis* may be evaluating the quantity and quality of fledglings from the previous breeding season. Juvenile *P. borealis* with poor body condition are more likely to disperse quickly from their natal territory in hopes of finding better resources (Pasinelli and Walters 2002), and dominant and healthy fledglings often remain in their natal territory and participate in conflicts against intruders (Ligon 1970, Walters 1990). During conflicts, prospecting *P. borealis* maybe evaluating the site's quality by observing number and physical condition of fledglings remaining in the territory. Unlike male helpers, inexperienced fledglings encountered during conflicts should be less of a threat to prospecting individuals. To get an accurate assessment of a territory's reproductive quality, *P. borealis* may need to revisit sites to estimate number of healthy fledglings because resident fledglings may also be periodically away from their natal territory to search for potential breeding sites.

Our data also suggest that juvenile female *P. borealis* are cueing into the fitness of potential breeding partners. For *P. borealis*, a group's reproductive success increases with the age of the breeding males (Walters et al. 1988, Walters 1990, Daniels and Walters 2000). However, our results showed that *P. borealis* visited territories more often with younger breeding males (Table 3.2). This tendency could be relevant to adult female dispersal behavior. Adult females experiencing an unsuccessful breeding during their first attempt usually relocate to a territory with an older breeding male (Daniels and Walters 2000). Therefore, territories with older breeding males may be unavailable to juvenile late-dispersing females due to their inability to displace an older and more experienced female.

Unfortunately, conspecific variables in the top-ranked model did not provide explanatory power when predicting independent dispersal events. Our lack of ability to associate observed dispersal events with conspecific cues could be due to difference in time scale between prospecting and dispersal data. Juvenile *P. borealis* either disperse soon after they obtain fledging status (earlier-dispersers) or just prior to the subsequent breeding season (late-dispersers). The observed dispersal events from banding data are a mixture of early and late dispersing individuals, while our telemetry data focused solely on late-dispersing *P. borealis*. The availability of most conspecific cues used by a prospecting individual to assess territory quality may shift through time, therefore individuals must evaluate conspecific cues when they convey the most reliable information (Boulinier et al. 1996, Doligez et al. 2004). For example, late-dispersers may be focusing on characteristics of the potential breeding partner (age of breeding male) to provided an accurate assessment of breeding site reproductive success, while early-dispersing juveniles may be using different conspecific cues to predict a breeding sites potential quality.

Conclusion

To increase the population persistence and biodiversity in human dominated landscape, it is important to understand how species movement behavior responds to varying natural and anthropogenic land-cover characteristics. Our results demonstrate the importance of social interactions and environmental cues when selecting breeding sites. *P. borealis* can serve as a useful model species to associate cooperative breeding behavior with conspecific interactions during prospecting. In addition, *P. borealis* is a habitat specialist that is negatively impacted by degraded habitat throughout their range. As landscapes change with human activities, prospecting individuals searching strategies will most likely have to be modified with the environment (Thomas et al. 2001). Altering search patterns could cause groups of territories to become isolated from the remaining population due to higher direst cost in terms of mortality risk and fewer successful dispersal events. Isolated territories within small habitat patches can also decrease the persistence of populations indirectly by causing more inbreeding events which can lower fitness levels. Cooperative breeder population sizes may be further affected if individuals are unable to locate potential breeding sites. Individuals may delay dispersal all together which will decrease the number of nests and young.

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CHAPTER 4

FIELD-CALIBRATED CONNECTIVITY ESTIMATES FOR RED-COCKADED WOODPECKER POPULATIONS

Abstract

The Red-cockaded woodpecker (*Picoides borealis*), is a federally endangered, cooperative breeding species endemic to the highly-fragmented longleaf pine forests in the southeastern United States. To assess the connectivity of *P. borealis*, we used pre-dispersal prospecting locations, collected with radio-telemetry, and LiDAR-derived landscape features to develop an empirical resistance surface. This surface is used to estimate the effective, or friction-weighted, distances between territories, which are incorporated into a graph-theory-based habitat connectivity model. This model predicts that if the dispersal ability, in terms of friction-weighted distance, is sufficiently reduced, the population will undergo an abrupt transition between a connected and disconnected. Using independently obtained mark-recapture dispersal data, we also found *P. borealis* that disperse up to 6 km are influenced by forest structure and impeded by human-modified landscapes. By correlating the network model at varying friction-weighted dispersal distances with our extensive set of observed dispersal events, we found that the abrupt transition from highly connected to disconnected territories occurs at the median dispersal ability of the population. Additionally, we found that highly connected territories reside within managed areas of continuous forest. However, these networks of connected territories are isolated from each other by agriculture or development on state-managed and private properties. These results will help identify areas to manage and improve habitat connectivity for *P. borealis*. More generally, our approach provides a basis for evaluating connectivity based on species-specific responses to intervening landscape features.

Keywords: Dispersal behavior, Graph theory, LiDAR, Natal dispersal, North Carolina, *Picoides borealis*, Radio-telemetry.

Introduction

Habitat fragmentation is one of the greatest threats to biodiversity, globally (Wilcove et al. 1998, Haila 2002, Fahrig 2003). Populations that once extended throughout large areas of habitat have become restricted within smaller and more isolated patches, reducing genetic diversity and increasing the probability of local extinction (Fahrig and Merriam 1994). Conserving animal populations in fragmenting landscapes requires strategic management activities that demand a greater understanding about the ability and willingness of organisms to move between habitat remnants (Dunning et al. 1992, Goodwin and Fahrig 2002). Connectivity between patches of habitat is partly a function of the degree to which the intervening landscape facilitates or impedes dispersal (Taylor et al. 1993). By adopting a broad definition of connectivity, it is possible to incorporate a wide range of information about the topology of the landscape as well as movement behaviors (Calabrese and Fagan 2004, Belisle 2005).

Currently, a variety of different connectivity metrics and modeling frameworks exist to evaluate the impact of fragmentation on wildlife movements (Calabrese and

Fagan 2004). The simplest connectivity metrics are based solely on the spatial distribution of the habitat patches and assume that connectivity is only a function of distance between patches. More complex estimates also incorporate population abundance, demographic information, land-use and land-cover characteristics, and varying ability to move through the environment (Moilanen and Hanski 2001, Calabrese and Fagan 2004, Minor and Urban 2007). Despite providing greater insight into a species connectivity, more complex connectivity models are rarely used due to insufficient information about land-cover characteristics and movement behavior (Cantwell and Forman 1993, Urban and Keitt 2001, Calabrese and Fagan 2004, Urban et al. 2009).

In particular, an organism's movement from its natal site to the first site where it obtains breeding status (Greenwood and Harvey 1982), i.e., the natal dispersal behavior, is fundamental to the connectivity between habitat patches (Wiens 2006) but it is one of the least understood animal behaviors. This in part is due to the brevity and complexity of the phenomenon (Kernohan et al. 2001). Knowledge about natal dispersal is often particularly lacking for rare and protected species due to their scarcity or restrictions regarding handling (Thompson 2004).

When natal dispersal information is not available, the flow of individuals between fragmented landscapes is estimated for a wide range of distinct threshold distances (Bunn et al. 2000, e.g., Urban and Keitt 2001). Habitat patches within the threshold distance are defined as connected while patches beyond the distance threshold are defined as disconnected (Keitt et al. 1997, Minor and Urban 2008). This approach evaluates connectivity to natal dispersal abilities and can reveal a sharp transition between connected and disconnected landscapes (Urban and Keitt 2001). This sharp transition is then compared to a fixed distance that represents typical or maximum dispersal distance and that is based on literature review (Roshier et al. 2001, e.g., Lookingbill et al. 2010b).

Intrinsically, connectivity models described with fixed distances are limited in they assume all individuals have equivalent movement ability and behavior. However, many species exhibit a right-skewed distribution with most individuals dispersing relatively short distances from their natal area, while a few individuals disperse considerably greater distances (Greenwood and Harvey 1982, Williamson 2002, Nathan et al. 2003). Thus, more complete estimates of connectivity should be obtained by correlating connectively models with independently obtained dispersal data that depict the distribution of a species' actual dispersal capabilities. Moreover, this approach will provide richer insights into connectivity that can be used to develop strategic conservation plans for populations residing within fragmented landscapes (Urban and Keitt 2001).

Much of the conservation emphasis in the southeastern United States has focused on preserving and restoring, the heavily fragmented longleaf pine (*Pinus palustris*) ecosystem. Logging and fire suppression have reduced longleaf pine forest to less than 3% of its original extent (Frost 2006), resulting in drastic declines in longleaf pine endemic Red-cockaded woodpecker (*Picoides borealis*) populations. Since its initial listing as a federally endangered species in 1970 (U.S. Department of the Interior 1970), *P. borealis* has been intensely studied throughout its geographic range, with several long-term monitoring projects evaluating their habitat requirements, demography, group composition, and dispersal behavior (Costa and Daniels 2004).

P. borealis is a territorial, cooperative breeder (Walters 1990), with juvenile males often remaining in their natal territories for several years to assist in caring for subsequent offspring (Walters et al. 1988, Walters 1990, Haig et al. 1994). In contrast, juvenile females usually conduct multiple forays from their natal territories before dispersing to a final breeding territory (Kesler et al. 2010, Kappes Jr and Walters In Preperation). While some juvenile females disperse distances as long as 31 km, most disperse less than 3.3 km (Walters 1990, Kesler et al. 2010). Thus, despite a potentially strong dispersal ability, *P. borealis* dispersal movements can be negatively influenced by the presence of dense hardwood forests and anthropogenic fragmentation of longleaf pine forests (Conner and Rudolph 1991,Chapter 2).

The purpose of this study was to relate *P. borealis* connectivity estimates derived from radio-telemetry-based movement data with observed dispersal ability obtained from independent mark-recapture and banding data. Specifically, we used the telemetry data to construct graph-theoretic network of breeding territories. *P. borealis* reactions to surrounding landscape features during natal dispersal were incorporated into the connectivity model to create an empirical resistance surface, from which friction-weighted distance values between territories (i.e., network edges) were derived (Bunn et al. 2000, Ferreras 2001, Adriaensen et al. 2003, Verbeylen et al. 2003). The network model at varying friction-weighted distances was then correlated with an extensive set of observed dispersal events, which allowed us to examine the patterns in *P. borealis* dispersal in terms of network topography. Finally, this biologically calibrated connectivity model, created by incorporating detailed dispersal ability data for the entire dispersing portion of the population, was used to identify territories that are necessary to maintain well connectivity and those where occupancy might be limited due to environmental barriers to dispersal.

Methods

Study Area

This study was conducted over a 3,721 km^2 area (79°12'12"W 35°7'31"N; Figure 4.1) in the Sandhills ecoregion of North Carolina (Griffith et al 2007). This region contains rolling topography and deep fluvial sandy soils intermixed with clay soils at an average elevation of 103 m (Skeen et al 1993). Historically, the prevailing vegetation type throughout the Sandhills ecoregion was the fire-dependent longleaf pine woodlands, characterized by an open canopy with minimal hardwood midstory and dense herbaceous understory vegetation (Frost 2006; Provencher et al 2001). Currently, the dominant vegetation types in the Sandhills ecoregion are cropland, pasture, and mixed woodland (Griffith et al 2007). The remaining evergreen forests are primarily mixed-pine (longleaf, loblolly [*P. taeda*], shortleaf [*P. echinata*], and pond pine [*P. serotina*]) in second-growth forest with varying amounts of hardwood understory and midstory (Griffith et al 2007). North Carolina’s largest tracts of federally owned longleaf pine forest are located in the study area on two military installations, Fort Bragg and Camp Mackall (Britcher and Patten 2004). These federal properties contain over 65% (n = 441) of the 670 established *P. borealis* territories located in the study area (Figure 4.1).

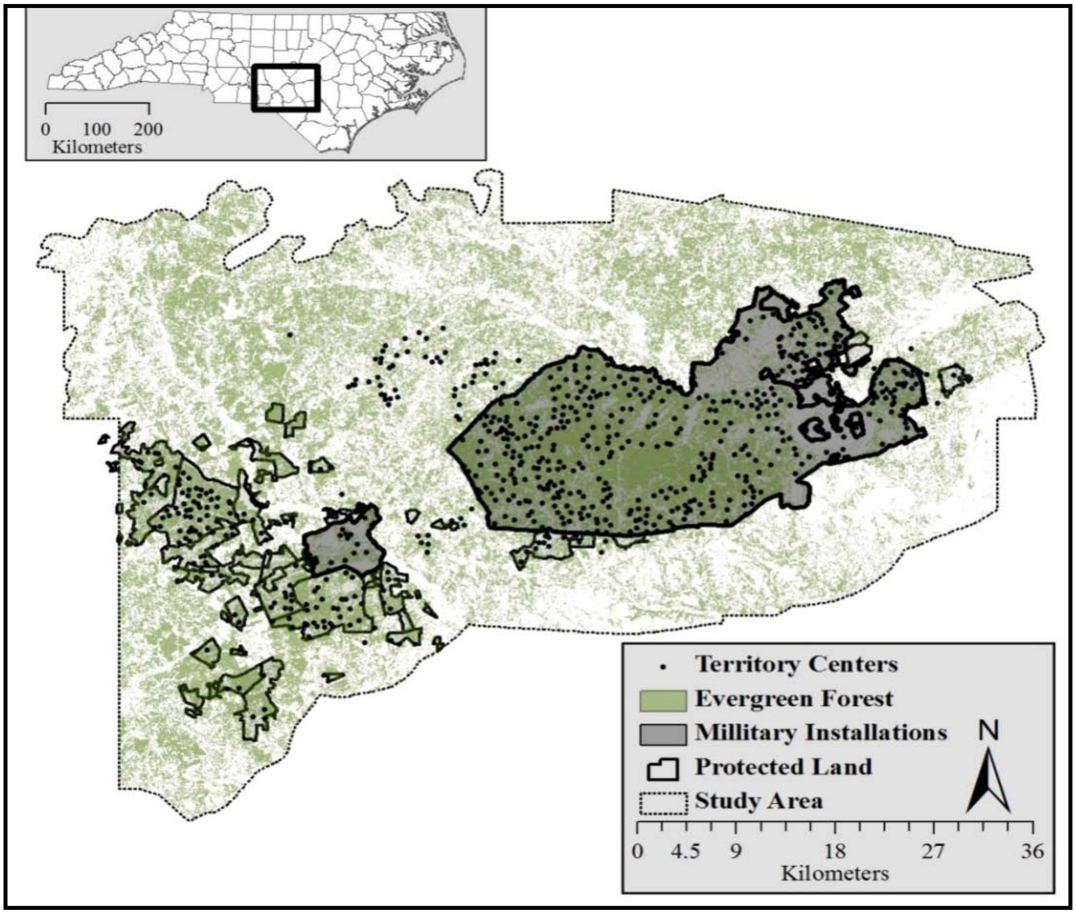

Figure 4.1 Study area depicting Red-cockaded woodpecker (*Picoides borealis*) territories in relation to military installations, protected properties, and evergreen forest in North Carolina (inset).

DATA

Movement Data– To evaluate how landscape features influence *P. borealis* movement behavior, we radio-tracked juvenile female birds foraying to potential breeding sites. In spring (March – May) 2006, 18 juvenile female *P. borealis* that had not yet obtained breeding status (average weight = 46 g) were captured in their roosting cavities and fitted with a 1.4 g transmitter glued to the base of 2 tail feathers (BD-2, Holohil Systems Ltd., Ontario, Canada). These birds were tracked for the life of their radio transmitters (~ 9 wks) on the western portion of Fort Bragg, which contains the largest unfragemented tracts of longleaf pine forest on the property. We also radio-tagged and tracked an additional 16 individuals during 2007 in the eastern section of Fort Bragg, which consists of highly fragmented forest surrounded by urban and agriculture land. We attempted to locate radio-tagged woodpeckers daily. Radio-tagged birds were ordered in a list by geographic location, and then a single individual was randomly selected to be the first daily observation. Animals were located using signal strength and direction with a receiver (R-1000, Communication Specialist, Inc. Orange, CA, USA) and a 3-element Yagi directional antenna (Wildlife Materials, Inc., Carbondale, IL, USA). Each time an individual was located outside its home territory we recorded a Universal Transverse Mercator (UTM) coordinate using a hand-held Garmin® global positioning system unit (GPS; Olathe, KS, USA).

In addition to the radio telemetry data collected as part of this project, all active *P. borealis* territories have been monitored by researcher from North Carolina State and Virginia Polytechnic Institute and State Universities, and biologists from Fort Bragg Endangered Species Branch and the Sandhills Ecological Institute, since 1981. Under their protocol, all juvenile and adult *P. borealis* are marked with a unique combination of bands and all active territories are monitored each breeding season. Banded juvenile females born between 2004 to 2007 were used as observed dispersal events to biologically calibrate the connectivity model to the dispersing portion of the population. These years were selected so that both datasets (radio-telemetry and banding) were collected under similar environment conditions and landscape composition. Detailed banding and monitoring methods are described in Walters et al. (1988).

Forest Structure Data – Forest structure attributes expected to influence *P. borealis* movement behavior were estimated using airborne Light Detection And Ranging (LiDAR) data collected during leaf-off canopy conditions between 31 December 2000 and 18 February 2001 for the North Carolina Floodplain Mapping Program. The flight paths of two subcontractors overlapped our study area with varying sample density and flight altitude. The average ground spacing between LiDAR postings ranged from 2 - 2.25 m, flight altitude ranged from 914 - 1676 m, and the elevation calibration ranged from 9 - 12 cm root mean square error of elevation (RMSE-*z*). The raw LiDAR data containing three-dimensional coordinates of laser hits were converted to raster format with Fusion software (McGaughey 2008). In Fusion, the height from the ground was calculated for the LiDAR points as the difference between the point's elevation values and digital elevation models from the North Carolina Floodplain Mapping Program. Six LiDAR-derived forest structure variables were estimated at a 30 x 30 m resolution, including maximum vegetation height, percent cover in each of the four distinct height classes (1-8 m, 8-13 m, 13-20 m, and greater than 20 m), and skewness of vegetation heights. Dense forest, such as plantations or hardwood forests, with few gaps in the canopy have a negatively skewed distribution of vegetation heights where the greatest densities of returns come from the canopy. Open canopy forest with minimal midstory vegetation, such as mature longleaf pine forest (Peet 2006), have a positively skewed distribution of vegetation heights with the majority of the returns reaching the herbaceous vegetation in the understory and a small, but consistent, density of returns from the canopy.

MODELS

Resistance surface – The resistance surface was generated from a habitat suitability model constructed with a maximum entropy modeling approach (Figure 4.2). We used the software Maxent, which uses a machine-learning algorithm to estimate habitat suitability based on known species locations (e.g., museum records or breeding sites) and maps of environmental data (Version 3.3.1, Phillips et al 2006). The algorithm finds the maximum entropy (i.e., closest to uniform) distribution constrained by the environmental data associated with species occurrences (Phillips et al 2006, Elith et al 2006).

Maxent requires two types of input data, coordinates of species occurrences and grids with environmental variables. We used all non-natal telemetry locations as the input data (n = 1710) and randomly divided the telemetry dataset into training (75%) and testing (25%) points. To account for variation in training and testing data sets, we used bootstrapping with 10 replicate samples (with replacement). The environmental variables used to create the habitat suitability model were the six forest-structure variables derived from LiDAR data. Maxent produces a raster representing habitat suitability for each grid cell covering the entire study area (Phillips and Dudik 2008). Habitat suitability values near one indicate the most suitable habitat conditions for the species while unsuitable habitat is indicated by values close to zero.

Since we modeled habitat suitability on the basis of telemetry locations for prospecting birds, we assume that habitat suitability is inversely related to resistance surface during dispersal (Figure 4.2). We converted habitat suitability values (h) into friction values (v) with the function,

$$v = 100 - 99 \times \frac{(1 - e^{(-4h)})}{(1 - e^{(-4)})}. \tag{1}$$

This non-linear relationship between habitat suitability and friction values was chosen based on a sensitivity analysis (Chapter 2). An arbitrary range of friction values from 1 to 100 was chosen, where the lowest value (1) is assigned to the highest suitable habitat (Maxent suitable habitat = 1) and the highest value (100) is assigned to the most avoided habitat (Maxent suitable habitat = 0).

Friction-weighted distance – The resistance surface was used to calculate the shortest accumulated travel cost, or friction-weighted distance (d_{ij}), from territory *i* to territory *j* for all territories in the study area using a Cost Distance model (ArcInfo Workstation, Environmental Systems Research Institute, 2008). Territories are composed of two or more trees with nesting cavities that are aggressively defended by a single family group (Walters et al. 1988). The friction-weighted distance was calculated to the center coordinates of each pairwise combination of territories in the study area.

Graph Networks – We used graph networks to quantify and visualize *P. borealis* connectivity at varying natal dispersal abilities. A graph is a set of nodes (points) connected to some degree by links or edges. For this study, the nodes in the graph networks denote territory centers and the edges represent ability to dispersal between pairs of territories (Figure 4.2). A distance matrix was populated with friction-weighted distances (d_{ij}) of the least-cost path between all pairwise combinations of territories. The distance matrix was then converted into a undirected graph network using the igraph package (Csardi and Nepusz 2006) in R (Version 2.11.1, R Development Core Team 2010).

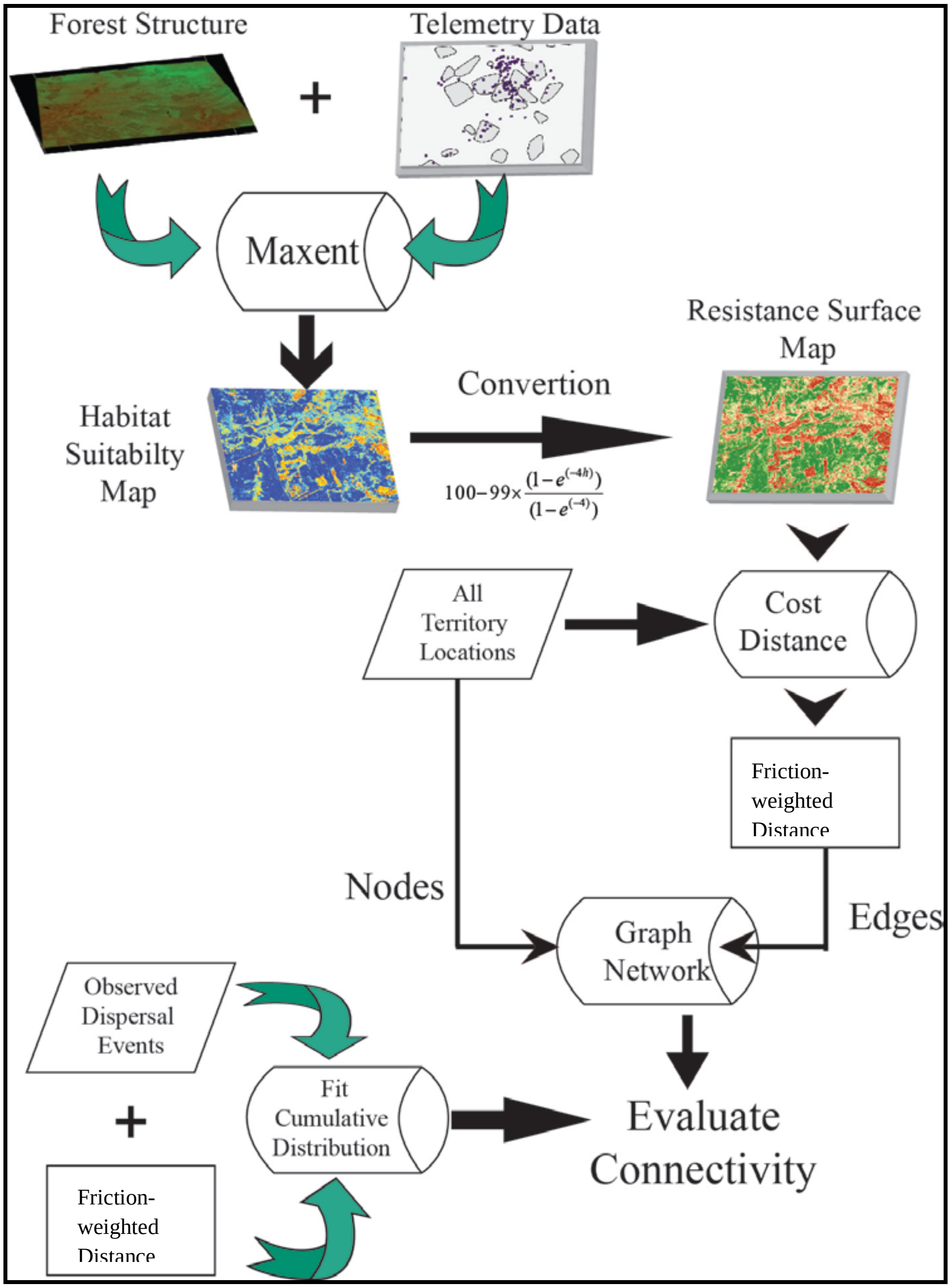

Figure 4.2 Overview of methods used to create resistance surface and graph network edges when estimating connectivity for Red-cockaded woodpeckers (*Picoides borealis*).

ANALYSIS

We compared the minimal friction-weighted distance with independently obtained mark-recapture dispersal data to validate that the friction values represented in the resistance surface explain how dispersing birds are influenced by landscape features between territories. This was accomplished by comparing the friction-weighted distance for each observed dispersal event to the average friction-weighted distance of all available territories with a similar geographic distance (within the 25th percentile) as the observed event. Available territories were only included if they were also within the maximum distance any juvenile female was observed dispersing from the natal territory during over 30 years of banding data.

We examined how different expectations about dispersal ability affect the structure and connectivity of the habitat network with Edge Thresholding Analysis (Urban and Keitt 2001). Starting with the most distant node pairs, edges were iteratively removed from the graph at 1,000 resistance friction-weighted distance intervals (d_{ij}). At each interval we estimated three landscape-level connectivity metrics (Table 4.1). The first metric is the number of isolated subgraphs in the entire network, also known as components (West 1996). The next metric is the number of nodes within the largest component (i.e., its order). The final metric calculated at each of the dispersal abilities is the largest component's diameter (Urban and Keitt 2001). Diameter is the longest minimal sequence of connected nodes (path) between any pair of nodes in a component (West 1996). The diameter of the largest component provides insight into the effective size of the graph (Urban and Keitt 2001).

Table 4.1 Definition of graph terms and metrics used to evaluate connectivity of Red-cockaded woodpeckers (*Picoides borealis*) in North Carolina's Sandhills ecoregion.

Graph Term	Definition
Node	Points (i.e., habitat patches or territory centers)
Edge	Friction-weighted distance between pair of nodes
Path	Sequence of connected nodes
Component	Connected subgraph with nodes separated from rest of the graph
Shortest Path	Shortest distance (number of edges or sum of weighted edge) through a component
Metrics	
Number Components	Number of subgraphs
Order	Number of nodes (territories) in the largest component
Diameter	Longest minimum path length between any pair of nodes in a component

The network model at each friction-weighted distance threshold was then correlated with observed dispersal events, which allowed us to examine the patterns in *P. borealis* dispersal to explore the current patterns in *P. borealis* connectivity. To accomplish this, we first calculated the minimal friction-weighted distance (d_{ij}) between a juvenile female's birth territory (i) and its subsequent breeding territory (j). The frequencies of all observed dispersal events (d_{ij}) were then fit to a lognormal probability density function where μ and σ are the mean and standard deviation of the natural logarithm of distances, respectively (Figure 4.3).

$$fx(d_{ij}, \mu, \sigma) = \frac{1}{d_{ij}\sigma\sqrt{2\pi}} e^{\frac{(\ln d_{ij} - \mu)^2}{2\sigma^2}}, \tag{2}$$

The lognormal distribution was selected because if the minimum range of the distribution is defined as zero, the two parameters are able to fit short and long-distance movements. The frequency distribution of the observed friction-weighted dispersal distances fit the lognormal distribution based on a Kolmogorov-Smirnov test ($p > 0.05$). The friction-weighted distances were converted into probability of dispersing from a territory to all territories with the fitted lognormal probability density function. The probability of dispersal given a friction-weighted distance was characterized as 1 – normalized frequency distribution. The trends in connectivity metrics at varying friction-weighted distance threshold values were compared with the cumulative probability of observed natal dispersal events for individuals born between 2004 and 2007 ($n = 257$).

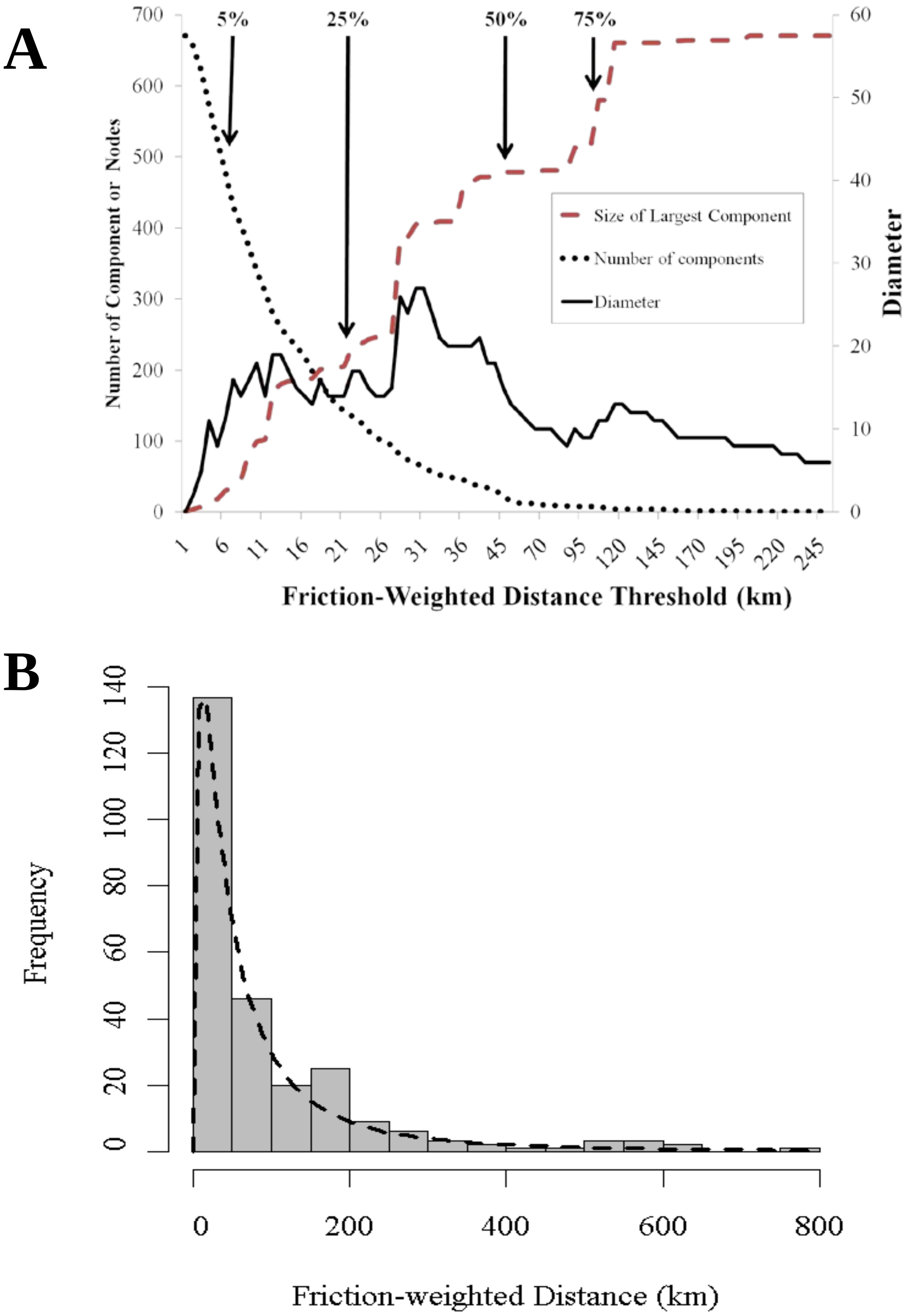

Figure 4.3 The number of graph components, graph order, and diameter of friction-weighted distance networks with iterative edge thinning (A). Arrows and percentages represent the cumulative percent of juvenile females Red-cockaded woodpecker (*Picoides borealis*) observed dispersing in North Carolina's Sandhills ecoregion. The frequency of observed dispersal distances based on least-cost path with the line representing the fitted distribution based on lognormal function (B).

Results

Maxent Models –The *P. borealis* habitat suitability model had an AUC greater than 0.82. The forest structure variables that strongly (> 20%) contributed to the habitat suitability model were percent cover of midstory vegetation (1 – 8 m), maximum vegetation height, and the skewness of the vegetation height distribution. Radio-tagged birds were unlikely to be observed in areas containing greater than 10% midstory cover but birds were very likely located in forested areas with maximum tree heights ranging from 13 to 25 m and areas with positively skewed vegetation height distribution. Percent cover classes above 8 m contributed minimally (< 17%) to the model.

Resistance Surface –When comparing observed dispersal events to potential destination territories, 172 individual out of 176 short distance dispersers (< 6 km) selected territories with friction-weighted distance less than the mean friction-weighted distance of all potential territories (Figure 4.4). Long-distance dispersers, in contrast, typically selected territories with much closer to, or greater than the average friction-weighted distance of available territories at similar Euclidean distances.

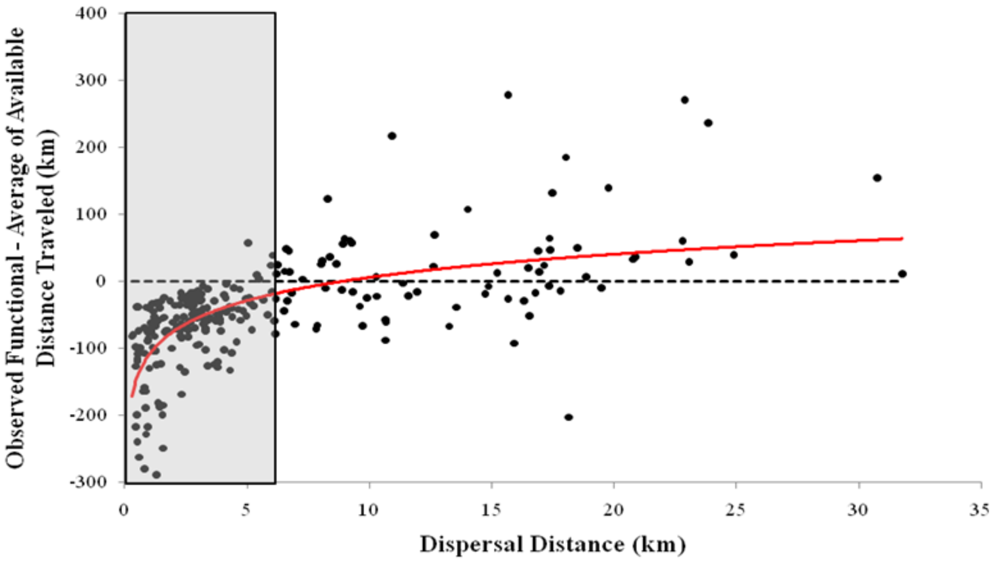

Figure 4.4 Observed friction-weighted distance dispersed minus the average friction-weighted distance of all territories with similar Euclidean distances from natal territory. Shaded box indicate individuals dispersing less than 6 km.

Network Models – The study area contains 670 territories that were represented in the network as nodes. The number of isolated components steeply declined up to a friction-weighted distance threshold of 22 km (Figure 4.3*a*). Twenty-five percent of the observed juvenile females dispersed up this friction-weighted distance threshold (Figure 4.3*b*). The network generated from edges with this threshold value contained 135 components scattered throughout the Sandhills region (Figure 4.3*a*) with an average of 5 territories (SE = 1.8) per component. However, six components contain more than 20 territories were located on government-owned properties (Figure 4.5*b*) with the majority of the largest component (233 territories) located on the western-portion of Fort Bragg (Figure 4.3*b*).

As friction-weighted distance threshold increased to 49 km, the median or 50% of observed dispersal events, the entire network of *P. borealis* territories was composed of

16 isolated components (Figure 4.3) with an average component size of 42 territories (SE = 29.7). The largest component included 479 territories radiating from Fort Bragg into nearby conservation properties. Most of the remaining *P. borealis* population was arranged into three components grouped by land-ownership. For example, the second (72 territories) and third (63 territories) largest components, were primarily located on state-managed properties while the smaller component (< 33 territories) was located on private property within the Southern Pines and Pinehurst city limits (Figure 4.5*b*).

By definition, components are isolated subgraphs with no connections between components (West 1996). The friction-weighted distance network based on 50% dispersal ability closely matched the observed dispersal events in relation to the delineation of components. For instance, most of the short-distance (< 6 km) dispersing individuals (99%, 215 out of 217) stayed within their natal component. The two individuals that did move between components dispersed to an adjacent component. In addition, 58 out of 80 long-distance dispersers (72%) remained in their natal component.

The 75% dispersal ability threshold was 110 km friction-weighted distance. At this threshold, *P. borealis* territories were composed of six components averaging 112 territories per component and ranging from a single territory to 580 territories in a component. The largest component contained territories on both military installations, one of the state-managed properties, and the territories within city limits of Southern Pines and Pinehurst. However, territories on one of the largest state-managed properties in the north western section of the study area were isolated at 75% dispersal ability (Figure 4.5*d*). The remaining three components were small (< 6 territories) and located on non-federal property surrounded by human-modified landscape features (e.g., agriculture and development) with high resistance values (Figure 4.5 *a* and *d*).

The overall traversability of a network can be indexed by the network's diameter (Urban & Keitt 2001). As dispersal ability increases with greater friction-weighted distance threshold and longer edges, the diameter growth initially corresponds to the largest component size or number of connected nodes (Figure 4.3*a*). When the network represented limited dispersal ability with many short edges created from small friction-weighted distance, the largest component was connected by long "stepping-stone" paths. As dispersal ability (represented with friction-weighted distance) increases further, these stepping-stone paths are replaced by longer, direct connections between nodes and the diameter of the largest component decreases. These two trends—the growth by accretion of the largest component and the replacement of long stepping-stone paths with shorter direct connections—results in network diameter reaching a maximum at intermediate dispersal distances (Urban et al. 2009).

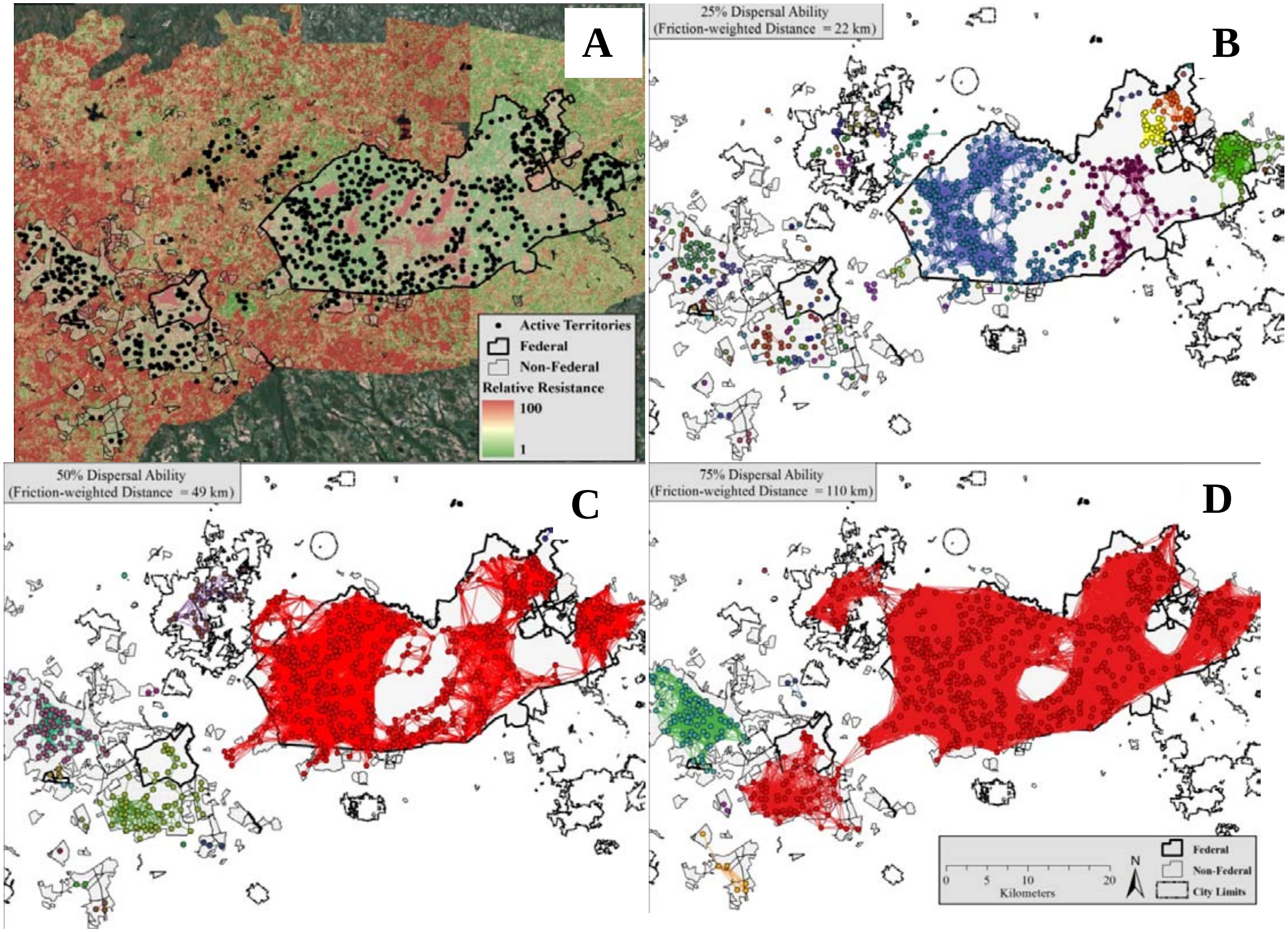

Figure 4.5 The resistance surface (a) and networks of territory groups for Red-cockaded woodpecker (*Picoides borealis*) with friction-weighted distance thresholds corresponding to 25% (b), 50% (c), and 75% (d) observed dispersal ability. Components are displayed with nodes (territories) and edges containing the same color.

Discussion

The extensive loss and fragmentation of longleaf pine ecosystem necessitates understanding *P. borealis* habitat connectivity in order to recover the species. Previous research suggests that *P. borealis* dispersal movements are inhibited by open and urban land-cover characteristics (Chapter 2). However, none of the over 250 peer-review articles regarding *P. borealis* since its federal protection in 1970 estimate habitat connectivity. We evaluated how connectivity changes with *P. borealis* reaction land-cover characteristics by creating network edges with friction-weighted distances. We took advantage of an extensive mark-recapture monitoring program to calibrate the friction-weighted distances to the probability of dispersal to explore the current patterns in *P. borealis* connectivity.

Evaluating the network structure in relation to easily accessible dispersal ability identifies well connected territories surrounded by high quality dispersal habitat. For instance, 25% of the juvenile females dispersed up to 22 km friction-weighted distances. The network created with this threshold distance showed clumps of highly connected territories on Fort Bragg (Figure 4.5*b*). Thus, extensive management for *P. borealis* breeding and foraging habitat with frequent prescribed burns implemented to increase population size (Britcher and Patten 2004) are also increasing connectivity between territories.

Even at relatively common dispersal ability of 25%, there is an enormous difference between connectivity estimates with and without including *P. borealis* reaction the surrounding environment. For instance, a simple network depicting 25% of the birds' dispersal ability in a featureless landscape (1.7 km) suggests that most territories are connected on Fort Bragg. When *P. borealis* relation to landscape features are including in the network model, military-specific land-use activities (drop zones and impact areas) in the central portion of Fort Bragg restrict movements across the property for individuals that up to 25% of the observed dispersal ability. Moreover, territories on the eastern-portion of Fort Bragg are composed of many small components in a highly fragmented longleaf pine forest surrounded by urban and agriculture land uses.

Network generated with edges occurs at the median dispersal ability of the population (49 km friction-weighted distance) suggests that territories are connected within Fort Bragg and adjacent properties. However, the entire Sandhills population was still segregated into four unconnected components (Figure 4.5*c*). With 99% of the short-distance dispersing birds remained within their natal components, there is strong evidence that this network portrays the current connectivity of the population. This network also suggests that *P. borealis* territories are highly connected on federal and state-owned properties that implement longleaf pine forest management practices. Unfortunately, these government-owned properties, are a small island of managed forests surrounded by urban development and agriculture land-use activities (Warren et al. 2007). As a result, few fledglings from Fort Bragg have been observed dispersing through surrounding development and agricultural fields to established territories on other conservation properties. Limited movement was observed between the three components situated in the western portion of the Sandhills region even though these components combined have similar spatial extent to Fort Bragg.

To incorporate a species' reaction to land-cover characteristics between habitat patches in connectivity models, species' relative ability to traverse different cover types can be integrated along the graph network edges using resistance surfaces (Bunn et al. 2000, Theobald 2006, Fall et al. 2007). When resistance surfaces are used to predict a species' connectivity, the most challenging step is to select biologically relevant friction values (Adriaensen et al. 2003). Friction values are usually defined based on subjective expert opinion and may not represent dispersal behavior (Beier et al. 2009). Instead of using the typical method of expert opinion to dictate how *P. borealis* react to the environment, we allowed *P. borealis* to inform the resistance surface with prospecting movements. Based on this resistance surface, *P. borealis* preferred to travel through forest stands similar to their foraging habitat characteristics, a tall canopy with minimal midstory vegetation (Rudolph et al. 2002, Walters et al. 2002, U. S. Fish and Wildlife Service 2003). The forest structure variables represented in the resistance surface suggest that land-cover characteristics strongly influenced birds dispersing up to 6 km (Figure 4.4). This 6 km distance coincides with juvenile female *P. borealis* prospecting range where individuals foray to potential breeding sites and return to their natal territory roosting site in the evening (Kesler et al. 2010, Kappes Jr and Walters In Preperation, Chapter 2 and 3).

Dispersal is a complex behavior that consists of three stages: a decision to leave the natal site, an intermediate transient phase, and the selection of a breeding site (Clobert et al. 2001). By creating resistance surfaces from breeding habitat characteristics, the selection stage is represented instead of the transient stage, which is more important when modeling connectivity. Resistance surfaces reflecting dispersal preference during the transient stage improved the realism of our connectivity model. Since most individuals dispersing up to 6 km are influenced by environment between their natal territory and the destination territory (Figure 4.4), edges in a *P. borealis* networks should be represented with friction-weighted distances from a resistance surface.

Since models simplify the real world, they all contain a level of uncertainty (Burnham and Anderson 2002). Habitat network models' greatest sources of uncertainty are associated with delineating habitat patches and characterizing dispersal ability (Minor et al. 2008, Lookingbill et al. 2010a). When complex habitat patches are simplified into nodes, within-patch movements are not included in the network model. This could significantly alter connectivity estimates for individuals in large patches. To mitigate this problem, many habitat connectivity studies define nodes with finer spatial resolution, such as animal locations, roosting sites, or breeding territories (Rhodes et al. 2006, this study, Garroway et al. 2008). These finer detailed nodes allow regional connectivity estimates to include local movement behavior within heterogeneous habitat patches. This approach makes it possible to directly compare connectivity to demographic processes which could provide insight into overall population function. Similar to mark-recapture studies, sampling bias the probability of capturing individuals or locating breeding sites for nodes in network model may provide inaccurate connectivity estimates (Naujokaitis-Lewis et al. In Preparation).

Defining edges for wildlife connectivity estimates is similar to testing alternate hypotheses in a modeling framework (Urban et al. 2009). Competing hypotheses can be evaluated by comparing edge values in a network to observed dispersal events. Selecting the edge value that best fits dispersal data will decrease some of the uncertainty when estimating connectivity. Our results provide important insights into management aimed to increase the connectivity of wildlife populations. For instance, a large portion of *P.*

borealis management practices have been directed towards preserving and restoring habitat at breeding territories and adjacent foraging areas (U. S. Fish and Wildlife Service 2003, Darden 2004). Our results suggest that persistence of healthy *P. borealis* populations requires management to extend beyond territories to connect isolated populations. In order to accomplish this goal conservation strategies can incorporate dispersal data between managed properties and habitat patches. Future management actions, such as prescribed fires, should be designed at large regional extents to include environments between established populations to encourage *P. borealis* movements between components and managing properties.

Understanding how individual movements connect populations is necessary to establish and implement effective management strategies to increase wildlife persistence and overall ecosystem function (Woodroffe 2003). Long-term monitoring projects and technological advances in radio-telemetry are starting to provide greater insight into species movement behavior. However, there is a significant delay in including movement data to estimate the flux of individuals and assessing habitat connectivity (Urban et al. 2009). For many species, including *P. borealis*, the graph theory has become a powerful tool to estimate and visualize species connectivity throughout fragmented ecosystems with modest data requirements (Calabrese and Fagan 2004). We showed that networks infused with biologically-relevant information substantially increases insight into habitat connectivity. This study provides a method to incorporate dispersal behavior via monitoring data to improve connectivity estimates with graph networks.

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CHAPTER 5

Evaluating Safe Harbor Program contribution to connecting resources: Case study of the Red-cockaded Woodpecker

Abstract

Through voluntary agreements, private landowners are becoming increasingly involved in managing biodiversity by participating in the incentive-based Safe Harbor Program (SHP). We evaluated the success of SHP with its inaugural species, the federally endangered Red-cockaded woodpecker (*Picoides borealis*) which is endemic to longleaf pine forests in the southeastern United States. We used movement data (mark-recapture and radio telemetry) and LiDAR-derived environmental characteristics to evaluate if *P. borealis* breeding sites' connectivity is positively impacted by habitat management actions fulfilled by private landowners' enrolled in the SHP. A graph-theoretic approach allowed us to prioritize which private properties could vastly improve *P. borealis* connectivity based on current conditions and encroaching urbanization. According to our results, SHP agreements increase the population's connectivity between publicly-managed and privately-owned properties, but connectivity on both properties are threatened by urban growth**.** While individual SHP properties are relatively small, our results show that coordinating conservation efforts with other SHP properties and collaborating with government agencies can increase population-level processes, such as connectivity. These results can help managers develop effective conservation plans on private land by incorporating the species specific movement ability on current landscapes, and projected urban growth. As movement data becomes available for other federally-protected species, the approach applied in this study can be expanded to further evaluate SHP impact on connectivity and strategically identify optimal locations for enrollment to mitigate current and future threats.

Key words: Connectivity, Dispersal, North Carolina, *Picoides borealis*, Radio-telemetry, Red-cockaded Woodpecker, Safe Harbor Program

Introduction

Human activities have drastically destroyed and fragmented productive ecosystems, thus reducing wildlife populations and eroding biological diversity (Dale et al. 2000, Fahrig 2003). Efforts to preserve diversity in the United States are complicated because most of the productive lands containing high wildlife diversity are allocated to private landowners (Scott et al. 2001, Miller and Hobbs 2002). That is, over 60% of the land area is privately-owned and contains habitat for more than 90% of the federally-protected species (GAO 1994, Hoppe and Wiebe 2002). Thus, to ensure the persistence and recovery of federally-protected species, habitat conservation efforts and management must focus heavily on habitat located on private property (Beatley 1996). However, private landowners are not legally required to directly manage habitat for the persistence and recovery of federally-protected species (Bingham and Noon 1998, U.S. Fish and Wildlife Service 2003, Wilcove 2004).

In the United States, the primarily regulatory legislation protecting biodiversity is the Endangered Species Act (ESA). The principle provision of this act is to restrict the “taking” of federally-protected species or the “harming” of individual organisms by adversely modifying their habitat (U. S. Fish and Wildlife Service 2003b). Unfortunately, this legislation has prompted some private landowners to fear land use restrictions and restrict conservation agencies access to private property or take preemptive actions (e.g., clear cutting or scorching land) to ensure federally-protected species do not occupy their properties (Bean 1998). As a result of these unintended consequences, the ESA has actually detrimentally impacted some federally-protected species on private land (Bean 1998). In response, many state and federal agencies have adopted incentive-based conservation strategies on private land that reward landowners for managing their lands to restore and enhance species' habitat (Bean 1998).

An increasingly popular tool for conserving biodiversity on private property is incentive-based programs is the Safe Harbor Program (SHP, U. S. Fish and Wildlife Service 2004). The initial agreement was developed in 1995 for the management of the federally endangered Red-cockaded woodpecker (*Picoides borealis*) (U.S. Department of the Interior 1995, Bonnie 1997). The program has now grown to include over 20 endangered species of various taxa with habitat restoration projects covering nearly two million acres nationwide (Wilcove 2004). The SHP participants agree to manage the current or "baseline" level of resources present on their property at the time of the agreement (Bonnie 1997, U.S. Department of the Interior 2006). In exchange for enhancing and restoring habitat, the USFWS guarantees that the SHP participants are not liable for additional land-use restrictions (Bonnie 1997, Wilcove and Lee 2004). Additionally, they are provided technical guidance and cost-share assistance to restore or improve habitat (Bonnie 1997, Bonnie et al. 2004, Wilcove and Lee 2004). While participants are allowed to terminate their contract at the end of the agreement, none of the private landowners have withdrawn from the program or altered restored habitat (Wilcove and Lee 2004, U.S. Department of the Interior 2006). As is highlighted by the program's growing participation and its complete retention of private landowners, by implementing the SHP the USFWS has improved relations with private landowners while increasing habitat quality for many federally-protected species (Wilcove and Lee 2004).

Since there will never be enough money to acquire resources to conserve all biodiversity on private land (Newburn et al. 2005). The flow of animal movements between habitat patches should be enhanced regardless if the property is publicly or privately owned. The USFWS strives to connect populations by increasing individuals' ability and willingness to move between relatively isolated and remnant habitat patches by increasing protected species' habitat quality with SHP agreements on private property (U. S. Fish and Wildlife Service 2004). However, the strategy of improving connectivity by enhancing habitat quality with SHP agreements has yet to be examined. In some cases, the recent establishment of SHP agreements prevents direct examination of populations' biological response to habitat improvements through the SHP (Wilcove and Lee 2004). More generally, the movement behavior of federally-protected species are incompletely documented and poorly understood (Thompson 2004). This lack of knowledge prevents richer insights into habitat connectivity (Urban and Keitt 2001) and thus impedes our ability to evaluate SHP influence on habitat connectivity.

Both of these obstacles can be overcome when evaluating SHP influence on connectivity for the federally endangered *P. borealis*. In the 15 years that have elapsed since the establishment of the SHP, over 50,000 acres of private land in North Carolina belonging to more than 100 individual land owners (Susan Miller, *personal* *communication*). *P. borealis* populations have also been extensively researched with several long-term monitoring projects evaluating their habitat requirements, demography, group composition, and dispersal behavior (Costa and Daniels 2004). Moreover, a 30-year monitoring program in the Sandhills region of North Carolina is within the boundary of the original SHP agreement. Recently, extensive mark-recapture natal dispersal data along with radio telemetry movement data were integrated into *P. borealis* habitat connectivity estimates (Chapter 4). With the available monitoring data (banding and radio-telemetry), it is possible to closely examine population-level and territory-level connectivity in relation to SHP properties.

Our first objective was to examine whether breeding sites on properties enrolled in SHP have a positive impact on connectivity than private properties not enrolled in the SHP. To increase the effectiveness of future conservation planning on private properties, we also prioritized which inactive breeding sites should be restored and are those breeding sites on SHP properties. We examined if the SHP properties contain active breeding sites that vastly improve *P. borealis* connectivity. Finally, we determined which breeding sites are threatened by encroaching urbanization and thus should be the focus of future enrollment in the SHP.

Methods

Focal species

P. borealis is a cooperative breeder that exhibits territorial behavior. Territories are composed of two or more trees with nesting cavities that are aggressively defended by a single family group (Walters et al. 1988). The family group is usually composed of a single breeding pair and up to four helpers that assist and care for subsequent offspring (Walters et al. 1992). Juvenile males often remain in their home territory as helpers for several years (Walters et al. 1988, Walters 1990, Haig et al. 1994). High-quality *P. borealis* territory habitat contains a moderate density of mature longleaf pine trees, low density of small and medium sized pines, little or no hardwood midstory, and abundant diverse herbaceous groundcover (Conner et al. 2002, Rudolph et al. 2002, Walters et al. 2002). Hardwood encroachment and degraded cavities are strongly correlated with abandonment of territories (Hovis and Labisky 1985, U. S. Fish and Wildlife Service 2003a). Territories can remain inactive for decades but territories are occasionally recolonized by dispersing individuals (Walters et al. 1988).

In contrast to males, juvenile females have been observed conducting prospecting forays from their natal territory to other territories before dispersing to a breeding site (Kesler et al. 2010,Chapter 2). During these forays, juvenile female *P. borealis* are influenced by environmental and conspecific cues (Chapter 3). Both foray and final dispersal distances of *P. borealis* exhibit a right-skewed distribution, with some juvenile females dispersing as long as 31 km, most disperse less than 3.3 km (Walters 1990, Kesler et al. 2010). *P. borealis* dispersing short-distances (< 6 km) are strongly affected by environmental features while long-distance dispersers (> 6 km) are less influenced by environmental features (Chapter 2 and 3).

Study Area

This study was conducted over a 3,721 km^2 area (79°12'12"W 35°7'31"N; Figure 5.1) in the Sandhills ecoregion in North Carolina (Griffith et al. 2007). This region contains rolling topography and deep fluvial sandy soil intermixed with clay soil at an average elevation of 103 m (Skeen et al. 1993). Historically, the prevailing vegetation type throughout the region was the fire-dependent, longleaf pine woodlands, characterized by an open canopy with minimal hardwood midstory and dense herbaceous understory vegetation (Provencher et al. 2001, Frost 2006). Currently, the dominant vegetation in the region is comprised of cropland, pasture, and mixed woodland forests (Griffith et al. 2007). The remaining evergreen forests are primarily composed of mixed-pine species (longleaf, loblolly [*P. taeda*], shortleaf [*P. echinata*], and pond pine [*P. serotina*]) in second-growth forest with varying amounts of hardwood understory and midstory (Griffith et al. 2007).

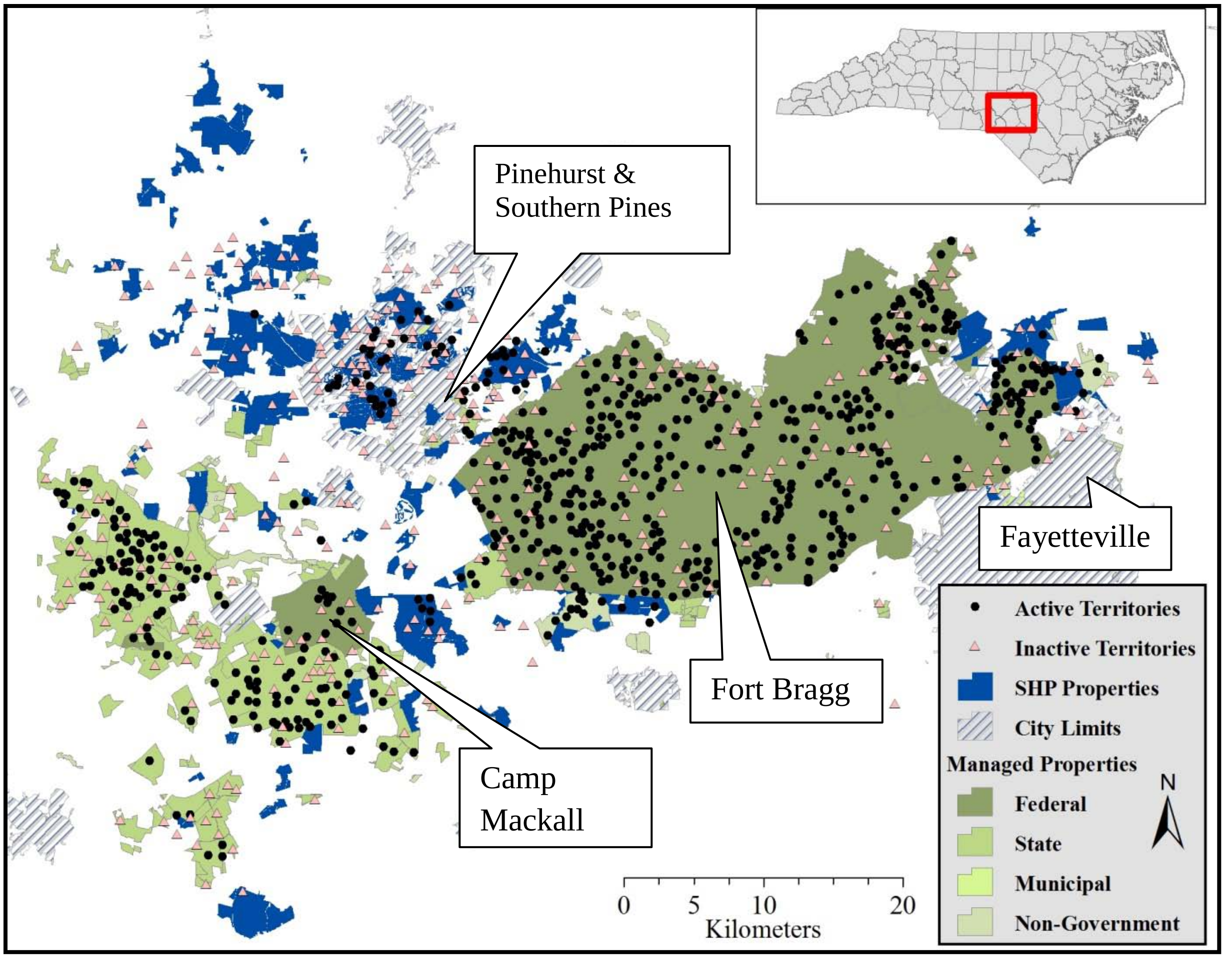

Figure 5.1 Red-cockaded woodpecker (*Picoides borealis*) active and inactive territories in relation to land ownership and Safe Harbor Program properties in the Sandhills region of North Carolina (inset).

As in many land management in the Sandhills region, natural areas are protected and managed by an assortment of landowners. The federal government manages large tracts of longleaf pine forests on two military installations, Fort Bragg and Camp Mackall (Britcher and Patten 2004, Figure 5.1). These federal properties cover 17% of the study area but contain 65% of the established *P. borealis* territories. The second largest group of active territories is located on 196 km^2 of state-owned game lands. Most of the remaining active territories (*n* = 48) are located on 116 private properties voluntarily enrolled in the SHP. These properties range in size from 0.15 km^2 to 16 km^2 and the land use actions include private forest, residential properties, horse farms, golf courses, and land-trusts. Data on all SHP agreements established as of 2009 were included in this study. For a complete breakdown of landownership in relation to *P. borealis* breeding territories see Table 5.1.

Table 5.1The number of Red-cockaded woodpecker (*Picoides borealis*) territories grouped by landownership in North Carolina's Sandhills ecoregion.

	Area		**Territories**	
Ownership	**Total (km^2)**	**% Area**	**Active**	**Inactive**
Government				
Federal	660	17.4	442	105
State	298	8.0	147	78
Municipal	9	0.2	0	2
Conservation NGO	74	2.0	18	3
Safe Harbor Properties	232	6.3	48	60
Private Land	2448	65.8	15	85

DATA

Movement **–** Active *P. borealis* territories have been monitored by researcher from North Carolina State and Virginia Polytechnic Institute and State Universities, and biologist from Fort Bragg Endangered Species Branch and the Sandhills Ecological Institute, since 1981. Under their protocol, all juvenile and adult *P. borealis* are marked with a unique combination of bands and active territories are regularly monitored each breeding season. Detailed banding and monitoring methods are described in Walters et al. (1988). Banding data from juvenile females born between 2004 to 2007 and dispersed within their first year were used to evaluate movements to and from territories located on SHP properties.

To evaluate how landscape features influence *P. borealis* movement behavior, we radio-tracked juvenile female birds foraying to potential breeding sites. In spring (March – May) 2006, 18 juvenile female *P. borealis* that had not yet obtained a breeding status were captured in their roosting cavities and fitted with a 1.4 g transmitter glued to the base of 2 tail feathers (BD-2, Holohil Systems Ltd., Ontario, Canada). Theses birds were tracked for the life of their radio transmitters (~ 9 wks) on the western portion of Fort Bragg, which contains the largest continuous tracts of longleaf pine forest on the property. An additional 16 female were radio tagged and tracked during 2007 in the eastern section of Fort Bragg, which consists of highly fragmented forest surrounded by urban and agriculture land use. We attempted to locate radio-tagged woodpeckers daily. Radio-tagged birds were ordered in a list by geographic location, and then a single individual was randomly selected to be the first daily observation. Animals were located via homing by using signal strength and direction with a receiver (R-1000, Communication Specialist, Inc. Orange, CA, USA) and a 3-element Yagi directional antenna (Wildlife Materials, Inc., Carbondale, IL, USA). When an individual was located outside its home territory we recorded a Universal Transverse Mercator (UTM) coordinate using a hand-held Garmin® global positioning system unit (GPS; Olathe, KS, USA).

***Forest Structure* –** Forest structure attributes expected to influence *P. borealis* movement behavior were estimated using airborne Light Detection And Ranging (LiDAR) data. The LiDAR data were collected during leaf-off canopy conditions between 31 December 2000 and 18 February 2001 by subcontracted engineering and surveying firms for the state of North Carolina (Greenhorne & O'Mara Inc. 2004). The flight paths of two different subcontractors overlapped our study area with varying sample density and flight altitude. The average ground spacing between LiDAR postings ranged from 2 - 2.25 m, flight altitude ranged from 914 – 1676 m, and the elevation calibration ranged from 9 – 12 cm root mean square error of elevation (RMSE-z). The raw LiDAR data containing three-dimensional coordinates of laser hits were converted to raster format with Fusion software (McGaughey 2008). In Fusion, the height from the ground was calculated for the LiDAR points as the difference between the point's elevation values and digital elevation models from North Carolina floodplain mapping program. With Fusion software, six LiDAR-derived forest structure variables were estimated at a 30 x 30 m resolution, including maximum vegetation height, percent cover in each of the four distinct height classes (1-8 m, 8-13 m, 13-20 m, and greater than 20 m), and skewness of vegetation heights. Dense forest, such as plantations or hardwood forests, with few gaps in the canopy produce a negatively skewed distribution of vegetation heights, where the greatest density of returns comes from the canopy. Forests with an open canopy and minimal midstory vegetation, such as mature longleaf pine forest (Peet 2006), produce a positively skewed distribution of vegetation heights, with the majority of the returns reaching the herbaceous vegetation in the understory and a small density of returns coming from the canopy.

MODELS

Habitat Quality – Habitat quality around *P. borealis* territories was characterized with a maximum entropy modeling approach. We used the software Maxent, which is a machine-learning algorithm that estimates habitat suitability based on known species locations (e.g., museum records or breeding sites) and layers of environmental data (Version 3.3.1, Phillips et al. 2006). Maxent uses the environmental data associated with species known occurrence locations to predict the distribution of a species using the distribution that maximizes entropy (i.e., closest to uniform) (Elith et al. 2006, Phillips et al. 2006).

The Maxent software requires two types of input data, grids with environmental variables and coordinates of species occurrences. To estimate habitat quality at breeding sites, we used the six LiDAR-derived forest structure variables for environmental data and active territory locations (n = 670) for occurrence data. These occurrence locations were randomly divided into training (75%) and testing (25%) points. To account for variation in training and testing data sets, we used bootstrapping with 10 replicate samples (with replacement). Maxent produces a raster containing the probability of habitat quality, with raster values near one indicating the most suitable habitat conditions and values near zero indicating unsuitable habitat (Phillips and Dudik 2008). Using this raster, we calculated the average habitat suitability within 174 m of each territory center. This radius was selected based on the median territory area defined by the outer boundary of the territories cavity trees (A. Trainor, unpublished data). The average habitat suitability values for each territory were then used as a node-level attribute in the connectivity model (*See Graph Networks*).

Resistance surface – We estimated *P. borealis* movement behavior in relation to the environment by assigning land-cover characteristics values that reflect the degree to which they impedes or facilitates dispersal movements, known as a friction value (Adriaensen et al. 2003). A continuous raster of friction values represents a resistance surface

(Adriaensen et al. 2003). For this study the resistance surface was estimated *P. borealis* dispersal behavior in relation to forest structure and radio telemetry data with Maxent. The same six LiDAR-derived forest structure variables were used for environmental grids, but occurrence locations (territory centers) were replaced with non-natal telemetry locations (*n* = 1710). Because we modeled movement behavior on the basis of telemetry locations for prospecting birds, we assume that Maxent's habitat quality raster is inversely related to a resistance surface for dispersal movement behavior. That is, *P. borealis* resistance to movement due to forest structure should increase as habitat quality decreases. Given this, the habitat quality values (h) estimated with Maxent and ranging from 0 to 1, were converted into friction values (v, where friction is a measure of resistance) with the function,

$$v = 100 - 99 \times \frac{(1-e^{(-4h)})}{(1-e^{(-4)})}. \tag{1}$$

This non-linear relationship between habitat suitability and friction values is a better predictor of *P. borealis* movement behavior than a linear transformation(Chapter 2). A range of friction values from 1 to 100 was chosen, where the lowest value (1) is assigned to the most suitable habitat (Maxent habitat quality h = 1) and the highest value (100) is assigned to the least suitable habitat (Maxent habitat quality h = 0). The resistance surface was then processed with the Cost Distance model (ArcInfo Workstation, Environmental Systems Research Institute, 2008), which determines the shortest accumulated travel cost between all territories. For our study the cost distance model calculated the friction-weighted distance (d_{ij}) from territory i to territory j for all territories.

Graph Networks **–** A graph is a set of nodes (points) connected to some degree by links or edges. For this study, the nodes in the graph networks represented territory centers. Graph nodes were attributed with the average habitat suitability of each territory. Graph edges were weighted to represent probability of direct dispersal between all pairs of territories. To accomplish this, we used observed dispersal events to calculated the population's least-cost friction-weighted distance (d_{ij}) between a juvenile female’s birth territory (i) and its subsequent breeding territory (j). The frequencies of all d_{ij} were then fit to a lognormal probability density function where μ and σ are the mean and standard deviation of the natural logarithm of distances, respectively (Figure 5.2). The lognormal distribution was selected because if the minimum range of the distribution is defined as zero and the two parameters are able to fit short and long-distance movements into a single function. The frequency distribution of the observed functional dispersal distances fit the lognormal distribution based on Kolmogorov-Smirnov test (p = 0.06).

The friction-weighted distances were converted into probability of dispersing between all pairwise combinations of active territories with the fitted lognormal probability density function. The probability of direct dispersal (p_{ij}) was characterized as 1 – normalized frequency distribution for a given friction-weighted distance (see Figure 5.2). This was calculated as

$$p_{ij} = 1 - \frac{1}{d_{ij}\sigma\sqrt{2\pi}} e^{\frac{\left(ln d_{ij} - \mu\right)^2}{2\sigma^2}}, \tag{2}$$

Probability of dispersal (p_{ij}) near one indicates a strong connection between two territories because they are functionally close to each other and p_{ij} near zero indicates a weak connection between territories.

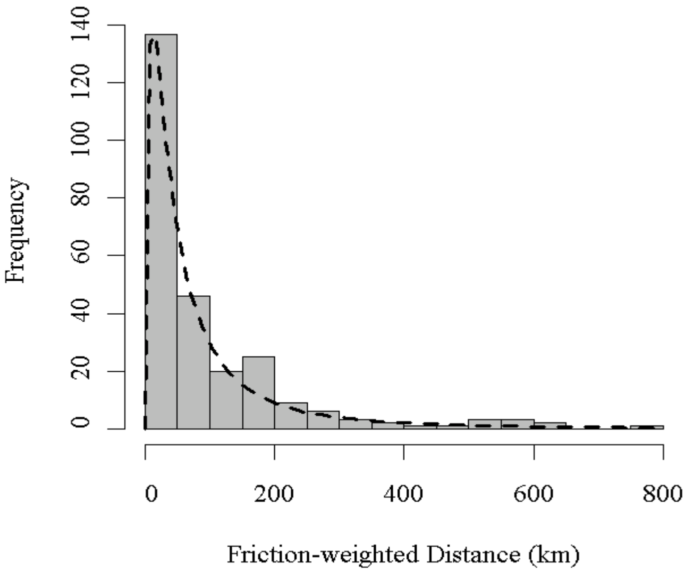

Figure 5.2 The frequency of observed least-cost friction-weighted dispersal distances with the dashed line representing the fitted distribution based on a lognormal function.

Analysis

To measure the contribution of SHP properties to the overall connectivity of *P. borealis* populations in the Sandhills region we used the network-level probability, Probability of Connectivity with Equivalent Connectivity (PCEC) with Conefor Sensinode software (Version 2.5.8, Saura and Torne 2009, Saura et al. 2011). PCEC integrates habitat availability, probability of dispersing between habitat patches, and graph network for all nodes. PCEC values increase with connectivity and represent the probability that two individuals randomly placed within the landscape fall into territories that are reachable from each other (interconnected) given the set of *n* nodes (territories) and the connections (p_{ij}) among them (Saura et al. 2011). PCEC is calculated as

$$PCEC = \sqrt{\sum_{i=1}^{n} \sum_{j=1}^{n} a_i a_j p_{ij}^*}, \tag{3}$$

(Saura and Pascual-Hortal 2007, Saura and Torne 2009). The node attributes a_i and a_j denote the average habitat quality of territories *i* and *j* and they range from 0 to 1. These values were Maxent-derived average habitat quality estimated at each territory (*see Habitat Quality).* The variable p_{ij}^{*} (Equation 3) is the maximum product probability, or the best route, of all possible paths between territories *i* and *j*, including single-step paths (Saura et al. 2011). For example, the best route between territories *a* and *d* (p_{ad}) in Figure 5.3 is the product of all dispersal probabilities if many small steps because this path has greater dispersal probability than the direct connection between *a* and *b*. Therefore, $p_{ad}^{*} = p_{a>b>c>d}$ (Figure 5.3).

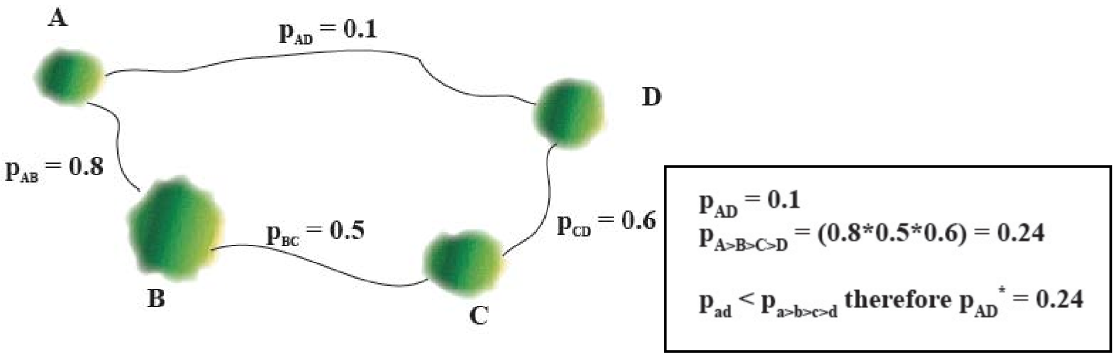

Figure 5.3 An example of the comparing the direct dispersal probability (p_{ad}) to dispersal probability of each connection ($p_{a>b>c>d}$). This comparison used to illustrate the calculation of the maximum product dispersal probability (p_{ad}^{*}) between territories A and D.

The population-level connectivity was evaluated by comparing PCEC metric for networks created with territories for each landowner type. Specifically, five separate networks were created with territories on 1) only federal property, 2) all managed properties (government and non-government agency conservation properties 3) all managed properties and private properties enrolled in the SHP, 4) all managed properties and private properties not enrolled in SHP, and 5) all territories in the study area.

The network with all territories was used for the remaining analysis. We ranked inactive territories according to how much connectivity they would contribute to the entire network. We applied the node addition option in the Conefor software, which iteratively adds each inactive territory to the network with active territories and recalculates the PCEC value (Saura and Pascual-Hortal 2007, Saura et al. 2011). For each inactive territory, the percent importance (d$PCEC$) was calculated as:

$$dPCEC_{add}(\%) = \frac{PCEC_{add} - PCEC}{PCEC} \times 100, \quad (4)$$

where $PCEC_{add}$ is the connectivity value after an inactive territory is included in the network (Saura and Pascual-Hortal 2007, Saura et al. 2011). Using $dPCEC_{add}$ as the ranking criteria, all inactive territories' on private land were ranked from having the highest potential to improve connectivity to having the least contribution.

We also evaluated the effect of losing active territories on private land due to lack of enrollment or participants leaving the SHP agreement. We iteratively removing each territory from the network and recalculating the PCEC connectivity according to the following equation,

$$dPCEC_{remove}(\%) = \frac{PCEC - PCEC_{remove}}{PCEC} \times 100, \quad (5)$$

where $PCEC_{remove}$ is the connectivity value after each active territory is removed from the network.

Our final objective was to evaluate if territories on SHP properties protect current connectivity when the region is facing urban encroachment. A SLEUTH (Slope, Land use, Exclusion, Transportation, and Hillshade) model was used to project spatially explicit urban growth throughout the study area. SLEUTH is a cellular automaton model that predicts the probability that each cell will become developed through time (Clarke and Gaydos 1998, Jantz et al. 2010). The model contains nested loops of five pre-defined and self-modifying growth rules (diffusion, breed, spread, slope resistance, and road gravity) with four types of urban growth models (spontaneous, diffusive, organic, and road influenced) (Clarke and

Gaydos 1998). The growth rules and models are then calibrated with historical data and Monte Carlo simulations to match observed local growth patterns (Silva and Clarke 2002).

Recently, the SLEUTH model was modified and executed by the North Carolina Cooperative Fish and Wildlife Research Unit at North Carolina State University for the Southeast Regional Assessment Project (McKerrow et al. 2010). They defined the current urban extent with road density and urban class within the National Land Cover Dataset. Within the Sandhills region, the SLEUTH model was processed for six combined statistical areas delineated on the basis of 2009 census data (Terando et al. In Preperation).

The input layers for this regional model were: the National Elevation Dataset (slope and hillshade), National Land Cover Dataset (general land cover and urban land use), National Gap Analysis Program (GAP) land cover (detailed land cover and land management and ownership), and U.S. Census Bureau's Topographically Integrated Geographic Encoding and Referencing (TIGER, transportation corridors) (Terando et al. In Preperation). The GAP dataset was also used to exclude urban growth on government-owned property, private conservation lands, and open water. Wetlands were assigned a low probability of development (Terando et al. In Preperation). Twenty-five iterative Monte Carlo simulations and four years of urban land-use maps (1992, 1996, 2001, and 2006) were used to calibrate the SLEUTH model. The product of the Sandhills SLEUTH model was forecasted urban growth at yearly increments from 2009 to 2100.

Projected urban growth in 2050 and 2100 was used to examine *P. borealis* change in connectivity. For both years, the cells on the resistance surface with > 50% probability of urban growth had their friction values increased to represent the predicted landscapes. The least-cost friction-weighted distances and dispersal probabilities (p_{ij}) between territories were recalculated for 2050 and 2100 predicted landscapes (Figure 5.4). The PCEC and d$PCEC_{remove}$ connectivity metrics were calculated for all territories with the 2050 and 2100 urban growth models.

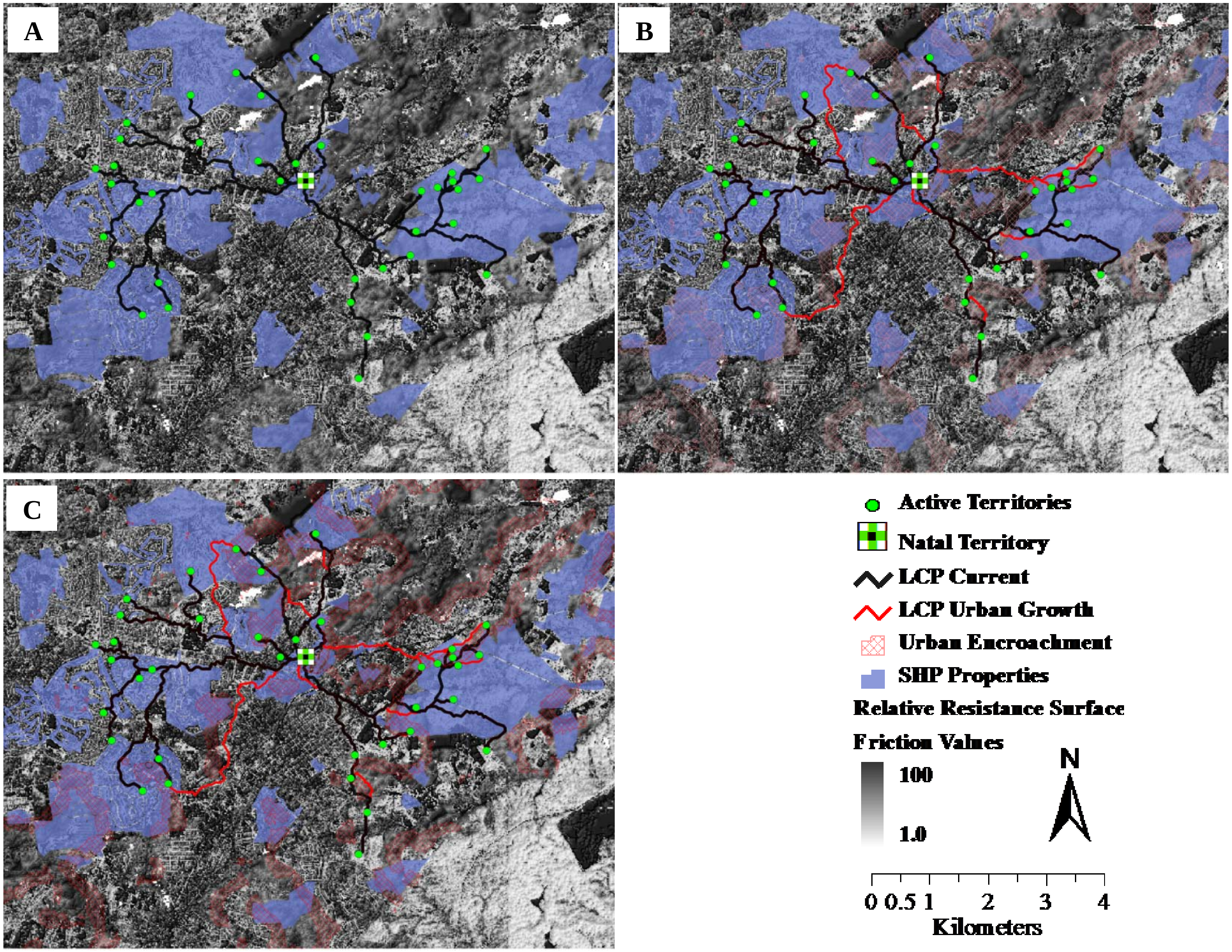

Figure 5.4 Example of the resistance surface and least-cost path (LCP) from natal territory to nearby (< 6 km) active territories for current conditions (a) and projected urban growth for 2050 (b) and 2100 (c).

Results

Seventy-three private property owners in the Sandhills region have participated in *P. borealis* SHP since its inception in 1995. The average property size is 2.0 km^2 (SE = 0.4). The largest property is 16 km^2. These SHP properties house an average of 2.73 (SE = 0.56) and 1.75 (SE = 0.25) active and inactive territories, respectively. The active territories contained higher habitat quality than inactive territories (Figure 5.5). Inactive territories situated on non-SHP private properties had the lowest average habitat quality. Within SHP properties, habitat quality for active and inactive territories differed for all land-use activities, except residential (Figure 5.5). Active territories in private forests and land trusts have the highest average habitat quality (Figure 5.5). The habitat quality for active and inactive territories is widely distributed throughout the region (Figure 5.6).

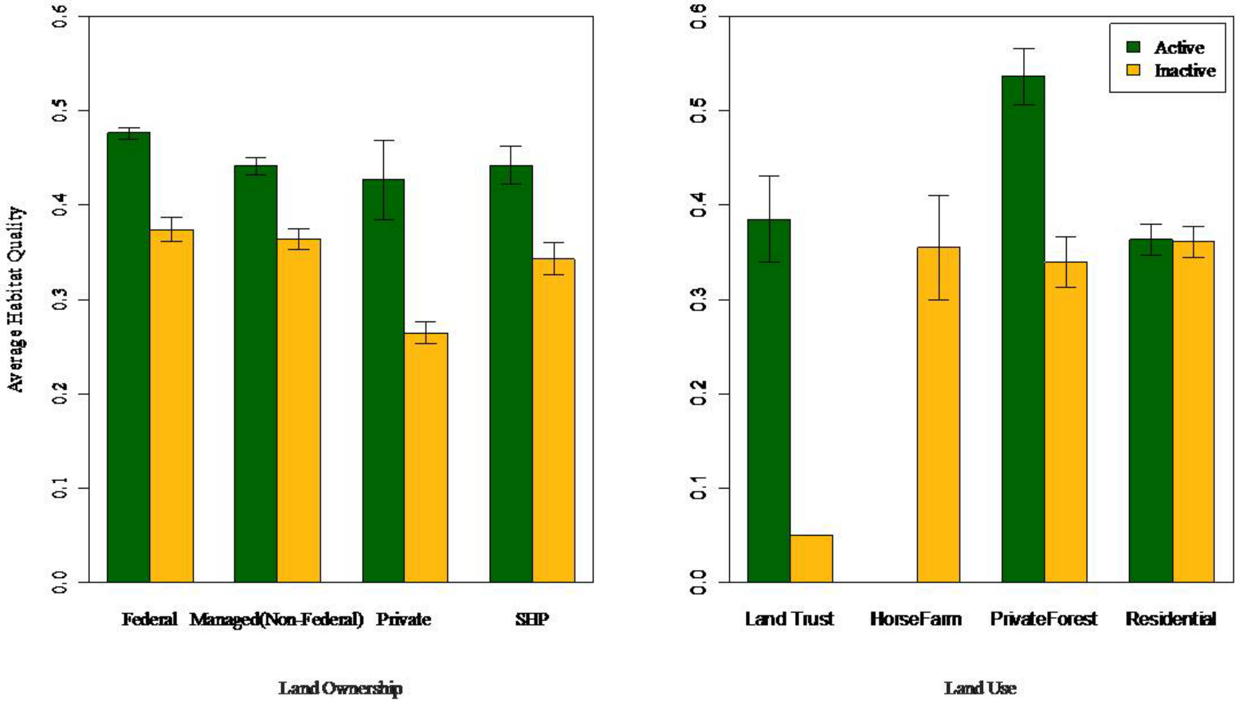

Figure 5.5 The average (+/- SE) habitat quality for territories by landowner (left) and private properties enrolled in the Safe Harbor Program (SHP) by the participants land-use activities (right).

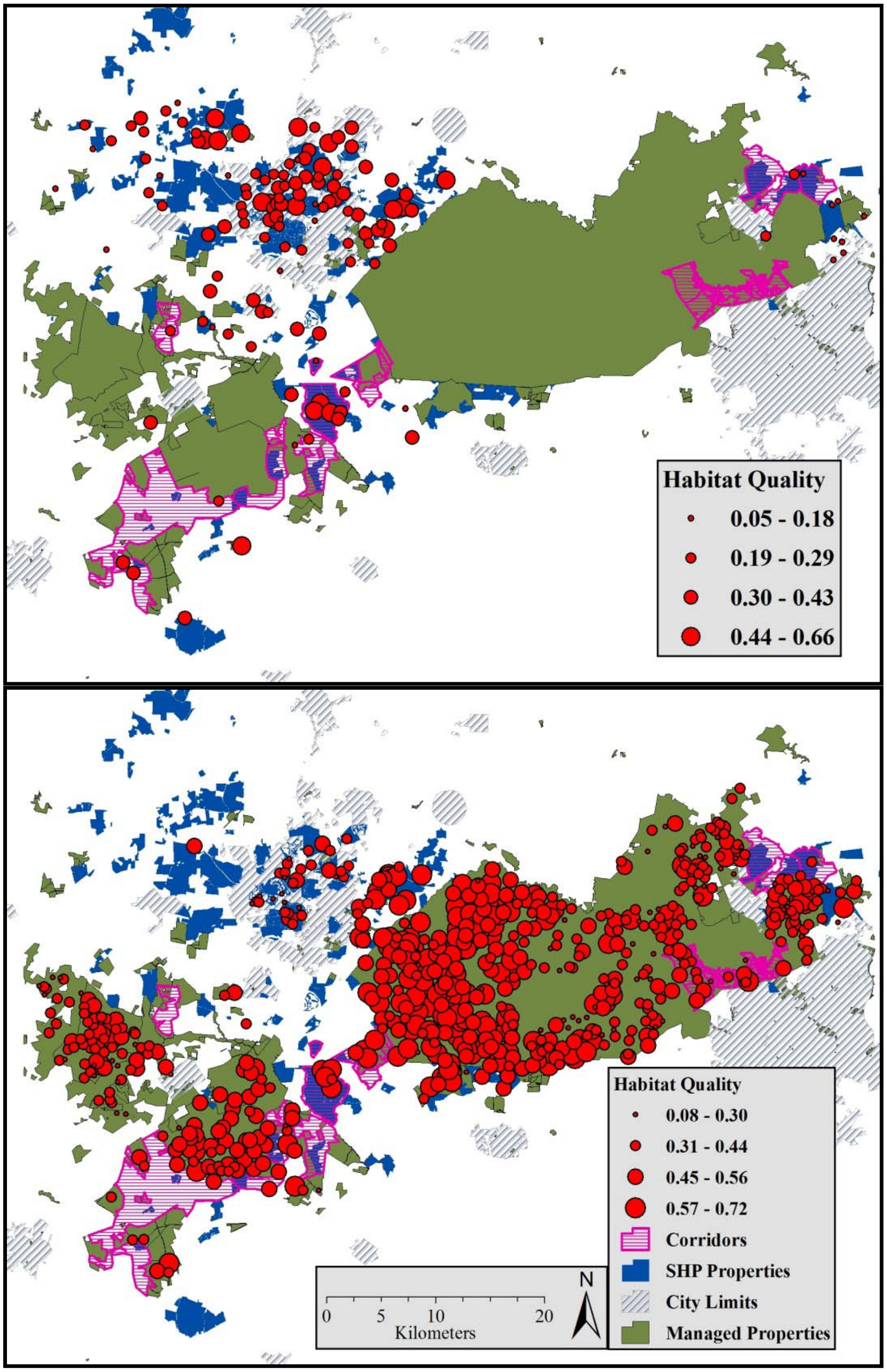

Figure 5.6 The habitat quality for inactive (top) and active (bottom) Red-cockaded woodpecker (*Picoides borealis*) territories in North Carolina's Sandhills region.

Mark-recapture banding data provided insight into SHP contribution to *P. borealis* connectivity (Figure 5.7). Out of the 259 observed juvenile female dispersal events from 2004 to 2007, 19 juvenile female *P. borealis* dispersed from a natal territory located on a SHP property to breeding territories on the same or another SHP property. The average and maximum dispersal distance for these birds were 2.2 km and 8.9 km, respectively. Twelve additional individuals born on SHP properties dispersed an average of 6.4 km (maximum = 22.9 km). Nine of these birds settled on properties owned by government agencies and non-profit conservation organizations while three birds settled on private properties not enrolled in the SHP. Fourteen juvenile females born on non-SHP territories obtained breeding status on SHP properties, dispersing an average of 14.6 km (maximum = 30.8 km).

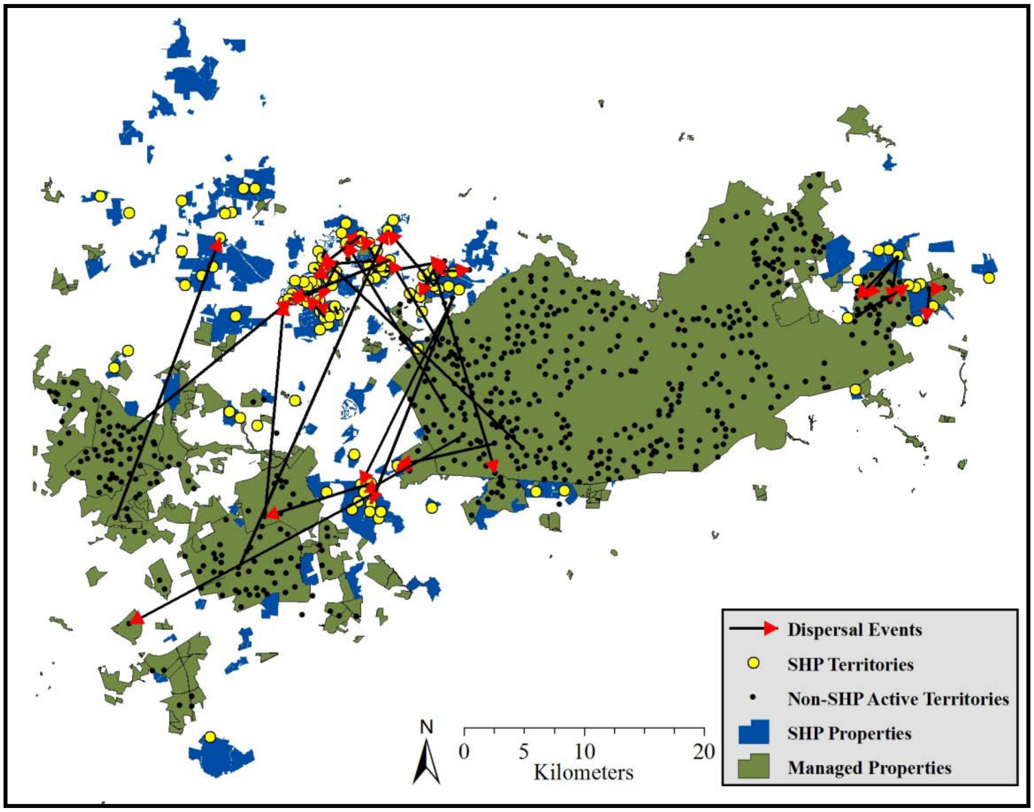

Figure 5.7 Observed natal dispersal events during 2004 to 2007 for juvenile female Red-cockaded woodpecker (*Picoides borealis*) born on and/or dispersed to territories on properties enrolled in the Safe Harbor Program (SHP) in the Sandhills region of North Carolina.

According to the landscape-level connectivity metric PCEC, connectivity increased with number of territories. The network with the fewest territories (*n* = 442) with only federally-owned properties had the lowest connectivity (PCEC = 111.1, Figure 5.8). When networks contained all territories on managed properties (federal, state, municipal, and non-government conservation lands, *n* = 607) PCEC rapidly increased to 121.2. The maximum PCEC value of 128.1 was reached when all 670 active territories were included in the network. The network contained territories on SHP properties was slightly higher than the network that included territories from non-SHP properties (Figure 5.8).

With the entire network we then ranked inactive territories by potential contribution to connectivity. Inactive territories on SHP properties contribute to connectivity greater (average dPCEC = 0.069, SE = 0.009) than territories on non-SHP participating private properties according to t-test (average dPCEC = 0.041, SE = 0.005, p = 0.011). Territories with the lowest contribution to connectivity were primarily located on the outer edge of the network. In contrast, the inactive territories with the greatest contribution to connectivity were located northwest of Fort Bragg and between Fort Bragg and Camp Mackall military installations (Figure 5.9). Of the 34 inactive territories ranked the highest 25th percentile that have the greatest contribution to connectivity and to improve connectivity, 18 were located on 10 SHP properties containing private forests (*n* = 4), residential properties (*n* = 5), and a horse farm (*n* = 1).

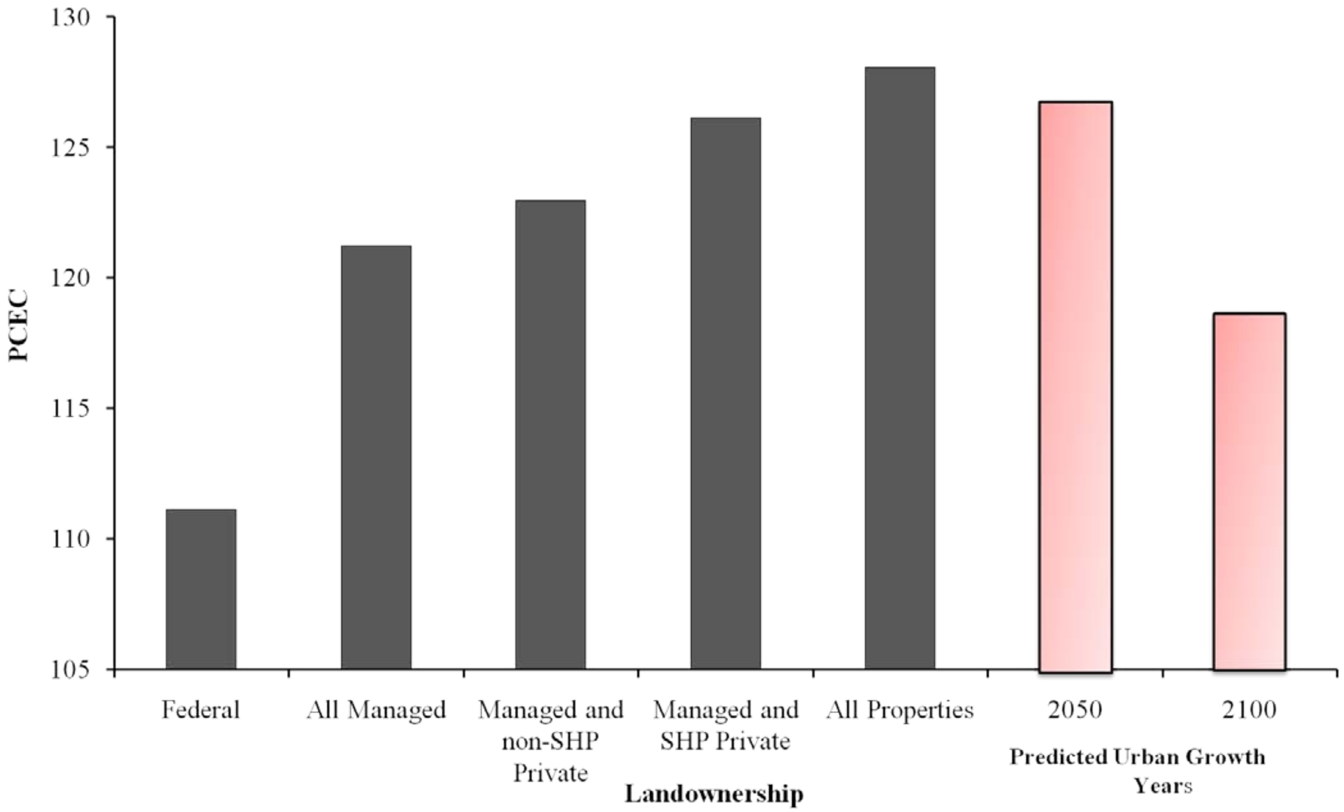

Figure 5.8 Red-cockaded woodpecker (*Picoides borealis*) connectivity represented with Probability of Connectivity with Equivalent Connectivity (PCEC) based on present landscape conditions with five separate networks landownership [1) federal-only property, 2) all managed properties (government and non-government agency conservation properties, 3) all managed properties and private properties enrolled in the SHP, 4) all managed properties and private properties not enrolled in SHP, and 5) all territories in the study area] and networks created based on projected urban growth (red bars).

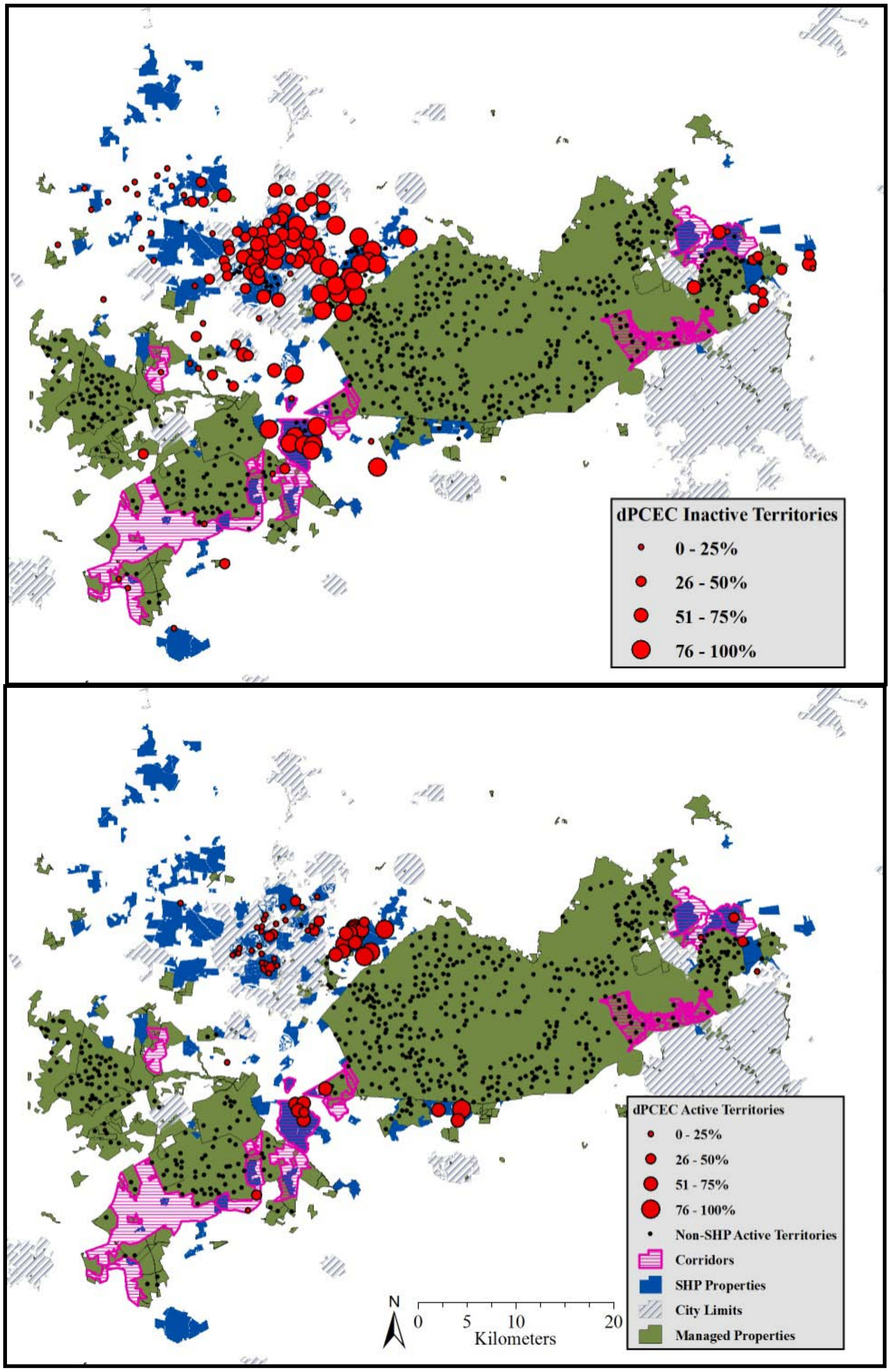

Figure 5.9 The distribution and relative contribution to connectivity (dPCEC) for inactive (top) and active (bottom) Red-cockaded woodpecker (*Picoides borealis*) territories on privately-owned land in North Carolina’s Sandhills region.

We also evaluated how active territories on private properties contribute to overall connectivity. Similar to the inactive territories, the highest ranking active territories (dPCEC > 76%) were primarily located near managed properties (Fort Bragg and adjacent non-government conservation property). Over 70% of the territories ranked the highest 25th percentile were located on private forests currently enrolled in the SHP. The remaining high ranking active territories (*n* = 4) were located within 2 km of Fort Bragg boundary on properties not participating in the SHP. A few of the lowest ranking active territories that contribute to connectivity the least were located east of Fort Bragg (Figure 5.9).

We then examined how urban growth could impact *P. borealis* connectivity and which territories are most vulnerable to urban encroachment. According to the landscape-level connectivity metric PCEC, the population's connectivity decreased with urban encroachment throughout the region (Figure 5.8). Projected urban growth in 2050 reduced connectivity by 1.2%, while connectivity decreased 5% with the 2100 urban growth projection. Based on the 2100 forecasted urban growth, 24 out of 670 active territories are vulnerable to encroachment. However, 13 out of the 24 territories are located on six SHP properties composed of private forests (*n* = 4) and residential properties (*n* = 2). The percent change in the distribution of relative important territories to overall connectivity (dPCEC) shifted throughout the population (Figure 5.10). For instance, the network created with 2100 urban growth suggests that territories on the western edge of Fort Bragg were impacted by urban growth while the territories on the eastern portion of Fort Bragg became more connected (Figure 5.10).

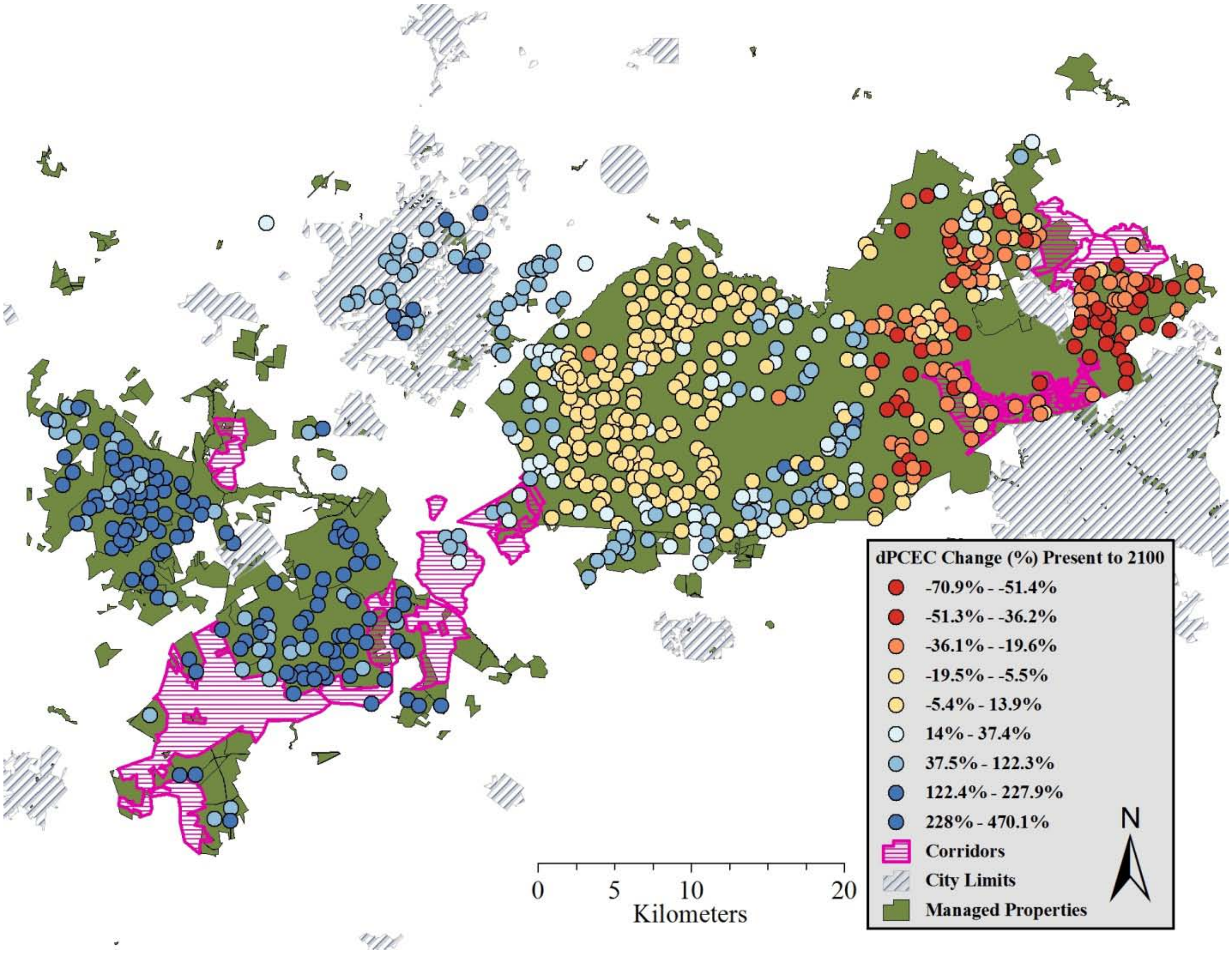

Figure 5.10 The percent change from current conditions to projected urban growth in 2100 based on relative importance of territories to connectivity (dPCEC). The hot colored territories represent connectivity increased with urban growth and colors represent territories' connectivity decreased due to urban growth.

Discussion

Previous reports evaluating *P. borealis* SHP agreements described individuals successfully colonizing new territories on SHP properties (U. S. Fish and Wildlife Service 2003a, Wilcove 2004, Walters et al. 2009). With additional mark-recapture banding data, we confirmed that juvenile female *P. borealis* regularly disperse to and from territories enrolled in SHP (Figure 5.7). This study goes further to show that territories on SHP properties contribute strongly to *P. borealis* connectivity. We also identified which territories on SHP and non-SHP private properties promote connectivity based on the current land-use conditions and projected urban growth.

As expected, a territories' relative contribution to connectivity is dependent upon its juxtaposition with other active territories. Connectivity models usually depict the proximity between resources with Euclidean distance (e.g., Keitt et al. 1997). However, animal movements can be predicted more accurately by replacing a uniform landscape with a resistance surface (Verbeylen et al. 2003, Magle et al. 2009, Richard and Armstrong 2010, Chapter 4). Since female *P. borealis* dispersal movements are affected by large open areas and subtle variation within forest structure (Chapter 2, Kesler and Walters In Review), we used a resistance surface that estimated the proximity between territories with friction-weighted distances. This methodology showed that territories within close geographic proximity of each other may be disconnected due to high friction-weighted distance if they are surrounded by poor quality longleaf pine forests, open fields, or development. Without creating additional territories, existing territories can become effectively closer and the population can be more connected by extending longleaf pine forest management and restoration activities onto private properties enrolled in the SHP.

With over 300 inactive territories in the Sandhills region (Table 5.1), restoring territories is an important management strategy employed by the USFWS. A common restoration activity is repairing nest cavities and inserting new cavities in nesting trees (U. S. Fish and Wildlife Service 2003a, Walters et al. 2009). However, cavity trees surrounded by poor quality habitat, such as dense mid-story vegetation, have lower reproductive success and are susceptible to abandonment (Conner et al. 1999, Davenport et al. 2000, Walters et al. 2002). Moreover, juvenile *P. borealis* rely upon social cues to evaluate a breeding site's reproductive potential (Chapter 3). Birds prospecting breeding sites will most likely not select unoccupied territories or territories few and unhealthy fledglings from the previous year which indicates low reproductive success. Therefore, restoring cavities alone may not be sufficient management to increase the abundance and viability of *P. borealis* populations. To increase connectivity, technical and financial assistance provided by USFWS should not only be used to restore cavities but to also increase breeding and foraging habitat quality on SHP properties.

To-date, most *P. borealis* management practices have been directed towards preserving and restoring habitat near territories on government-owned land (U. S. Fish and Wildlife Service 2003a, Darden 2004). This trend is partially due to the difficuly in coordinating conservation efforts beyond government boundaries because of limited access by private landowners (Bean 1998, Theobald and Hobbs 2002). Without site visits, we were able to identify which properties have the highest potential contribution to the populations' connectivity. This was accomplished by using publically available LiDAR data, territory locations, and movement behavior into a connectivity network. This approach will allow agencies to allocate more time and resources to promote SHP benefits to a targeted set of private landowners not yet enrolled into the program.

Due to natural and anthropogenic land-cover characteristics preventing movements, species may not detect or reach new/restored resources (Trainor et al. 2007). Even though *P. borealis* are strong fliers, their movements can be impeded by open fields or development (Kesler et al. 2010, Kesler and Walters In Review, Chapter 2). Thus, improving habitat quality and restoring cavities does not guarantee a bird is going to detect or recolonize a restored territory. To mitigate this problem managers have translocated juveniles to restored territories (Rudolph et al. 1992, Allen et al. 1993, U. S. Fish and Wildlife Service 2003a). However, the USFWS has recently suspended permission to translocate *P. borealis* in Sandhills population (Jeffery Walters, *personal communication*). Since *P. borealis* can only recolonize territories naturally, properties with high probability of being connected to the remaining population should have greatest priority when allocating funds to restore territories.

Recovery of federally-protected species' are not only dependent upon quality and quantity of available resources but on the spatial arrangement of habitat on the landscape (Bonnie 1999). For example, *P. borealis* territories are highly connected with federal (Fort Bragg and Camp MacKall) and state-owned properties with limited movements between government properties (Chapter 4). Unfortunately, these government-owned properties are a small island of managed forests surrounded by urban development and agriculture land-use activities (Warren et al. 2007). To increase connectivity throughout the Sandhills region, a working group composed of *P. borealis* experts delineated five corridors expected to better connect Sandhills population. Each corridor was ranked according to available habitat and potential for conservation actions (Unpublished data, USFWS). The top-ranked corridors, according to the working group, were located east of Fort Bragg and south of Camp MacKall. In contrast, our connectivity model suggests that territories located northwest of Fort Bragg have the greatest potential to increase the population's connectivity (Figure 5.8). Our results were also consistent with those of Walters and colleagues (2009), who suggest that stabilizing group dynamics and demography in the north west of Fort Bragg will improve the population's habitat connectivity. The working group noted the importance of this area, but assigned it the lowest priority partially because of the great financial cost involved in acquiring land for conservation (Unpublished report USFWS). Voluntary incentive-based programs, such as SHP, avoid the high cost associated with purchasing and maintaining public land by offering nonmonetary incentives (e.g., insurance from future land-use regulations) (Bonnie 1997, Main et al. 1999).

Since the SHP is voluntary, it is important to understand landowners' motivation to participate in the programs (Merenlender et al. 2004). Recently, Moon and Cocklin (2011) reported that private landowners' deriving income from the land (e.g., livestock grazing or crops) likelihood of participating in conservation agreements differently than nonproduction private landowners. To optimize SHP participation with a limited budget, SHP agreements should contain a variety of incentive options that appeal to private properties deriving income from the land (e.g., private forests) and nonproductive private property (e.g., residential). By incorporating habitat connectivity with SHP, it is possible to identify private properties that are able to significantly enhance a population's persistence. Once these properties are located, agencies can approach these private landowners to determine which type of incentives would increase their likelihood of participating in the SHP.

Since the primary cause in the decline of many federally-protected species is urban growth (Wilcove et al. 1998, Miller and Hobbs 2002), conservation planning on private property also needs to consider future threats to biodiversity. The development of urban growth models, such as SLUETH, has allowed researches to forecast urban encroachment for many cities throughout the world (Silva and Clarke 2002, Jantz et al. 2003, Yang and Lo

2003). To our knowledge, this is the first study to directly examine how urban encroachment influences a species' connectivity with a SLEUTH model. By combining the SLEUTH and the connectivity models, conservation plans can become proactive in protecting resource patches threatened by urban encroachment. We showed that increasing urban growth will negatively impact *P. borealis* connectivity (Figure 5.9). We also observed a decline in connectivity for territories on government-owned property, which was an unexpected result because government properties were excluded from future urban growth. This suggests that urbanization on private land can further isolate populations from populations on private land. SHP agreements can reduce the rate of urban growth through the region by directly preventing development on participants' properties. The wide spatial distribution of SHP properties will help maintain connectivity by providing stepping stones to allow movements between protected properties.

Conclusion

For many federally-protected species, conservation has focused on parks and reserves with minimal consideration about the surrounding land use activities.(Waller 1990). However, these public lands are inadequate to sustain viable populations or maintain all biodiversity (Grumbine 1990). Moreover, degraded landscape between these properties can restrict movements and increase the probability of local populations becoming extinct (Fahrig and Merriam 1994).

Incentive-based programs like SHP are needed as an additional conservation options on private property (Noss et al. 1997). We have shown that the voluntary incentive SHP increased connectivity by improving longleaf pine forests and protecting *P. borealis* resources from urban growth on SHP properties. While individual SHP properties are relatively small, coordinating conservation efforts with other SHP properties and collaborating with government agencies can greatly improve species persistence. As movement data becomes available for other federally-protected species, the approach applied in this study can be expanded to further evaluate SHP impact on connectivity and strategically identify optimal locations for enrollment to mitigate current and future threats.

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CHAPTER 6

CONCLUSION

Summary of major results

My research integrated animal behavior, landscape ecology, and wildlife management disciplines. Using multiple spatial and temporal scales of animal movement data with remote sensing technology, I estimated Red-cockaded woodpecker (*Picoides borealis*) connectivity among fragmented longleaf pine forests. This multi-scale approach demonstrated the importance of including detailed dispersal behavior when estimating and validating habitat connectivity. The connectivity model was correlated with an extensive set of observed dispersal events, which allowed me to examine the patterns in *P. borealis* dispersal in terms of network topology. This biologically calibrated connectivity model, created by incorporating detailed dispersal ability data for the entire dispersing portion of the population, was used to identify territories that are necessary to maintain well connectivity and those where occupancy might be limited due to environmental barriers to dispersal. The conclusions from my research are:

1. According to an empirically-derived resistance surface, *P. borealis* are influenced by subtle changes in forest structure and land-use activities and the influence of land-cover types were distinct for long and short-distance dispersers.

2. Prospecting individuals’ are cueing into environmental characteristics between breeding sites and complex social dynamics at potential breeding sites. By correlating the network model with and extensive set of observed dispersal events, I found that the abrupt transition from highly connected to disconnected territories provides insight into habitat connectivity within and between habitat patches.
3. Voluntary incentive-based conservation programs on private land are able to increase the connectivity of federally-protected species in fragmented landscapes.

Fundamental Contributions

The research I carried out for this dissertation contributed to bridging the gap between wildlife management and landscape ecology. For decades both disciplines have made many contributions to preserving biodiversity with different approaches. Wildlife management originated from natural history discipline that primarily links detail field observation with environmental features. As a result this discipline developed extensive toolsets to monitor and manage wildlife populations affected by human-induced stresses (Caughley 1994, Braun 2005). In contrast landscape ecology is an interdisciplinary field strives to understand causes and ecological consequences of spatial heterogeneity across a landscape by examining landscape structure, function, and change by linking pattern and process (Liu and Taylor 2002).

Landscape ecology studies typically integrate only a few details regarding species behavior and resource requirements when examining landscape-level processes at variety of spatial and temporal scales (Turner et al. 2002). Moreover, wildlife management studies do not usually expanded their research objected far beyond managing for specific species at small spatial scales (Turner et al. 2002). My dissertation connects these two disciplines by using detailed movement behavior and resource requirements to evaluate a population's reaction to fragmentation at regional scale (Table 6.1). I used monitoring data from mark-recapture and radio-telemetry methods along with remote sensing data (LiDAR and Landsat) to evaluate how species react to detailed land-cover types. This information was then used to determine the optimal location for future conservation and management activities at local and regional scales.

This dissertation also contributed to the growing knowledge of *P. borealis* biology. Based on previous mark-recapture data, *P. borealis* have a complex social structure, are sensitivity to degraded longleaf pine forests, and are potentially strong disperses. In Chapter 2 and 3, I suggested that extensive extra-territorial forays are guided by subtle changes in land-cover characteristics while the social cues encountered at the breeding sites help the prospecting individual to predict the site reproductive potential. The complex dispersal behavior collected for this research and previous studies were combined to estimate *P. borealis* connectivity within and between forest patches (Chapter 4). The connectivity model then showed that voluntary incentive-based programs aided in the recovery efforts for *P. borealis* populations by increasing connectivity with habitat improvements on private land (Chapter 5).

Table 6.1 Overview of landscape ecology and wildlife management disciplines and how this dissertation bridges the gap between the two fields.

	Landscape Ecology	Wildlife Management	Bridging the Gap
Goals	Understanding causes and ecological consequences of spatial heterogeneity	Understanding species biology and resource requirements	Incorporate movement behavior and resource requirements to understand the consequence of fragmentation.
Scale	Process oriented	Management oriented	Applied multiple scales of resources (breeding site to forest patch) and behavior (prospecting and dispersal movements) to evaluate connectivity within and among managed properties.
Data	Remote Sensing and simulation	Mark-recapture, Radio-telemetry, and Vegetation sampling	Integrated mark-recapture and radio telemetry data with LiDAR and Landsat data to evaluate species response to land-cover types and vegetation structure.
Tools	GIS, Spatial statistics, and Simulation modeling	Monitoring, Estimating demography, and Resource selection	Combined detailed monitoring information in GIS and spatial statistics to prioritize future management practices.

Future contributions

The research conducted in this dissertation sheds light on how landscape ecology and wildlife management disciplines can be integrated to achieve more effective conservation strategies. The ultimate objective of conservation and management activities are to insure persistence of the target species, which is achieve through increasing species survival and reproduction. This research evaluated the necessary first step for population-level process, movement and connectivity between breeding sites. Since I defined nodes as breeding sites in the graph network model, it is very easy to linking reproduction and survival dynamics with detailed movement behavior and regional habitat connectivity. In addition, this approach allows juxtaposition of breeding sites composition of the intervening landscape to assess population persistence in fragmented landscapes.

The movement data used in this study only focuses on a small portion of the population (e.g., prospecting late-dispersing juvenile females and dispersing juvenile females). The inference of this research is limited to juvenile female *P. borealis* connectivity. Recognizing that dispersal pattern can vary by sex, age, and reproductive status, means that the response late-dispersing juvenile females may be different than early-dispersing females who are exploring novel environments. Therefore, radio-tracking individuals as they beginning fledgling from their nest can provide greater insight into species reaction to these new landscapes. Further, radio-tracking males could reveal complex dispersal behavior and provide insight into why some males stay as helpers and some search for breeding vacancies.

This research would not have been possible without the extensive and continuous monitoring effort put forth by many agencies, academic institutions, and research institutes. Few common species, and even fewer federally-protected species have such wealth of data to provide detailed movement behavior and population-level knowledge. For the small number of protected species with monitoring projects, such as Northern Spotted owl (*Strix occidentalis caurina*), Northern goshawk (*Accipiter gentilis*), and Canadian lynx (*Lynx Canadensis*), reproductive and survival rates are well known with long-term mark-recapture data and movements have been monitored with radio-telemetry. However, habitat connectivity models for these species, if conducted at all, do not take use all the available tools available from landscape ecology discipline to estimate connectivity in heterogeneous landscapes. In addition, remote sensing data and technology is becoming readily available to general public. The monitoring and remote sensing data can be easily input into the approaches developed in this dissertation as movement behavior and land-cover types to allow the species movements explain how landscape characteristics influence their dispersal behavior. This information can then be used to get better insight into how species respond to environment and estimate habitat connectivity to improve the effectiveness of regional conservation efforts.

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