FINAL REPORT

Mapping Habitat Connectivity for Multiple Rare, Threatened, and Endangered Species on and Around Military Installations

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LIST OF ACRONYMS

ABB	Appalachian Brown Butterfly (surrogate species for SFS)
ACUB	Army Compatible Use Buffer Program
AIC	Akaiki Information Criterion
DEM	Digital Elevation Model
DoD	Department of Defense
EPA	Environmental Protection Agency
GAM	Generalized Additive Model
GAP	Gap Analysis Program
LiDAR	Light Detection and Ranging
NCSCP	North Carolina Sandhills Conservation Partnership
NLCD	National Land Cover Dataset
NWI	National Wetland Inventory
RCW	Red Cockaded Woodpecker
SFS	St. Francis' Satyr

KEYWORDS

***Ambystoma tigrinum tigrinum*, boundary behavior, Camp Mackall, Carolina Gopher Frog, Circuitscape, CONNECT, decision-support system, Dispersal, Eastern Tiger Salamander, Fort Bragg, graph theory, Habitat Management, Individual-based Model, Landscape Connectivity, LiDAR, model complexity, *Neonympha mitchellii francisci*, North Carolina Sandhills, *Picoides borealis*, *Rana capito capito*, Red-cockaded Woodpecker, St. Francis Satyr, Umbrella Species**

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1 ABSTRACT

1.1 OBJECTIVE

Military and non-military land-use demands can adversely affect habitat connectivity for endangered and at risk animal populations on military installations and surrounding landscapes. Meeting legislative requirements regarding the protection and recovery of these species on Department of Defense (DoD) lands likely requires not only the protection of primary habitats, but adequate management of habitats that promote dispersal between habitat patches.

The specific goals of the project are 1) to understand dispersal patterns of four endangered or at-risk animal species on Fort Bragg: The red-cockaded woodpecker (RCW), Saint-Francis satyr (SFS) and two at-risk amphibians; 2) model and map the connectivity of landscapes on and around Fort Bragg for the study animals; 3) Evaluate the ability of the red-cockaded woodpecker to serve as a surrogate to guide management of landscape connectivity for multiple species; and 4) Develop a modeling strategy and spatial decision-support system that will allow wildlife managers to examine the influence of habitat management practices on connectivity.

1.2 TECHNICAL APPROACH

To achieve our objectives, we used a simulation modeling approach. First, we collected movement data on each target species using a combination of experimental and observational techniques. Next we synthesized these movement data into general rules that describe how landscape features influence dispersal. Then we mapped these features across the study area using remote-sensing data and ground-based inventories. These empirical data allowed us to parameterize and validate dispersal simulations for each of our target species and use those models to predict the relative importance of dispersal habitat use for each species across the study extent. We then used a reserve-design algorithm to find the most important dispersal habitats across all of our target species and evaluate RCW's ability to serve as a suitable management surrogate for the others.

1.3 RESULTS

The target species differ drastically in their overall dispersal ability. We found that RCW populations are highly connected on Fort Bragg, but are less connected in the surrounding landscape. Our other target species have limited dispersal ability and dispersal of these species from known populations off of the installation itself is probably rare. Small areas near current populations of SFS and amphibians are also important dispersal habitats for RCWs, but overall the patterns of dispersal habitat use are widely divergent across species. On private lands, conservation strategies intended to preserve or improve connectivity for RCWs will only benefit other species if the areas conserved are extensive.

1.4 BENEFITS

This project has created new knowledge about habitat connectivity for the target species that can be used by DoD to manage their populations more effectively. We have also created a multi-species connectivity evaluation framework that may be generally useful in guiding habitat

management for DoD installations that harbor multiple species of conservation concern. The GIS toolbox that we have developed, called "CONNECT", will allow DoD wildlife managers and others to model connectivity for a variety of species, evaluate the effects of multiple habitat management options on connectivity, and prioritize lands for connectivity across multiple species.

2 OBJECTIVE

The main objective of our project was to develop a set of methods for prioritizing land parcels in terms of their value for conserving connectivity for multiple species of management concern. We focused our attention on a group of rare, threatened, and endangered species with divergent life histories, range requirements, and dispersal abilities (red-cockaded woodpecker, St. Francis' satyr butterfly, Carolina gopher frog, and eastern tiger salamander). Our objectives were to model habitat-mediated dispersal for each of these species, map the value of the landscape for connectivity conservation, and integrate individual species models to produce maps of multi-species connectivity value. The objective of this process was to rank land-parcels according to their priority for connectivity conservation. Part of this process, and an additional goal of the project, was to develop software that will help land-managers integrate relevant data and generate useful products for assessing the relative value of land parcels for multi-species habitat connectivity conservation.

2.1 BACKGROUND

2.1.1 CONSEQUENCES OF HABITAT FRAGMENTATION

Most landscapes contain a mosaic of habitat types, presenting different levels of difficulty for dispersal by native species, depending on each species' habitat affinities, behavioral attributes, and risk of mortality while dispersing. Anthropogenic land uses change the quality and topology of landscapes, often leading to the reduction of habitat area as well as habitat fragmentation, both of which are recognized as major threats to biodiversity and causes of species loss globally (Wilcove et al. 1998). Reduction of total habitat area, increase in spatial isolation of remaining habitat fragments, and increased resistance of intervening landscapes to dispersal can result in reduced population sizes, reduced flow of individuals and genes between populations, and greater risk of extinction of native species (Fisher and Lindenmayer 2007).

2.1.2 RELEVANCE TO DOD

The problem of habitat fragmentation and reduced habitat connectivity is an especially salient issue pertaining to military installations and DoD's mission for sustainable management of wildlife resources. Many military installations contain large proportions, and large areas of natural habitat. These habitats are becoming increasingly insular as continuing land-use changes beyond installation boundaries convert natural or semi-natural habitats into residential, commercial, or public use developments. As an example, 49% of Fort Bragg, NC is covered in evergreen forest, which is twice that found in the 20 km wide buffer area beyond the perimeter of the installation (24%) (Figure 1). Fort Bragg, like many U.S. military installations, is becoming an island of native species and their supporting ecosystems in a sea of land that is relatively inhospitable to some native wildlife, including numerous at-risk species.

2.1.3 CONNECTIVITY CONSERVATION FOR MITIGATION OF FRAGMENTATION

The main tool for mitigating the effects of habitat fragmentation and population isolation is to protect and manage or restore lands that maintain the ability of wildlife to move between existing blocks of habitat. A major distinction is made between structural connectivity, which considers only the spatial arrangement of habitat patches, and functional connectivity which incorporates knowledge about dispersal behavior, albeit usually determined from expert opinion. Connectivity facilitates population persistence in at least two ways: maintaining meta-population dynamics and providing safe harbor from environmental changes like development and climate change.

Protecting lands that connect habitat patches can especially benefit rare, threatened and endangered species, many of which exist in small populations confined to relatively small areas of habitat (Beier and Noss 1998, Tewksbury et al. 2002). At regional scales, habitat corridors can be used to restore or maintain habitat connectivity for species with large range requirements, which often are also at risk due to habitat fragmentation at larger scales (Kikoti et al. 2010). Often such mega-corridors, as they are often described, follow mountain ranges or river valleys.

Identifying which lands to conserve is typically done using using expert opinion alone, or increasingly, using computational methods such as least-cost path analysis in a geographic information system framework, or models that simulate individual animals dispersing through digital, gridded representations of actual landscapes (Will and Tackenberg 2008). The latter are often referred to as "individual-based" models. Both modeling approaches require maps of the resistance the landscape will present to the movement of animals that are passing through it. However, resistance itself is usually inferred in a crude manner from published data on habitat preferences or expert opinion, with little consistency in approach between different projects, or comparison of approaches within projects (Beier et al. 2008). This raises one questions that was at the heart of our project: **How do models based on crude estimates of habitat resistance, compare to models using data on specific animal movement behaviors collected in the field in different habitat types?**

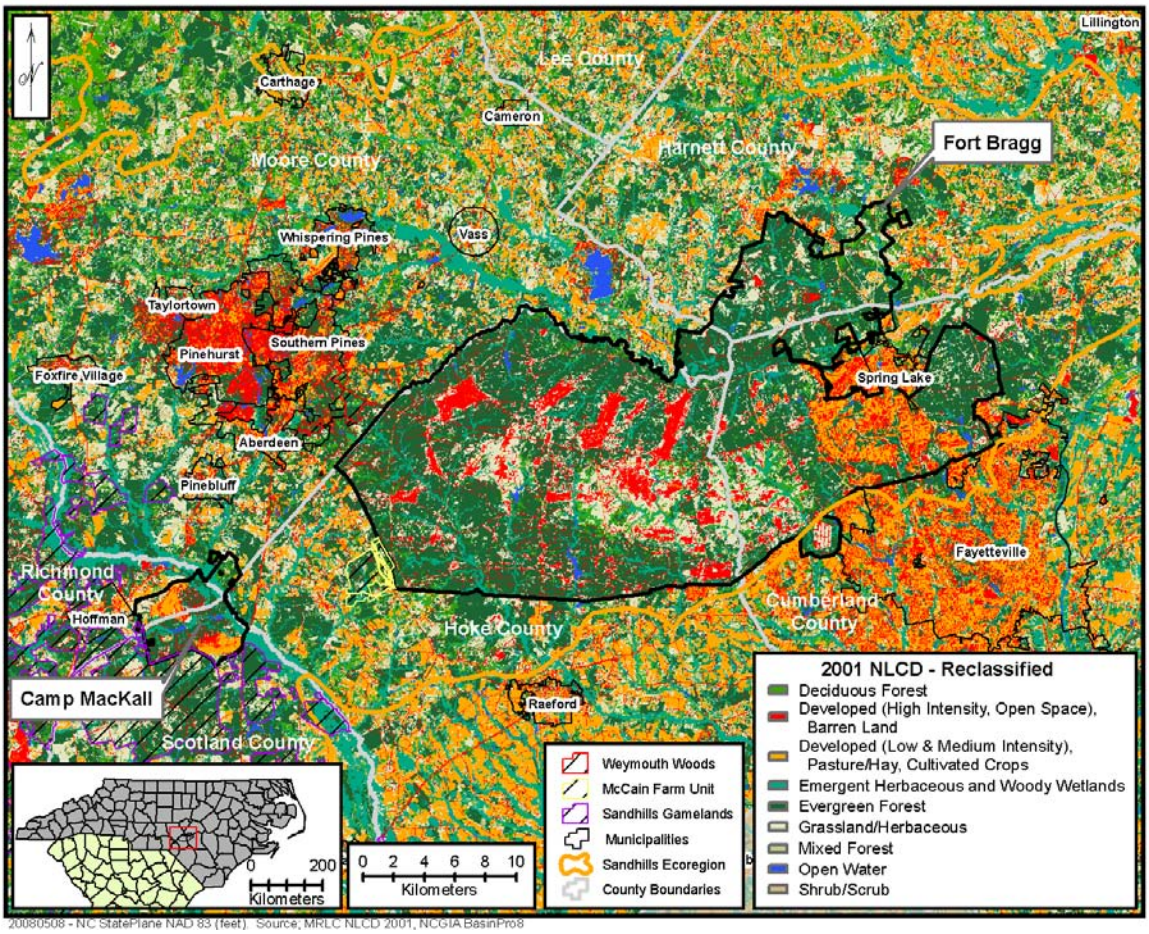

Figure 1: Map of the study area highlighting location of Fort Bragg.

2.1.4 IMPORTANCE OF A MULTI-SPECIES APPROACH

An additional issue is that conservation management decisions typically are made to protect habitat connectivity for a single species, whereas many actual conservation scenarios, including on DoD installations, involve managing for multiple at-risk species. This is partially because species differ in their dispersal strategies, their sensitivity to the landscape, and the landscape features that might facilitate or impede dispersal, and partially because conservation historically has been oriented around large charismatic vertebrates, including game species, or species that have been federally listed as endangered. However, single-species conservation has been widely criticized for neglecting biodiversity and failing to recognize the critical role of biodiversity in maintaining ecosystem function and integrity (van Dyke 2008). This raises the question: **How to identify the best patches of land for conserving habitat connectivity in a *multi-species* context, accounting for differences in life history, habitat affinity, and spatial distribution of all target species?**

In addressing these questions, we sought ways to maximize the conservation effectiveness of DoD land use, procurement, and management by explicitly incorporating knowledge of animal movement behavior, and landscape resistance to dispersal for multiple rare taxa. Our framework will allow evaluation of the conservation impact of alternative land-management scenarios, in

order to determine strategies for managing connectivity for suites of rare species present on and around installations.

While dispersal is the primary force that generates animal distributions, dispersal data are often difficult to collect, and reflect patterns at a scale generally much larger than the processes determining them (Lima and Zollner 1996). In comparison to dispersal data, movement data are generally much easier to collect, and occur at the same spatial scales as environmental factors determining individual movement. Thus, an alternative approach to quantifying habitat connectivity, and the approach used in our work, was to model dispersal on the basis of more easily obtained data on local movement behavior (Turchin 1988; Morris 1993). Using this approach, movement behaviors provided a quantitative and objective basis for predicting which land has highest connective value for conservation (Levey et al. 2005; Revilla et al. 2004).

Our general approach was to A) collect behavioral data on animals in the field in different habitat types and at habitat boundaries; B) produce digital maps of habitat variables either known or expected to affect animal movement; C) model habitat connectivity using simplest to most complex available data, and using least-cost path, and simulation methods; D) compare maps of habitat connectivity across species and across levels of complexity.

We tested a range of modeling approaches for several species with very different life-histories and distributions. Our models spanned a continuum of complexity from extremely simple – where habitat connectivity is solely a function of Euclidean distance between populations or habitat patches – to highly complex. Our most complex models involved simulating movement through the landscape for thousands of virtual individuals. As virtual organisms move across a gridded computer model of the actual landscape, behavioral decisions at boundaries and within the different habitat types are drawn from probability distributions obtained from experimental and observational field data.

2.1.5 MULTI-SPECIES CONSERVATION PARADIGMS

In working towards a conservation framework that balances the conservation needs of each of our focal species we drew upon two major multi-species conservation paradigms. The umbrella species paradigm posits that conservation can be focused on a single large area-requiring species, and other species are protected by coincidence with the umbrella species. In the context of our study area the red-cockaded woodpecker (RCW) is a potential umbrella species, which allowed us to test the suitability of this paradigm for conservation of multi-species habitat connectivity. Alternatively, the core-habitat conservation or hotspots paradigm would lead to optimizing for all species of concern and prioritizing lands that connect habitat for the maximum number of species.

2.2 STUDY AREA

Our study area encompasses Fort Bragg Army Base in the Sandhills ecoregion of the North Carolina coastal plain (Figure 1). The base itself is approximately 65,000 ha in size, comprised mainly of longleaf pine forest and riparian habitats and open areas. Longleaf pine forest on base is subject to controlled burning on a 3-yr rotation. Fire planning is designed to complement management for military training.

Our study makes use of data from pre-existing efforts primarily in terms of historical dispersal records for RCW on Fort Bragg, and data on butterfly and amphibian populations on Fort Bragg. Many endangered and at risk species are found on DoD lands, and managing for their persistence and recovery poses major challenges to land-use planning on and around these areas, where training on base and development off base intersect or interfere with wildlife habitat. This project has relevance for other installations in the southeastern US coastal plain with extant populations of red cockaded woodpeckers (RCW), installations elsewhere that harbor at risk amphibians and butterflies, and all installations that manage for at risk or endangered animals.

2.3 HABITATS OF PRIMARY INTEREST

This project focused on identifying "dispersal habitats," which can include both high quality breeding and foraging habitats, as well as poorer quality "matrix habitats" that animals must traverse in colonizing suitable breeding and foraging sites. For all of our study species, and especially for butterflies, dispersal through less suitable matrix habitat is the only way for individuals to move between patches of quality habitat.

Habitats of primary emphasis for this project, and those included in our land-cover taxonomy (Table 1) captured the landscape differences that matter for occupancy and dispersal of our study animals. Our landscape taxonomy was designed to provide the needed information and to be complete, parsimonious, and achievable. Suitable breeding and foraging habitats differ among the four species we are considering. RCWs nest and forage in high quality longleaf pine woodlands with an open understory. St. Francis' satyr (SFS) and related butterflies live and reproduce in wetland meadows that occur intermittently along streams. Both the eastern tiger salamander and the Carolina gopher frog breed in ephemeral ponds that are isolated from streams, and, in the non-breeding season, they migrate to upland longleaf-pine and other forest where they live in holes or under coarse woody debris.

Our taxonomy differentiates between forest and non-forest because this is an important distinction for dispersal of all of our study animals. Beyond this, we needed sub-categories within the forest class. Upland forest, particularly mature long-leaf pine, is used by amphibians for hibernation in between breeding periods, and is ideal dispersal territory for them. Plantations are presumed to, at best, provide intermittent breeding or foraging habitat for RCW and hibernation for amphibians, and are also important to differentiate. Mature Hardwood is primarily located in riparian and swamp areas, and is suitable dispersal habitat for RCW, but not for breeding or forage. The same is true for Mature Plantation. Mature Non-Plantation Pine is sufficient to characterize RCW habitat as suming artificial cavities could be used. However, Mature Non-Plantation Pine with Hardwood Understory (i. e. mixed) is less suitable habitat for amphibians and for RCW than Mature Non-Plantation Pine, and so is also separated out as an additional class. Regenerating stands act as open areas for all animals and are distinguished for this reason. In addition to our interest in dispersal through each habitat type, we were also interested in the influence of boundaries (i. e. edges or transition zones where two land-cover types come together) on dispersal. Boundaries can affect connectivity, for example by creating barriers to dispersal, or by directing dispersers through the landscape (Levey, et al. 2005). Thus, we also studied how animals behaved at boundaries.

Landscape characterization involved land-cover mapping (according to the taxonomy in Table 1) and also included mapping of amphibian breeding ponds, and mapping canopy density within three different height classes.

Table 1: Landscape classification taxonomy

Classification Level			Species
1	**2**	**3**	
Forest	Upland		All
		Mature Plantation	RCW, Amphibians
		Mature Non-plantation Pine	RCW, Amphibians
		Mature Non-plantation Mix	RCW, Amphibians
		Regenerating (<10y)Pine	RCW, Butterflies
	Riparian		All
	Herbaceous wetland		Butterflies
Permanent Open	Open Land		Amphibians
		Asphalt Road	Amphibians
		Dirt Road	Amphibians
		Field	RCW
		Water	Amphibians
	Developed	Urban	All
Streams			Amphibians

2.4 FOCAL SPECIES

Below we outline the life history characteristics of each focal species, and provide the reasoning for inclusion in the study.

2.4.1 RED-COCKADED WOODPECKER

The federally endangered red-cockaded woodpecker is endemic to mature longleaf pine (*Pinus palustris*) forest 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 (Peet and Allen 1993, Outcalt and Sheffield 1996, Frost 2006). High quality RCW 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 RCW 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. Dispersal distances of RCWs exhibit a right-skewed distribution, with most juvenile females dispersing no more than 3.3 km and a small proportion dispersing long distances as high as 31 km (Walters 1990, Kesler et al. 2010). Previous research with mark-recapture data suggested that RCWs acquire information about surrounding territories using extra-territorial forays before the final dispersal event (Pasinelli and Walters 2002). Using radio telemetry, we confirmed that juvenile female RCWs conduct prospecting behavior with extensive forays from their natal territory before settling on a single breeding site (Kesler et al. 2010). Previous models depicting RCW dispersal behavior have failed to account for this prospecting behavior and for long-distance dispersal events (Letcher et al. 1998, Daniels and

Walters 2000, Schiegg et al. 2002, Pasinelli et al. 2004, Schiegg et al. 2005) and, thus, may provide unrealistic depiction of RCW dispersal behavior. Despite the extensive RCW monitoring and widespread fragmentation of the longleaf pine ecosystem, because dispersal behavior was poorly known before this project, connectivity has yet to be quantified for RCW populations.

2.4.2 ST. FRANCIS' SATYR

St. Francis' satyr (SFS; *Neonympha mitchellii francisci*) is a federally endangered species that occurs only at Fort Bragg in wetland meadows that occur along small streams. Wetland meadows are created by pond inundation and abandonment by beavers, which were once abundant, but were eliminated from North Carolina by the late 19th Century. This may explain the loss of habitat and the currently restricted distribution. Initially, flooding has a negative impact on butterfly subpopulations, as caterpillars cannot withstand submergence. Following beaver lodge abandonment and flood recession, however, the plant communities progress through succession from wetland meadow, which provides SFS habitat, to woody and shrubby vegetation that excludes the butterfly's food plants. Thus, because available habitat is constantly shifting, the butterfly needs to disperse to new habitat in order to persist in the landscape. Because beavers have been restored to the landscape, there may be suitable habitat on or off Fort Bragg that has yet to be colonized. One of the goals of our project was to identify these suitable habitats, and identify lands that preserve connectivity among them.

2.4.3 AMPHIBIANS

Eastern tiger salamanders (*Ambystoma tigrinum tigrinum*) and Carolina gopher frogs *(Rana capito capito*) are both NC-state listed as threatened species. The Carolina gopher frog is also considered a federal species of concern. These amphibians breed in late fall (*A. tigrinum*) and winter (*A. tigrinum* and *R. capito*) in temporary pools within upland sandhills habitats (Petranka 1998; Palis 1997; A. Braswell personal communication). Adults spend the summer (non-breeding) months in upland longleaf pine woodlands, spending most of their time in holes created by rotted or burned out roots (A. Braswell, E. Hoffman, R. Sutherland personal communication). Both species must migrate between breeding and non-breeding habitats.

3 MATERIALS AND METHODS

This report describes all of our accomplishments during the funding period of SERDP SI-1471. Subtasks completed this year fall into three categories. First, we have validated the dispersal models for each species and applied them to the larger area surrounding Fort Bragg (Subtask 4.6). Second, we have developed a user-friendly tool for managers to perform multi-species connectivity analyses on any number of species for any conservation area (Subtask 4.7). Finally, we have completed the integration of the individual species models into multi-species habitat prioritization maps and used these maps to that evaluate a number of conservation scenarios both on Fort Bragg and in a 5km buffer off-installation (Subtasks 4.5 and 4.8).

In the following sections we present a detailed description of the methods developed to accomplish this project. These include: 1) the development of the environmental datasets necessary for the occurrence and dispersal modeling, 2) empirically parameterized dispersal models for each of the focal species, and 3) the integration of the dispersal models into a multi-species conservation priority maps that inform conservation values for the areas surrounding Fort Bragg and the installation itself.

3.1 DATA CONTRIBUTING TO THE DEVELOPMENT OF DISPERSAL LANDSCAPES

We draw upon a variety of remotely-sensed data to generate the environmental templates for our models, including raw products such as LiDAR and LANDSAT and classified products such as the National Land Cover Dataset and National Wetland Inventory (NWI). The environmental maps we generated describe the landscape surrounding Fort Bragg in ways that are biologically meaningful to our study organisms. This includes three-dimensional estimates of forest cover, discrete land-cover classifications that correspond to our release experiments, and RCW-specific dispersal environments. All of our environmental datasets share a common spatial reference. This is important for the final steps of integrating the dispersal models of each species. While some of our intermediate steps may use different spatial references, all of our final environmental datasets are projected to North Carolina State Plane, meters, and all rasters have a 30m resolution.

The environmental data were developed at two extents. The extents are a rectangle bounding Fort Bragg, and a rectangle enclosing a 5km Buffer around Fort Bragg and Camp Mackall (Figure 2). The smaller extent was used to make inference about the movement of species on the installation itself, while the larger extent was used to make inference about conservation values of lands off-installation. Our justification for using two extents stems from the limitations of the data we collected, and from the biology of the organisms themselves. Existing populations of SFS and the amphibians are limited spatially and these species have limited vagility. In our most conservative simulations of the species, there was little or no dispersal off-installation. So, we limited our inference from these models to the installation itself. Using alternative methods, such as Circuitscape or simulations with relaxed assumptions we could model dispersal off-installation, and these models play a key role in making inference about conservation priority of off-installation lands, however these predictions are subject to a greater amount of uncertainty than the on-base analyses because of the quality of available off-installation data.

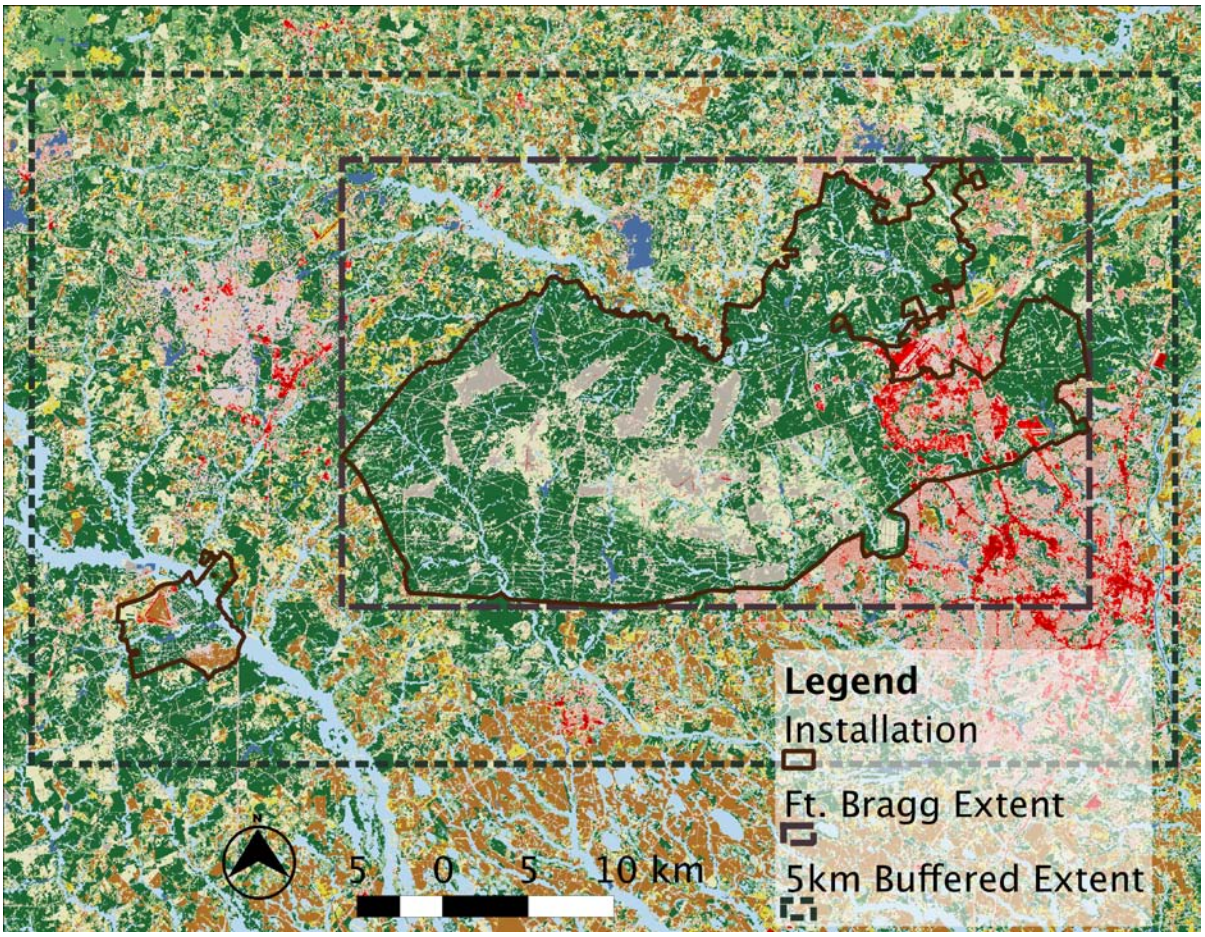

Figure 2. Map of the study area showing our two analysis extents, along with the National Landcover Dataset. Green represents forest, blue represents wetland or water, brown represents agriculture, and red and Pink represent urban development. The smaller extent encompasses Fort Bragg alone and was used when inference from our most conservative simulation models. At the larger extent we used dispersal models with relaxed assumptions to assign conservation priorities to off-installation areas.

3.1.1 LiDAR Forest Cover Estimates

Airborne LiDAR data are ideally suited and commonly used to infer three-dimensional forest canopy structure, which can provide information on habitat diversity (MacArthur and MacArthur, 1961), ecosystem productivity (Waring, 1983), harvestable timber (Maltamo et al., 2004), and forest type (Maltamo et al., 2005). This is one of the most promising new applications of remote sensing technology for the study of forested ecosystems. However, as with many remote sensing applications, most models for estimating canopy attributes from LiDAR provide limited information on the uncertainty of estimates. This manuscript presents a method for inferring the vertical canopy density of forests from LiDAR data, which includes reliable estimates of uncertainty due to the LiDAR sampling process.

LiDAR data consist of geolocated return times for pulses from a scanning laser. Distances and elevations of objects intercepted by the pulses are derived from these return times. Because grain

can be small (more than one return per square meter) and extent can be very large (entire states have been mapped), LiDAR data are spatially dense, even by remote sensing standards. A common application of LiDAR data is to create high-resolution digital elevation models from returns that reach the ground. Pulses also reflect off of vegetation and buildings, yielding estimates of elevation for these surfaces as well. Foresters use LiDAR to estimate forest stand characteristics, such as basal area and harvestable timber (Means et al., 1999), net primary productivity (Lefsky et al., 2005), and to identify individual tree crowns (Popescu, 2007). Ecologists use LiDAR data to define habitat quality for endangered species (Nelson et al., 2005), quantify the intensity of insect defoliation (Solberg et al., 2006), and associate bird diversity with forest structure (Goetz et al., 2007; Muller et al., 2009) (See Vierling et al., 2008, for a full review).

Most inferential models of forest structure from LiDAR data do not explicitly treat different sources of error. For example, a typical approach is to regress field derived forest stand characters (e.g. basal area, stem density) against LiDAR-derived metrics (eg Goodwin et al., 2006; Harding et al., 2001; Lefsky et al., 1999). In such regressions there are at least three major sources of error: 1) measurement error associated with field-collected data, 2) error in the correspondence between the field metric and the LiDAR metric, which are typically measuring different phenomena, and 3) sampling error associated with the LiDAR metric itself. Sampling error in particular is heterogenous because sample density is dependent upon the response variable. That is, the total number of possible returns at any height is attenuated by the forest canopy above. Generalized linear regression lumps all these three error sources into a single error term. The heterogenous sampling effects introduced by the LiDAR data collection process are not considered in such models. In this paper, we present an inferential model describing the error distribution of a canopy density metric derived from discrete return LiDAR. Here, canopy density is defined as the vertically projected stem and leaf area between two heights. Across many consecutive heights these canopy densities form a canopy height profile (Lefsky, 1997). We present this inferential model in a simple Bayesian framework, one that is easily extended to include other sources of error present in LiDAR data, such as scan angle and spatial autocorrelation of returns.

3.1.1.1 DATA

We selected a single 1km^2 quadrat (35◦10’48.617”N, 79◦12’15.863”W, Figure 3) on Fort Bragg for intensive analysis. This quadrat contained all the major types of forest canopy density present on Fort Bragg. We chose this quadrat because we could easily classify the forest types based on aerial photos and surveys on the ground. We compared these heads-up classifications within the quadrat to the canopy density estimates we derived from LiDAR.

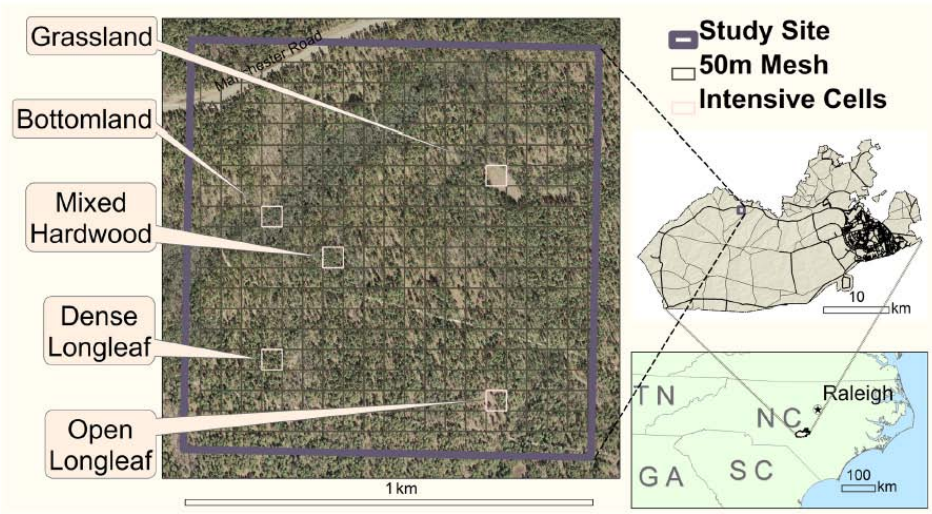

Figure 3: Locations selected for ground validation of LiDAR canopy density model.

We used 2-return LiDAR data with an average spacing of 0.33m^2 (1m ground return spacing). These data were flown on July 1-3 2006 by Airborne 1 corporation (http://www.airborne1.com/) at a height of 900m, with a pulse frequency of 20Hz, and scan angle of ±18 degrees. The pulse footprint at the ground was approximately 24cm. The dataset contains approximately 2 billion returns and covers all of Fort Bragg save the far NE corner. Returns were agglomerated into 50mx50m cells with approximately 10,000 returns per cell. We applied our model to the distribution of returns within each of these cells.

The Bayesian framework we have adopted requires that prior information about forest canopy density be included. The influence of the prior in Bayesian inference depends upon the nominal precision of the prior data. This precision can be informed by a known or estimated error distribution, and commonly different prior weights are used on the same model to assess the prior's role in the posterior estimates.

Our prior knowledge of forest canopy density was derived from data collected in 2001-2002 following the protocol laid out in the U.S. Forest Inventory and Analysis National Program (Alerich et al., 2004, FIA). These forest stand data consist of a polygon shapefile with attributes for abundance of hard and softwoods of different diameters. We correlated these estimates of hardwood and softwood abundance with canopy height, depth and canopy density measured in 10 mapped plots. From the mapped plots we developed allometric relationships between the diameter at breast height (dbh), mean and variance of canopy density, and mean and variance of canopy height for a tree. Then, we convolved the allometric probability distribution on the frequency distribution of tree diameters recorded in the forest stand data. The result of this process was an estimate of the canopy density for each height class in the model in every polygon of the forest stand data. These values became the prior for each 50m×50m grid cell on Fort Bragg.

3.1.1.2 INFERENTIAL MODEL

We consider the number of returns (including both first and last returns) within a 50m × 50m cell, n, at a single height interval, k, out of a K height intervals to be drawn from a series of

Bernoulli trials consisting of successes (returns in height k) and failures (returns below height k). We assume that vegetation structure at a given height is randomly distributed horizontally. This assumption is necessary, because returns are aggregated with the 50m × 50m cells though the geolocations of returns vary within the cell. The likelihood of a given number of returns n_k is a binomial distribution with canopy density, θ_k:

$$
\begin{aligned}
p\left(n_k|\theta_k, n_{k+1}, \ldots, n_K\right) &= \text{Binom}\left(n_k|\theta_k, \sum_{i=k+1}^{K} n_i\right) \\
&= \begin{pmatrix} n_k + \sum_{i=k+1}^{K} n_i \\ n_k \end{pmatrix} \times \\
&\theta^{n_k}\left(1-\theta\right)^{\sum_{i=k+1}^{K} n_i}
\end{aligned}
\tag{1}
$$

3.1.1.3 ANALYSIS

We derived posterior canopy density estimates for Fort Bragg at the following height intervals: 1-2m, 2-5m, 5-10m, 10-20m, and > 20m. Within our focal tile we selected 5, 2500m^2 cells capturing the variety of forest types in the study site (Figure 3) and calculated canopy density estimates at height intervals of 1m from 0-35m. We also calculated a 95% credible interval for each estimate.

To assess the role of the prior in the posterior estimates, we repeated the analysis with different prior weightings. The variance of the beta-distribution is dependent upon the mean canopy density. So, we selected prior weightings based on the maximum variance achieved in the prior beta distribution across all canopy densities (the first partial derivative of the variance against the mean). These weightings yielded a maximum standard deviation of 0.1% and 1% for any canopy density. We recorded the difference in posterior estimates for the range of prior weightings against the posterior estimates.

3.1.2 CREATING THE DISPERSAL LANDSCAPES

Landcover maps that specified habitat-specific resistances were needed for the dispersal models of each focal species. These landcover maps provide the template on which the individual-based simulations run. We created them to mirror the 4 different habitat classes for the release experiments (See Methods-Saint Francis' Satyr). Maps were created at our two analysis extents: Fort Bragg, and a 5km beyond Fort Bragg and Camp Mackall. Our land cover map for Fort Bragg was developed using the National Land Cover Dataset (NLCD), the National Wetland Inventory (NWI), forest stand data from Fort Bragg, color-infrared aerial photography, and LiDAR data. Of these datasets only the NLCD, NWI, aerial photography, and a courser resolution LiDAR product extend off base. To map land cover off base we modified our classification procedures to use these more limited datasets (Figure 4).

The basic classification algorithm is: 1) map all NLCD open, developed, and water classes as open habitat; 2) map NLCD upland habitats as upland forest; 3) map all remaining pixels as riparian; 4) within the riparian class map wetland habitat from the NWI polygons. Open, upland forest, riparian, and wetland habitats are then spot checked for consistency with LiDAR canopy height estimates, color infrared aerial imagery, and digital elevation data.

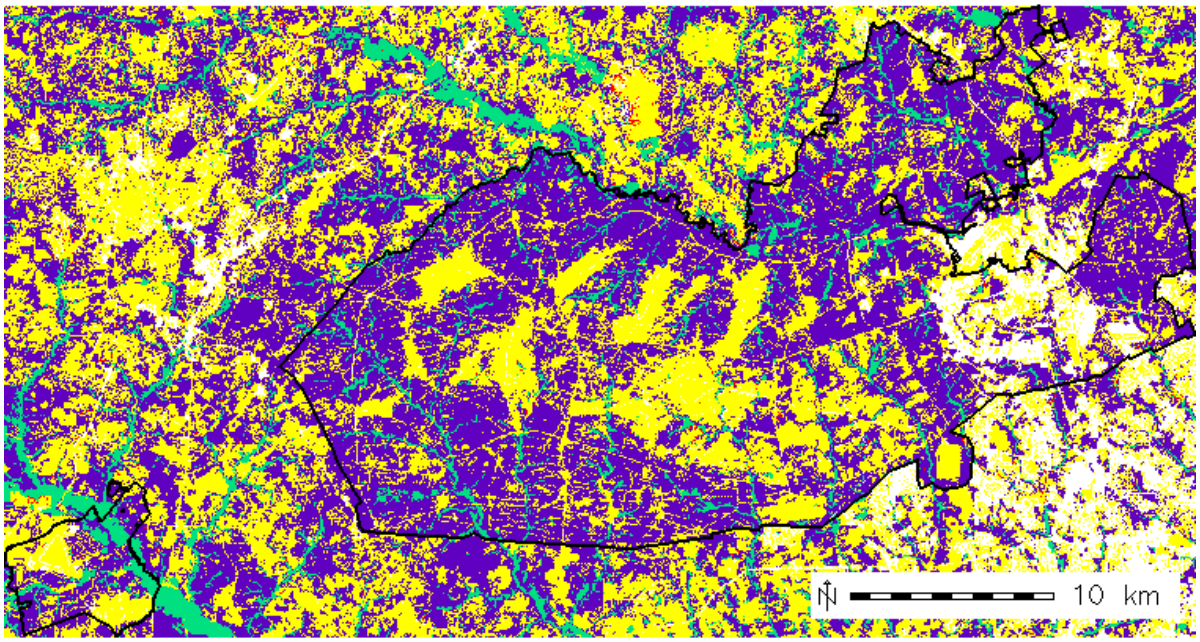

Figure 4: The land cover map for SFS and amphibians at the extent of Fort Bragg. Classes correspond to the four habitats for which we have empirical movement data. These are open (yellow), riparian (cyan), upland (blue), and wetland (red). Highly developed areas are shown in white and are not considered in the simulations. The boundary of Fort Bragg is shown in black.

3.1.3 RCW-SPECIFIC DISPERSAL LANDSCAPE

The red-cockaded woodpecker is much more widespread in the landscape around Fort Bragg and Camp Mackall than the other species considered. As a consequence, we developed a single dispersal landscape for this species that applied to dispersal simulations both on-installation and off-installation. This dispersal landscape utilized a variety of remotely-sensed data.

3.1.3.1 CATEGORICAL LAND-COVER CLASSIFICATION

Fort Bragg and Camp Mackall were classified into four land-cover classes (longleaf pine, non-longleaf pine evergreen species, hardwood, and non-forested [open, 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).

3.1.3.2 LANDSAT

Two Landsat-5 Enhanced Thematic Mapper (ETM) images (Path16, Row 36) collected 12 December 2006 and 5 May 2007 were georeferenced to < 1-pixel root mean square error (RMSE) and atmospherically corrected to estimates of surface reflectance. These two image dates were chosen to represent leaf-on and leaf-off conditions to facilitate differentiation of evergreen and deciduous canopies. Three variables were computed from these data to determine if RCW respond to environmental cues related to vegetation composition.

The ratio of infrared (0.75 to 0.90 µm, ETM band 4) to middle infrared (1.55 to 1.75 µm, ETM band 5) of the December image, known as Structural Index (SI, Kushla and Ripple 1998) was used to indicate the presence of mature evergreen forest. The SI has been found as a good predictor of stand age and as strong 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 (ETM band 4) due to increased amounts of vegetation growth with forest age (Fiorella and Ripple 1993). The middle infrared reflectance (ETM 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 ETM 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 used two additional variables derived from a transformation of the Landsat image bands into composite bands. The Tasseled-Cap transformation rotates the image data into composite bands, the first three of which are strongly associated with brightness, greenness, and wetness of the scene (Crist and Cicone 1984). Since RCWs avoid hardwood forest for nesting habitat (Wood et al. 2008), we wanted to test whether the presence of hardwood affected dispersal behavior. Greenness, which is the second component of the Tasseled Cap transformation, is correlated with the amount of photosynthetically active canopy present. The difference in greenness between the two dates (May minus December) was used to indicate the presence of hardwood forest. In order to account for the effect of spatial congruency of forest on RCW movements we used the spatial heterogeneity in summer greenness as the standard deviation of the greenness values within a 3 x 3 pixel window (8,100 m^2 area) surrounding each pixel. Low variation in standard deviation of greenness would indicate large forest patches, while high values would suggest small segments of forest surrounded by non-forested land-cover features (i.e., agricultural fields).

3.1.3.3 NORTH CAROLINA FLOODPLAIN MAPPING LIDAR

RCWs prefer forested areas containing longleaf pine trees greater than 60 years old for foraging (U. S. Fish and Wildlife Service 2003). RCW may use longleaf pine trees between 30 and 60 years old which usually range from 13 to 20 m tall, but avoid stands of this age when older stands are available (Platt et al. 1988, U. S. Fish and Wildlife Service 2003). RCW also tend to avoid forested areas with dense hardwood midstory vegetation (i.e., less than 8 m). We used LiDAR data to estimate percent cover at four biologically relevant height classes (1-8 m, 8-13 m, 13-20 m, and greater than 20 m) at a 30 x 30 m resolution. In 2001, the state of North Carolina subcontracted engineering and surveying firms to collect LiDAR data during leaf-off canopy conditions from 31 December 2000 to 18 February 2001. Our study area overlapped the flight paths of two subcontractors with varying sample density and flight altitude. The post spacing averaged 2.25 m, flight altitude ranged from 914 m to 1676 m, and the elevation calibration ranged from 9 cm to 12 cm elevation RMSE. The raw LiDAR data containing three-dimensional coordinates of laser hits were converted into .las 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. Maximum and median vegetation heights were also derived from LiDAR data. In order to represent the overall forest structure in a single variable, we calculated skewness of vegetation heights within 30 x 30 m pixel. Dense forest, such as

plantations or hardwood forests, with few canopy gaps should translate into a negatively skewed distribution of vegetation heights where 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.

3.2 RED COCKADED WOODPECKER

3.2.1 FIELD DATA ON RCW DISPERSAL

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 RCW territories located in the study area. Since 1981, active RCW territories have been monitored by Fort Bragg Endangered Species Branch, researchers from North Carolina State University and Virginia Tech, and Sandhills Ecological Institute and university biologists. The species' dispersal behavior has been assessed by marking juvenile and adult RCWs with a unique combination of bands, monitoring territories during the breeding season, and recording dispersal outcomes, that is, movements from one territory to another between breeding seasons, which includes both natal and breeding dispersal (Daniels and Walters 2000a, 200b). For this study, dispersal events between 2004 and 2007 were used to validate dispersal behavior in relation to environmental features and estimate the population's current connectivity. Detailed banding and monitoring methods are described in Walters et al. (1988).

To parameterize models that predict how environmental cues influence prospecting behavior and connectivity of RCWs, we collected movement data on prospecting birds using radio telemetry. Many juvenile females remain on their natal territory with their family group through the winter and disperse just prior to the next breeding season. We focused on these individuals to increase efficiency in obtaining data on dispersal behavior. In spring (March – May) 2006, 18 juvenile female RCWs that had not yet dispersed from their natal territory 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 RCW 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 (Figure 5). Four of the subjects in 2007 had already dispersed from their natal territories and were floaters, that is, individuals not belonging to any territorial family group.

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). 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). We attempted to relocate radio-marked woodpeckers daily. Study subjects were ordered in a list by geographic location, and then a single individual was randomly selected to be the first daily observation. During 2006, we attempted to locate all radio-tagged birds at least once a day, although positions of foraying birds

occasionally could not be determined due to military training or zoning, topographic interference, or vegetation. Radio tracking protocols varied slightly in 2007 to account for increased tracking personnel (2 and 3 individuals conducted radio tracking in 2006 and 2007, respectively) in order to increase probability of detecting forays. In 2007 the radio-tagged population was divided into 3 sampling sections. Each section consisted of approximately 5 radio-tagged individuals within close proximity to each other. All sections were sample in 4 hour sessions throughout the day with the first individual randomly selected for each session. Each person looped through the radio tagged individual in a section and record if they are in or out of their natal territory. If radio-tagged birds were not initially found with the natal group, we drove throughout the study area using vehicle-mounted omnidirectional antennas until the foraying individuals were located. Once located, we remained with the individual to collect GPS locations, social observations, and landcover characteristics. Monitoring continued for the other radio tagged individuals as long as we were able to return to individuals off their natal territory at 30-minute intervals.

Birds were considered to be on forays when they were twice as close to a cavity tree on a non-natal territory as they were to a cavity tree on their natal territory and were not with other members of their natal group. Radiotelemetry observations ceased when transmitters failed or with the onset of the breeding season and egg laying. Based on the telemetry data, we calculated the number of days a bird visited a non-natal territory (Frequency of Territory Visits). Foray distances were approximated using the linear distance between the roosting site on the natal territory and the visited territory. We defined each individual's prospecting range as the maximum foray distance traveled from the roosting site.

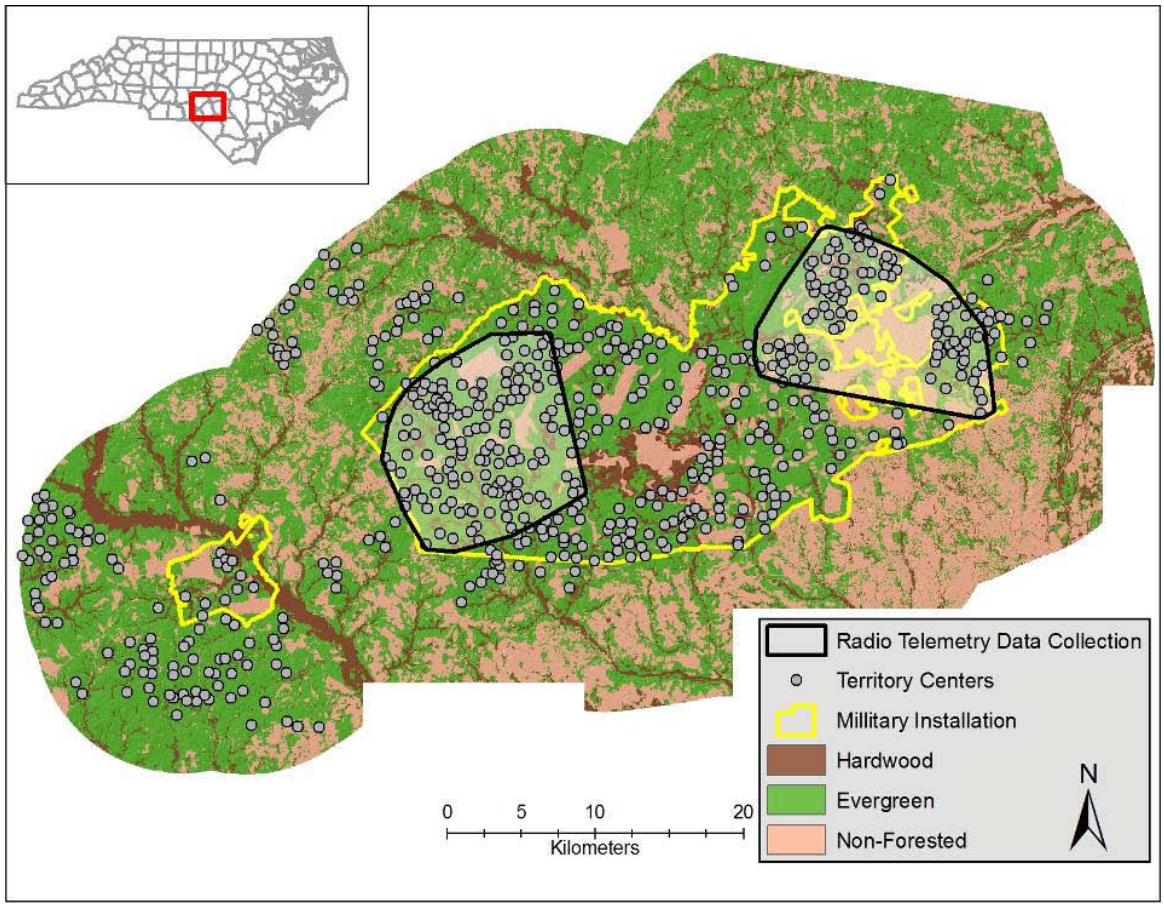

Figure 5: The study area extent with the centers of Red-cockaded woodpecker (Picoides borealis) territories and military installation boundaries. The two shaded polygons illustrate the spatial coverage of radio telemetry data collection (2006 = west, 2007 = east).

3.2.2 MOVEMENT MODELING

3.2.2.1 GENERATING RESISTANCE SURFACES USING MAXENT

The Maxent software package (Phillips et al. 2006) is a species distribution modeling (SDM) approach that has recently gained popularity, especially with rare species for which there are few spatial records. Maxent contrasts the environment underlying input presence points against a random sample of background points, which represent the availability and range of environmental conditions of the study area, to predict the maximum likelihood distribution of a species. This distribution is applied to the entirety of the study area and can be displayed as a raster grid. Each grid cell of the resulting map is ranked in a continuous index from 0-100 indicating relative landscape suitability.

Maxent is particularly useful as it relies only on presence data, so avoiding the possibility of indeterminacy of habitat versus non-habitat and poor resolution of habitat models due to the lack of detailed presence/absence information (Sexton et al. 2006). It frequently outperforms other SDM techniques, notably with limited datasets (Elith et al. 2006; Wisz et al. 2008; Hernandez et al. 2006; Phillips et al. 2006; Pearson et al. 2004). Furthermore, Maxent is not limited to

modeling linear relationships, which are rare in nature. Instead, because variables are considered individually, disparate relationships are possible for each variable, giving a more complete and holistic representation of the study area than a restrictive linear model (Phillips et al. 2006).

The Maxent software 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. To characterize environmental features at breeding sites we used territory centers as occurrence data (n = 604). Environmental variables recognized during prospecting movements were identified by creating habitat suitability models with all non-natal telemetry locations (n = 1710). For each type of occurrence data, we created five different sets of environmental data, with increasing complexity, to determine which set of remote sensing data best explains RCW prospecting movements. The simplest representation of the environment was with a raster containing four general land-cover 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. 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.

Due to our relatively large samples of occurrence data (> 80 occurrence points), we allowed Maxent to fit all feature functions (linear, quadratic, product, threshold and discrete) by selecting the "auto feature" option. In addition, the regularization constants (β) were not adjusted in Maxent. 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, for each of the Maxent models we used bootstrapping with 10 replicate samples with replacement for both types of occurrence data. In addition, 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 with the classification. The AUC values range from 0 (habitat predictions worse than random) to 1 (perfect prediction of habitat), with 0.5 indicating random classification. Maxent then produces a logistic probability of habitat suitability for the entire study area (Phillips and Dudik 2008). Values near one indicate the most suitable habitat conditions while unsuitable habitat is indicated by values close to zero.

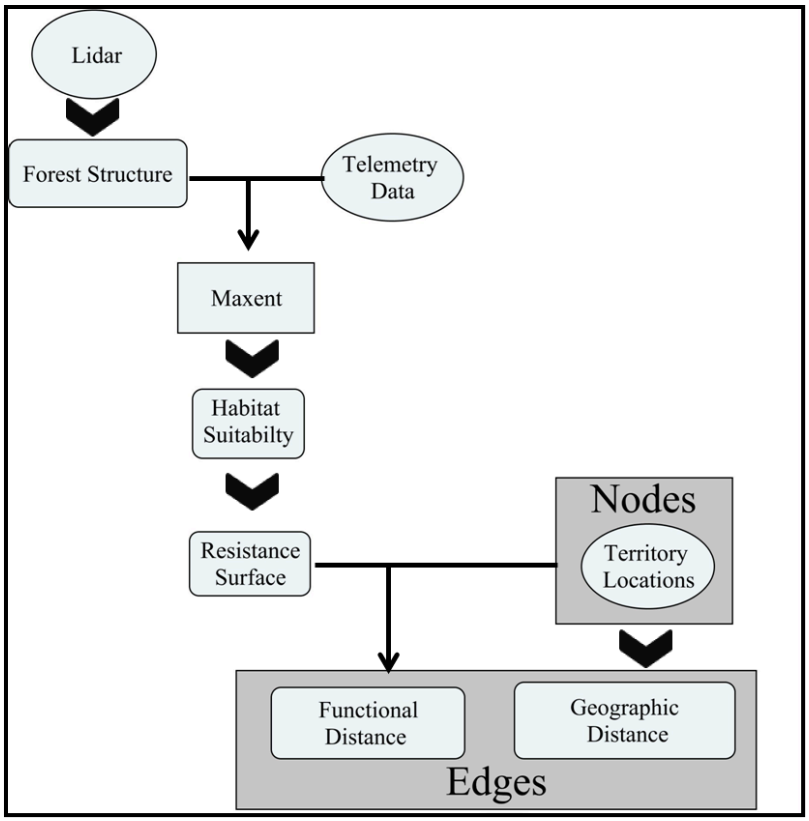

Figure 6: Overview of methods used to create resistance surface for effective distance and graph network edges when estimating connectivity of Red-cockaded woodpecker (*Picoides borealis*) habitat.

The habitat suitability map created with Maxent software was converted into a resistance layer (Figure 6). Effective 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 RCW roosting territories. Destination points are defined as all territories within prospecting range. The friction values on the resistance surface are usually converted from the species habitat suitability preferences with a single function, such as linear (Ferreras 2001, Singleton et al. 2004, Richard and Armstrong 2010). However, there is no overwhelming reason to assume that habitat preferences are linearly associated with friction values. We tested the sensitivity of the relationship between habitat suitability and friction values for the prospecting RCW. A resistance surface was derived for each Maxent model by converting the habitat suitability values (h) into friction values (f) with the function:

$$f = 100 - 99\frac{1-\exp(-ch)}{1-\exp(-c)} \tag{2}$$

A rescaling constant, c, was included in the above function to vary the relationship between habitat suitability (h) and friction values (f). An arbitrary scale 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). We then selected seven rescaling values (c), ranging from 0.25 to 16 (Figure 7), to produce a broad range of curves to evaluate which relationship between habitat suitability and friction values best predicts RCW reaction to environmental cues. Based on the ten habitat suitability models and seven rescaling constants (Figure 7), a cost distance model was applied to each of the 70 resistance layers resulting from the combination of the ten habitat suitability models and seven rescaling constants in ArcInfo Workstation (Environmental Systems Research Institute Inc. 2008). For each resistance surface, we calculated the effective distance of the least-cost path from each of the radio-tagged RCW roosting territories to all possible territories within each individual's prospecting range.

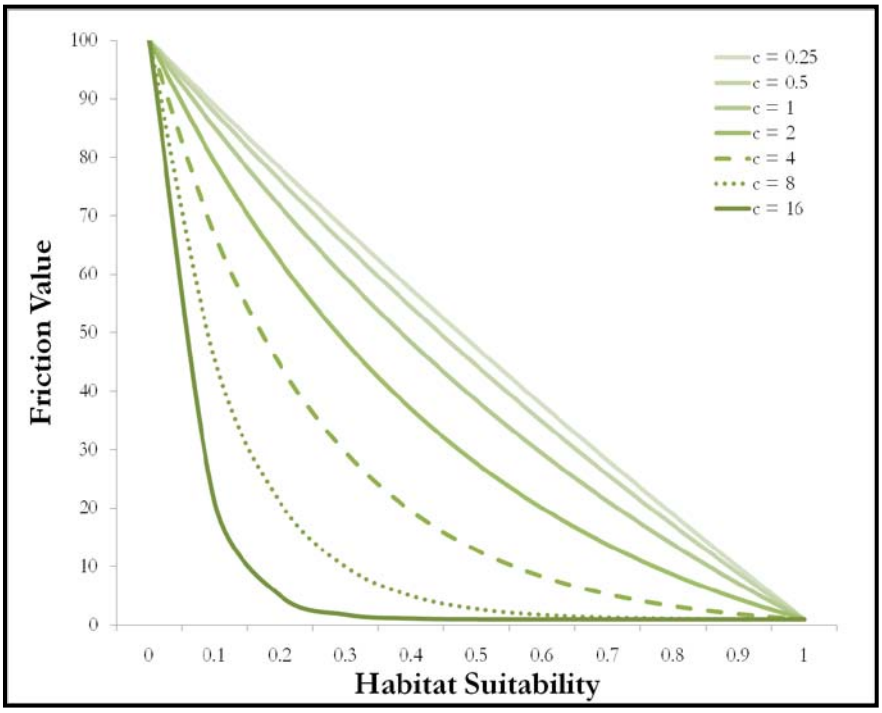

Figure 7: The seven curves used to rescale habitat suitability values into friction values. The dash and dotted curves produced the top-ranked and second-ranked predictive rescaling for prospecting behavior, respectively.

3.2.2.2 GRAPH NETWORKS

We also estimated connectivity for RCW populations using a graph-theoretic approach. The influence of effects of landscape features between territories was accounted for with the empirically estimated resistance surface that optimally represents RCW prospecting movements. For this study, the nodes in the graph networks were denoted as territory centers. A distance matrix, **F**, was populated with functional distances (f_{ij}) between all pairwise combinations of territories. For comparison, a geographic distance matrix, **G**, was created to portray a graph network in a featureless matrix. The functional (**F**) and Geographic (**G**) distance matrices were converted into unidirectional graph models with igraph package in R statistical software (R Development Core Team 2010). For each graph (Functional and Geographic), we examined the

overall trend in connectivity with decreasing dispersal ability. Edges were iteratively removed at 100 and 1000 m intervals for the Geographic and Functional distances, respectively. When the distance matrix values were greater than the threshold distance, the territories were defined as connected. At each interval we estimated three connectivity metrics, 1) number of components, 2) size of the largest component, and 3) diameter of largest component (Table 2).

Table 2: Definition of graph terms and metrics used to evaluate connectivity of red-cockaded woodpeckers (*Picoides borealis*) in North Carolina's Sandhills ecoregion.

Graph Terms		**Definition**
	Node	Points (i.e., habitat patches or territory centers)
	Edge	Flux 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	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

To evaluate the current connectivity of RCW populations, the trend in connectivity metrics from the geographic and functional distance networks were then compared with cumulative probability of observed dispersal events between 2004 and 2007 (n = 257). We selected this subset of dispersal data to have similar environment and landscape composition as radio-tagged individuals. The observed functional distances from natal territory to breeding territory (x) were fitted to a lognormal probability density function,

$$fx(x,\mu,\sigma) = \frac{1}{x\sigma\sqrt{2\pi}} e^{\frac{(\ln x-\mu)^2}{2\sigma^2}} \tag{3}$$

where μ and σ are the mean and standard deviation of the distances' natural logarithm, respectively. The lognormal distribution was selected because if the minimum range of the distribution is defined as zero, the two parameters provide flexible distribution of short and long-distance movements. The cumulative distribution functions (cdf) were extracted from the functional lognormal probability density functions. We then evaluated how the cumulative probability of dispersal based on observed movements corresponded to the sharp transitions in the connectivity metrics.

To determine which network optimally represented RCW connectivity, we used the observed dispersal events to evaluate if individuals are influenced by landscape features between territories. This was accomplished by comparing the effective distance for each observed dispersal event to the average effective distance of available territories with similar geographic distance. Available territories were defined as territories with similar geographic distances (with the 25th percentile) from the natal territory to the observed destination territory and are within the

maximum distance any juvenile female was observed dispersing from the natal territory during all the years of banding data.

3.3 SAINT FRANCIS' SATYR

3.3.1 FIELD DATA - EXPERIMENTAL RELEASES OF APPALACHIAN BROWN

We have already published the results of experimental releases to measure butterfly movement behaviors (Keufler et al. 2010), but we include an overview of the key methods and results in this Final Report.

We performed two types of experiments using Appalachian brown butterflies (ABB), *Satyrodes appalachia* (Chermock) as a surrogate species for SFS. First, we quantified the choices butterflies made when released at boundaries between habitat types. Second, we quantified movement parameters for individuals released within large areas of each habitat type. As our experiments involved moving individuals away from their native wetlands to measure their movement behaviors in other habitats, and we could not be certain that we would be able to recapture all released butterflies to return them to the wetlands, we judged it would be unethical to perform these experiments on the endangered SFS directly. However, when we observed naturally moving (non-released) individuals in wetlands, we found that ABB has movement behaviors very similar to those of SFS, supporting the use of ABB as a behavioral surrogate species for SFS (Keufler et al., unpublished).

We identified five common habitat types for our experiments: upland forest, riparian forest, open field, wetland meadow (high-quality habitat for our species), and urban development. Within our study landscape, upland-forest and open-field habitats each cover ~40–45% of the land surface; wetlands and riparian tracts each account for < 5% of the land surface.

We examined habitat choices made by ABBs that we released at distinct boundaries between pairs of habitats. We performed releases because encounters with most boundaries would occur too rarely for us to study. We established release sites at all realistic habitat boundaries across Fort Bragg for a total of six boundary types at 16 different locations. There were release sites at three different locations for each of five different boundary types: wetland to riparian forest, wetland to upland forest, riparian forest to upland forest, upland forest to open field, and upland forest to urban development. Additionally, we established one site at a rare boundary type, riparian forest to open field. At each site, we released ABBs that were collected and transported from an area where they occurred in abundance (as in Conradt et al. 2000 and Kuefler and Haddad 2006). Upon their release we visually tracked each butterfly until it was lost in one of the two habitats. We recorded the habitat it first flew into, the habitat it spent the most time in before it was lost by the observer, and the habitat in which it was lost. We defined the ''preferred habitat'' to be the one that the butterfly chose by two or more of the above three criteria. For each pair-wise choice we then calculated the frequency of selecting either habitat based on these preferences. Finally, for each habitat, we calculated an overall probability of entry as the average selection frequency across all the pair-wise choices where that habitat was an option. Each butterfly used was uniquely marked on the wing with an ultra-fine-tip marker to ensure that we did not use the same individual twice. Butterflies were observed until they were lost in a habitat or until no movement had occurred for 30 minutes. We collected data from 59 individual butterflies released at boundaries, with at least 8 individuals for every boundary type with the

exception of only 3 individuals at the riparian forest–open field interface. For more common boundary types, such as an upland forest–open field interface, we were able to collect choice data from an additional 9 butterflies that were released for movement-path experiments (described in the section below). For each boundary type, we tested the hypothesis that there was no preference for either habitat using a binomial test. Additionally, for each habitat type we analyzed butterfly choices using the Freeman-Halton extension of Fisher's exact probability test (effectively a G test for low sample sizes) to test whether the probability of choosing a certain habitat depended on the adjacent habitat.

To quantify habitat-specific movement, we conducted releases within continuous areas of single habitat types. We established release sites at three different locations for each of four habitat types: wetland, riparian forest, upland pine forest, and open field. We then released naive butterflies at each site and collected data on spatial aspects of movement. Butterflies were uniquely marked, individually released, and, whenever possible, re-caught after the trial and returned to their original place of capture.

We collected spatial data on butterfly movement using two different techniques, depending on the type of habitat. In upland pine forests and open fields, we were able to walk or run behind butterflies while maintaining a suitable distance so as to not influence their movements in any obvious way. One observer called out at 5-s intervals, and at each call the second observer dropped a numbered marker at the butterfly's location. This process was repeated until the butterfly perched for 30 min or was lost from sight. We then measured the bearing and distance between sequential markers (which we defined as a ''move'') and used them to calculate a sequence of move lengths and turn angles (i.e., the angle between successive bearings) for each movement path. If a butterfly did not move during an interval, we designated that interval as a ''rest period.'' For these movement-path analyses we used data from releases at boundaries if butterflies clearly flew in a specific habitat for two or more moves. If butterflies moved through both habitats, then flight paths of the same butterfly in each respective habitat were treated as independent paths. In bottomland forests and wetlands, where walking was difficult and the habitat was sensitive to trampling, we could not physically follow butterflies. In these habitats, we used pairs of digital compasses and triangulation techniques, rather than numbered markers, to determine move lengths and turn angles for each movement path (see also Zalucki et al. [1980]). We worked in pairs, with each observer standing at a fixed location. Each observer operated a KVH DataScope (digital compass; KVH Industries, Middletown, Rhode Island, USA) affixed to a swivel on a PVC pole. The poles were pushed into the ground to maintain their position relative to each other. Upon release the observers worked cooperatively to take synchronous bearings of the butterfly's position at 5-s intervals, until the butterfly either perched for 30 min or was lost from sight. We also used this observational approach to track the movements of undisturbed ABB in their native wetland habitats and used these data on nonreleased butterflies to gauge the effect of release on ABB's behavior. To collect data for undisturbed butterflies, paired observers stood at fixed locations within areas where butterflies were abundant, began taking data as soon as an individual was sighted, and continued until the butterfly was lost from sight or perched >30 min.

We used Kolmogorov-Smirnoff (K-S) tests to determine whether the distributions of move lengths and turn angles differed between all pair-wise combinations of habitats. To compare

movement rates among habitats, we computed a single index of motility that integrates the two components of movement, move lengths and turn angles, based on the correlated random-walk model of Kareiva and Shigesada (1983). This motility index represents the asymptotic amount by which the mean squared displacement of a butterfly from its starting point increases with each move. For details, see Keufler et al. (2010).

3.3.2 HABITAT MODELING WITH MAXENT

Landscape connectivity was analyzed with respect to maps of known or high potential habitats for SFS breeding. Habitat maps were created as follows. Using variables derived from terrain, land cover, and vegetation structure data, we created two maps characterizing the study area's suitability for SFS at two different extents: (1) a habitat suitability map covering only Fort Bragg, and (2) a buffered habitat suitability map that covers Fort Bragg as well as a 10km buffer around Fort Bragg's outer boundary. Because of the temporary (i.e. successional) nature of SFS habitat, we based these habitat suitability models on those locations where we saw SFS during, and within one year of 2008 (the year for which we obtained Landsat data, see below). Butterfly locations were obtained as Universal Transverse Mercator (UTM) coordinates using a Trimble hand-held Global Positioning System (GPS) unit, resulting in a total of 217 points representing SFS presence locations.

A wide range of terrain-derived variables has been found important in vegetation modeling (Franklin 1995) and by extension, in modeling the distribution of fauna dependent on vegetation, such as butterflies. Terrain variables derived for this study included moisture (flow accumulation and slope), solar radiation (aspect), temperature (elevation), and topography (relative slope position, topographic position index, terrain shape). (For more information on each index used see e.g. Tarboton 2009). All terrain-based variables were derived from a Digital Elevation Model (DEM) at the 10m resolution, acquired from the USGS national elevation dataset using tools contained in the ArcGIS Spatial Analyst and TauDEM v. 4.0 packages (Tarboton 2009).

To obtain land cover data of the study area, we georectified one cloud and snow-free winter (January 2008) and one cloud-free summer (May 2008) LANDSAT-5 Thematic Mapper (TM) image of the study area to the NC State Plane projection. We then converted the six non-thermal TM bands (bands 1-5, 7) to radiance (Chander et al. 2007) and estimates of surface reflectance using the DOS3 approach (Song et al. 2001). Surface reflectance values were transformed to Tasseled-Cap "brightness", "greenness" and "wetness" indices (Kauth & Thomas 1976, Crist & Cicone 1984) using coefficients calibrated for Landsat TM-5 surface reflectances (Crist 1985). For each surface index, we considered the value of each pixel as well as the difference in values between the two images.

To characterize the study area's vegetation structure, we obtained two datasets. First, for the buffered Fort Bragg habitat suitability map, we obtained, at a 10m resolution, two spatially explicit datasets representing canopy height and surface height respectively. These two files were derived using LiDAR data obtained by the North Carolina Floodplain Mapping Program (NCFMP; http://www.ncfloodmaps.com) and processed by the USF&W office in Raleigh, NC. For the habitat suitability map covering only Fort Bragg, we used the LiDAR data obtained through this project (see **LiDAR Forest Cover Estimates)**. We derived mean vertical density of vegetation at heights 1-2m, 2-5m, 5-10m, 10-20m and higher than 20 m, also at the 10m

resolution. Vegetation density was chosen as it best characterizes the relative vertical structure of a habitat, an important aspect of habitat suitability for this butterfly (Kuefler, et al. 2008).

We created habitat suitability maps for both extents (Fort Bragg and buffered Fort Bragg map) using the Maxent software package (for a more complete description see Section 3.2.2.1). For both Maxent models, we retained the default regularization multiplier (1), convergence threshold (10^{-5}), maximum number of iterations (500), and maximum background points (10,000). Furthermore, we conducted ten bootstraps of each model (with training data for each bootstrap sampled with replacement), and replicate species distribution models were averaged to create a final output. Because our environmental data were derived from different sources, not all data conformed to the same spatial extent. Maxent will adapt the coarsest spatial grain during modeling, causing us to lose the fine-scale detail present in the LiDAR and DEM-derived products. As such, we resampled all Landsat data to the 10m scale using nearest neighbor scaling to retain the file-scale information provided in the terrain and LiDAR-derived data. This did not improve the spatial resolution of the Landsat images but aligned the pixels of the various data sources for the analyses.

We used a cumulative threshold value that balances errors of commission (sensitivity) and errors of omission (specificity) to distinguish suitable from unsuitable habitat. Specifically, we used a method of thresholding the point on the ROC curve where the sum of the sensitivity and specificity is maximized (for more information see Phillips et al. 2006). Once suitable habitat patches were identified, we filtered unlikely locations first by eliminating those habitat patches smaller than the smallest known habitat patch that supports SFS ($100m^2$) and thereafter locations present within human habitation.

3.4 AMPHIBIANS

3.4.1 FIELD EXPERIMENTS

We conducted field experiments with amphibians to provide empirical data that could be used to create movement models that would be comparable to movement models developed for RCWs and St. Francis' satyrs.

In addition to providing data for modeling, these experiments examined how movement behavior is affected by several different factors that are subject to modification by people and are associated with the ecology of amphibians, ranging from conditions within breeding ponds, to coarse transitions between habitats at their boundaries, to changes within habitats in ground cover. This research tests three assumptions that are often made implicitly in studies of movement behavior and connectivity, including: 1) individuals within a population exhibit similar behavior, 2) species respond more strongly to canopy structure than variation in ground cover, and 3) the movement behavior of common species is an appropriate surrogates for rarer species. These empirical results are used in simulation studies with amphibians that are reported elsewhere (see Movement Simulations for SFS and Amphibians). Here we report our findings from field experiments with amphibians and provide recommendations for connectivity research.

We conducted a series of experiments to examine factors associated with the movement ecology of amphibians as they leave breeding ponds (Figure 8). First, we manipulated larval density of ornate chorus frogs to determine how variation in larval conditions affects movement behavior in good and bad dispersal habitat. Although the dispersal of juvenile amphibians has been studied

by others, important questions remain unresolved. Chelgren *et al*. (2006) observed juvenile red-legged frogs (*Rana aurora aurora*) leaving natal ponds and found that smaller body size and delayed timing of metamorphosis resulted in slower dispersal rates. Patrick et al. (2008) examined patterns of habitat selection and mortality for juvenile wood frogs (*Rana sylvatica*) and found that habitat selection was affected by coarse-scale rather than fine-scale variation in habitats, which resulted in high densities of juveniles in suitable habitats that were associated with higher density-dependent mortality. However, experiments examining the effects of larval conditions on juvenile movement behavior in habitats that vary in suitability are lacking. Here we manipulate larval density of ornate chorus frog tadpoles to test for the effects of variation in body condition on movement behavior in high and low quality habitats where low quality habitat reflects common management practices. We initially compared movement behavior of frogs reared at different densities in forest and field habitats. We then compared the movement behavior of frogs from different densities in forested habitat where leaf litter is raked or left in place. We predict that frogs raised at low densities will be larger and move more rapidly than frogs reared at high densities regardless of the habitat in which they are released following the pattern observed by Chelgren *et al*. (2006).

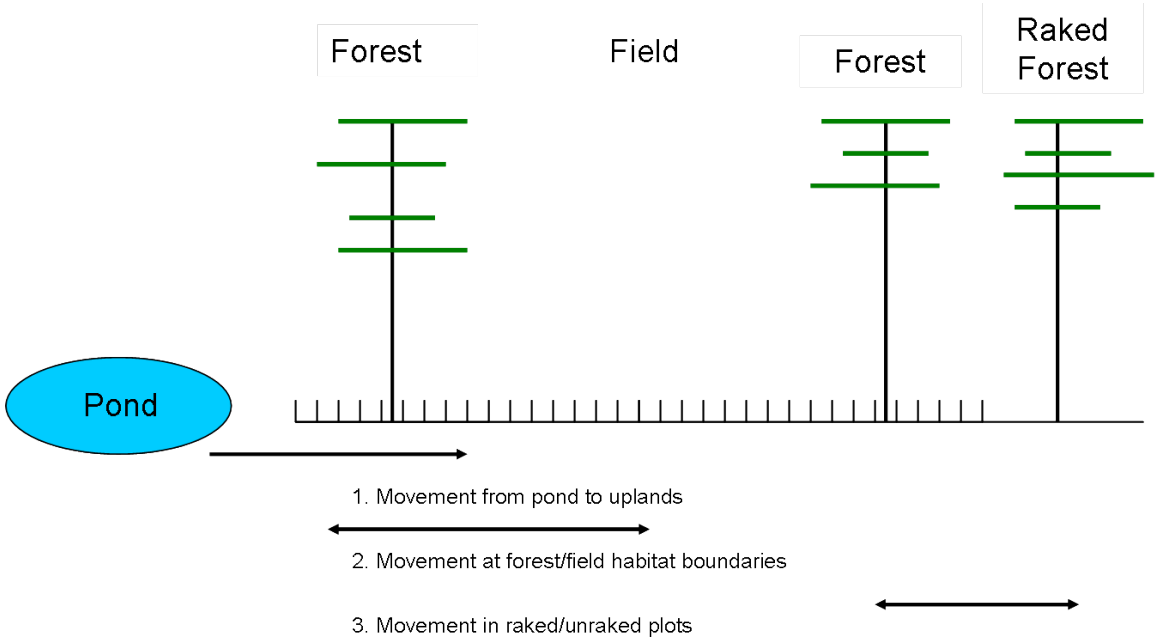

Figure 8: Amphibian field experiments collected movement data on species as they moved: (1) from ponds to upland areas, (2) from forest to field habitats, and (3) from raked to unraked forest plots.

We then examined how manipulating microhabitats affects movement behavior of eastern newts (*Notophthalmus viridescens*) and ornate chorus frogs (*Pseudacris ornata*). Habitat manipulation is an important process that affects species in fragmented landscapes. Although habitat fragmentation is caused by loss of habitat patches, remaining habitat may vary in quality as a result of different management practices or disturbance regimes that are found in an area. Amphibians could be sensitive to the manipulation of microhabitats because individuals require different habitats for different life stages and often exhibit site philopatry (Blaustein 1994,

deMaynadier and Hunter 1995, Rothermel and Semlitsch 2002). We manipulated microhabitats by raking pine straw because this has been linked to changes in amphibian behavior (Moseley *et al*. 2004) and it is a widespread forestry practice in the southeastern U.S. Because amphibians are expected to move faster through lower quality habitats (Rosenberg *et al*. 1997), we expected that both of our study species would move faster through areas in which pine straw had been harvested. We also hypothesized that, in their escape from unfavorable habitats, amphibians would move in more direct paths in order to minimize their time spent in those habitats (Rosenberg et al 1998). Through this experiment, we were able to assess the direct influence of microhabitat structure heterogeneity on amphibian movement rates and behavior, a topic of which little is understood (but see Roznik & Johnson 2009).

Finally, we evaluated how interspecific variation affects movement behavior by comparing the behavior of juvenile southern leopard frogs (*Rana sphenocephala*) and juvenile gopher frogs (*Rana capito*). Frogs and salamanders might be expected to show differences in movement behavior because the body shape of salamanders makes them more sensitive to desiccation (Todd et al. 2009). By comparing the movement behavior of these congeneric frog species with a management relevant context – that is, at the boundary of forest and cleared habitat – we provide important ecological insights by testing the generality of movement behaviors among different species. Boundary behavior data is used to determine the permeability of different habitats, and this strongly influences dispersal behavior. Further, we provide critical information for conservation of amphibians since southern leopard frogs are a widespread and common species throughout much of their range while gopher frog populations have experienced severe declines in recent years.

In conducting our experiments, we test 3 key assumptions that are frequently implied in studies of landscape connectivity: (1) species respond to environmental factors in a similar fashion, (2) species respond more strongly to the structure of coarse habitat types rather than fine-scale variation in microhabitats, and (3) individual variation within a population does not affect movement behavior. These assumptions are seldom tested empirically in studies of landscape connectivity, so our findings provide important lessons for understanding the movement ecology of amphibians and how different ecological factors affect landscape connectivity for species in fragmented landscapes. In the process of gathering data to test our hypotheses, we obtained detailed movement data needed for simulation models in complex landscapes.

3.4.2 EMPIRICAL DATA FOR SIMULATION STUDY

Because of concerns about losing animals in unsuitable habitats, we conducted amphibian releases necessary to parameterize dispersal simulation using a surrogate species, the ornate chorus frog. The ornate chorus frog has a distribution on and around Fort Bragg similar to Carolina gopher frogs, suggesting that their dispersal may be constrained by similar factors, but is found with greater predictability and in greater numbers at breeding sites making them a more amenable to study.

We quantified movement behaviors of adult ornate chorus frogs captured exiting breeding pools in three of the four habitats described for SFS experiments, upland forest, riparian forest and open fields. Animals captured exiting breeding pools were taken to locations at least 1 km away to a release location. Each animal was dipped in fluorescent dye powder before release, and its location was marked in 5-minute intervals for up to 30 minutes or until the animal was lost. We

measured step length as the distance between consecutive locations and turn angles as the change in direction between consecutive steps. We released 10, 6, and 4 chorus frogs into upland forest, open field and riparian corridor habitats, respectively.

We also released 29 ornate chorus frogs and 3 Carolina gopher frogs at upland forest-open field edges to determine boundary behaviors and assess how dispersion rates differ between the two species. The release protocol was as above except that the only a single timed location was recorded from the end of each release, corresponding to movement over the course of 12-60 minutes.

3.4.3 EXPERIMENT 1

We collected 24 ornate chorus frog egg masses from one wetland on 2 February 2010. Egg masses were held in a lab for 7 days until larvae hatched. After larvae became free swimming they were randomly assigned to cattle tanks. Twenty cattle tanks were fitted with screened standpipes and allowed to fill naturally with rainwater over a 3-month period prior to the introduction of tadpoles. Three days prior to the introduction of tadpoles, cattle tanks were filled with 100 L of dry longleaf pine needles raked at Fort Bragg. We collected plankton from the pond where egg masses were collected with a net and added 500 mL of pond water containing concentrated plankton to each tank. Each tank was randomly assigned a high or low density of tadpoles (40 or 20, respectively).

We monitored tanks 3 – 5 times per week over 12 weeks, and we allowed tanks to dry down naturally in late April as tadpoles began to mature. Water levels declined 8 – 10 cm over this time period, and all tanks were lowered to a depth of 20 cm when tadpoles initiated metamorphosis. We collected individual frogs from cattle tanks as they completed metamorphosis, weighed them to the nearest 0.01 g, held them in controlled conditions in a laboratory, and fed them wingless fruit flies *ad libitum* until they were used in field experiments.

To test the effects of larval density and habitat structure on movement behavior of juvenile frogs, we conducted two sets of experiments. First, we released frogs from high and low density tanks into open fields and longleaf pine forest to examine the effects of larval density and habitat type on movement behavior. We established 2 release plots at each of 4 sites. We randomly assigned one frog from a high-density tank and one frog from a low density tank to each plot during each night of releases. We continued releasing frogs to track their movements until 4 – 6 frogs had been tracked on all plots. We conducted releases at night between 2100 and 0300. Frogs were released one at a time. We marked each animal with fluorescent dye powder, randomly selected a cardinal direction for the animal to face, and placed it in the center of the plot and checked the location of the frog at 3-minute intervals for a total period of 12 minutes. Frog locations were initially checked at longer intervals, but this resulted in the loss of individuals because of the small amount of dye powder on the frogs. In a second experiment, we selected 3 additional 20 x 20-m forest plots where pine straw had been previously raked (see details below in experiment 2) to evaluate the effects of larval density and microhabitat on movement behavior.

After tracking each animal, we mapped the trail segments with compass and measuring tape. We measured the straight-line distance between each location marked at three-minute intervals to the nearest centimeter and summed these to obtain a measure of cumulative total distance. We also measured the direction between these locations with a compass, and recorded the straight-line

distance and direction from the release point to the last observed location of the animal (net total distance and net direction) with the same precision.

We examined the effects of larval density and habitat type on movement behavior with a two-way ANOVA. We used two measures of movement behavior as response variables: the average speed (m/min) and the linearity of movement paths, which was determined by dividing the net distance of a path by the total distance moved along each segment of a path. We tested movement rates and path linearity for normality with a Kilmogorov-Smirnov test, and we log-transformed data when necessary.

3.4.4 EXPERIMENT 2

Our experiment to test for effects of microhabitat variation on movement behavior consisted of two treatments: closed-canopy forest plots dominated by pine straw (henceforth referred to as control plots) and closed-canopy forest plots dominated by pine straw in which a 20 by 20 meter (m) area had been raked free of pine straw (henceforth referred to as raked plots). For eastern newts, the experiment consisted of four replicates per treatment, and for ornate chorus frogs, the experiment consisted of three replicates per treatment. The replicates were established in separate locations due to transit logistics.

Between October 22 and December 2, 2009, we captured 35 adult male eastern newts from a pond using minnow traps or dip nets on nights when weather conditions were favorable to amphibian movement. Newts were then transported to experimental sites within five to six miles of the capture location. Between January 21 and March 28, 2010 we captured 16 adult ornate chorus frogs from breeding ponds surrounded by drift fences using pitfall traps. Individuals were then transferred to experimental sites within one mile of the capture locations.

As in experiment 1, we tracked animals using fluorescent dye powder. We left the immediate area (at least 30 m away) for five minutes to allow the individual sufficient time to move away from the release point. We then returned and followed the trail with an ultraviolet flashlight, and marked the location of the individual. This process was repeated until an individual had moved for a total of 45 minutes, failed to move from one location after at least 15 minutes, or was lost in the habitat. (In the case of four newts and two frogs, we ceased data collection less than 45 minutes after release due to a fourth reason: insufficient time available to continue tracking.)

For each species, we compared the average speed and linearity of movement paths in control plots with raked plots. We also compared net total distance traveled. We tested data for normality and transformed it when necessary prior to comparing movement behavior in different treatments with an ANOVA.

3.4.5 EXPERIMENT 3

To test the value of surrogate species and the role of habitat boundaries in affecting movement behaviors, we used newly metamorphosed Carolina gopher frogs (*Rana capito*) and southern leopard frogs (*Rana sphenocephala*), both of which occur on Fort Bragg. Carolina gopher frogs are a federal species of concern while southern leopard frogs remain common throughout much of the United States. We removed approximately 50 eggs from each of 8 egg masses of both species from ponds on Fort Bragg in January, 2008. Partial egg masses were held in the laboratory for approximately 2 weeks until they hatched and larvae were free swimming. After

hatching, larvae were transferred to polyethylene cattle watering tanks and remained in tanks until they completed metamorphosis. Cattle watering tanks contained ~900 l of water and 1.5 kg of leaves (a mix of sweetgum (*Liquidambar styraciflua)*, oak (*Quercus* spp.), and pine straw), and were regularly stocked with plankton from natal ponds. Tadpoles were reared at a density of 18 per tank in 20 tanks.

A total of 4 replicate dispersal arenas were established on forest/open field boundaries along the Overhills power-line corridor on Fort Bragg. Open field was clear-cut longleaf that was mowed seasonally by the utility company. Forest was longleaf pine savanna. Each experimental arena was centered on an artificial pool (90 cm diameter, 10 cm deep, constructed of black plastic pond liner) placed directly on habitat boundaries (Figure 9). Arenas extended 25 m into forest and 25 m into open field habitat (total area 50 x 5 m). They were constructed of 90 cm high, plastic-weave silt fencing, supported by wooden stakes, the bottom edge of which was buried 15-20cm below the ground surface.

When animals metamorphosed from cattle tanks, they were released into experimental arenas at dawn or dusk following rain. Individuals were uniquely marked using toe clips, weighed to the nearest 0.1 gram, and measured as snout-vent length (mm). Initial releases were in the center of the arena at the habitat boundary. Once individuals were released into arenas, pitfall traps were monitored daily and recaptured individuals were identified, measured and released back into the center of the arena next to the point of capture. The first recapture of each individual was used to determine the initial distance and initial rate of emigration. Additionally, these data were used to determine initial direction of movement with respect to habitat type. Subsequent captures of individuals allowed estimation of total distances migrated and overall direction of movement. Experimental animals were removed from arenas upon their third recapture or upon capture at the end of each experimental corridor, and returned to the natal pond.

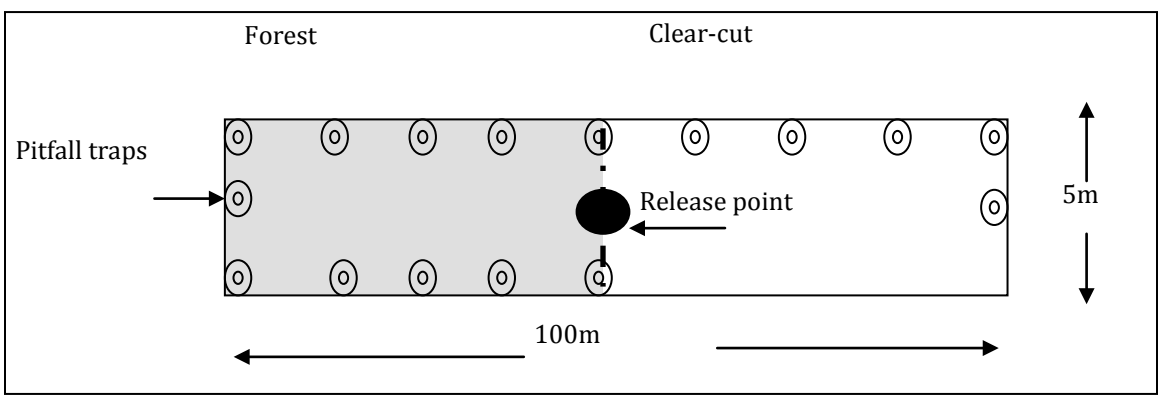

Figure 9: Schematic of arenas used for releases in experiment 3.

3.4.6 VERNAL POOL MAPPING

Assessing connectivity for amphibians requires knowledge of where breeding ponds are located, but amphibian breeding sites are not well mapped by existing spatial data. Breeding ponds that are suitable for amphibians typically remain flooded for only a portion of any given year, and they are small relative to the spatial resolution of GIS data, so even National Wetlands Inventory data may not provide a good map of small, isolated ponds. Moreover, in our study area amphibians use both natural and artificial wetlands that are created by various human activities.

We developed predictive models for both natural and artificial ponds and verified the locations of suitable breeding ponds with field surveys. We intentionally selected data sets that should be available at comparable resolution for many other areas. We obtained a 20-foot resolution digital elevation model (DEM), stream data (1:24,000 hydrography data from the U.S. Geological Survey), and data from Fort Bragg on the locations of dirt roads. We processed the DEM to identify depressions within the landscape and a few other metrics including a wetness index that reflects the amount of area located upslope of a point in a landscape and a landform index that indicated whether a point is located along the top of a ridge, the side of a hill, or the base of a slope. We also used the DEM to calculate slope and elevation for points within the study area. Finally, we calculated the distance from dirt roads and streams for all points within our study area.

Preliminary analyses of wetland sites using generalized linear models revealed spatial autocorrelation in the data, so we switched from using logistic regression to generalized additive models (GAMs) to have a more flexible analysis that would allow us to deal with spatial autocorrelation directly. GAMs are similar to logistic regression, but allow for nonparametric smoothing functions to be used in fitting data to predictor variables. If spatial autocorrelation is present in the residuals of a GAM, then a smoothing function based on geographic coordinates of survey sites can be added to control for the spatial structure of the data (Wood 2006).

We developed predictive models for natural and artificial wetlands separately. We generated models using data for known locations of natural and artificial wetlands as well as random points in the landscape that were not natural or artificial wetlands. We initially examined a full model which included parameters for distance from streams and dirt roads, wetness index, landform index, slope, and elevation, and then used a backward selection procedure to systematically remove parameters from the original model and determine whether the new model with fewer parameters provided a more parsimonious fit. We assessed the accuracy of our predictive models with receiver operating characteristic curves (Freeman and Moisen 2008). Models with an area under this curve that is greater than 0.9 show strong discrimination between sites that are and are not wetlands.

3.5 MOVEMENT SIMULATIONS FOR SFS AND AMPHIBIANS

In order to predict important dispersal corridors for SFS and rare amphibians on and around Fort Bragg, we built spatially explicit movement simulations parameterized with the landscape data described in the habitat modeling section 3.3.2 Habitat Modeling with MaxEnt and movement data from the butterfly and amphibian releases described in the SFS and amphibian methods sections 3.4.1 Field Experiments and 3.3.1 Field Data - Experimental Releases of Appalachian Brown). These simulations are identical in structure for butterflies and amphibians, and followed virtual animals originating in current, historic, or potential breeding sites as they moved throughout the Fort Bragg landscape. The simulations used five types of information as input: 1) a map of the locations of the 4 major habitat classes (wetlands, riparian corridors, upland forest, and open areas including roads and human development); 2) a map of the locations and sizes of waterways (important for amphibian models only, with streams ranked as first, second, third, or $\geq$ fourth order); 3) a map of the locations of potential breeding sites for the focal species (suitable wetlands for butterflies and suitable temporary ponds for the amphibians); 4) species-specific step length and turn angle distributions in each habitat; and 5) species-specific habitat choices at

the edges of each pair of habitats that has common boundaries on the landscape. For butterflies only, we also included habitat-specific probabilities that each move would be followed by a rest, and a distribution of rest period lengths. For amphibians only, crossing probabilities for first through third order streams were input, and crossing probabilities of larger waterways were set to 0. All habitat data were input at a 30 x 30 m grain covering Ft Bragg, Camp Mackall, and a 5 km buffer surrounding the bases. The simulation produced as output the number of times a 30 x 30 m cell was used by emigrating animals, the number of times a 30 x 30 m cell was used by animals successfully dispersing among potential breeding sites, and the number of animals successfully dispersing between each pair of potential breeding sites.

Separate simulations were carried out for SFS and amphibians. Butterfly simulations were based on movement data taken at 5-second intervals (see Field Data - Experimental Releases of Appalachian Brown) and amphibian simulations were based on ornate chorus frog movement data taken at 5 minute intervals (see Amphibian empirical results section). We also attempted to determine connectivity for gopher frogs assuming that they moved through different habitats similarly to chorus frogs. In particular, we assumed that differences between the species in the displacement rates over longer movement paths could be wholly attributed to differences in the mean step lengths (i.e., habitat-specific turn angle distributions did not differ between the species). If we further assume that the coefficient of variation (CV) for step length distributions was constant between the species, we could use the method of matching moments to parameterize habitat specific gamma distributions for gopher frog step lengths from chorus frog movement paths. We did not have sufficient movement data from eastern tiger salamanders to model their dispersal, and did not think it appropriate to model their movement based on chorus frog movement.

To estimate the relationship between gopher frog and chorus frog step length distributions, we used release experiments for which we had two locations (the release and recapture points) separated by 12-60 minutes (N=7 chorus frog paths, 5 gopher frog paths). We estimated squared displacement rates for each species as the slope linear regression of the squared distance between release and recapture locations compared to the elapsed time between release and recapture. We then calculated habitat specific mean and standard deviation for gopher frog step lengths as the ratio of gopher frog:chorus frog squared displacement (ρ=7.79) times the mean and standard deviation, respectively, for chorus frog step length in each habitat.

For butterflies and amphibians, simulations began with a virtual animal placed in the center of each cell located within a potential breeding site. Consequently, larger breeding sites produced more dispersers than smaller sites, corresponding to observations that habitat area was related to population size in SFS (Kuefler et al. 2008). Each animal began moving in a random direction. The distance moved was drawn from a gamma distribution fit to the distribution of step lengths in breeding (i.e., wetland) habitats input to the model.

Whether or not the animal continued to move was then determined based on the resting probabilities observed during all release experiments and observations of naturally occurring butterflies. The length of time a butterfly rested before continuing to move was similarly drawn from a gamma distribution fit to the observed distribution of rest times. Because rest data were not taken for amphibians, we did not include resting behavior in dispersal simulations (i.e. resting probabilities were all set to 0), effectively lengthening the total dispersal period simulated.

Following a rest (if any), the length of the next step was drawn from the wetland-specific step length distribution. The direction of successive moves was determined by drawing a random turn angle from the observed distributions of turn angles using the following procedure, which retained the overall shape of the observed turn angle distribution while generating a more continuous set of possible angles than were represented in the finite set of observed angles. First, the 30 degree bin (0-30, 30-60,…150-180) of the turn angle was drawn from a multinomial distribution fit to the wetland turn angles input to the model. Next, the exact turn angle was drawn from a uniform distribution spanning the appropriate 30 degree bin. Finally, the sign of the turn (right or left) was determined from a uniform random distribution (i.e., with 50% chance of either sign).

These steps were repeated until the projected end point of a move was in a cell covered by a new habitat type. If the new position resulted in the butterfly crossing a boundary to a different habitat, the program then determined if the move was allowed. In our experimental releases, we quantified the fraction F of butterflies starting at rest at the boundary between two habitats that moved into the more preferred habitat. To parameterize the simulation models, we had to translate F into the probabilities that moving butterflies approaching the boundary from both the more- and less-preferred habitats would cross the boundary. To do so, we first assumed that half of the butterflies encountering the boundary would come from the more-preferred and half from the less-preferred habitat. Next we assumed that all of the latter would cross the boundary (into the more-preferred habitat). Let P represent the probability that a butterfly in the former group does not cross the boundary (i.e., remains in the more-preferred habitat). With these assumptions, we have the relation:

(4)

(where the two terms on the right hand side are contributed by butterflies approaching the boundary from the less- and more-preferred habitats, respectively). Thus we estimate P as $2(F-1/2)$, and the probability that a butterfly moves from more- to less-preferred habitat is $1 - P$.

If the move into less preferred habitat was allowed, the butterfly's location was updated. If not, a new step length and turn angle were drawn, and the process repeated until either the new location was in the original cell or the boundary crossing was allowed. If a new location would take a butterfly across multiple cells in a single step, all boundary crossings had to be allowed.

For amphibian simulations, cells containing streams and rivers were considered to be distinct habitats, with different entry probabilities for streams of first, second, third, and fourth or greater order and distributions of movement upon entry equivalent to riparian habitats. Because we lacked data on stream crossing probabilities, we considered several scenarios in which 1st-3rd order streams had different impacts on amphibian movement. Here we present the two extreme scenarios: that streams below fourth order present no barrier to dispersal (crossing probabilities=1) and that all streams act as complete barriers to dispersal (crossing probabilities=0).

Animals continued to move for a number of steps determined by their effective dispersal period and the time interval of movement data. For SFS, the lifespan of each butterfly was drawn from an exponential distribution with mean of 3 days, corresponding to the average lifespan of marked SFS (Kuefler et al. 2008). Based on observations of butterfly activity during annual population surveys, we assumed that butterflies were active for six hours each day, corresponding to 4,320

five-second moves per day. Because we do not have similar information about amphibian dispersal we modeled dispersal periods of 1, 10, and 100 days for ornate chorus frogs, and 100, 200 and 300 days for gopher frogs to capture a wide range of possibilities. We assumed 10 hours of activity each day corresponding to 120 five-minute steps.

To test the validity of the model, we compared simulation predictions of butterfly dispersal probabilities among occupied breeding sites to observed dispersal rates from capture-mark-recapture (CMR) data taken during annual SFS population monitoring (Kuefler, et al. 2008). In these simulations, we included only occupied and historic breeding sites, all of which occur on Fort Bragg. For these simulations, larger breeding sites containing multiple survey transects used during annual SFS population surveys separated by at least 30 m were designated as separate breeding sites. SFS movement was simulated as described above, but the simulation also tracked the location of each butterfly over a 20 minute period (i.e., 240 steps) every 24 hours (six of which were "active" hours) after it began moving until it died. If a butterfly was located within a colony at any time during the 20 minute period it was considered to have been "recaptured" and the sites where that butterfly originated, was most recently recorded, and was recaptured were recorded. A butterfly was also considered to be "recaptured" if it occurred in any of four upland forest areas near surveyed colonies where survey crews typically spent 30-40 minutes every 2-3 days (approximately half the effort spent in surveyed breeding sites) and would have likely seen an SFS flying by (no such butterflies were observed, even for upland sites close to wetlands, indicating SFS aversion to upland habitat).

From these data we calculated the probability that a recaptured butterfly originating in breeding site A was recaptured in breeding site B for all pairs of breeding sites, including nondispersal events (i.e., butterflies released and recaptured in the same site). Because effort in uplands was not equal to effort in breeding sites, we weighted predicted recaptures in breeding areas 2:1 compared to predicted recaptures in upland areas before calculating predicted dispersal probabilities. We then tested the predictive power of the model as the Pearson's correlation coefficient between the predicted dispersal probability and the relative frequency of dispersal observed from marked butterflies. We only included pairs of sites located within the same drainage since SFS do not appear capable of dispersing the longer distances that separate breeding survey sites on different drainages (see ResultsResults and Discussion - Dispersal Modeling - Model Results). Because very few butterflies were recaptured multiple times, we restricted our comparisons to first recapture events (including secondary recaptures did not change our results). We conducted 1000 replicate simulations for each year (2002-2007), varying the landscape so that only breeding sites occupied and surveyed during each year were included. We also updated the extent of breeding sites to reflect observed changes in suitable habitat caused by beaver activity (leading to breeding site expansion) and succession (leading to breeding site contraction).

3.6 EVALUATING MODEL COMPLEXITY

Two elements are required for a formal assessment of the value of increasing model complexity in predicting dispersal. First, the modeling framework must allow for changes in the representation of movement behavior while holding other elements of the model constant. This provides a measure of experimental control when comparing across models. Second, an independent testing dataset must be available to allow researchers to measure changes in model

fit with increasing complexity. For this project, these two elements were present for our studies of the Red-cockaded Woodpecker and St. Francis Saytr. We did not have sufficient independent testing data to do a similar analysis with amphibians.

3.6.1 MODEL COMPLEXITY IN RCW

A maximum likelihood approach was used to find which resistance surface (see Section 3.2.2.1) optimally represents RCW prospecting movements. These surfaces varied in complexity from a featureless landscape to one that incorporated both spectral (landsat) and structural (LiDAR) attributes. Each fledgling emerging from its natal territory is surrounded by a unique set of environmental features that may influence prospecting behavior. Thus, a discrete-choice model used to account for variation in available territories and surrounding environmental features. We defined the choice set for each individual as all territories within its prospecting range.

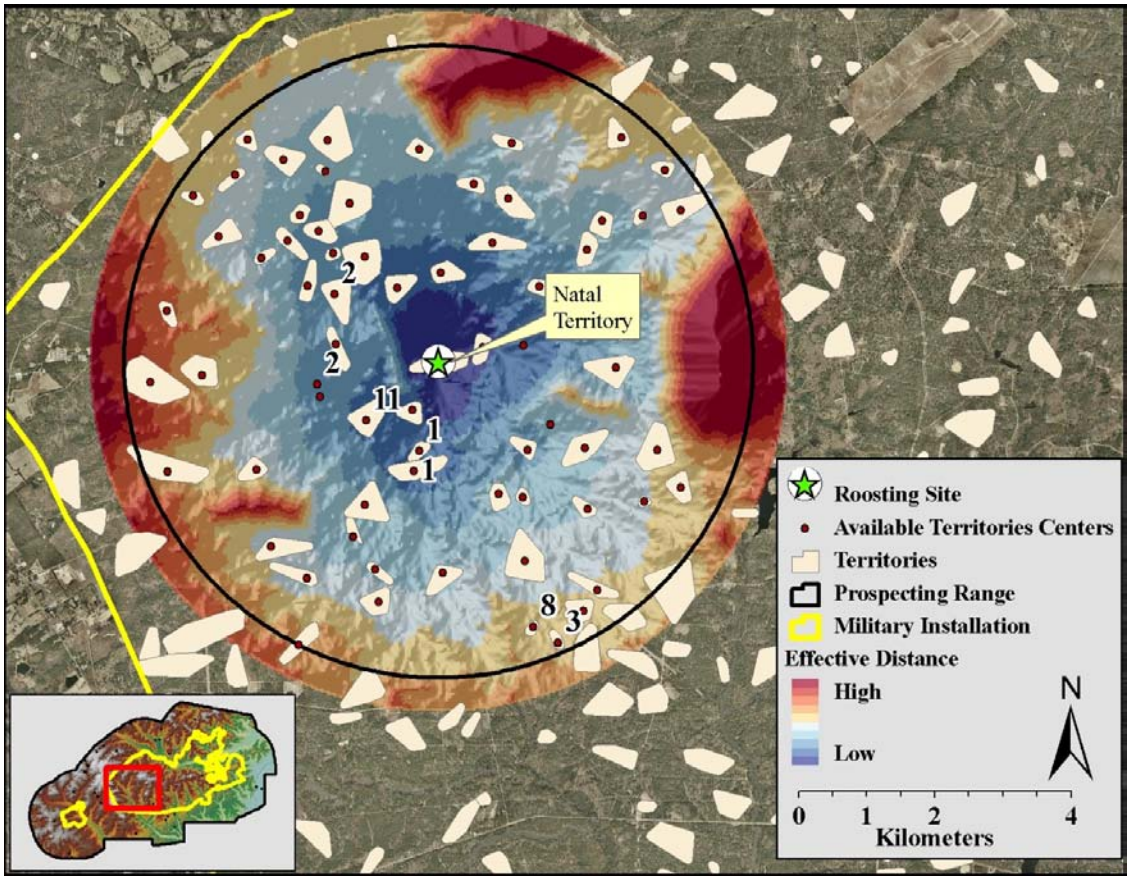

Figure 10: An example of prospecting movements of a radio-tagged juvenile female red-cockaded woodpecker's (*Picoides borealis*) in relation to effective distance surface. A number to the upper right of a territory indicates the frequency the bird was observed visiting that territory. Territories without numbers were never visited.

Our discrete-choice analysis evaluated RCW response to landscape features during prospecting by comparing the 70 resistance surfaces (2 types of occurrence data x 5 levels of environmental complexity x 7 resistance curves) against Euclidean distance in a featureless landscape. The response variable in the discrete-choice models was the frequency of territory visits during

observed prospecting behavior (Figure 10). 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 (AIC) 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 package Survival in R (Version 2.11.0, R Development Core Team 2010).

We evaluated the best resistance surface using an independent dataset of observed juvenile female dispersal events from 2005 (n = 57) and 2006 (n = 39). For each dispersing individual we created corridors in ArcInfo Workstation (Environmental Systems Research Institute Inc. 2008) by adding the accumulated cost from all least-cost paths between the natal territory and all available territories. Sets of available territories for each dispersal event were defined as territories with similar distance (with the 25th percentile) from the natal territory as the observed destination territory and are within the maximum distance any juvenile female was observed dispersing from the natal territory during all the years of banding data (Figure 11). Within this analysis we assessed if RCW short-distance dispersers (SDD) interact with the environment differently than long-distance dispersers (LDD). We defined the long-distance threshold at 6 km, the 95th percentile of the observed foray distance 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 11).

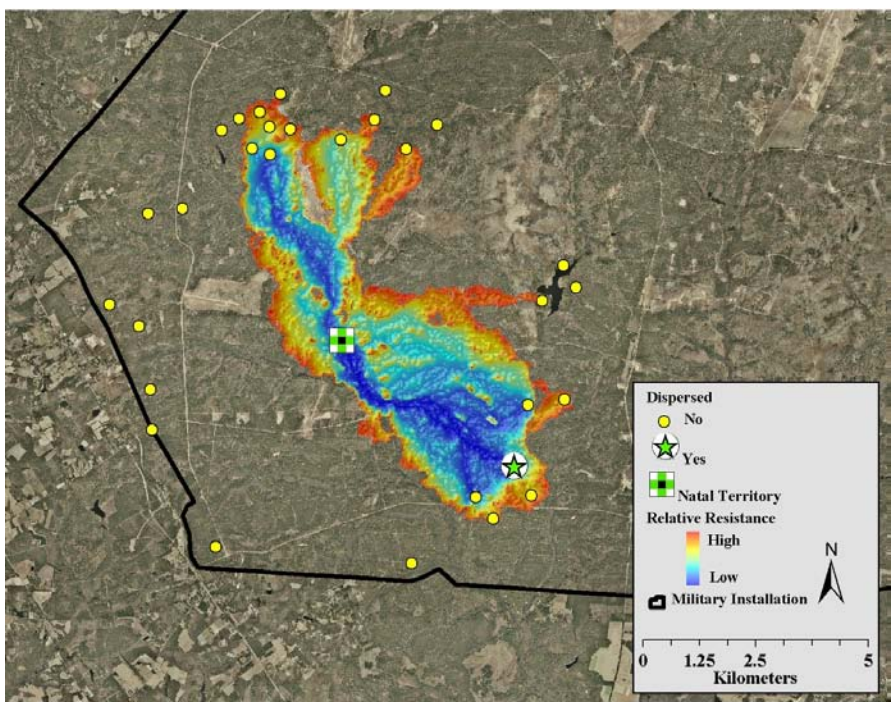

Figure 11: Examples of long-distance dispersing juvenile female red-cockaded woodpecker (*Picoides borealis*) that settled in a territory within the 25% least-cost corridor.

3.6.2 MODEL COMPLEXITY IN SFS

To determine the movement detail that is needed to predict dispersal in SFS, we compare dispersal predicted in simulations of varying complexity to dispersal events observed in a capture/mark/recapture (CMR) study of SFS marked in multiple breeding sites in 5 years (Haddad et al. 2008). Specifically, we assessed the ability of simulation models of increasing complexity to predict the observed dispersal patterns. Importantly, the dispersal data we used in the assessment are independent of the movement data we used to estimate model parameters.

As we noted above, building a more complex model involves greater cost. Therefore, even if a more complex model does a better job of predicting observed moves than does a simpler model, the simpler model might be preferred if it is easier to build and parameterize but still does a reasonable job predicting dispersal. We assessed the value of building more complex models in three ways. First, we adopt a parsimony approach using information criteria, weighing overall ability to predict the observed moves against the number of parameters that needed to be estimated to run the model. Second, we compare the predictive ability of the models to the financial costs of estimating the parameters.

The third way we assessed the value of model complexity recognizes that the utility of adding greater complexity to predictive models likely depends on the landscape context of a managed metapopulation. For example, most pairs of potential source and destination sites in our CMR study were separated by either a short distance of wetland matrix or by very large distances SFS would not be expected to traverse regardless of matrix composition. Therefore including details of movement differences in multiple habitats and at different boundary types may have been unnecessary for the simulations to mimic reasonably well the CMR results. However, an important goal in constructing dispersal models is to provide a tool for evaluating the consequences of management actions that may create a landscape that differs from the one on which the model was validated. This is certainly the case for SFS. Efforts are now under way to create (through flooding and tree removal) restored wetlands near current breeding sites and to translocate SFS into them. Some of these restoration sites will be located closer to habitat types that butterflies currently encounter only rarely in the vicinity of breeding sites. The movement models we have constructed are intended to help inform the decision of where restoration sites should be located to maintain connectivity between breeding sites (both current and restored ones). Therefore, we also ask if model complexity (i.e., the degree of detail about animal movement a model embodies) affects its predictions about the level of dispersal between breeding sites on a landscape that includes restoration sites, and thus differs from the landscape on which the CMR study was conducted.

The Full Simulation (hereafter FS) described above represented the most complex model we used. To evaluate the need for such a complex model, we compared its ability to predict observed dispersal events to that of three simpler models. In the No Edge (NE) model, we retained habitat-specific movements (i.e., distributions of turn angles, step lengths, and rest durations) but eliminated boundary behaviors (so that simulated butterflies moved freely from one habitat to another). In contrast, in the No Habitat Differences (NHD) model, we applied the movement characteristics from the breeding habitat (wetlands) to all locations on the landscape, but we retained boundary behaviors where different habitats meet. Finally, in the Distance Only (DO) model, we applied wetland movement characteristics to the entire landscape with no

boundary behaviors (thus simulating a pure correlated random walk, in which dispersal should depend only on the distance between sites).

We compared simulation predictions to CMR data to determine how well the simulation predicted observed dispersal among SFS breeding sites. We assessed the fit between model predictions and observed dispersal events in the CMR study in two ways. First, we simply computed the correlation between the observed and predicted fractions of dispersers starting from each breeding site recaptured at all breeding sites (including the original site). This approach does not discount for the number of parameters used in the model. Second, we computed the multinomial likelihood (appendix) of the observed recaptures for each model, and used them to compute the sample-size-corrected Akaike's Information Criterion (Hurvitch and Tsai 1989), which does penalize models with more parameters (see appendix for a description of how we determined the number of parameters in each model).

We compared model fit to the marginal cost of estimating additional parameters in more complex models. The background cost of performing the CMR study would have to be paid to validate any of the models, or even to test predictions made in the absence of movement data, such as those based on simple map distance, incidence function models, or expert opinion. Beyond this background cost, the simplest (i.e., DO) model required the additional (marginal) cost of measuring movement behaviors in breeding (i.e., wetland) habitat, and parameterizing the three more complex models incurred costs of measuring movement in multiple habitats (NE), behavior at habitat boundaries (NHD), or both (FS).

3.7 CIRCUITSCAPE MODELS

We used the software Circuitscape (McRae et al 2006, 2008) as a complimentary approach to individual-based simulations. Circuit-based dispersal models assume that dispersing organisms are analogous to electrical current flowing over a landscape composed of conductors with various amounts of resistance, represented by a raster dataset. Circuit-based models can be considered an efficient analytical equivalent to simple individual-based models known as "biased random walk" models (McRae et al. 2008), and allow dispersal corridors and "pinch points", where animal movements are constricted to only a few possible paths, to be mapped quickly and effectively. These models also allow us to quantify the relative strength of connections between all habitat patches, based on their distance and the quality of intervening habitat.

Circuitscape models require two inputs. The first input is a raster where valued cells represent occurrences of the focal species. The second input to Circuitscape is a raster of resistances that represent the relative impermeability of different landscape features to dispersing organisms. Frequently, these resistances are based on expert opinions, but our resistance surfaces were based on the empirical movement data we collected. In the case of SFS and the amphibians, resistances were calculated from release experiments. RCW resistances were taken from the optimal discrete-choice model, described in the previous section.

Unlike the individual-based models that we have developed, boundary behavior is not included in Circuitscape models. Additionally, our individual-based models are constrained to a finite number of individuals and movements. There are many grid cells in our individual-based simulations that have not dispersals through them. In contrast, every grid cell in a landscape receives a relative dispersal estimate in Circuitscape. We developed Circuitscape models for

each focal species at the largest extents of our anlaysis (a 5km buffer surrounding Fort Bragg and Camp Mackall). These maps were then used in separate, Circuitscape-only, conservation prioritization maps (see supporting data).

We also used a Circuitscape model for RCWs as a substitute for an individual-based model in our multi-species analysis. Although an appropriate individual-based dispersal model does exist for RCWs as a component of the spatially explicit population model (Letcher et al. 1998, Scheigg et al. 2005), the only landscape features that RCWs respond to in the model are large canopy gaps. Our more detailed analysis of RCW foray movements (Section 3.2) suggest that this model may be less-than ideal for spatial predictions of dispersal habitat use for this species. While we are in the process of revising the RCW SEPM to reflect our new analysis, this modified version of the SEPM is not yet ready for production use. We anticipate that using Circuitscape as an alternative modeling framework for RCWs with the best empirically derived resistance surface from Section 3.6.1 will result in very similar results to what we would achieve with an individual-based simulation.

3.8 MULTI-SPECIES INTEGRATION

The key to integration of the different modeling approaches is that each model produce similar output. Though the models differ in complexity and approaches used, they all produce raster maps with identical geographic projection, cell sizes, and total extent. The output from each model thus overlies precisely on the output from each of the other models. The values contained in these maps always represent the same variable: the *relative probability of visitation* during dispersal. This is a measure of connectivity for individual species. Each model may derive this probability using different data and assumptions appropriate for the particular species being modeled, but they all estimate how frequently each pixel is visited as the organisms move across the landscape.

3.8.1 ZONATION

The outputs of all our simulation models and Circuitscape models were rasters where each cell represented an estimated probability of dispersal. In the case of simulations, outputs were the relative frequency that a cell was used by any individual during the simulation run. In the case of Circuitscape, outputs were the relative probability of movement through each cell. The objective of the study was to take these dispersal models outputs and combine them to assess the multi-species conservation value of landscape locations.

A variety of methods exist to integrate the species dispersal maps. The simplest would be a linear combination of the dispersal maps for each species. There are a few weaknesses to this approach. First, species with a greater area of quality dispersal habitat tend to dominate the results. Second, the larger spatial structure of habitats is ignored in a linear combination of dispersal maps. That is, the method does not take into account neighboring cells when evaluating conservation priority. The algorithm that we used, Zonation, addresses these weaknesses in the way it assigns conservation value to pixels.

Zonation creates a conservation priority map of ranked pixels where high ranks are given to areas of high priority and low ranks are given to areas of low priority. It is an edge deletion algorithm, meaning that the algorithm begins on the periphery of the map, assigns a rank to the cell with the lowest conservation priority, removes that cell and sequentially ranks and removes

cells from the outer edge until no pixels are left to rank. For each grid cell on the periphery of the map, the zonation algorithm sums the species-specific connectivity measure weighted by the total amount of connectivity in the remainder of the landscape. The connectivity value, delta, of cell i is evaluated for all species j as

$$\delta_i = \max_j \frac{Q_j(S) w_j}{c_i} \tag{5}$$

where $Q_j(S)$ is the proportion of the distribution of species j remaining in the set of all of the unranked patches S, w_j is the weight given to species j, and c_i is the economic cost of protecting patch i. The single grid cell with the lowest multi-species connectivity value is then removed. Since the periphery of the map is changed once a grid cell is removed, the algorithm then compares all the cells along the new periphery in the same manner, always removing the least valuable grid cell. The output from the zonation algorithm is a ranking of raster cells by conservation value. Because the algorithm begins at the edges of the raster, it will give a high ranking to connections between patches. There are many possible parameterizations of the Zonation software. We used the standard zonation settings to generate our conservation priority maps.

3.8.2 Multi-species Analysis

We generated a set of conservation priority maps from both our Circuitscape dispersal models and the individual-based simulations using Zonation. These priority maps provided the multi-species conservation recommendations that were the ultimate goal of this study. They are a test-bed for evaluating the realism of our simulation outputs and the Circuitscape models. We generated these maps for both of our spatial extents.

3.8.3 Flagship Species Test

The management of RCW populations strongly influences conservation decisions in the Sandhills region. In order to test whether RCWs are a good proxy for connectivity of other species, we generated two landscape prioritizations using the Zonation algorithm. One scenario considered RCWs only, while the other was a "balanced" scenario that was based on dispersal habitat use for all of our target species, giving each species equal weight. We compared the highest-priority habitats (90th percentile) across the two scenarios to evaluate the extent and distribution of important dispersal areas for other species that might be "missed" by focusing just on RCWs.

3.8.4 Development Scenarios

We compared our conservation priority maps against a likely scenario of human development in the area. This comparison highlighted areas that were both important for maintaining connectivity across species and were likely to experience pressure from urban or suburban development. This "threat map" was developed from a set of land-use suitability products from the environmental nonprofit Sustainable Sandhills along with an urban growth simulation for the year 2100 generated for the US Geological Survey's Southeast Regional Assessment Project (Jantz et al. 2009, Dalton and Jones 2010).

Sustainable Sandhills created a set of three suitability maps that represent relative suitability of lands for residential, commercial, and industrial development based on criteria such as population density, road and sewer access, and flood risk. For each map, lands were assigned a rating between 1 (low suitability) and 9 (high suitabilty). The criteria for each map were developed in a series of focus groups held with county planners and other experts. Details appear in the Technical Report, which is available at

http://www.sustainablesandhills.org/Release2Workshop.html. We averaged the three different suitability indices to arrive at a relative score that we have taken to represent an overall index of suitability for the development of human infrastructure. Notably, no explicitly environmental criteria were included in the suitability indices. We converted this index into a binary map using a threshold that represents "moderate suitability for development".

The areas highlighted as suitable for development by Sustainable Sandhills do not take into account anticipated trends in population that drive urban growth. To select those areas that are truly threatened, we used an urban growth simulation based on the SLEUTH cellular automaton model (Jantz et al. 2010) which was generated by the Biodiversity and Spatial Information Center. The urban growth model generates spatial estimates of urban development probabilities for the years 2010 - 2100. From this model we considered lands with a 5% or greater probability of urban development as "threatened". The areas that we consider most at risk for urban development are those "threatened" areas that are also considered "suitable" by Sustainable Sandhills. Although future patterns of urban development are highly uncertain, focusing on lands identified by these two independent methodologies reduces that uncertainty somewhat.

4 RESULTS AND DISCUSSION

In this section we review the results of our efforts to characterize dispersal landscapes, collect empirical data on movement behaviors for our target species, and discuss the results of our simulations of wildlife movement. We also present the results from our integration of these different dispersal models to identify areas of the landscape that are important for maintaining landscape connectivity for multiple species and describe a GIS toolbox that we have developed to allow wildlife managers to evaluate the influence of landscape change on connectivity for wildlife.

4.1 LIDAR FOREST COVER ESTIMATES

Posterior estimates captured the vertical characteristics of forests types within the 5 intensively studied cells (Figure 3). The open longleaf pine estimates showed a peak at 15-20m, with a relatively low density at 5-10m (the absence of an oak understory) and a relatively high density below 3m (grass density near the ground). The bottomland hardwood showed high density at all heights below 20m. The longleaf forest with oak understory showed intermediate understory density between the bottomland hardwood and open long-leaf pine forests. The mixed-hardwood forest canopy density distribution was the roughly the same shape as dense longleaf forest, but the estimated canopy density at all heights was approximately 10% greater. The open grassland cell had a relatively low density of vegetation at all heights. Canopy density below 18m was greater than 0, however, because there was some longleaf pine encroachment at the edges of the cell (Figure 12).

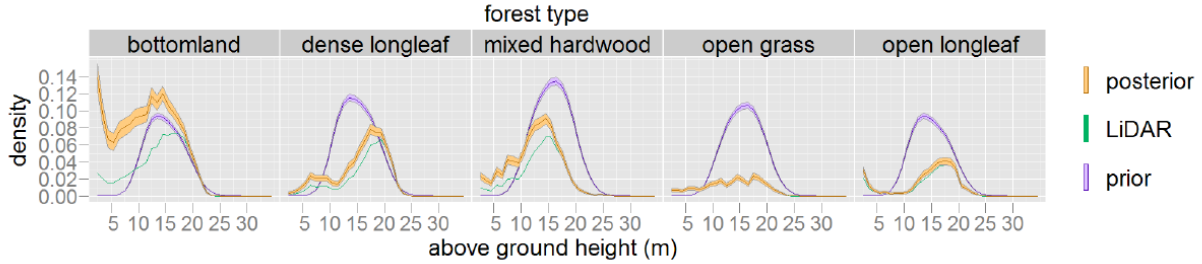

Figure 12: Posterior canopy height profiles of 1m height intervals for the five intensive cells along with the raw LiDAR return densities and prior densities. 95% credible intervals are shown for the posterior, and 1 standard deviation for the prior.

The most important result of the model is the increase in the credible interval width at lower heights. This effect is more pronounced in sites with greater canopy density at the highest points on the canopy. With a dense overstory, the number of returns at lower canopy heights is reduced resulting in broader credible intervals. In sites like the open grassland, credible intervals are narrow at lower heights because the number of returns from these heights is greater than in the forest interior.

The effect of the prior on posterior estimates was small. Changes for maximum standard deviations of 0.1% yielded only a 0.03% change in mean canopy density and for maximum standard deviation of 0.01%, a 0.3% change. Even when the average error in empirical estimation of canopy density was less than 0.1%, the change in the posterior estimates of canopy

density was less than 1%. This was due to the sheer number of LiDAR returns. The mean of the posterior beta-distribution is

$$\mathrm{Exp}\left(\theta_k\right) = \frac{n_k + \mu_k \phi_k}{\sum_{i=k}^{K} n_i + \left(1 + 2\mu_k\right)\phi_k} \tag{6}$$

where μ_k is the mean of the prior expectation of canopy density and φ_kIis the degree of belief or weight of that expectation. It is apparent that $\mu_k\varphi_k$ would have to be close to the number of returns n_k for the effect of the prior to be significant. There were about 1×10^4 returns per cell. The prior data accuracy parameter would have to be extremely small for $\mu_k\varphi_k$ to be close to 10000 or even 100. The effect of the prior will increase at lower heights as the signal is attenuated and the number of returns decreases.

Across the entire study site, the pattern of density estimates reflects the distribution of forest types observed on the ground. For example, the dense understory of bottomland hardwood forest running from NE-SW in the NW corner of the site is apparent in the 2-5m posterior estimates.

Previous studies have shown that LiDAR data does not predict canopy density in the understory as well as it predicts the density of the canopy surface (e.g. Lefsky, 1997; Harding et al., 2001). Our model shows that these poor predictions are dependant upon attenuation of the LiDAR returns in the overstory. This attenuation affects both the mean and the variance of canopy density estimates. The mean is affected because, for a given canopy density at a low height, the number of returns changes with overstory density. So in a dense forest, 100 returns of heights 2-5m may have the same canopy density as an open field that has 1000 returns at 2-5m. By considering canopy density to be the result of a binomial sample whose size is the number of returns at the focal height class and below, the estimates become conditionally independent of the returns at heights above. When we consider the sampling process of LiDAR in this way, statistical analyses that include only raw quantiles of LiDAR data become suspect.

The second effect of attenuation in the overstory is to increase the variance of estimates in the understory. Because many returns are reflected in the overstory of dense forest, there are fewer returns from which to make inference about canopy density at lower heights. This is a mechanistic property inherent in LiDAR data, and there's no clear way to overcome this during data collection. However, we can quantify this effect and explicitly include the changes in confidence of our estimates of density in the lower canopy. The model we have presented does that in the simple context of binomial sampling, providing a means to quantify the variability of canopy density estimates for the understory.

Even though we have presented a Bayesian model that uses prior information to help train the estimates of canopy density from LiDAR, the choice of prior does little to affect the estimates. There are two conclusions to draw from this. The first is that the Bayesian perspective could be supplanted by a maximum-likelihood approach, which did not include prior information. In doing this, our approach could dovetail directly with common regression approaches used to measure the correspondence between field-derived forest metrics and LiDAR-based metrics. Using a mixed-effect model, beta-distributed error in LiDAR returns could be included as a

random effect in canopy density dependent upon the number of returns. The advantage of the simple Bayesian model lies in the potential to add other complexities, such as spatial dependence and scan angle to the model, and we expect future application to move toward this approach.

The second interpretation of the small prior effect is that LiDAR data provide more precise estimates of canopy density than is feasible using practical field methods except certain ground-based LiDAR systems. Prior information of canopy density needed to be accurate within 0.1% to alter the posterior estimates of canopy density by 1% for our grain size of 50m×50m. We know of no field method which can estimate canopy density to within 1%, and, in any case, research questions in forestry and ecology rarely require canopy density estimates that are accurate to less than 1%.

There is a trade-off between the precision of canopy density estimates and the grain at which LiDAR data are binned. Smaller grains have fewer LiDAR returns and wider credible intervals. It is just the opposite for larger grains. The advantage of smaller grains, even though their credible intervals are larger, is that the model more closely fits one of its key assumptions, namely, that canopy density is randomly distributed horizontally. The same logic applies with the vertical binning of heights. More bins means fewer samples per bin but a more finely divided canopy.

So, what is the best grain for a given dataset? We suggest that this decision be made based on the precision of the canopy density estimates needed to answer the research question at hand. We have presented our model as a way to include error in estimates of canopy density. An alternative approach is to fix the maximum error at, say, 10% canopy density, then build estimates for a variety of grains choosing the smallest grain for which the 10% credible intervals are achieved. In this way, the smallest reasonable grain is used for answering the research question.

Because we did not include spatial dependence in our inference, the credible intervals of our model are narrower than the data might suggest under a more complex model. We have treated the number of returns at a given height as conditionally independent of the returns higher in the canopy. In one sense, this is necessary because the populations of inference at the focal heights are the successes (returns at the focal height) and failures (returns below the focal height). Returns above the focal height do not affect the number of reflections.

The estimates of canopy density, however, are not spatially independent because vegetation is spatially autocorrelated (Legendre and Fortin 1989), both vertically and horizontally. So, horizontally at a given height, two adjoining cells are more likely to have similar covers than two distant cells. Likewise, in the vertical dimension, given a canopy density of 50% at a height of 2-5m, canopy density at 5-10m is more likely to be 50% than it is to be 0% or 100%. This autocorrelation reduces the effective sample size, because some of the returns at a given location and height are due to its proximity to neighboring voxels. This should result in increased credible intervals for canopy density estimates.

We have presented a simple probabilistic model for inferring canopy height profiles from multiple return LiDAR data. This model has a closed-form solution so estimates and credible intervals can be quickly calculated for large datasets, and it adopts a Bayesian perspective so that prior estimates of canopy density can be included. Given that this probabilistic model is as easy to implement as its deterministic counterparts such as FUSION (McGaughey, 2007), we see no reason to continue with the deterministic approach to estimating canopy density.

4.2 RED COCKADED WOODPECKER

4.2.1 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 282 and 533 territory visits by prospecting individuals in 2006 and 2007, respectively. The number of visits ranged from 1 to 23 territories per female with 49% of the individuals visiting at least one territory multiple times. The maximum prospecting range from a roosting site was 8.9 km ($\overline{X}$ = 3.54, SE = 0.28). This study is the first to document prospecting via forays by juvenile RCWs. We also discovered another previously unknown dispersal behavior, which we termed jumping. Following a period of typical foraying, jumpers make long-distance, unidirectional movements far beyond previous foraying range in a single day, and thereafter remain at and foray from the new location to which they jumped. We describe jumping and its significance in explaining the "fat tail" of the RCW dispersal distance distribution in Kesler et al. (2010).

4.2.2 MAXENT MODELS

Maxent models with an AUC value above 0.75 are considered informative (Elith et al. 2006). The simplest habitat suitability model based on four land-cover classes did not reach the 0.75 cutoff (Figure 13). All other habitat suitability models performed much better (AUC > 0.85), with the models' accuracy increasing with the complexity of environmental data (Figure 13). The accuracy of habitat suitability models increased by 5% with the combination of Landsat and LiDAR data relative to either alone. There was then a slight increase in accuracy when the discrete land-cover data were included with all the remote sensing parameters (Figure 13). Based on AUC, Maxent models trained with environmental data at breeding sites were slightly better than models trained with environmental variables at prospecting locations (Figure 13).

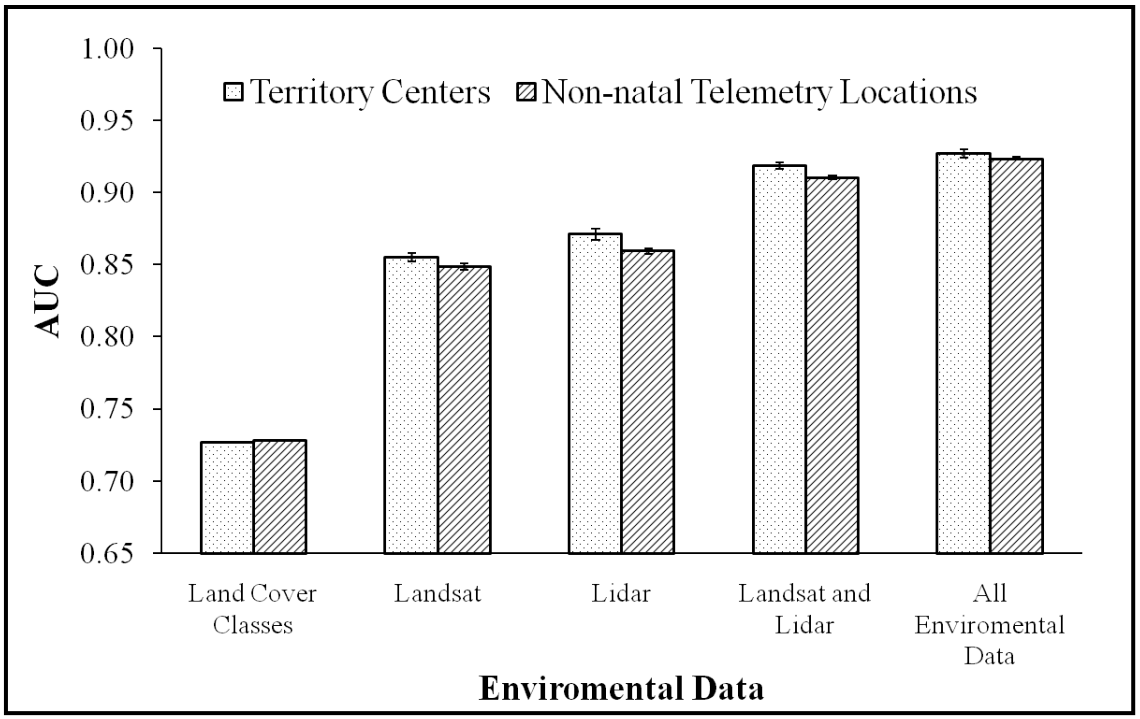

Figure 13: The Area Under the Curve (AUC; +/- SE bars) for each Maxent model used to create resistance surfaces that predicted how red-cockaded woodpeckers (Picoides borealis) interact with environmental cues during prospecting in the Sandhills ecoregion of North Carolina.

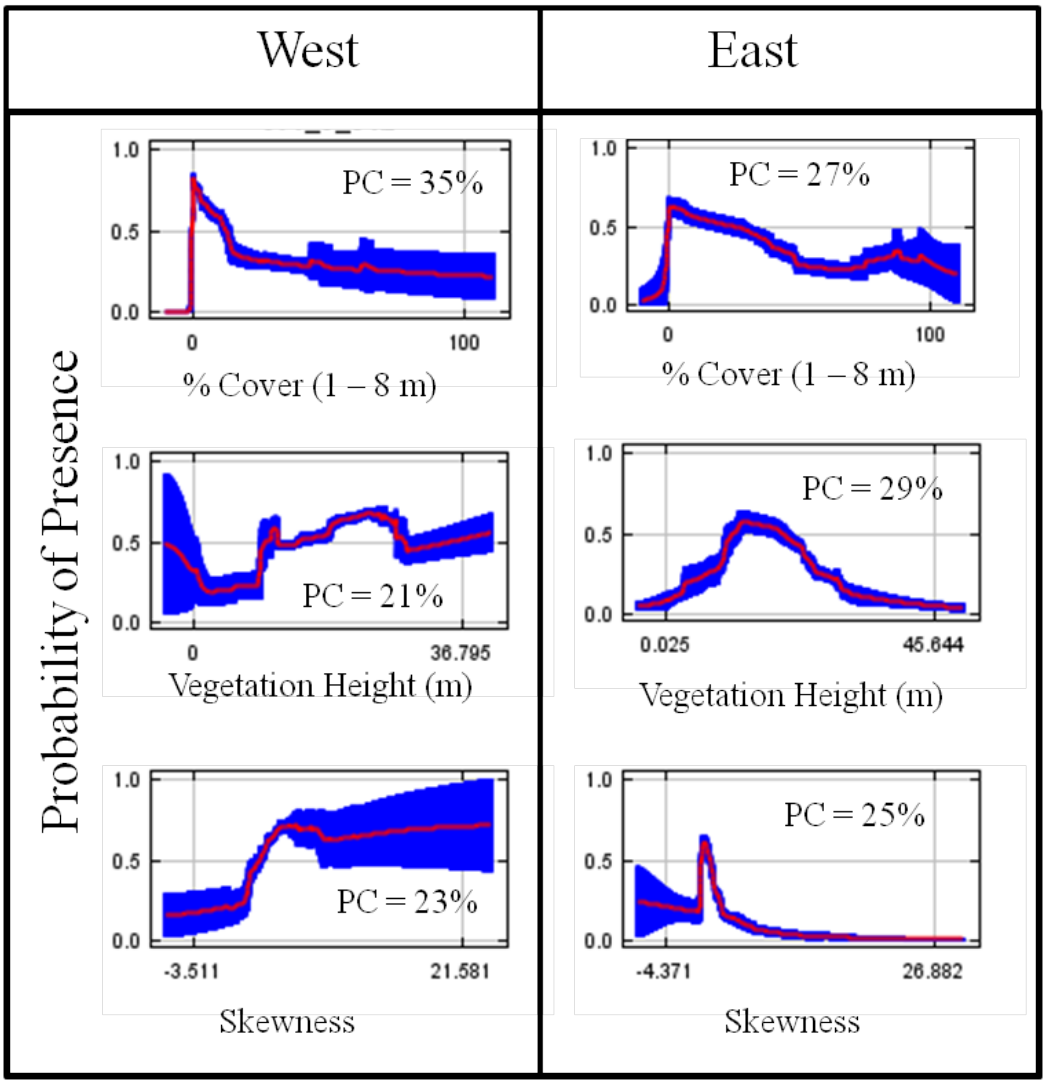

Figure 14: The probability of red-cockaded woodpecker (*Picoides borealis*) presence based on forest structure variables located at non-natal telemetry locations and percent contribution (PC) of each variable in the top-ranked habitat suitability model for the Sandhills of North Carolina. red line indicates average and blue shading indicates standard error.

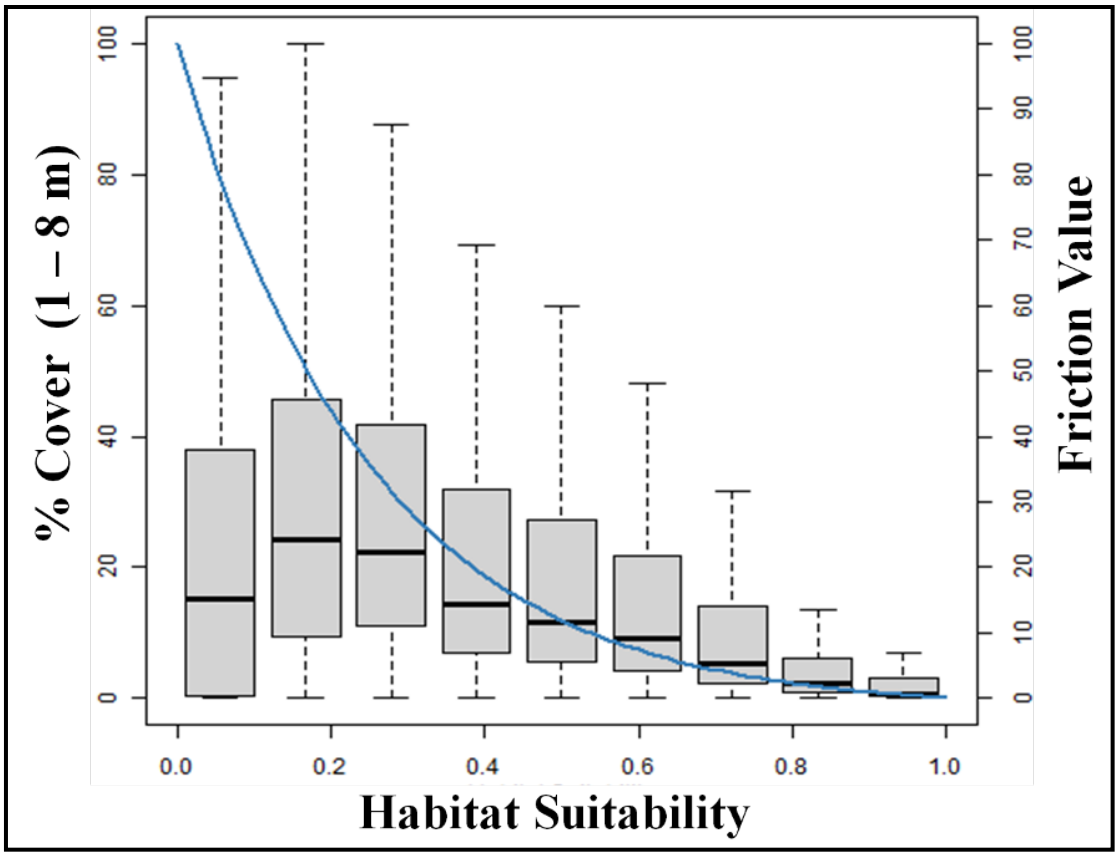

Figure 15: Box plot of percent midstory cover (1 to 8 m) in relation to habitat suitability and the friction value in the top-ranked model predicting red-cockaded woodpecker (*Picoides borealis*) prospecting movements. The line indicates the top-ranked rescaling constant explaining the relationship between habitat suitability and friction values.

The forest structure parameters that contributed most to the best habitat suitability model 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 14). Prospecting individuals tend to avoid areas containing even small percentages of midstory cover. The median percent midstory cover (1 – 8 m) was less than 10 % when habitat suitability was greater than 0.6. Decrease in habitat suitability from 0.6 to 0.1, corresponded to a steady increase in the average percent midstory cover. Very unsuitable habitat (< 0.1) is primarily composed of open and non-forested areas. RCWs used forested areas where maximum tree heights ranged from 13 to 25 m. The relationship between probability of observing RCWs and maximum tree height varied by LiDAR sensor (Figure 14). The eastern sensor (2 m spacing and 9 cm RMSE-z calibration) predicted maximum tree height to have a unimodal shape peaking at 13 m, while the western sensor (2.5 spacing and 12 cm elevation RMSE calibration) had a broader range of tree heights associated with a high probability of observing RCWs (15 – 28 m). The probability of an individual prospecting through a forest increased when the distribution of vegetation heights had a slight positively skewed distribution. A positively skewed distribution of vegetation heights represents a small but consistent density of returns depicting the canopy with the majority of the returns reaching the herbaceous vegetation in the understory. This description matches mature

longleaf pine forest with an open canopy and minimal midstory vegetation (Peet 2006). Skewness varied slightly between LiDAR sensors (Figure 14). The eastern sensor predicted slightly positive skewness values, while the western sensor had a broader range of positive skewness values related to a high probability of observing RCWs. Median vegetation heights and percent cover classes greater than 8 m did not strongly contribute to the forest structure habitat suitability model.

We used the habitat suitability models of varying complexities described above, and different rescaling constants (Section 3.2.2.1) to evaluate which resistance surface optimally predicted RCW forays. The details of this analysis can be found in the section on model complexity (Section 4.6.1). The discussion below uses the top-ranked model from that analysis.

4.2.3 MODEL VALIDATION

We used a separate set of observed juvenile female dispersal events from 2005 and 2006 to test the ability of the top-ranked discrete-choice model based on foraying behavior to predict natal dispersal destinations. We counted instances in which a female occupied the breeding position in a territory other than the natal territory at age one as natal dispersal. Very few individuals dispersed to territories located in corridors with high (>50%) cumulative cost distances, even when they were a similar straight-line distances from the natal territory as territories with lower cost-distance (Table 3). Over 60% of the individuals selected territories within the 25% least-cost corridor. There was a sharp decline in number of individuals dispersing to territories located on the wider and effectively more difficult to traverse corridors. More than 70% of the short-distance (i.e., $\leq$ 6km) dispersal events for both years fell within the 25% least-cost corridor. Accuracy of prediction of long-distance dispersal events varied by year. In 2006, 60% of long-distance dispersal events fell within the 25% least-cost corridor, compared to 39% in 2005.

Table 3: The percentage of short-distance (SDD) and long-distance (LDD) dispersing juvenile female red-cockaded woodpeckers (*Picoides borealis*) that settled into territories within corridors derived from resistance surface based on non-natal telemetry locations, forest structure and a moderate rescaling constant (c = 4).

Year	Percentile Corridor	SDD	LDD	Total
2005	0 – 25	79 %	39 %	63 %
	25 – 50	18 %	39 %	26 %
	50 – 75	3 %	18 %	9 %
	75 – 100	0 %	4 %	2 %
2006	0 – 25	71 %	60 %	67 %
	25 – 50	25 %	40 %	31 %
	50 – 75	4 %	0 %	2 %
	75 – 100	0 %	0 %	0 %

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 dispersal events. Most of the short-distance dispersing RCWs selected breeding sites within the lowest 25% least-cost path created from the resistance surface. However, the long-distance dispersers did not overwhelmingly select territories within the 25% least-cost path. These results suggest that short-distance dispersers are strongly affected by forest structure represented in the resistance surface. Long-distance dispersers were much less consistent with the 25% least cost path, suggesting that they are not strongly influenced by environmental features during dispersal, or the environmental cues affecting long-distance movements are not represented in our resistance surfaces. In fact our observations during the radio telemetry study indicate that long-distance dispersal involves different behavior (i.e., jumping) than the foraying behavior used by short-distance dispersers, on which our resistance surfaces are based. It is likely that jumpers interact differently with the landscape than foraying birds, for example some were observed to cross very large openings, something that foraying birds do not do (Kesler et al. 2010).

In one of the few recent studies to validate resistance surfaces with empirical data Driezen and colleagues (2007) correctly predicted approximately one third of hedgehog (*Erinaceus europaeus*) dispersal routes based on the best resistance surface, a result similar to our long-distance dispersal results. They suggested that conspecific interactions could have contributed to their limited ability to predict dispersal events with environmental variables alone. However, combining the resistance surface with conspecific cues did not increase explanatory power when predicting RCW dispersal events (Trainor et al. In Preparation).

4.2.4 GRAPH NETWORK MODELS

The geographic and functional networks contained similar trends in metrics as the edges were iteratively removed by decreasing the threshold distances (Figure 16a and Figure 16). Both networks have a relatively abrupt transition between connected and disconnected networks. As dispersal ability increased, the number of components sharply decreased and the largest component grew in size. However, the transition between connected and disconnected networks was more distinct with the geographic distance networks. The largest component in the geographic networks quickly increased until the edge threshold distance reached 1.7 km. The connectivity of RCW territories then remained relatively constant until the dispersal ability reached 4.5 km, which is when the network represented a completely connected RCW population (Figure 16a). The functional network contained a more gradual transition between connected and disconnected network of RCW territories (Figure 18*a*). The functional distance networks' largest component gradually increased with dispersal ability through a wide range of natural and human-modified landscape features.

A species' capability or quickness to traverse between any pair of nodes within the largest component corresponds to the network's diameter (Urban & Keitt 2001). The trend in diameter varied greatly between the two types of networks. The geographic network's diameter quickly transitioned from relatively disconnected to connected network with a sharp increase in the diameter that closely corresponded with the abrupt increase in the component size (Figure 16a). This suggests that the largest component was slow to traverse because it contained many short connections. Once the network is connected, increasing dispersal ability allows faster

connections between territories. In contrast, the functional distance network's diameter was consistently smaller and did not have the drastic change with dispersal ability (Figure 17a).

The frequency distributions of the observed geographic and functional dispersal distances were fitted to the lognormal distribution based on Kolmogorov-Smirnov test ($p > 0.05$). The threshold between connected and disconnected RCW populations for the geographic network was equivalent to the 25% cumulative distribution of the observed dispersal distances (1.7 km, Figure 16b). The population is expected to be completely connected when the observed dispersal ability reached a cumulative distribution of 60% at 4.5 km. According to observed dispersal ability with functional distance, the abrupt transition into connected RCW population is reached at 32% and the network is not completely connected until the dispersal ability reached 80% cumulative distribution (Figure 17b).

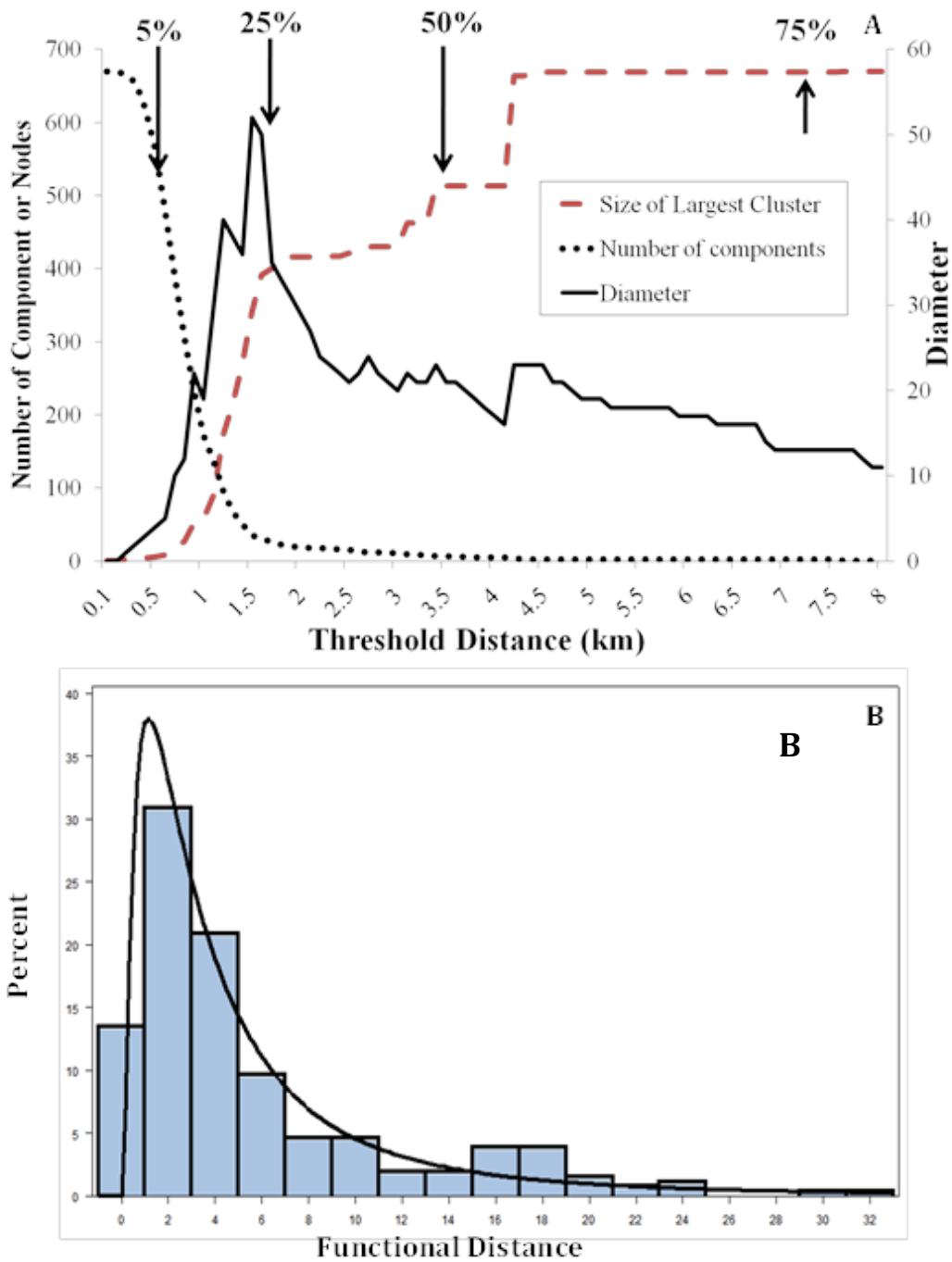

Figure 16: The number of graph components, graph order, and diameter of geographic networks with iterative edge thinning (a). Arrows and percentages represent the cumulative percent of juvenile red-cockaded woodpecker (*Picoides borealis*) observed dispersing in the North Carolina Sandhills ecoregion. The frequency of observed geographic dispersal distances with the line representing the fitted distribution based on lognormal function (b).

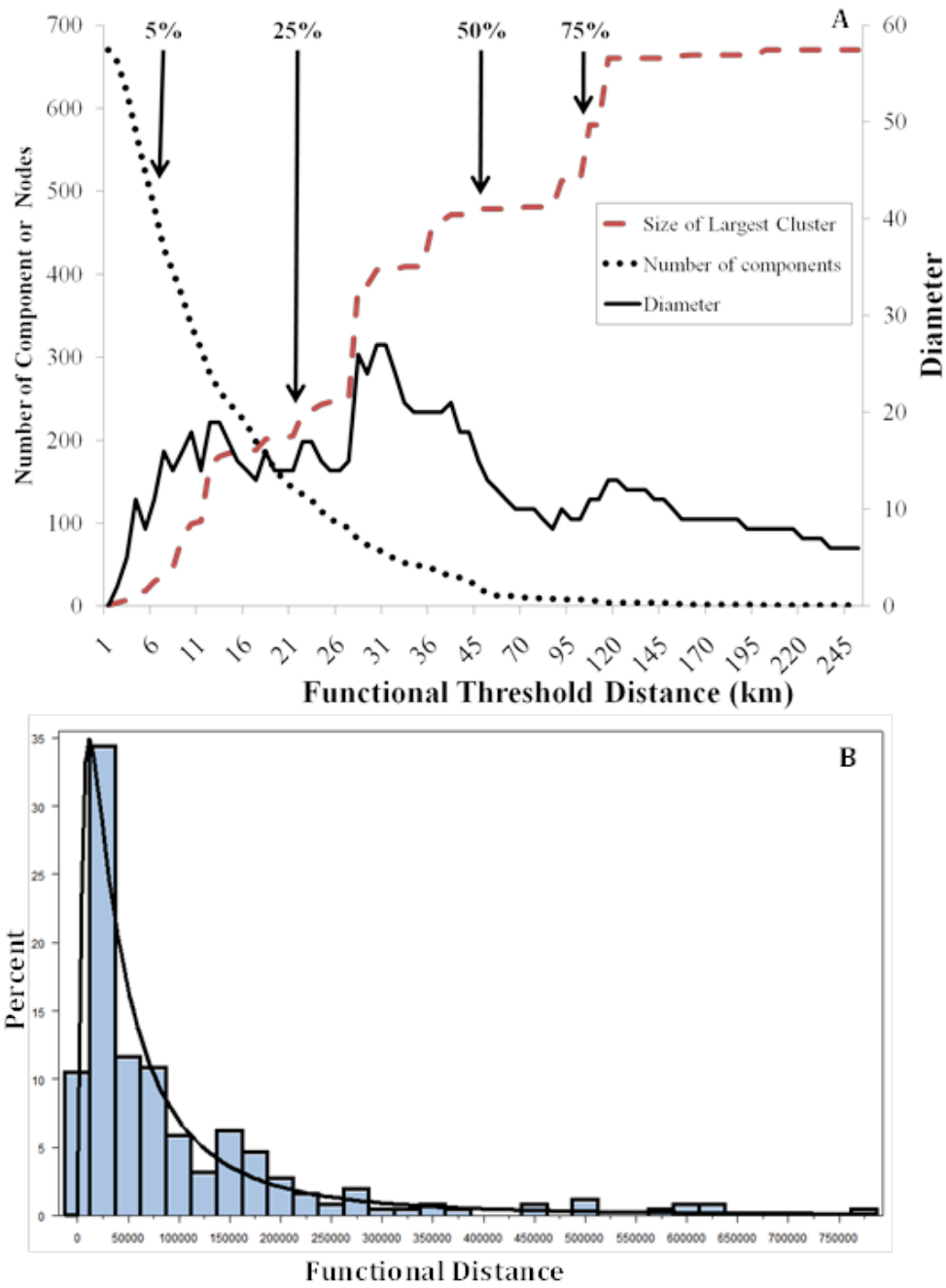

Figure 17: The number of graph components, graph order, and diameter of functional distance networks with iterative edge thinning (a). Arrows and percentages represent the cumulative percent of juvenile red-cockaded woodpecker (Picoides borealis) observed dispersing in the North Carolina Sandhills ecoregion. The frequency of observed dispersal distances based on least-cost path with the line representing the fitted distribution based on lognormal function (b).

When comparing observed dispersal events in relation to potential destination territories, most individuals dispersing less than 6 km selected territories that were effectively closer than territories with similar Euclidean distances (Figure 18). Individuals that dispersed greater than 6 km (i.e., long-distance dispersers) did not consistently select territories that were effectively closer than territories with similar distances. These results suggest that short-distance dispersing RCW are influenced by the landscape features, specifically forest structure, between their natal territory and the destination territory. RCWs dispersing greater than 6 km are less influenced by the intervening landscape features, as suggested by our observations of jumpers (see above). Thus, RCW dispersal behavior within foray distance of 6 km is best represented by a graph network created with the functional distances. This suggests that the dispersal ability represented with geographic distances within a RCW graph network should be replaced with functional distances. The functional distance network with moderate dispersal ability (50% cumulative distribution function) closely matched the observed dispersal movements (Figure 19 and Figure 20).

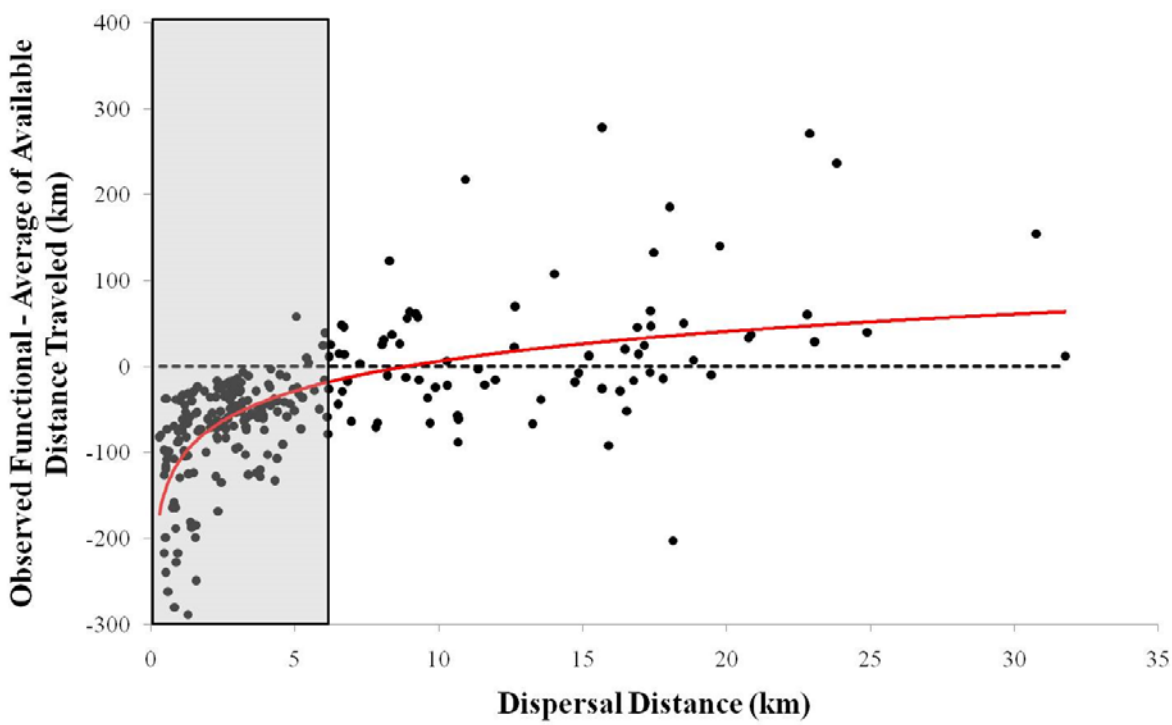

Figure 18: A plot comparing observed functional distance dispersed and the average functional distance of territories with similar Euclidean distances. Shaded box indicates the short-distance dispersal events (< 6 km) and arrow is pointing to the above example.

Most of the short-distance dispersing individuals (99%, 215 out of 217) stayed within their natal component defined by a 50% probability of dispersal with a functional distance network (Figure 20). The two individuals that did move between components dispersed more than 5 km and moved to adjacent components. In contrast only 58 out of 80 long-distance dispersers (72%)

remained in their natal component and the majority of these individuals (76%) remained in the largest component, which was primarily composed of the territories on Fort Bragg. Most of the long-distance dispersing individuals leaving their natal component traveled to a component that was connected by a 25% least-cost corridor (Figure 20). Four individuals dispersed to components that were not connected by the 25% least-cost corridor. The validated connectivity estimates suggest that groups of RCW territories are relatively isolated in the Sandhills population due to limited flow of individuals between managed areas.

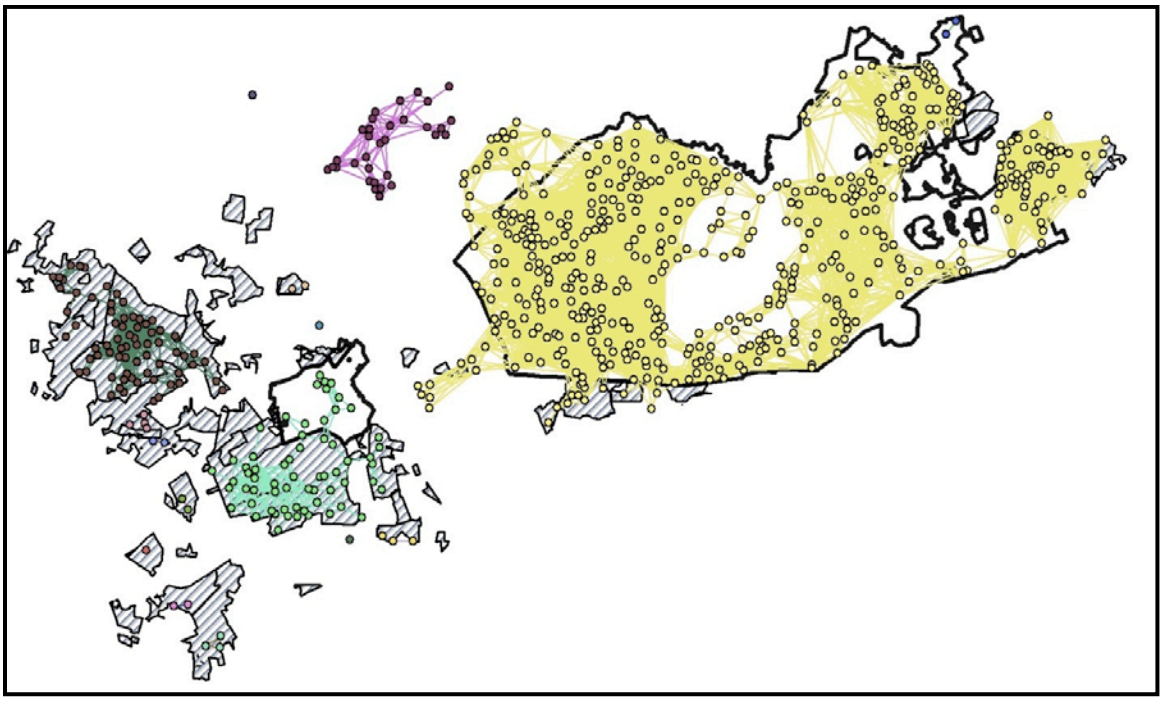

Figure 19: The connectivity of juvenile female red-cockaded woodpecker (*Picoides borealis*) territory groups based on the functional distance network with a dispersal ability at the 50% cumulative distribution function of observed dispersal distance. Edges connecting the Fort Bragg/Southern Pines network are yellow, edges connecting the Pinehurst network are pink, Edges connecting the Camp Mackall / Sandhills Gameland Block B network are light green, and those connecting the Sandhills Game Land Block A network are dark green.

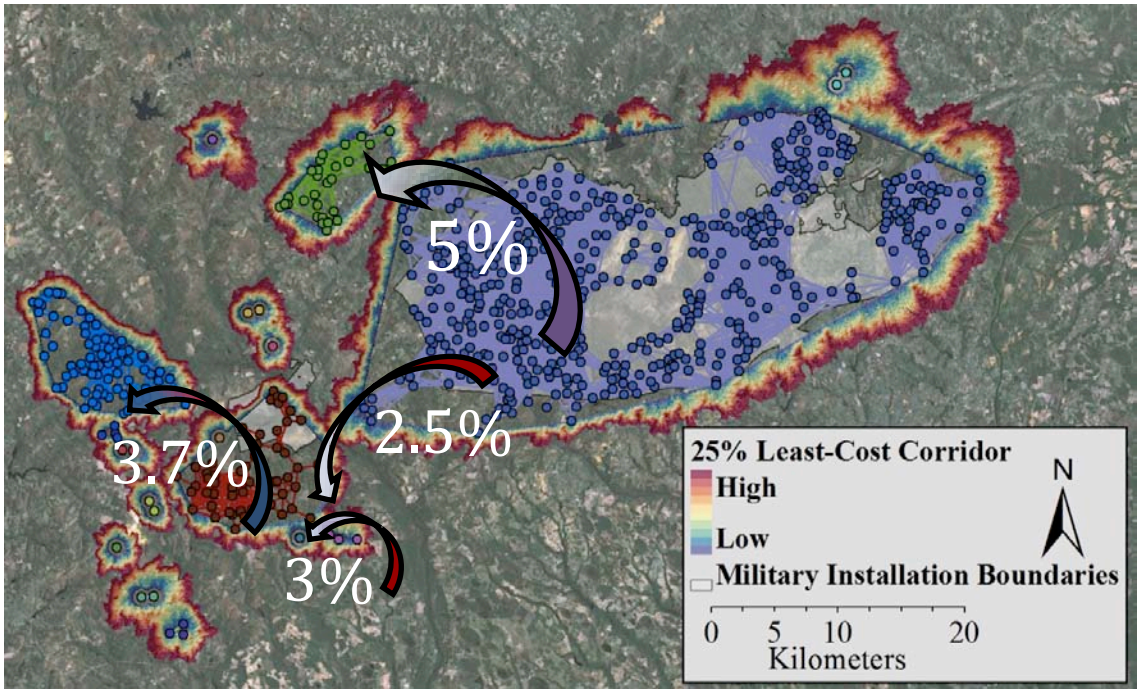

Figure 20: The percent of long-distance dispersing red-cockaded woodpeckers (*Picoides borealis*) selecting a breeding site in a different component. Warmer colors indicate larger functional distances from the boundary of each sub-population.

The graph-theoretic approach has become a useful tool to estimate and visualize species connectivity throughout fragmented ecosystems with modest data requirements (Calabrese and Fagan 2004). However, infusing biologically relevant information into graph networks substantially increases the accuracy and insight into species connectivity. For example, a geographic network with median dispersal ability of 3.5 km (Kesler et al. 2010) implies that almost all RCW territories would be easily connected in the Sandhill ecoregion (Figure 16). This simple depiction of dispersal ability fails to account for varying RCW movement behavior within and between patches of longleaf pine forest. RCWs preferred to travel through forest stands similar to their breeding and foraging habitat characteristics, a tall canopy with minimal midstory vegetation. Juvenile female RCWs 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 (Kesler et al. 2010, Trainor et al. In Preparation). Our results also suggest that within the prospecting range of 6 km, juvenile females dispersed to territories that were effectively closer based on forest structure and human-modified landscape features. Positive and negative environmental cues guiding movements of individuals during prospecting may influence subsequent dispersal events. Therefore, incorporating movement behavior in relation to the surrounding environment by using a resistance surface provided insight into RCW connectivity in the currently fragmented landscape.

One way to validate a graph is to determine if observed dispersal events follow the graph network assumptions. By definition, components are isolated subgraphs with no movement

observed between components. The functional distance network based on 50% cumulative distribution probability closely matched the observed dispersal behavior in relation to the delineation of components. Based on observed dispersal events, 99 % of the individuals dispersing up to 6 km remained within their natal components. This provides strong evidence that this network portrays the current connectivity of the population.

According to the validated network, RCW territories were strongly connected within managed properties. High connectivity of RCW territories within properties is most likely associated with current habitat management practices. A large portion of RCW 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). For example, on Fort Bragg extensive management of RCW cavity trees and foraging habitat with frequent prescribed burns has created a well-connected network of over 400 territories within the longleaf pine ecosystem (Britcher and Patten 2004). Unfortunately Fort Bragg, like many military installations, is a small island of managed ecosystems surrounded by urban development and agricultural land-use activities (Warren et al. 2007). As a result, few fledglings from eastern Fort Bragg were observed dispersing through surrounding development and agricultural fields to other conservation properties with established territories. Movement between the three components in the western portion of the Sandhills region was also limited even though these components combined have similar spatial extent to Fort Bragg (Figure 19).

There was an asymmetric flow of individuals from military installations into the other conserved properties (Figure 20). This is possibly due to higher requirements for federal land management. Federally owned land has the most restrictions and active management requirements through the Endangered Species Act (ESA). The federal government is mandated to avoid "take" as it is defined in Section 9 and to implement conservation programs (Kennedy et al. 1996). Section 7 (a) of the ESA requires federal agencies to use their authorities to carry out programs for the conservation of endangered and threatened species (U.S. Department of the Interior 1996). In addition, military installations containing endangered species are required to develop endangered species management plans to identify, protect, and manage the recovery of the listed species and habitats (Frost 2006).

Our results suggest that persistence of healthy RCW populations requires management to extend beyond territories. In order to accomplish this goal conservation strategies need to incorporate species movement behavior between managed properties and habitat patches. RCWs prefer to travel through forest stands with a tall canopy with minimal midstory vegetation (Figure 14) while movements are strongly inhibited by open or developed areas (Kesler et al. 2010). Therefore, environments between established populations should encourage RCW movements by managing longleaf pine forest with reduction and removal of dense midstory vegetation.

Understanding how individual movements in fragmented landscapes 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 incorporating movement data to evaluate the flux of individuals predicted with graph networks (Urban et al. 2009). This study provides a method to incorporate dispersal behavior via monitoring data to improve species connectivity estimates with graph networks.

Using data to parameterize nodes and edges can decrease the uncertainty in a network model and connectivity estimates. The overall network is sensitive to delineating and selecting the minimum patch size for the nodes (Minor et al. 2008, Lookingbill et al. 2010). Recently, wildlife conservation studies are expanding the definition of nodes to include locations of individuals or roosting sites (Rhodes et al. 2006, Garroway et al. 2008). By defining nodes as territory centers in our study we were able to remove the decision of minimum patch size. More importantly we were able to examine the connectivity within habitat patches by allowing small changes in movement behavior due to fine detailed landscape features.

The simplest type of connectivity is based only on the spatial arrangement of habitat patches (i.e., Euclidean distance between patches) surrounded by a featureless landscape (Calabrese and Fagan 2004). However, species movement behavior is strongly linked to the spatial configuration of the landscape, as a result both aspects are needed to evaluate how species respond to and orientate themselves within and between habitat patches (Bell 1991, Gautestad and Mysterud 1993, Brooks 2003). This study gives further evidence that edges created with resistance surfaces increase the biological relevance of species connectivity.

When resistance surfaces are used to predict a species' connectivity, the most important step is to select biologically relevant friction values (Adriaensen et al. 2003). However, friction values are usually defined based on subjective expert opinion or are converted from species habitat preferences during common daily activities or at breeding sites, and therefore are not representative of dispersal behavior (Schultz and Crone 2001, Schadt et al. 2002). Friction values derived from 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). Due to difficulty of obtaining detailed dispersal data, few studies have validated friction values with independent movement data (Driezen et al. 2007, Rabinowitz and Zeller 2010). We were able to empirically estimate resistance surface at a regional scale by combining radio-telemetry data during prospecting behavior and LiDAR data. Then with empirically estimated resistance surfaces and observed dispersal data we were able to confidently predict the flux of individuals between territories and overall RCW connectivity.

4.3 SAINT FRANCIS' SATYR

4.3.1 CHOICES OF APPALACHIAN BROWN BUTTERFLIES RELEASED AT HABITAT BOUNDARIES

Across all types of experimental releases, ABBs had the highest probability of moving into riparian forest habitat (0.84) and wetland habitat (0.59), and they exhibited a strong aversion to open-field and urban-developed habitat types (0.03) (Table 4). In all cases where open-field habitat was a potential choice, released butterflies rejected it in favor of the other habitats. Likewise, in all but one case in which urban development was a choice, butterflies favored the other habitat. Overall, upland forest was neither strongly favored nor rejected (entry probability = 0.53). Comparisons across pairwise combinations show that the adjacent habitat can make a difference in selection frequency of a habitat. By every measure (initial choice, most occupied, final choice) preference (p) for either riparian ($p = 0.026, 0.006, 0.002$ for each respective measure, $df = 2$) or upland forest ($p < 0.001$ for all measures, $df = 3$) differed among pair-wise choices. There was a strong preference for riparian habitat unless it was adjacent to a wetland.

Upland forest was strongly favored when paired against open or developed habitat but strongly avoided when paired against riparian forest and mildly avoided when paired against wetlands. By no measure did preferences differ among choices involving either wetlands or open habitats, as we observed a consistent preference for wetlands and a consistent avoidance of open habitats. Our analyses with binomial tests mirrored these results. Butterflies showed no preference between wetland and riparian forest habitats, and between wetland and upland-forest habitats (Table 4). Wetter habitats tended to be selected over drier ones, although only significantly so for the riparian forest-to-upland forest comparison. However, upland forest habitat was chosen significantly more frequently than developed or open-field habitat.

Table 4: Results from a series of binomial tests for choices at habitat boundaries (Table 1 from Keufler et al. 2010)

TABLE 1. Results from a series of binomial tests for choices at habitat boundaries.

Boundary type		Butterfly choices										
		Initial choice			Habitat most occupied			Final choice			Selection frequency§	
Habitat, *a* vs. *b*†	No. released‡	*a*	*b*	*p*	*a*	*b*	*p*	*a*	*b*	*p*	*a*	*b*
R vs. O	5	5	0	0.0313	5	0	0.0313	5	0	0.0313	1	0
R vs. U	16	12	4	0.0280	14	2	0.0018	15	1	0.0002	0.87	0.13
U vs. D	12	12	0	0.0000	11	1	0.0029	10	2	0.0161	0.92	0.08
U vs. O	11	10	1	0.0050	11	0	0.0005	11	0	0.0005	1	0
W vs. R	11	7	4	0.1610	7	4	0.1610	7	4	0.1610	0.64	0.36
W vs. U	13	4	9	0.0873	7	6	0.2095	9	4	0.0873	0.54	0.46

Note: For the column heads, "*p*" denotes the probability of observing each result, assuming that each habitat (*a* or *b*) in a paired choice has an equal chance of being selected.

† Habitat key: R, riparian forest; O, open field; U, upland forest; D, urban development; W, wetland.

‡ Sample size reflects the number of individual *Satyrodes appalachia* butterflies released at each boundary type.

§ A frequency of selection is provided, where a positive habitat choice is defined by a butterfly satisfying two of the three criteria described in the text

4.3.2 HABITAT-SPECIFIC MOVEMENT CHARACTERISTICS

We analyzed data from the individual movement paths of 116 ABBs, including habitat-specific movement data from 62 of the butterflies released for habitat-choice experiments, 25 additional butterflies that were released in continuous stretches of habitat, and 29 naturally occurring butterflies observed moving through large areas of native habitat. Movement paths ranged from 1 to 32 moves, with median and mode each being 4 moves. Move lengths varied between habitats, with Kolmogorov-Smirnoff (K-S) tests showing significant differences ($P < 0.001$) between mean step lengths for all pair-wise combinations of habitat types with the exception that step lengths did not differ between riparian forest and wetland habitats (motility index = 0.150, $P > 0.2$; Figure 21). Specifically, the step lengths decreased in order from open (median, 25–75% quartiles = 14.2, 7.5–19.5 m) to upland forest (9.0, 5.1–12.9 m) to riparian forest (3.1, 1.5–5.5 m) to wetland (2.9, 1.3–6.2 m) habitats. We collected too few data from butterflies in developed habitats to include in analyses. ABB turn angles varied among habitats (Figure 22). Turn angle distributions were most similar in upland forest habitats ($52.5^o \pm 5.0^o$ [mean ± SE]) and open habitats ($63.6^o \pm 7.3^o$), where movements tended toward greater linearity (i.e., turn angles were clustered near 0°). Movement distributions were also similar in riparian forest ($79.1^o \pm 15.7^o$) and wetland habitats ($78.8^o \pm 5.1^o$), where movements tended toward greater sinuosity. K-S tests showed that turn-angle distributions differed significantly between wetlands and both open and upland forest habitats (wetland, open motility index = 0.276, $P < 0.001$; wetland, upland motility index = 0.280, $P < 0.001$). No other comparisons were significantly different. However, the lack

of a significant difference in turn-angle distributions between riparian forest and either open or upland forest habitats is likely due to a lack of power associated with few (n = 19) turn angles available from riparian forest habitats.

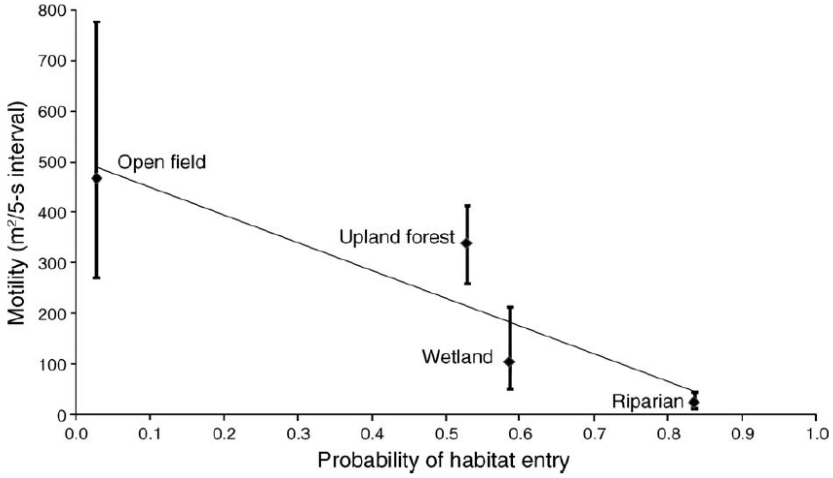

FIG. 2. Relationship between the probability of entering a given habitat and the motility within that habitat. Probability of entry is derived from values in Table 1 as the mean of all possible choices for a given habitat type. The probability of entry into open habitats pools choice data for open fields and urban developments. Data are means and 95% CI around each estimated value. All data were collected from experimentally released *Satyrodes appalachia*. Data used to estimate mean displacement were not collected for developed habitat.

Figure 21: Relationship between the probability of entering a given habitat and the motility within that habitat (Figure 2 from Kuffler et al. 2010).

The squared displacement rate of ABB was highest in open habitats (estimate, 95% CI: 467 m^2/5-s interval; 95% CI, 273.2–777.3 m^2/5-s interval), slightly lower in upland forests (339 m^2/5 s; 95% CI, 260.8–414.4 m^2/5 s), nearly one third as large in wetlands (105 m^2/5 s; 95% CI, 51.4–213.8 m^2/5 s), and one fourth as large again in riparian forests (24 m^2/5 s; 95% CI, 14.7–46.6 m^2/5 s).

4.3.3 INTEGRATING BOUNDARY BEHAVIOR AND WITHIN-HABITAT MOVEMENT

Across habitats, movement rate was negatively correlated with the probability of entry (Figure 21; $r \cong 0.91$; df = 3, $P < 0.09$). Thus our comparison of different matrix habitats illustrates the potential importance of nonbreeding habitat in promoting landscape connectivity. In the Fort Bragg landscape, wetland and riparian-forest habitats support populations of our focal species, and are most frequently selected by butterflies, yet they promote the lowest rates of movement. Open fields, by contrast, promote rapid movement, yet butterflies very rarely cross into this habitat. Perhaps surprisingly, upland forest may be one of the most important habitat types for facilitating dispersal of our focal species among populations across this landscape. Upland forest habitats do not support breeding populations of wetland butterflies, yet they promote relatively high rates of movement and present a relatively ''permeable'' boundary. Unlike suitable wetland and riparian-forest habitats that account for a very small proportion (< 10%, combined) of the landscape, upland forests account for nearly 50% of the landscape. Because upland forest habitat has relatively high permeability and rates of displacement (that is, it is the point well above the

regression line in Figure 21), and also occupies a large fraction of the landscape, connectivity created by this habitat type may be highest. When habitat preference, habitat-specific movement, and the natural fragmentation of suitable wetlands are taken into account, the value of breeding habitats in promoting landscape connectivity may be relatively low.

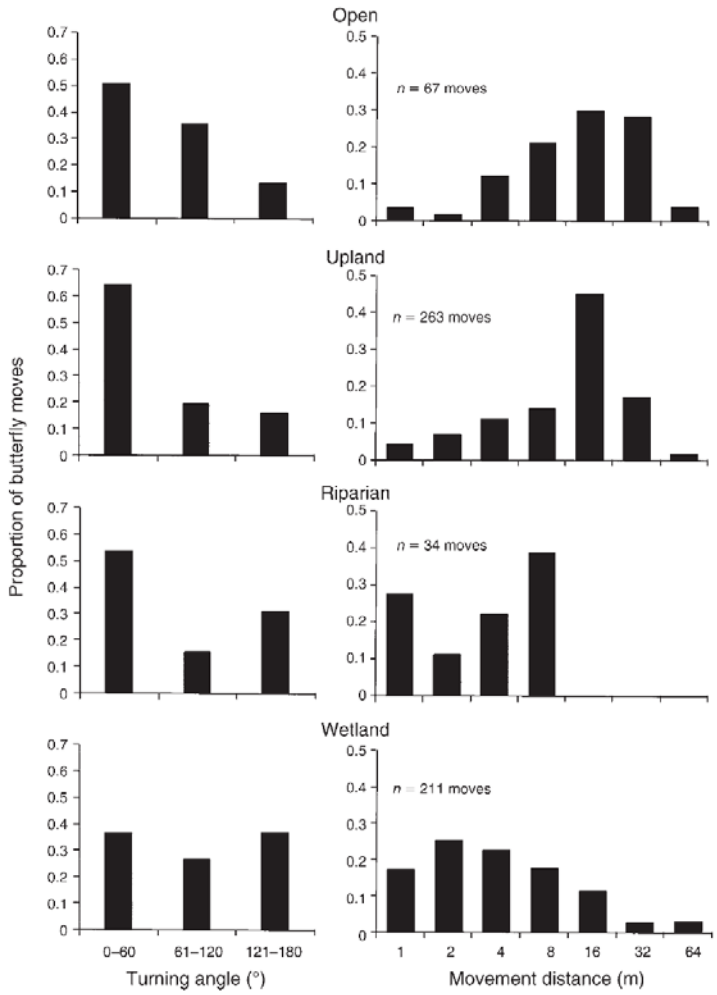

FIG. 1. Histogram of turning angles and movement distances of each movement step for experimentally released *Satyrodes appalachia* (Appalachian brown) butterflies in four dominant natural habitat types. The lower two panels illustrating wetland habitats include data from released and naturally occurring butterflies combined.

Figure 22: Histogram or turning angles and movement of each movement step for experimentally released *Satyrodes Appalachia* (Appalachia brown) butterflies in four dominant natural habitat types (figure 1 from Kuffler et al. 2010).

4.4 AMPHIBIANS

4.4.1 EMPIRICAL DATA FOR SIMULATION STUDY

We found no significant differences in turn angle distributions among the three habitat types for ornate chorus frogs (Figure 23). However, step lengths in riparian forest habitat were shorter than those in upland forest or open habitats. Further discussion of the use of these data can be found in the simulation section 3.5 Movement Simulations for SFS and Amphibians.

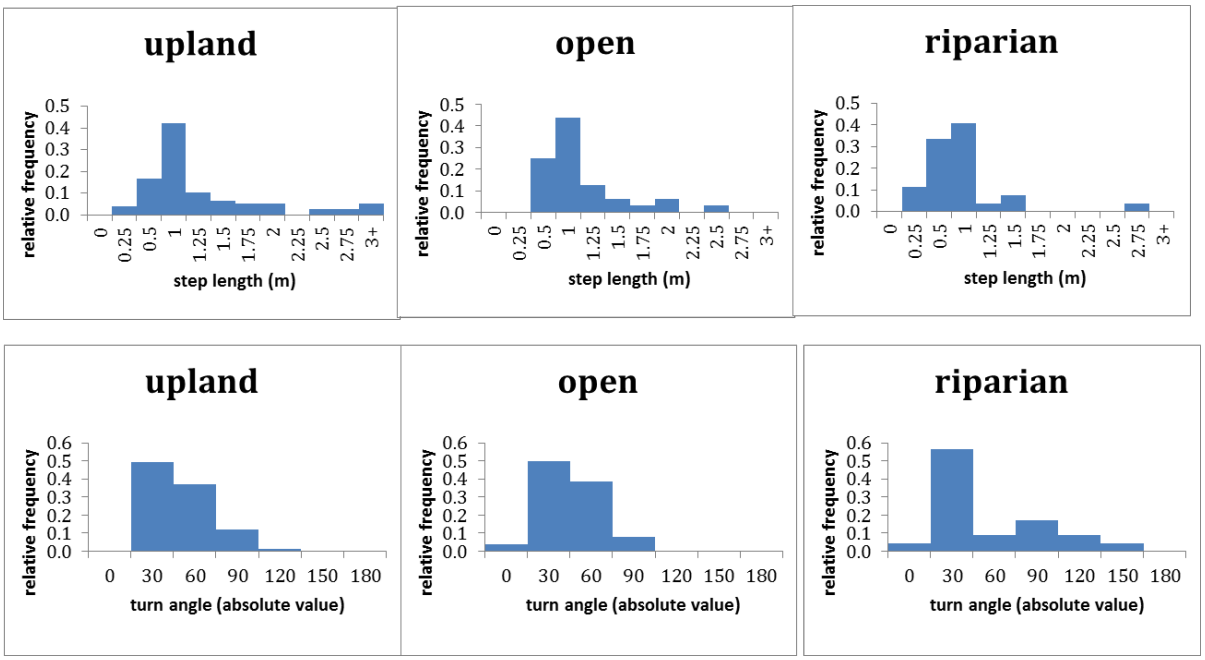

Figure 23: Frequency distributions of step lengths and turn angles for adult ornate chorus frogs tracked in open habitats, upland forest, and riparian forests that were used in conducting movement simulations.

4.4.2 EXPERIMENT 1

We released 19 juvenile ornate chorus frogs in 4 forest plots and 19 juvenile ornate chorus frogs in 4 field plots between 17 May 2010 and 27 May 2010. An additional 17 juvenile ornate chorus frogs were released in raked plots within forested areas between 27 May 2010 and 29 May 2010. There was an interaction between larval density and habitat type. Juvenile frogs raised at low densities traveled faster in fields than in forests, and this pattern was reversed for frogs raised at high densities (Table 5, Figure Figure 24). However, there was no effect of larval density on the linearity of movement paths in forest and field plots.

In contrast to the behavioral differences in different habitat types, juvenile frogs moved at similar rates in forested areas that were raked or unraked (Table 5). There was also no effect of raking or larval density on the linearity of frog movement paths. Frogs used in releases at forest and field sites from low density tanks were heavier than frogs from high density tanks (t=5.8427, p-value=0.0215), but frogs released at raked plots show no difference in size due to larval density (t=0.0824, p-value=0.9375).

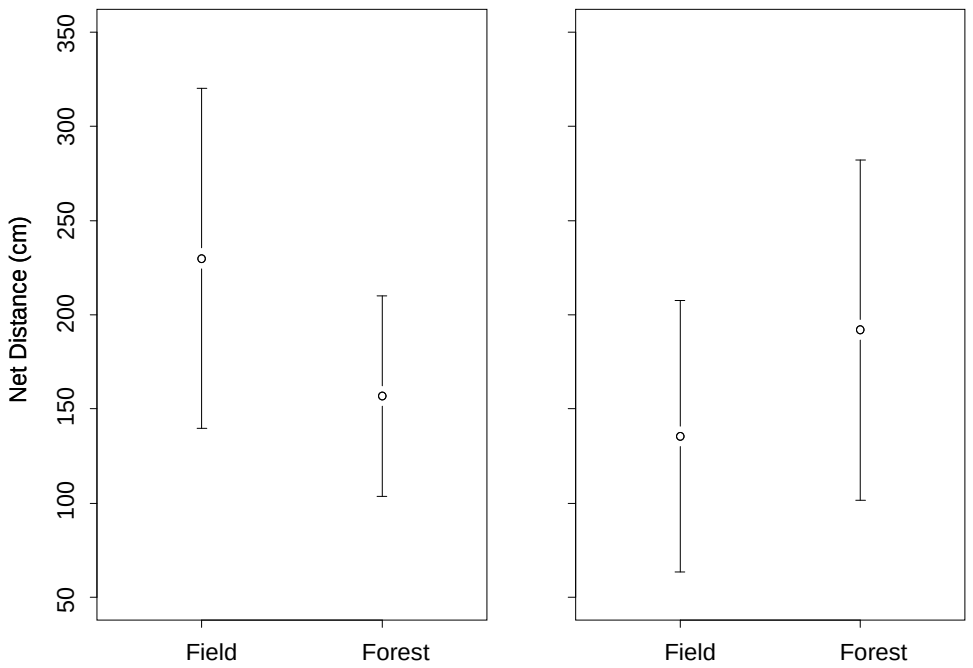

Figure 24: Average net distance moved by juvenile ornate chorus frogs reared at low (left) and high (right) densities in different habitats when checked at 12-minute intervals.

Table 5: Two-way ANOVAs comparing the effects of larval density and habitat type on juvenile ornate chorus frog movement speed and path linearity.

Release Experiment	**Effect**	**df**	**F**	**p-value**
Forest v s. F ield: M ovement				
	Larval Density	1	0.3803	0.5415
	Habitat Type	1	0.0048	0.9453
	Larval Density * Habitat Type	1	4.6712	0.0378
Forest vs. Field: Path Linearity				
	Larval Density	1	0.2594	0.6140
	Habitat Type	1	1.5019	0.2291
	Larval Density * Habitat Type	1	0.1197	0.7315
Raked v s. Unraked: M ovement				
	Larval Density	1	0.3550	0.5557
	Raking	1	1.4533	0.2374
	Larval Density * Raking	1	0.5850	0.4503
Raked v s. U nraked: P ath				
	Larval Density	1	1.5540	0.2229
	Raking	1	0.1124	0.7399
	Larval Density * Raking	1	0.0335	0.8561

4.4.3 EXPERIMENT 2

4.4.3.1 EASTERN NEWTS

Of the 35 individuals tracked, two were lost during the first five minute interval and therefore not used in any analyses. Data from five newts that failed to move at all (four in control plots and one in a raked plot) were also discarded, leaving 28 newts for analyses (14 in the control plots and 14 in the raked plots). (An ANOVA including the five newts that failed to move also yielded the same qualitative result as reported below). Eastern newts traveled faster in raked plots than in control plots (F = 15.85, df = 1,26, p-value = 0.001, Figure 25). Newts were tracked for a total of about four time intervals in the control plots (mean = 22.50 minutes, SD = 9.76) and about six time intervals (mean = 32.86 minutes, SD = 13.41) in raked plots, however newts did not move different distances per time interval in raked plots (F = 0.99, df = 5,66, p-value = 0.433) or in control plots (F = 1.22, df = 5,69, p-value = 0.31). The average net total distance moved by eastern newts was 0.65 m (SD = 0.54) in control plots versus 1.68 m (SD = 1.09) in raked plots. Eastern newts traveled further in raked plots than in control plots (F = 9.92, df = 1,26, p-value = 0.004). For the linearity analysis, we removed data of two additional newts because they were lost after only one five minute time interval. Eastern newts moved in less direct paths in raked plots than in control plots (F = 4.64, df = 1,24, p-value = 0.04, Figure 25).

4.4.3.2 ORNATE CHORUS FROGS

We used movement data from 16 frogs for analyses (seven in control plots and nine in raked plots). Ornate chorus frogs did not travel at significantly different speeds in raked plots versus control plots (F = 0.70, df = 1,14, p-value = 0.42). Frogs were tracked for a total of about five time intervals in control plots (mean = 26.43 minutes, SD = 9.45) and in raked plots (mean = 25.56 minutes, SD = 8.08). The average net total distance moved by ornate chorus frogs was 6.08 m (SD = 9.41) in control plots versus 8.52 m (SD = 9.62) in raked plots. Ornate chorus frogs did not travel different net total distances in raked plots versus control plots (F = 0.26, df = 1,14, p-value = 0.62). For the linearity analysis, we excluded data from two individuals that were lost after only one five minute time interval. Ornate chorus frogs did not move in significantly different paths in raked plots versus control plots (F = 2.98, df = 1,12, p-value = 0.11Figure 26).

4.4.3.3 SPECIES COMPARISON

Eastern newts traveled slower than ornate chorus frogs (F = 12.3082, df = 1,42, p-value = 0.0011), in less direct paths (F = 15.2151, df = 1,38, p-value = 0.0004), and achieved lower net total distances (F = 12.7902, df = 1,42, p-value = 0.0009) in roughly the same amount of time (F = 0.2407, df = 1,42, p-value = 0.6262).

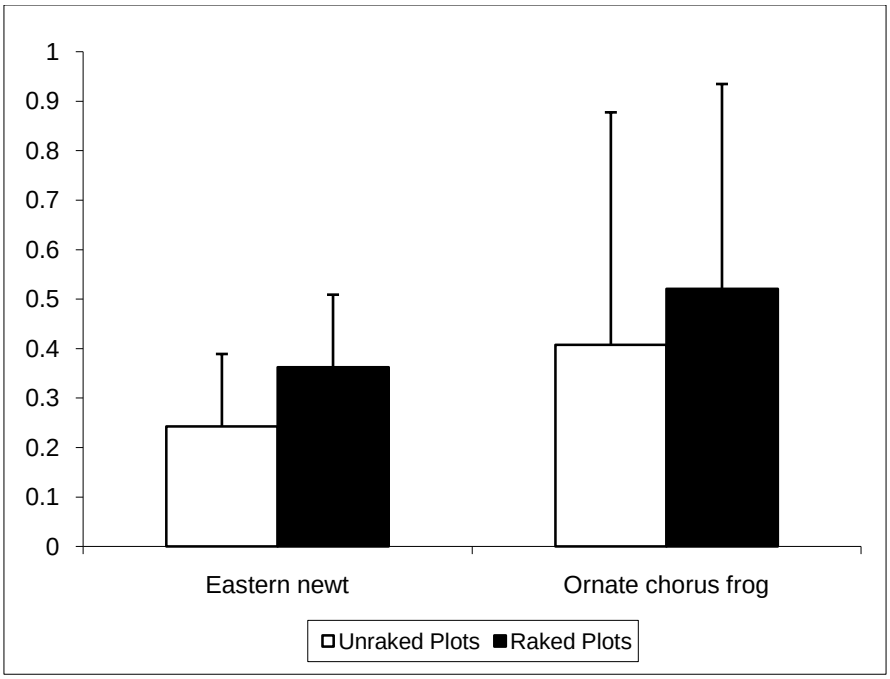

FIGURE 25. Average speed (m/min) traveled by both species in control (unraked) versus raked plots. Points displayed represent means and y-error bars are 95 % confidence intervals from ANOVA.

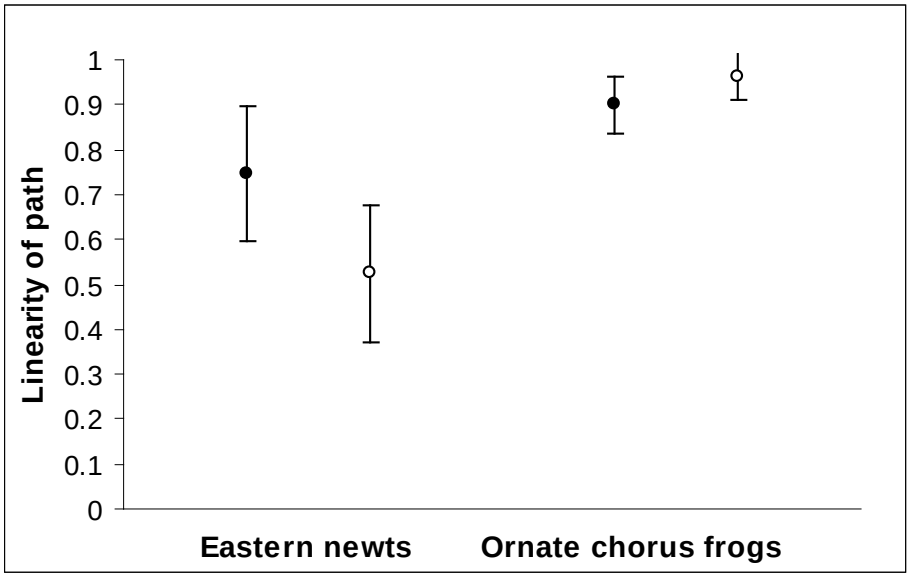

Figure 26: Linearity of paths traveled by both species in control (unraked) versus raked plots. Points displayed represent means and y-error bars are 95% confidence intervals from ANOVA. Closed circles indicate control treatments, open circles indicate raked treatments.

4.4.4 EXPERIMENT 3

We released 84 newly metamorphosed Carolina gopher frogs and 77 southern leopard frogs into enclosures from June to August 2008. Of these, 68 gopher frogs and 59 leopard frogs were recaptured at least once. Initial habitat choice (the location of the first recapture of an individual) was significantly different ($p<<0.001$) for Carolina gopher frogs, with the majority of animals choosing to move into clear-cut (Figure 27). Southern leopard frogs trended towards the forest habitat, however this difference was not significant ($p=0.09$).

Gopher frogs moved rapidly into their chosen habitat. Of the 68 gopher frogs recaptured, 56 (86.7%) were recaptured at the end of the enclosures. Animals reaching the end of enclosures were defined as having dispersed into that habitat. The majority of gopher frogs reaching the end of enclosures moved there within 1 day (73.2%), with the overall mean time to disperse being 1.25 days (Figure 27). Fewer leopard frogs reached the end of the enclosures, and only 37 of the 59 (62.7%) recaptured had dispersed. Leopard frogs were slower to disperse through habitats and the mean time to disperse was 2.44 days (Figure 27).

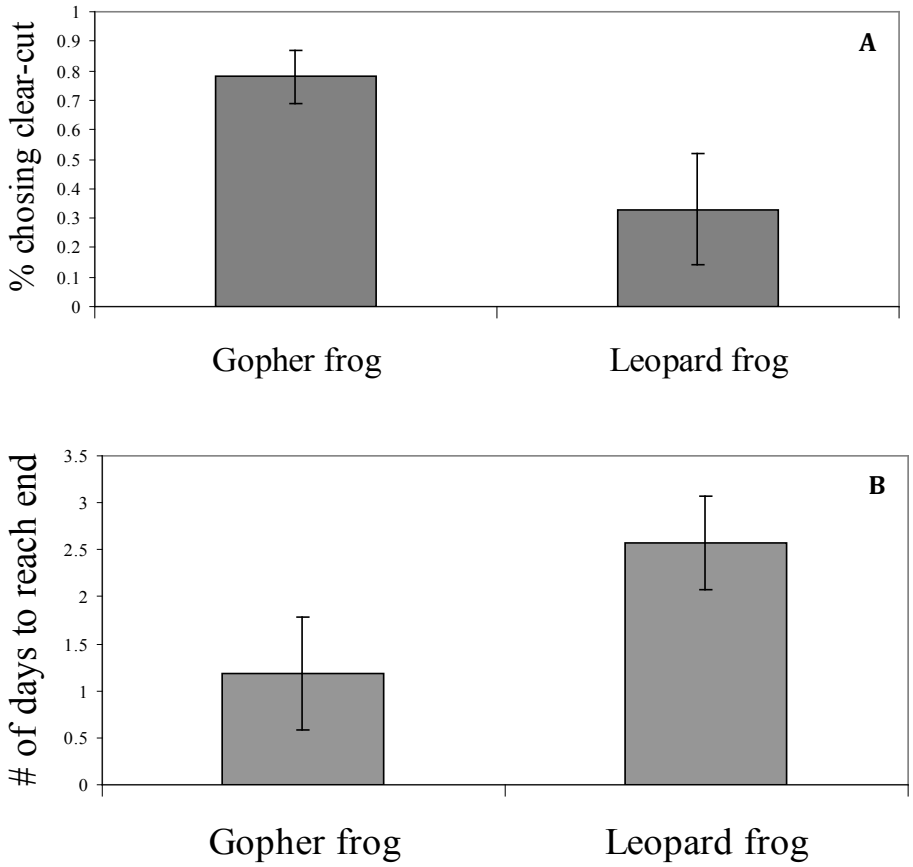

Figure 27: The proportion of animals choosing clear-cut habitat (A), and the mean time for animals to disperse (B).

4.4.5 VERNAL POOL MAPPING

This backward selection procedure identified distance to streams and elevation as the two parameters in the best model for predicting natural wetlands, which reflects the fact that natural wetlands in the Sandhills region of North Carolina are associated with ridgetop areas and tend to be located farther away from streams. In contrast to this, the best model for predicting artificial wetlands indicated that artificial wetlands were more likely to occur closer to dirt roads and at moderate elevations. Predictive models for natural and artificial wetlands correctly classified most sites as wetlands or not wetlands (Figure 28 and Figure 29).

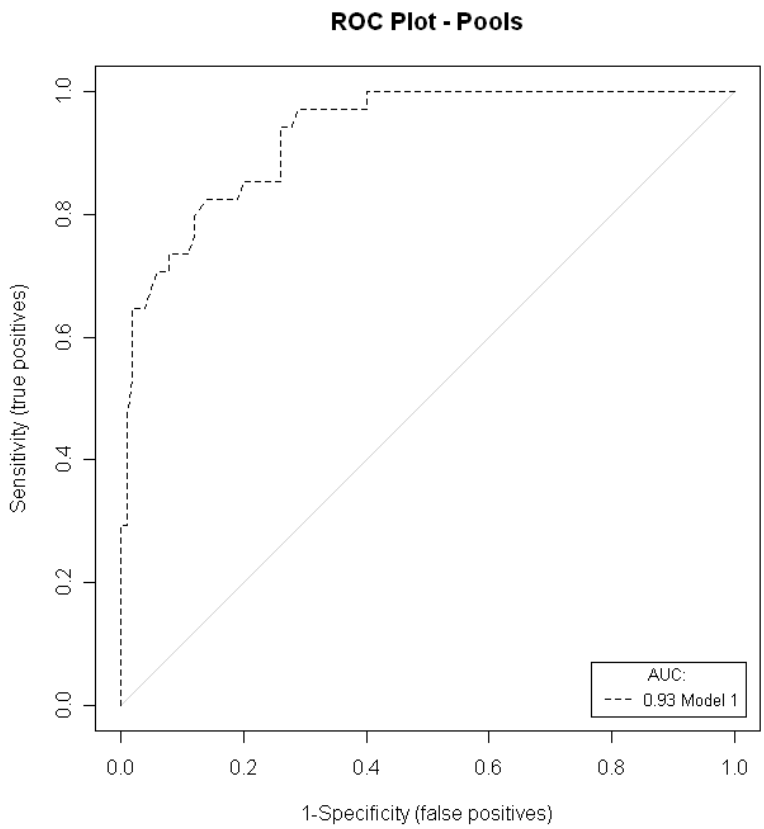

Figure 28: Receiver operating characteristic curve and area under the curve (AUC) for a predictive model of natural wetlands in the study area.

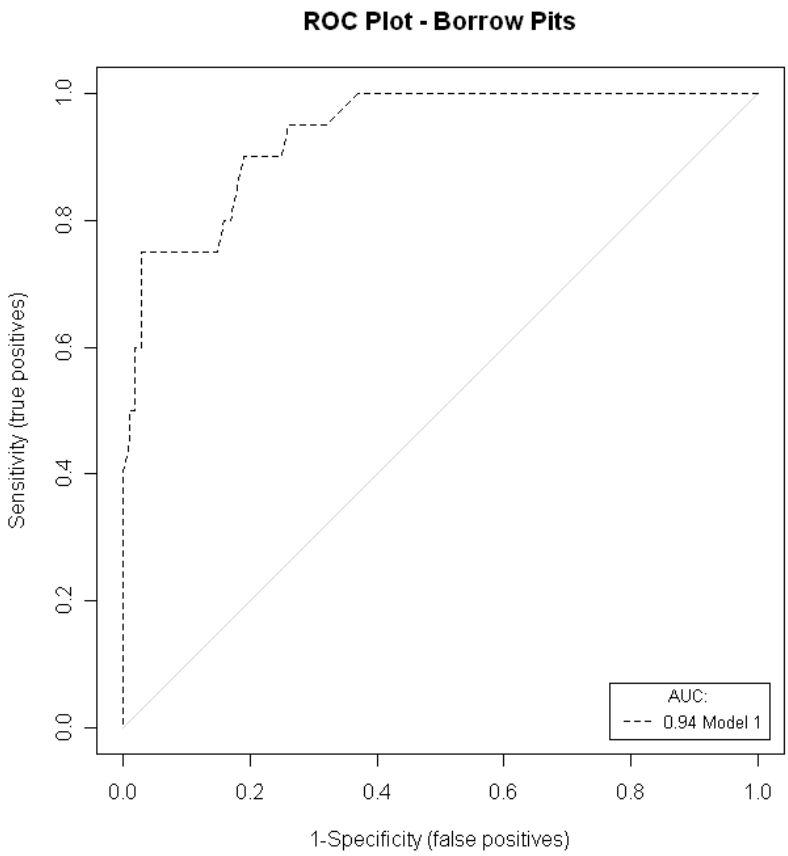

Figure 29: Receiver operating characteristic curve and corresponding area under the curve (AUC) for a predictive model of artificial wetlands in the study area.

Although natural and artificial wetlands that are suitable for amphibians are poorly mapped by existing GIS data, we were successful in predicting areas where these sites should occur. Our predictive models showed a good ability to discriminate between sites that were wetlands and random sites within the landscape. We used GIS data that is commonly available throughout the state of North Carolina and for many publicly managed lands in the southeastern U.S., so our method of predicting wetland sites could easily be transferred to other locations.

Following field surveys to ground truth predicted wetland sites, we generated a new map of suitable wetland habitat for amphibians in our study area. This map included both natural and artificial wetlands, and it provided the locations for suitable breeding habitat that were used in both simulation and circuit models of amphibian dispersal.

4.4.6 Discussion

Our findings highlight several important lessons for studying movement ecology of amphibians. Assessing landscape connectivity for a rare species often involves making assumptions, such as that movement rules for a species are habitat specific, that variation in habitat at a coarse scale is more important than at a fine scale, and that surrogate species can provide appropriate data for use in the place of data on rare species. Our experiments provide data that contradict these

assumptions: juvenile ornate chorus frogs exhibited changes in movement behavior that reflected the larval conditions they experienced, movement behavior of adult eastern newts and ornate chorus frogs was affected by habitat manipulation at a fine scale within the dominant forest habitat type, and juvenile gopher frogs and leopard frogs exhibited preferences for different habitat types.

There are two implications of our findings. First, much modeling of landscape connectivity is based on expert opinion about the resistance of various habitats to dispersal. These opinions are based on assumptions that are unlikely to be met. One way to determine the consequences of these assumptions is through simulation models that assess the sensitivity of model results to assumptions. Additional simulations could examine the effects of changing the complexity and distribution of habitat types as well as movement rules for individuals. Second, our movement data likely lead to a conservative assessment of connectivity for amphibians in the Sandhills region of North Carolina. Body size may be positively associated with tolerance to desiccation in amphibians, and this could result in individuals of larger species, like tiger salamanders and gopher frogs, moving longer distances. Radio telemetry studies of tiger salamanders and gopher frogs conducted in this region have found that tiger salamanders are capable of moving hundreds of meters within a night, and gopher frogs have been found in burrows 2 – 3 km away from breeding ponds. Thus, it is possible that rare amphibians are capable of moving substantially larger distances than we observed. Further research will test the correspondence between the fine scale movement we measured and larger scale dispersal.

4.5 DISPERSAL MODELING

4.5.1 MODEL VERIFICATION USING RESIGHT DATA FOR SFS

For existing SFS colonies and surveyed upland sites there was a strong positive correlation between dispersal probabilities predicted by the simulation and those observed in the mark-resight study ($r=0.824$, $p< 0.001$; Figure 30). The largest discrepancies came from source colonies where few marked butterflies were subsequently recaptured (Figure 31), suggesting that some of the discrepancy may be simply due to sampling error. The strong overall correspondence between the observed moves and the simulation predictions provides validation that the simulation is an accurate tool for predicting dispersal within novel landscapes.

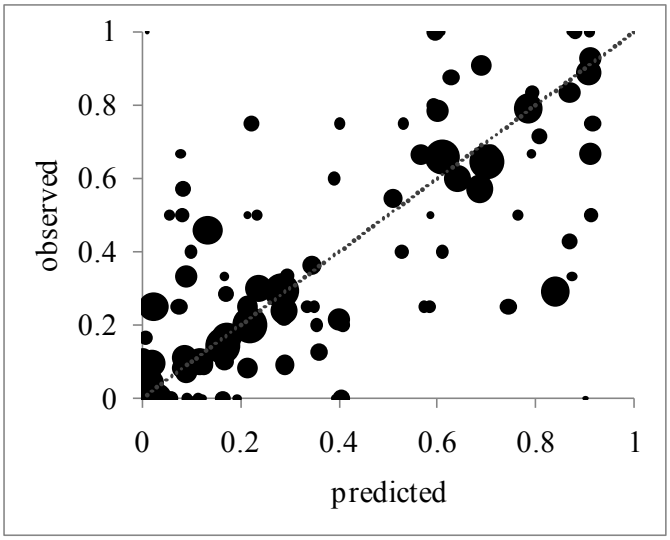

Figure 30: Observed vs. predicted dispersal between surveyed SFS colonies. Each point represents the observed dispersal rates of recaptured butterflies during mark-resight surveys from 2003-2007 plotted against the predicted dispersal probability from the SFS simulation. Only pairs of sites located within the same drainage are plotted.

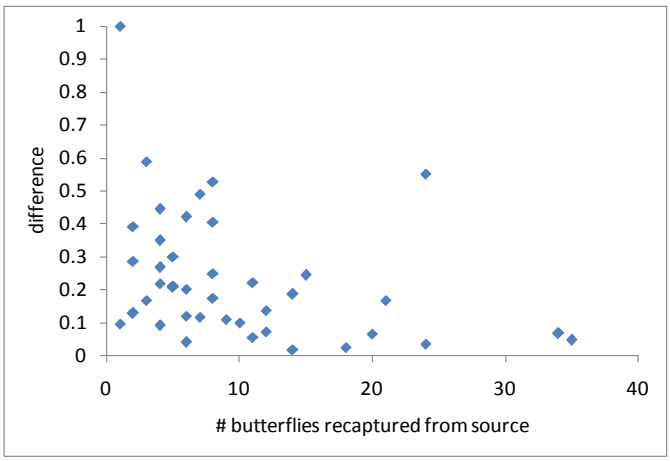

Figure 31: Magnitude of the difference in the predicted probability and observed dispersal rate compared to the number of marked and resighted butterflies from a given source.

4.5.2 MODEL RESULTS

At Fort Bragg, both SFS and the two amphibian species appear to persist in spatially structured networks of distinct breeding sites linked by dispersal (i.e., metapopulations, Figure 32). Further, our results strongly suggest that these species will need to be able to persist in such a metapopulation structure in areas surrounding Fort Bragg if they are to be established and/or managed there in the future.

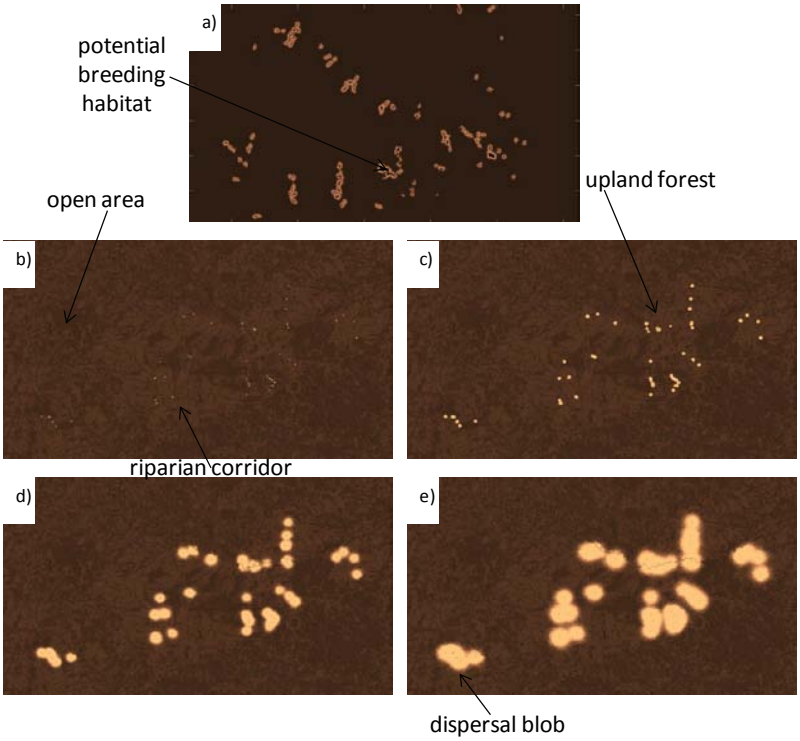

Figure 32: Simulated dispersal paths. Panels depict the relative use of 30 X 30 m grid cells by simulated dispersing a) SFS, b) chorus frogs assuming a 10 day dispersal period, c) chorus frogs assuming a 100 day dispersal period, d) gopher frogs assuming a 100 day dispersal period and e) gopher frogs assuming a 300 day dispersal period. In each panel, potential source patches are indicated by dark brown surrounded by a "dispersal region" of light brown fading into darker browns. Withing the dispersal region, lighter colors indicate greater use by dispersers (i.e., more paths entered the cell). Panels depicting frog dipsersal are overlaid on a map of the study region with different shades indicating different habitats as indicated. Because of concerns about revealing the location of SFS breeding sites, panel a) is not overlain on a map, and covers only a part of the study region.

For purposes of managing landscape connectivity for our focal species, we define pairs of sites as being linked if an animal leaving one site has at least a 0.01% chance of reaching the other. Nearby breeding sites within each network appear to have a relatively high likelihood of being connected by dispersal. SFS sites that are connected by dispersal are all within 300-500 m of each other. Chorus frog sites that are connected by dispersal are all within 100-150 m if the dispersal period is 10 days and within 350-400 m if the dispersal period is 100 days. Gopher frog sites that are connected by dispersal are within 2-2.5 km if the dispersal period is 100 days and 4-5 km if the dispersal period is 300 days (Figure 33). For all three species examined through simulation, the likelihood of dispersal drops rapidly with the distance from source patches. Although not all breeding sites within a single network necessarily share a direct link,

all sites within the same network are connected (directly or indirectly) through a continuous line of linked sites (e.g. Figure 34). In contrast, sets of nearby core areas that are separated from each other by even a few kilometers are likely to be almost completely isolated on a time-scale relevant to management. Rare moves between these sets of core areas may very occasionally occur, but such events are probably so unlikely that they should not be considered when designing management plans.

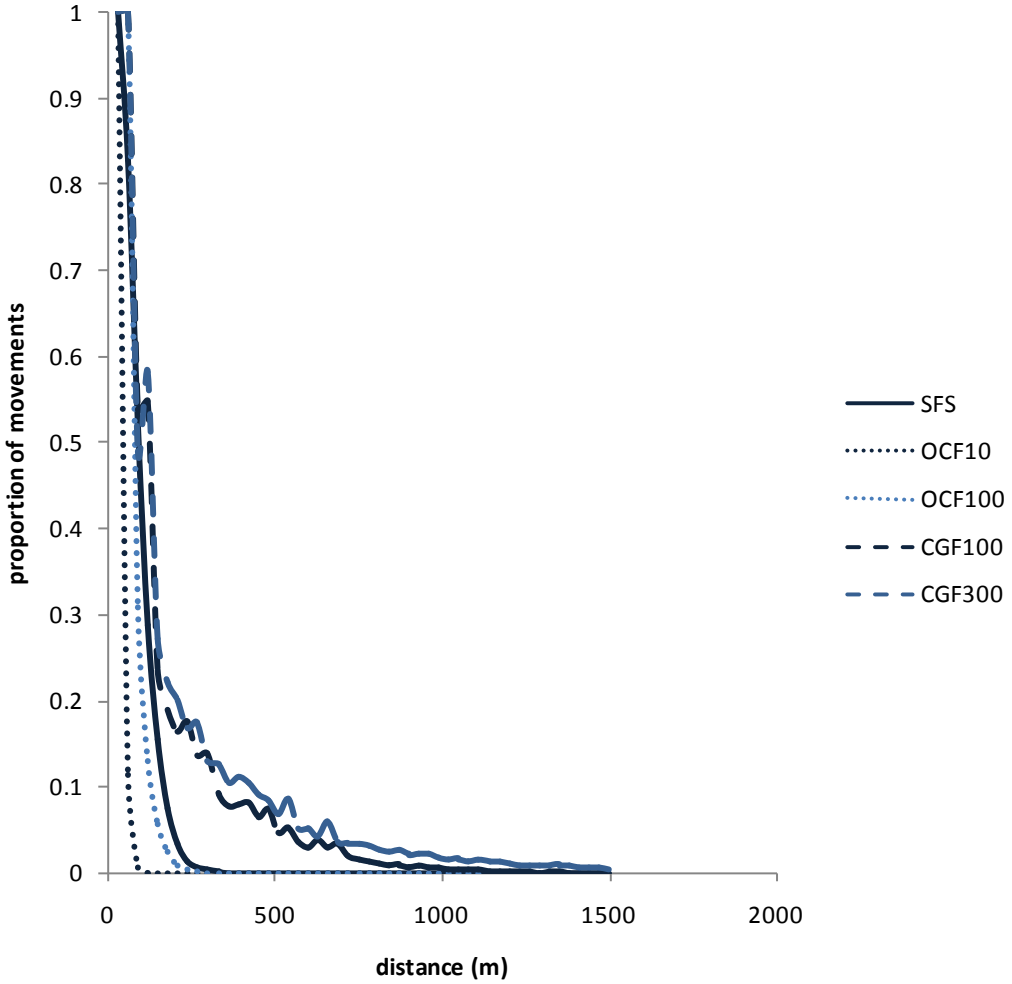

Figure 33: Fractions of the movement paths of simulated SFS, chorus frogs (OCF), and gopher frogs (CGF) that fell at various distances from the breeding site starting points. Numbers after frog identifiers indicate the dispersal period simulated.

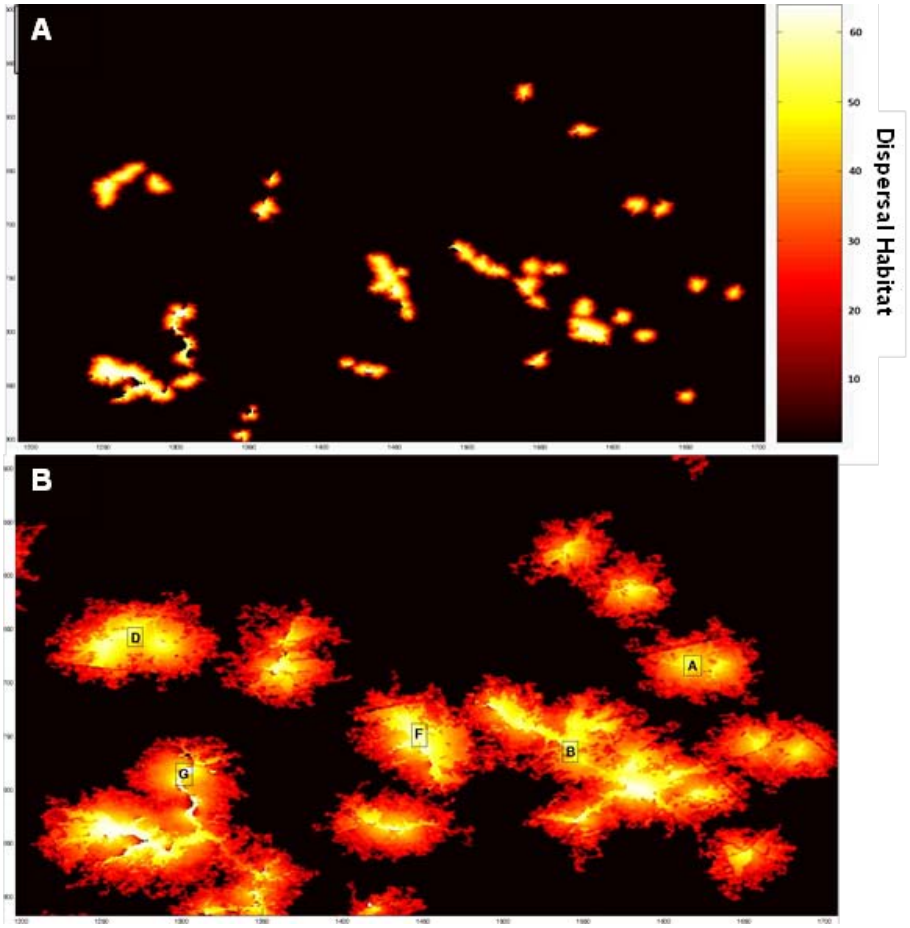

Figure 34: Heatmaps. A: SFS dispersal within the core area. B: SFS dispersal within the core area assuming no rest and 10 hr activity per day. Boundaries are the same as in A). Labels indicate drainages described in Vogel and Haddad in press.

Dispersal was influenced both positively and negatively by habitat differences. We visualized the influence of habitat on dispersal potential by plotting habitat use as a function of distance from a breeding site. In this case, our measure of habitat use was the ratio of the percentage of migration paths that passed through a particular type of habitat at a given distance from a potential source to the percentage of the landscape at that distance composed of that habitat type (Figure 35). For both SFS and the amphibians, open habitat acted as a barrier to dispersal, and was used disproportionately rarely compared to its availability in all simulations. The influence of other habitats was species specific. SFS dispersal was promoted by riparian corridors, but the butterfly used upland forest roughly in proportion to its availability (Figure 35). In contrast upland forest promoted chorus frog dispersal while riparian corridors acted as barriers to its movement (Figure 35). Simulated gopher frog dispersal paths (Figure 35) also fell within upland forests more frequently than expected based on the availability of that habitat type, especially for longer dispersal paths. The influence of riparian corridors on gopher frog dispersal was more complex, but simulated gopher frog dispersal paths generally fell within riparian habitats less frequently than expected based on availability of that habitat.

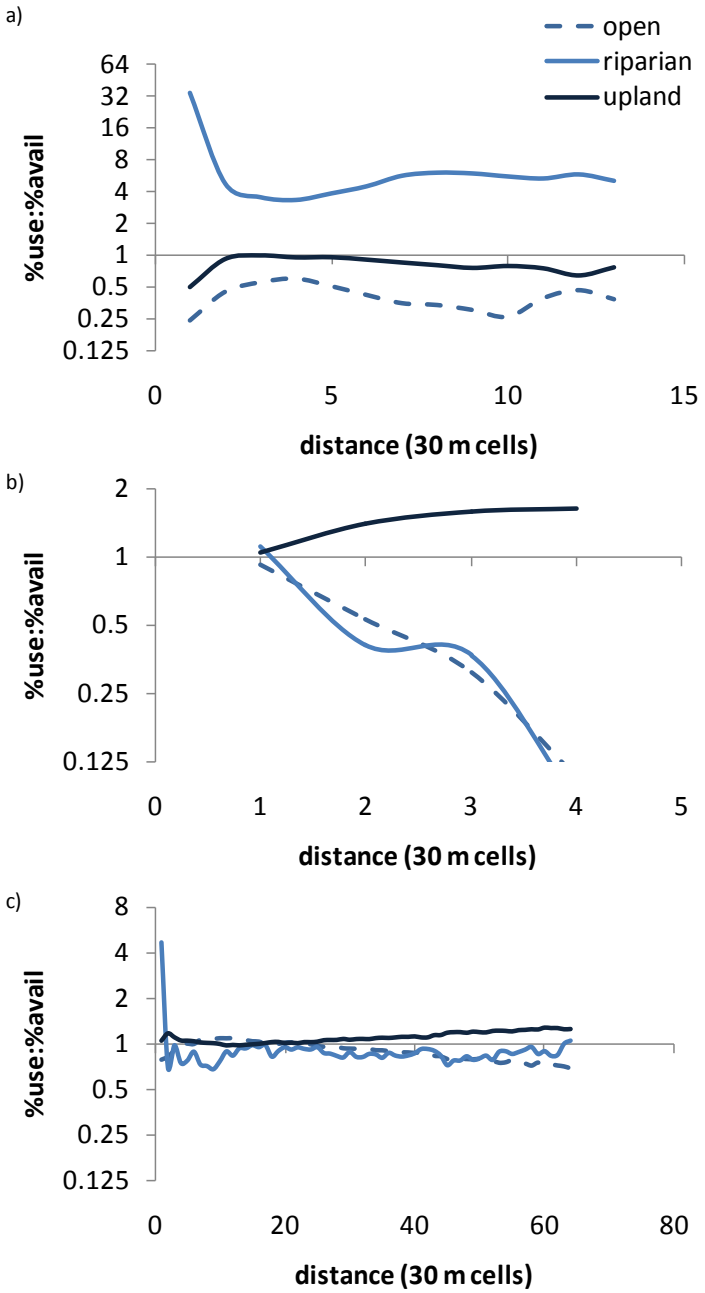

Figure 35: Ratio of relative use to availability of major habitat types vs. distance from source for simulated a) SFS, b) ornate chorus frogs and c) Carolina gopher frogs. Distance is measured as the minimum number of cells a disperser would have to cross to reach the focal cell from its point of origin.

4.5.3 Discussion of Simulation Results

Simulated dispersal probabilities were congruent with field-based measures of SFS dispersal. Within drainages, simulated dispersal was extremely limited, especially among sites separated by more than 200-300 m This result is similar to the low dispersal found in mark-resight studies

(Haddad et al. 2003-2007) and is consistent with low genetic differentiation among colonies in the same drainage but high genetic differentiation among colonies in different drainages (Vogel and Haddad *in press*). For some pairs of drainages, our simulations suggest that dispersal is even more restricted than indicated by genetic structuring. Increasing the amount of SFS dispersal in simulations to three times that expected in the lifespan of an adult SFS yields the prediction of connectivity between two of the three drainages which likely experienced recent historic genetic exchange (Figure 34). Thus underestimation of adult lifespan could partly explain cases of mismatch between simulation estimates of exchange rates and genetic data. Discrepancies in connectivity between genetic and simulation studies may be further explained by the presence of upstream historic breeding sites lost to succession that would have increased historical gene flow.

4.5.3.1 HABITAT MANAGEMENT

Our results lead to a few general recommendations for promoting the dispersal of SFS and the amphibians in fragmented landscapes at Fort Bragg. First, because the dispersal abilities of SFS and the amphibians are severely limited relative to that of RCW, management of SFS and amphibians should focus on promoting dispersal within networks of closely-spaced patches. Second, beyond the localized vicinity of a breeding area, stepping stones will be needed to promote relatively long-distance dispersal. Stepping stones are locations between existing occupied networks that are restored to habitat suitable for SFS or amphibians, and close enough to one another and to occupied networks that dispersers can successfully move between them (Leidner and Haddad 2010). To hasten such connection, it may even be necessary to "seed" these restored stepping stones with translocated or captive-reared individuals. Before that is attempted, it would be best to determine whether these restored sites are of sufficiently high quality to support healthy populations of the target species. Third, perhaps the best way to ensure the long-term persistence of SFS and amphibians in the landscape in and around Fort Bragg is to increase the number of patch networks (i.e., local metapopulations), which could be accomplished through captive rearing and release, through restoration, or both.

With regard to future restoration and reintroduction in our study area, there are probably more easily exploited opportunities to create new networks on Fort Bragg itself rather than off base. Because all existing SFS colonies are on base, adding new networks between existing (but isolated) networks there has the added advantage of increasing the amount of exchange (both demographic and genetic) between existing colonies, which may increase the likelihood of overall persistence more than would be expected by simply increasing the number of (isolated) networks alone. If, however, establishing a persistent connection between Fort Bragg and other nearby conservation areas (such as the Sandhills Gamelands) is deemed desirable, our results suggest that, given the extremely limited dispersal abilities of SFS and amphibians, such a connection cannot be accomplished for these species by acquiring widely scattered parcels. Instead, true connectivity will likely necessitate a full-scale, continuous corridor that is wide enough to allow a series of local networks spanning the areas to be connected.

The Endangered Species Branch at Fort Bragg is well positioned to use the computer simulation we have created as a tool for evaluating potential sites for new restored breeding habitats in and around Fort Bragg. Our field-tested and validated simulations can provide a quantitative assessment of whether a proposed site (or network of sites) is likely to be colonized naturally from extant populations, or whether a "seeded" population established there is likely to exchange

migrants with neighboring existing colonies (or networks). If there are multiple such proposed sites, this quantitative assessment can provide a basis for adjudicating between them. In addition, the simulation can be used to predict which site or sites within a newly restored network of (initially empty) sites will receive and contribute the most to other sites within the network. This information will be key to deciding which is the best "beachhead" site at which to perform initial releases, given financial and/or logistic constraints in terms of the availability of captive reared individuals that prohibit all potential or restored sites from being seeded initially. The simulation may be especially useful as a management tool when used in conjunction with other tools, including but not limited to Maxent, for locating patches of suitable (or restorable) habitat on the landscape, including sites that have potential sites for use as stepping stones. Moreover, tools to evaluate suitable habitat may be used to predict the likely future population size that might be attained given the actual amount of suitable habitat at different locations.

The MATLAB code for the movement simulations can be used to make predictions for other species or on other landscapes with the proper input. The simulations will be maintained for future use at the Institute for Wildlife Studies (IWS), Arcata California (www.iws.org).

4.6 EVALUATING MODEL COMPLEXITY

4.6.1 MODEL COMPLEXITY FOR RCW

Euclidean distance was a very poor predictor of prospecting behavior (Table 6). 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). The top 17 models, according to AICc, explained prospecting behavior with environmental cues recognized from non-natal telemetry locations. This result suggests that environmental variables encountered away from roosting territories were a better predictor of prospecting movements than environmental features found only at roosting territories.

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 6). The top-ranked discrete-choice model had a moderate rescaling constant ($c = 4$) creating a non-linear function converting forest structure into friction values on the resistance surface. This model suggested a negative relationship between probability of visiting a territory and effective distance ($\beta = -7.44 \times 10^{-5}$, $SE = 1.347 \times 10^{-5}$, $p < 0.001$). That is, within the prospecting range, territories with greater effective distances from the roosting site were less likely to be visited during forays.

Table 6: 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	5478.580	0.000	0.702
2		LiDAR	8	5480.341	1.760	0.291
3		LiDAR	2	5488.054	9.474	0.006
4		LiDAR	1	5499.407	20.826	0.000
5		LiDAR + Landsat	2	5509.093	30.513	0.000
6		LiDAR	0.25	5509.698	31.118	0.000
7		LiDAR	0.5	5512.346	33.765	0.000
8		LiDAR + Landsat	1	5513.835	35.255	0.000
9		LiDAR	16	5519.418	40.837	0.000
10		LiDAR + Landsat	4	5520.478	41.898	0.000
15	Telemetry	All Environmental data	0.25	5554.001	75.421	0.000
18	Territory	Landsat	16	5563.018	84.438	0.000
48	Telemetry	Land-cover Classes	0.5	5607.292	128.712	0.000
56	Euclidian Distance (m)			5620.006	141.426	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).

Replacing a uniform landscape with a resistance surface often improves animal movement predictions (Verbeylen et al. 2003, Magle et al. 2009, Richard and Armstrong 2010). Insight into species' reactions to the environment between habitat patches has been enhanced by increasing the complexity of resistance surfaces (Moilanen and Nieminen 2002). Evaluating observed movement data in relation to multiple resistance surfaces with varying complexity of environmental features and a range of friction values helps identify which environmental features influence animal movements (Ricketts 2001, Adriaensen et al. 2003, Beier et al. 2008). For example, Verbeylen and colleagues' (2003) ability to explain red squirrel (*Sciurus vulgaris*) movements with a resistance surface increased with complexity of land-cover data. However, the moderately complex landscape predicted the species' dispersal behavior better than the most complex resistance surface. In our study, 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 model explaining RCW prospecting behavior focused only on forest structure. Adding further environmental complexity to this model did not improve performance (Table 6).

RCW prospecting behavior was best explained by the model developed using environmental data from extra-territorial telemetry points recorded during forays of radio-tagged birds. Our study suggests that RCWs preferred to travel through forest stands with a tall canopy with minimal midstory vegetation and a slightly positively skewed distribution of vegetation heights. These environmental characteristics closely correspond to features of preferred foraging habitat, with which juveniles would have experience on their natal territories. RCWs prefer to forage in canopy trees at least 20 m tall and greater than 60 years old (Rudolph et al. 2002, Walters et al. 2002), and tend to avoid longleaf pine trees less than 30 years old and 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 14). Foraging RCWs also avoid hardwood vegetation and breeding pairs abandon sites with encroaching midstory (Hovis and Labisky 1985, Wood et al. 2008). Our data suggest that the probability of detecting a prospecting individual sharply dropped as percent midstory vegetation increases and that even a small percentage of midstory cover influences RCW movements (Figure 15).

RCW habitat quality is related to a complex set of forest structure characteristics and is difficult to represent with a single variable (Walters et al. 2002). Along with canopy height and midstory cover, RCW prospecting behavior was also related to the skewness of the overall distribution of vegetation heights. The best Maxent model suggested that prospecting RCW are located in forest with a positively skewed vegetation height distribution (Figure 14). The positively skewed distribution matches the characteristics of mature longleaf pine forests with a low density of points consistently hitting the tall sparse canopy of longleaf pine trees while the majority of the points reach the herbaceous understory.

Most studies that have converted habitat suitability into friction values have used a single transform 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 suggest that a non-linear relationship between habitat preference and friction values is a better predictor of prospecting behavior than linear transformation. Specifically, the moderate

rescaling constant (c = 4) had overwhelming support (ω = 0.70) and the model using this conversion was twice as important as the next ranked model with a more extreme rescaling constant (c = 8, ω = 0.29; Table 6). The sensitivity between habitat suitability models and friction values provides insight into RCW reaction to landscape features during prospecting movements. For example, RCW prospecting movements may be slightly impeded by environmental factors such as percent midstory cover even in high quality environments (Figure 15). The resistance surface's smallest friction values are typically assigned to the entire habitat patch without evaluating if the habitat quality varies throughout the patch. Our study suggests that even within high quality habitat there are environmental cues that could impede movements. More complex dispersal models that incorporate data other than general habitat type may be more suitable in these situations.

4.6.2 MODEL COMPLEXITY FOR SFS

For all four movement models, the predicted probabilities of dispersal among sites within the same drainage were highly (and statistically significantly) positively correlated with observed dispersal fractions from the capture-mark-recapture data (Figure 36, Table 7). No marked butterfly was observed to move between drainages, and the model-predicted probabilities of such movements were zero. The estimated correlation between observed and predicted dispersal fractions was highest for the FS model (the most complex model) and lowest for the DO model (the least complex model). However, the three less complex models produced correlations that were only very slightly lower than, and fell well within the 95% confidence interval for, the correlation produced by the FS model. Similarly, the log likelihood was highest for the FS model and lowest for the DO model, but the likelihoods of the three simpler models were only slightly lower than that of the FS model. Discounting these log likelihoods for the number of parameters in each model, the DO model emerges with the lowest AICc value. Thus a strict parsimony approach based on the available CMR data favors the simplest model.

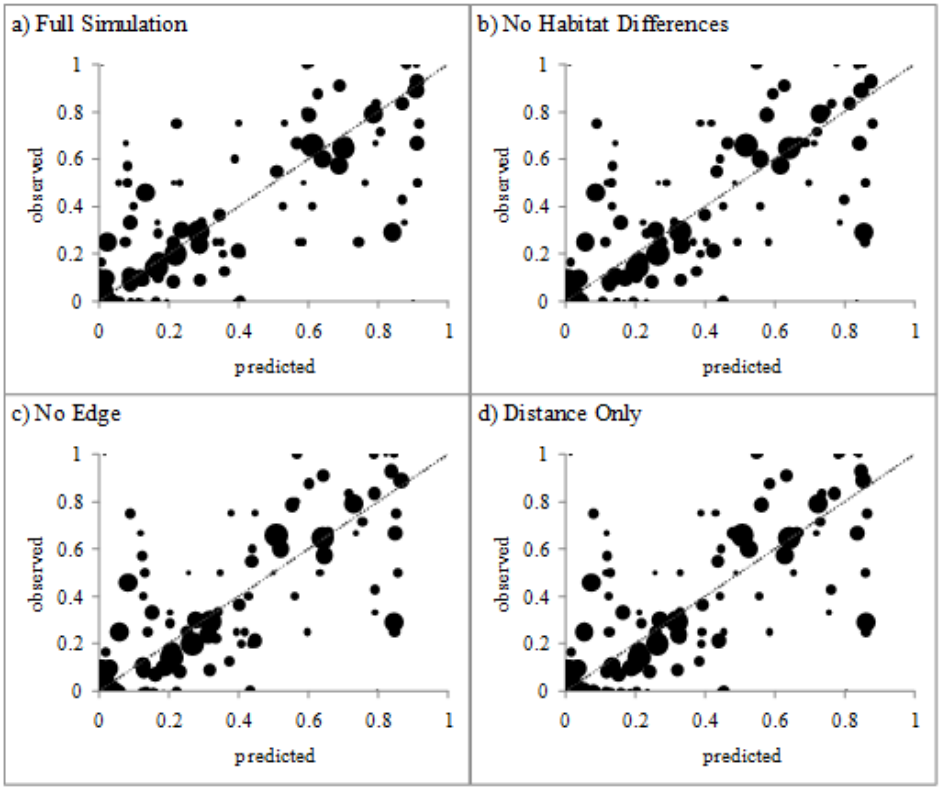

Figure 36: Scatter plots showing predicted and observed dispersal rates between paired surveyed sites in the capture-mark-recapture study (all years combined). Each point represents the fractions of simulated and observed marked SFS dispersing between a pair of surveyed sites, including SFS resighted in the same site where they were originally marked, during a single flight period. The size of the point indicates the number of SFS marked in the breeding site (range 1-35).

Table 7: Measures of fit and cost for simulation models of differing complexity. "Correlation" gives the Pearson correlation coefficients (with 95% confidence intervals) between the observed fractions of recaptured SFS moving between specific pairs of origin and destination sites in the CMR study and the probabilities of dispersal between those site pairs predicted by the four movement models. All correlations are significantly greater than zero (one-sided test, P< 0.001). Log likelihood is for a multinomial model.

	Full Simulation	**No Edge Effects**	**No Habitat Differences**	**Distance Only**
Correlation	0.824	0.813	0.816	0.811
Log Likelihood	-357.445	-361.027	-359.621	-364.643
No. parameters	28	22	13	7
AICc	775.24	768.72	746.18	743.57
Marginal costs (U.S. dollars)	10,600	5,800	7,000	2,200

The landscape immediately surrounding existing breeding sites has very little open habitat, so incorporating the behaviors we have estimated in this habitat and at boundaries between open and the other types of habitat into the FS, NE, and NDH models did little to improve their fit to the CMR data relative to the DO model. However, establishing new SFS breeding sites in the proposed restored wetlands would put some butterflies in closer proximity to open habitat. Consequently, we compared the dispersal predictions among models for the modified future landscape with restored wetlands.

As observed in the landscape without the restored wetlands (spatial maps not shown), for the simulations with restored wetlands, all models predicted little or no dispersal between habitat patches separated by more than a few hundred meters, such that SFS is predicted to occupy a collection of isolated networks containing one or a few nearby breeding sites (Figure 37). However, at a smaller scale, predicted dispersal distances and routes differed among models. The DO model (without boundary behaviors or habitat-specific movements) predicted the furthest distance traveled from breeding sites, with dispersal paths extending out to 480 m from breeding sites. Dispersal patterns predicted by the NHD model (with boundary behaviors only) were generally similar to those of the DO model. In contrast, dispersal paths in the FS model (with both boundary behaviors and habitat-specific movements)did not extend beyond 360 m from sources. The NE model (habitat specific movement rules but no boundary behaviors) predicted dispersal patterns similar to those of the FS model.

Models differed in predicted dispersal rates between the established SFS populations and nearby proposed restoration sites. The DO model predicts relatively high dispersal among proposed restoration sites and that most of these sites will be linked to established SFS populations, while the FS model predicts relatively low dispersal among proposed restoration sites, with three sites completely isolated from any other breeding site, and no dispersal between restored and currently occupied sites (Figure 37). Incorporating habitat effects on movement behaviors leads to the greatest reduction in dispersal among most sites, while boundary behaviors act to isolate sites separated by open areas or roads (Figure 37).

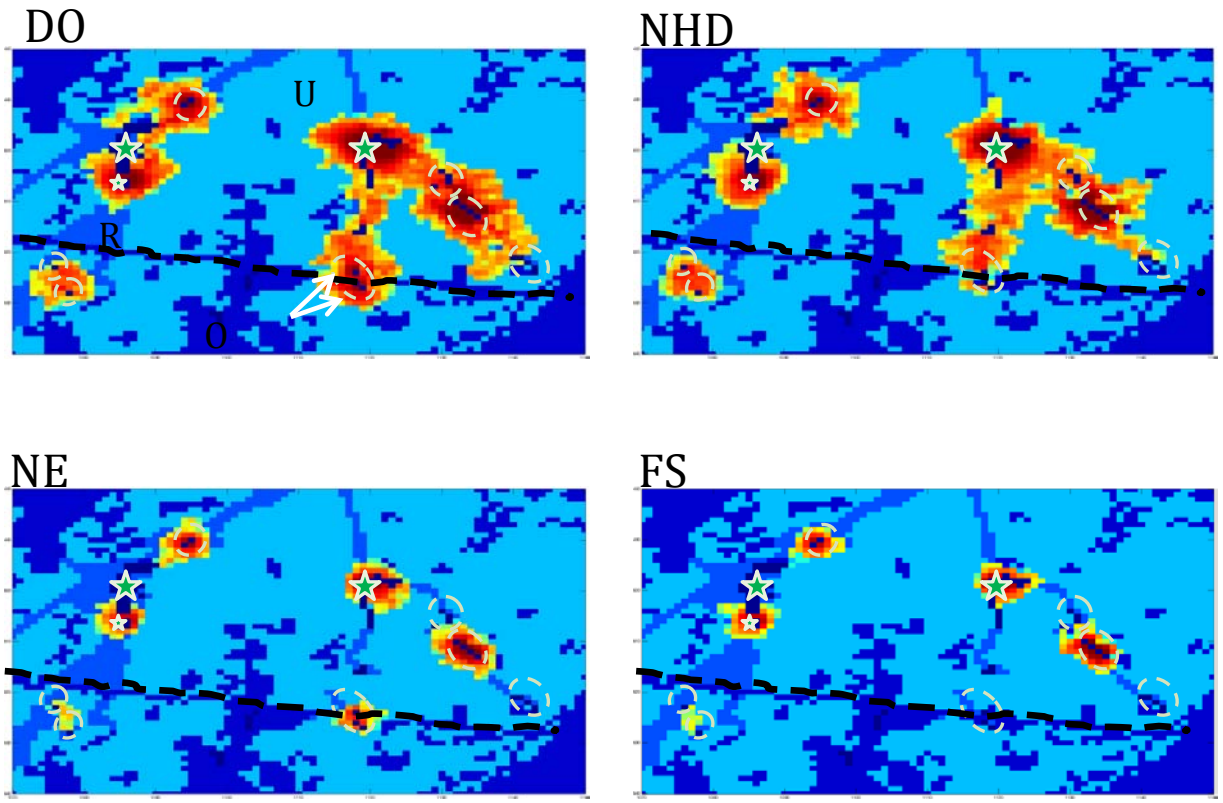

Figure 37: Predicted dispersal on the managed landscape with added restoration sites. Each panel shows a heat map indicating the frequency at which a cell was crossed during simulated dispersal among existing breeding sites (green stars) and proposed restored breeding sites (dark blue rectangles within dashed ovals) for the four movement models. Each pixel represents a 30 × 30 m cell. Color indicates the relative number of times a cell was crossed during successful moves between breeding sites (existing or restored); warmer colors indicate more frequent use. Except for breeding sites, areas shaded blue were not used by simulated butterflies, and different shades of blue indicate the habitat type of the cell: upland forest (lightest hue, indicated by "U" in upper left panel), riparian corridor (next darkest hue, indicated by "R" in upper left panel), or open habitats (two darkest hues, indicated by "O" in upper left panel). The dashed black lines indicate a dirt road running between a pair of restored sites in the lower left of the panels from existing sites above them and between a pair of restored sites in the lower right of the panels (indicated by white arrows in the DO panel).

Since the simulations of the landscape with restoration sites show that more complex models may indicate barriers to dispersal that simpler models miss (Figure 37), it is worthwhile to assess the financial cost effectiveness of increasing model complexity, which we did by comparing the ability of the models to predict the CMR results to the marginal cost of estimating model

parameters (Figure 38). Even though the gain in fit (measured by either the correlation or the log likelihood) is small, the marginal cost of achieving that gain is also relatively modest. Moreover, there is no sign of diminishing returns, as would be indicated by a plateau in fit with increasing marginal cost. Importantly, because we can only assess model fit on the landscape without restoration sites on which the CMR results were obtained, the cost effectiveness of constructing more complex models may be higher than this analysis indicates, if it turns out that the more complex models accurately predict that open habitat will pose a barrier to dispersal between restored and current breeding sites (which can only be evaluated after the restoration has been completed).

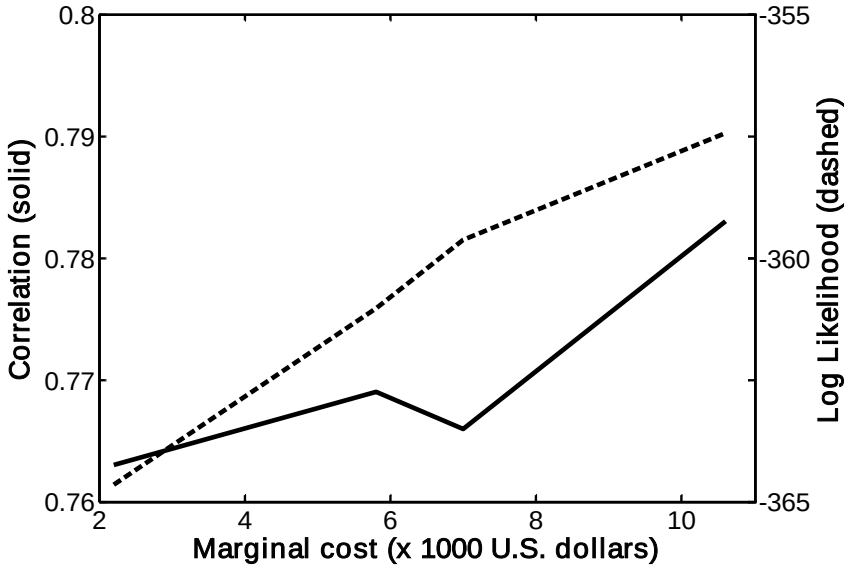

Figure 38: Measures of model fit vs. the marginal cost of collecting more data to parameterize more complex models.

We obtained different answers to the question "how valuable is it to construct more complex models of dispersal through matrix habitats?" depending on how value was assessed. From a strict parsimony viewpoint, the small increase in the ability of more complex models to predict the capture-mark-recapture (CMR) results was negated by the substantial increase in the number of parameters that had to be estimated before those models could be used. Thus an information criterion approach using the CMR data favors the simplest model we examined. However, when we applied the models to a landscape that had been modified relative to the one on which the CMR study was performed, our results suggest that the simplest model may fail to identify an important barrier to dispersal, namely a strip of open habitat where a road separates some of the proposed restoration sites from other breeding sites (Figure 37). Finally, we found that, although the gain in fit to the CMR data with increasing complexity was small, so was the increase in financial cost, and greater fit continued to accrue with greater financial cost, suggesting that constructing more complex models might be justifiable on financial grounds. In the following

paragraphs, we discuss the apparent conflicts between these different views of the conservation value of more complex movement models.

The mismatch between the values of complex models that we found when we assessed value in different ways is best understood in terms of the conflict between what is practical and what is desirable when managing rare species. We conducted our CMR study using every known, easily accessible breeding site for SFS, an extremely rare butterfly with a highly restricted geographical range. Because dispersal of SFS out of its breeding habitat (wetlands) is extremely limited, the marked butterflies in the CMR study only "sampled" a limited proportion of the landscape, specifically the region located very close to the existing breeding sites. That region happens to have low representation of "open" habitat, as we have classified fields and roads. Movement of the surrogate species (Appalachian browns) was very different in open habitats, and individuals were reluctant to move into the open when released at the boundary between open and other types of habitats (Kuefler et al. 2010). Nevertheless, those details are irrelevant if butterflies rarely encounter open habitat, as was the case for the marked butterflies in the CMR study, and thus adding complexity to the model by allowing it to account for the consequences of rare encounters with open habitat is difficult to justify solely on the basis of a model's ability to predict the CMR results in a parsimonious way. An alternative approach to our CMR study which might have more power to identify the value of complex models would be to capture and mark butterflies in the breeding habitat, release them in other locations where they would be forced to move through a variety of habitats - including open habitat - while searching for a breeding site, and attempt to recapture them at known breeding sites. However, as individuals moved from their preferred habitat to less preferred matrix habitats may suffer higher mortality, performing such an experiment with an extremely rare butterfly cannot be justified on ethical grounds.

The locations of existing breeding sites restrict the types of matrix habitats butterflies "see" when they explore the neighborhood surrounding those sites. However, establishing new breeding sites in restored wetlands is a desirable goal in the management of SFS, given that the current number of breeding sites is very low, threatening persistence of the metapopulation (and thus the subspecies). The most suitable locations for those restored wetlands would put them in closer proximity to habitat types, notably open habitat, that are rarer in the vicinity of existing breeding sites. Moreover, several of the proposed restoration sites are completely separated from existing sites by a strip of open habitat (a road; Figure 38).

Our results suggest that it may be dangerous to base decisions about which potential restoration sites to use solely on the simpler movement model, even if it explains more parsimoniously the CMR results. In particular, more complex models that incorporate documented responses of butterflies to open habitat predict that restoration sites separated from existing breeding sites by open habitat may experience only very rare exchange of dispersers with existing sites. If the goals of restoration are not only to increase the number of local populations but also to increase connectivity between them, either to enhance genetic exchange, to allow recolonization of both original and restored breeding sites where the local population has gone extinct, or simply to increase the chance that restoration sites are colonized naturally once they are established, more complex models make different, and perhaps more justifiable, recommendation about locating restoration sites than does the distance-only model.

For management of SFS, if enhancing connectivity is an aim of restoration, the complex models suggest either that potential sites not separated by open habitat from existing sites should receive higher priority for restoration, or that open habitat that currently isolates some potential restoration sites should be reduced or eliminated (e.g., by rerouting roads) as those sites are restored. It is important to note that even in the vicinity of the proposed restoration sites, open habitat represents a relatively small proportion of the landscape (although a larger proportion than in the neighborhood of existing sites). Nevertheless, the strong behavioral aversion to open habitat that we have documented in earlier work (Kuefler et al. 2010) suggests that it may be disproportionately valuable to include such behaviors when predicting dispersal on novel landscapes.

Our results also indicate that an important component to deciding whether or not additional complexity is required to accurately model dispersal is an understanding of the match between the spatial scale of dispersal and the spatial scale of landscape heterogeneity. For example, limitations on SFS dispersal distances imposed by habitat-specific movement behaviors (reduced dispersal in the NE vs. the DO model; Figure 38) occur at a smaller spatial scale than do limitations imposed by boundary behaviors (reduced dispersal between the NHD vs. the DO model; Figure 37). Furthermore, neither type of additional model complexity should be expected to inform predictions of dispersal between drainages given the current, sparse distribution of breeding sites on the landscape; for any movement model, such long-distance dispersal is effectively non-existent. Complex movement models may, however, be better predictors of SFS dispersal among breeding sites in areas that are currently inaccessible to us (due to unexploded ordinance) where breeding sites are separated by smaller distances, or of past SFS connectance when breeding sites were more common on the landscape.

4.7 MULTI-SPECIES INTEGRATION

4.7.1 EVALUATING MODELING STRATEGIES

Clear differences in predicted dispersal habitat use emerge when comparing our most sophisticated individual-based models for SFS and gopher frog to models fit with Circuitscape (Figure 39). Circuitscape models link all populations on the landscape by dispersal, whereas our individual-based models suggest that these species have limited dispersal ability. Our results suggest that Circuitscape may not be an appropriate modeling framework for organisms of low vagility unless a maximum dispersal distance threshold is specified *a-priori*.

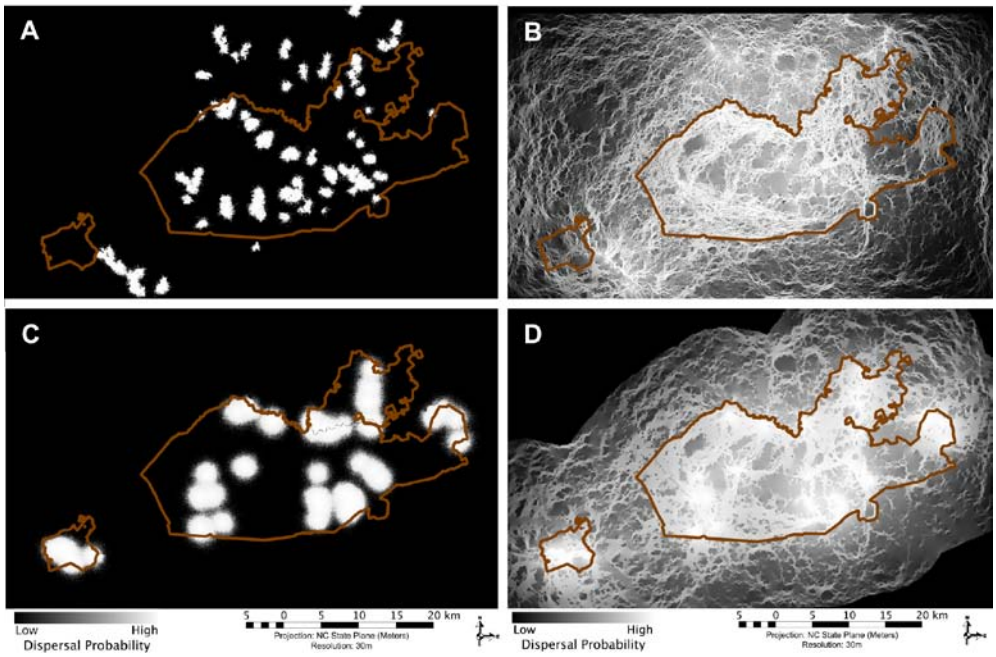

Figure 39: Comparing dispersal habitat use between individual-based models to those generated by Circuitscape. A. Dispersal habitat use for SFS based on the most sophisticated individual-based model and predicted habitat. B. Circuitscape model for SFS. C. Individual-based model for gopher frog using predicted habitats. D. Circuitscape model for the gopher frog.

The connectivity of a landscape for species of management concern depends on both the distance between potential breeding sites and the habitats forming the intervening matrix. We find that various methods for predicting dispersal perform differently depending on what aspect of dispersal is under consideration, but that only movement simulations can fully inform managers about both potential dispersal distances and habitat influences on where dispersers are likely to travel. Exponential decay models may be used to predict the distance threshold beyond which dispersal is highly unlikely, and fit quite well the decline in simulated movement paths with distance (r^2=0.988 for SFS). However, distance models alone cannot account for the influence of riparian habitats in enhancing (for SFS) or inhibiting (for chorus frogs) dispersal (Vogel and Haddad 2010, Leidner and Haddad 2010).

Our approach of combining displacement rates with edge behaviors represents a major step forward in developing methods to parameterize circuit models using field data that are feasible to collect. Nevertheless, even when parameterized with field data as we have done here, circuit models make different predictions about how diverse habitats influence dispersal than do our models explicitly simulating movement behaviors on the Fort Bragg landscape for SFS and amphibians. Both models agree that open habitats close to source patches are used relatively rarely by both SFS and frogs, and that riparian habitats are relatively frequently used by dispersing SFS. However, movement simulations predict increasing use of upland habitats and increasing avoidance of open areas by dispersing frogs as they move further from source patches (Figure 35), while circuit models predict a decreasing influence of habitat differences with distance (all lines converge to and then vary around unity in Figure 40).

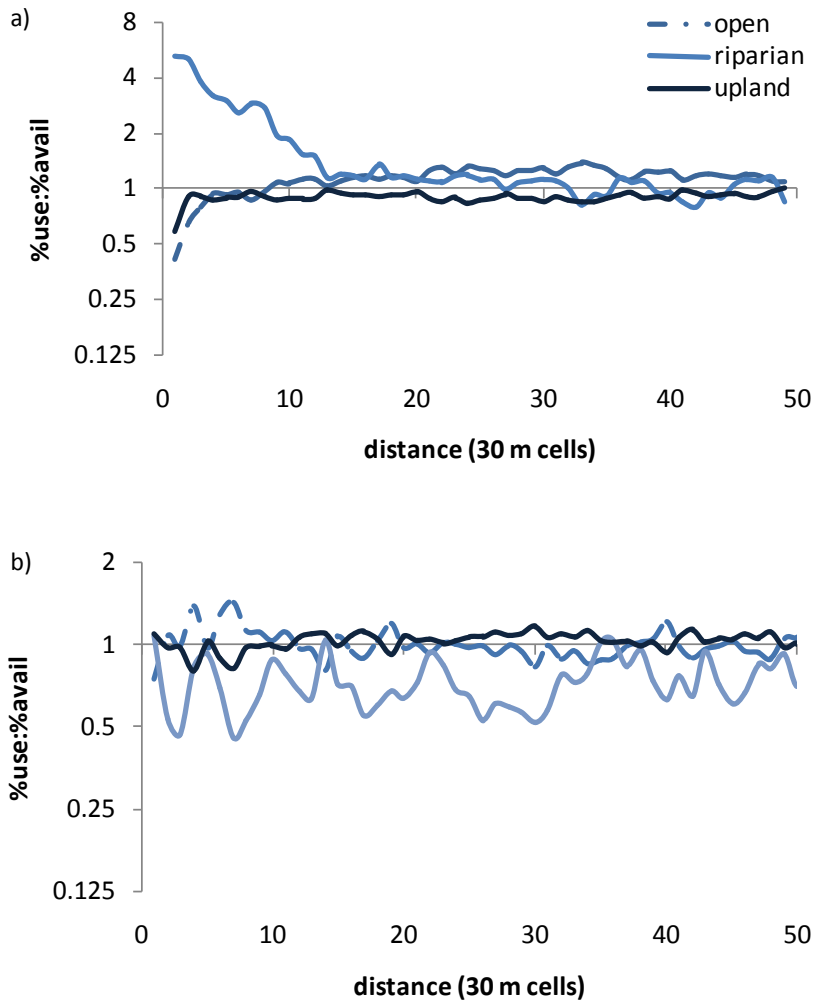

Figure 40: Ratio of relative use predicted by Circuitscape to availability of major habitat types vs. distance from source for simulated a) SFS and b) ornate chorus or Carolina gopher frogs. Distance is measured as the minimum number of cells a disperser would have to cross to reach the focal cell from its point of origin.

4.7.2 Synergies and Tradeoffs

Comparing our most realistic dispersal models on Fort Bragg proper shows that there is relatively little congruence between core dispersal areas for our target species (Figure 41). This reflects differences in the habitat requirements of species and their dispersal behavior. Our models of Saint Francis Satyr dispersal suggest that there is little dispersal between wetland complexes. Our amphibian models suggest that, although there may be substantial use of upland habitats within 1.5km of breeding sites for at least one species (Carolina gopher frog), dispersal between breeding sites that are spatially disjunct is predicted to be rare. In contrast, our models (and long-term mark-recapture data) show that RCW clusters are connected by frequent dispersal throughout Fort Bragg.

Because it is so extensive, RCW dispersal habitat would provide an "umbrella" for the other species in a few areas if all RCW dispersal habitat were to be protected or managed. There is some overlap between predicted amphibian dispersal habitat, and RCW dispersal habitat in the Macridge Impact Area, along Preachers Road, and near Area O (Figure 42, blue-green shading in Figure 41). In addition, there is a small area that may be important for both RCW and SFS dispersal to the west of Mac Ridge Road (Figure 42 and yellow shading in Figure 41). Despite these small areas of overlap, focusing on the most important dispersal areas for RCW will not capture the most important dispersal areas for the other species. We anticipate that core dispersal areas for the different species can be managed essentially independently in most areas of Fort Bragg.

We identified few spatial tradeoffs in habitat management for connectivity between species. SFS dispersal habitats, located along drainages with extensive hardwood floodplains, are areas that present some barrier to RCW dispersal, but because these areas are small relative to the amount of RCW dispersal habitat, we anticipate no significant decrease in RCW connectivity with habitat management or restoration for SFS. Upland habitats managed for amphibian dispersal can also promote dispersal of RCWs, so we anticipate little management tradeoff in areas that are important for the dispersal of both RCW and amphibians. Although SFS and our target amphibian species inhabit wetlands, habitats for SFS are spatially segregated from important amphibian breeding ponds. The limited dispersal ability of these species means that there are few potential synergies or tradeoffs in habitat management between SFS and the target amphibian species.

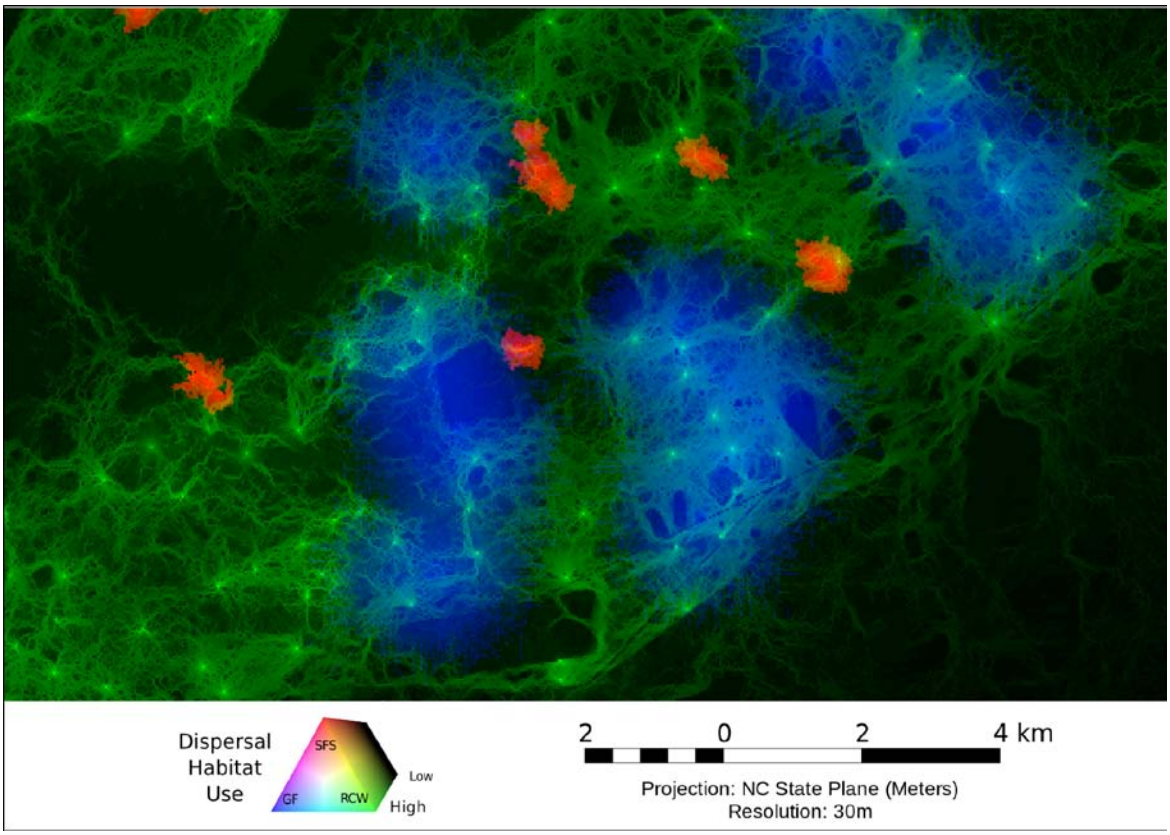

Figure 41: RGB composite of dispersal habitat use on Fort Bragg for our target organisms, Red-cockaded Woodpecker (RCW, green) Carolina Gopher Frog (GF, blue), and Saint Francis Satyr (SFS, red). High luminance (brighter colors) represents relatively higher dispersal habitat use. Habitat use maps are based on the most sophisticated model for each species incorporating conservative assumptions about dispersal times and distances. Full base extent not shown for data security reasons. See text for additional details.

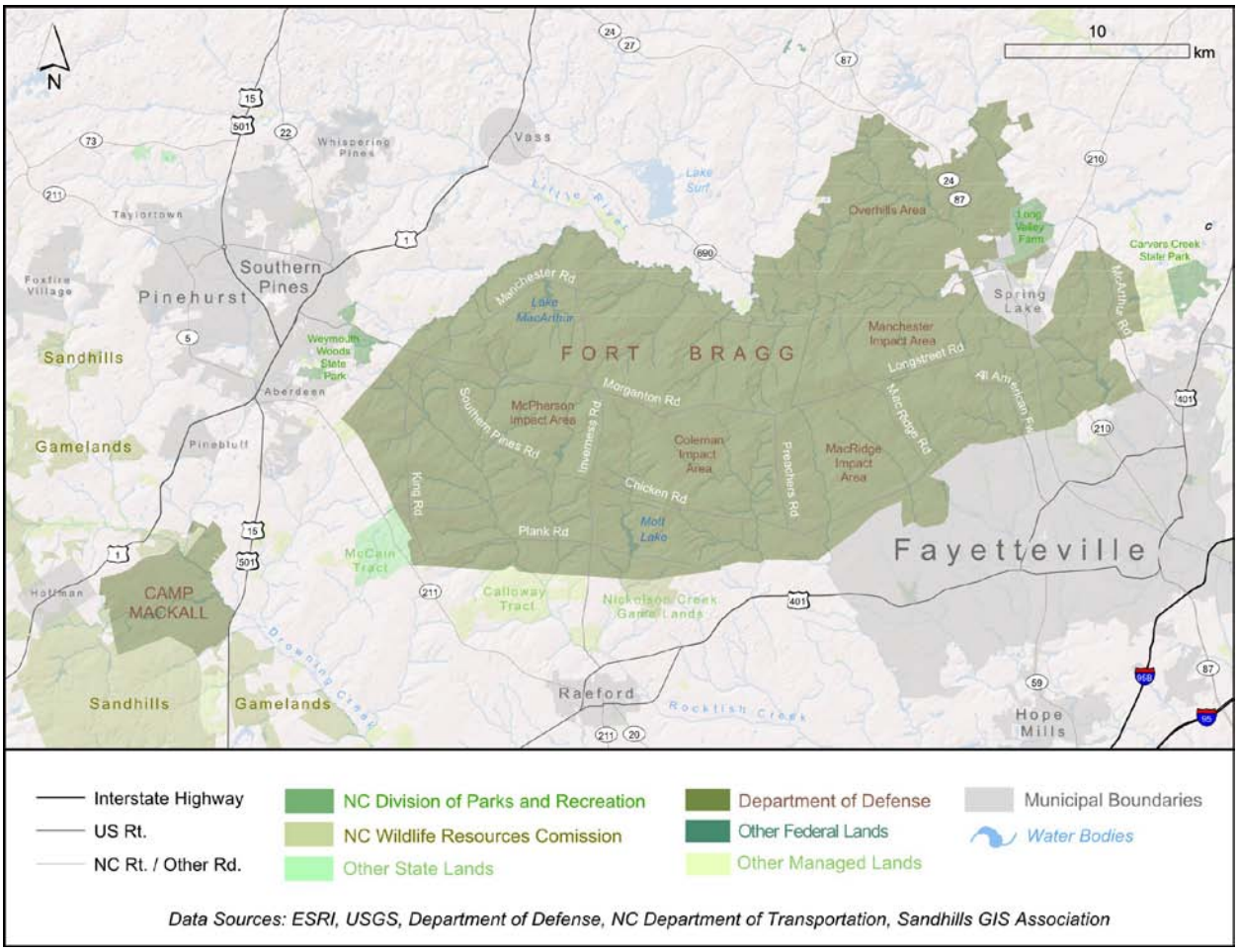

Figure 42: Reference map for specific locations mentioned in Sections 4.7.2, 4.7.3 and 4.7.4.

4.7.3 ZONATION CONSERVATION PRIORITIES

When we used the Zonation algorithm to prioritize areas on Fort Bragg according to their connectivity value across all of our target species, the highest priority areas were in the immediate vicinity of RCW clusters, in the immediate vicinity of wetlands where SFS occurs, and in areas surrounding amphibian-breeding ponds (43). Because Zonation produces a rarity-weighted ranking of all areas, dispersal habitat for SFS and Amphibians are prioritized above most dispersal habitat for RCWs because habitat for these species is less prevalent.

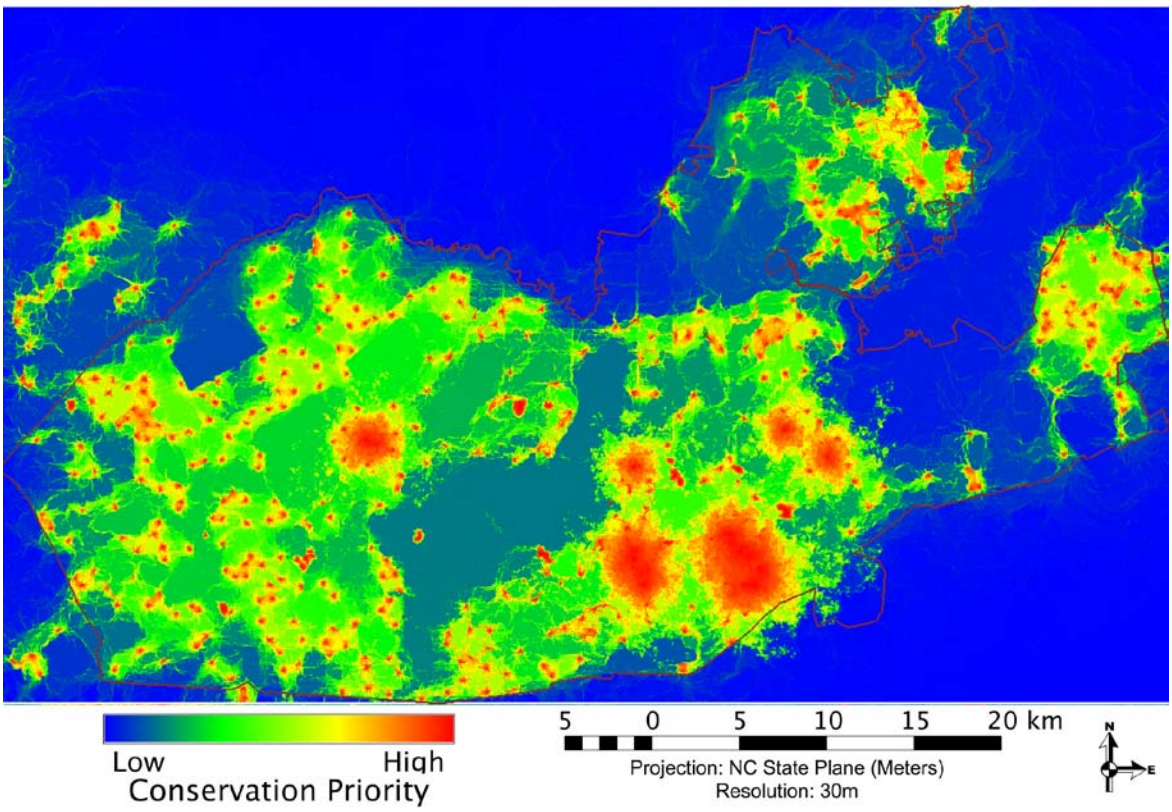

Figure 43: Multi-species dispersal habitat conservation priorities on Fort Bragg from a Zonation run that weights each species equally. Inputs are the most sophisticated dispersal models based on known populations and conservative dispersal assumptions.

4.7.4 OFF-INSTALLATION CONSERVATION PRIORITIES

A major result of this study is that populations of SFS and the target amphibians have limited vagility and probably do not frequently disperse off of the installation itself from known populations. This conclusion is subject to two major types of uncertainties. First, the survey techniques that are used to detect these species are imperfect. Survey effort has been unequally distributed across public and private lands in this region, and there may be populations of the target organisms that have not yet been detected. Second, parameters that describe total daily activity times and maximum step lengths are highly uncertain in even our best dispersal models. As a result, there may be off-installation areas that contain undiscovered populations of our target organisms or are important for infrequent, long-distance dispersal.

To deal with these uncertainties, we developed alternative dispersal models for our target species that are based on predicted, not actual habitat, and that have somewhat relaxed assumptions about total activity times and dispersal distances. These models were developed for a spatial window that incorporates all lands within a 5km buffer around Camp Mackall and Fort Bragg. Because distributional data for RCWs is considered to be quite complete, we have not used predicted habitat for this species.

The map below (Figure 44) shows an RGB overlay of potential dispersal habitat use for RCWs (green), Carolina Gopher Frog (blue) and SFS (red) based on modeled habitat with relaxed

assumptions regarding dispersal abilities of the target organisms. This analysis shows that there is some potential for dispersal habitat use by all three species along Drowning Creek east of the boundary of Camp Mackall, south of Lake Bay Road along the northern boundary of Fort Bragg, and southeast of Long Valley Farm (Figure 42 and 44). Areas near the southern base boundary north of Cliffdale Road as well as near the eastern Fort Bragg boundary near McArthur Road may be dispersal habitat for both RCWs and amphibians (Figure 42 and 44). Because of the high degree of uncertainty involved in basing dispersal models on distribution models, these results should be interpreted with care.

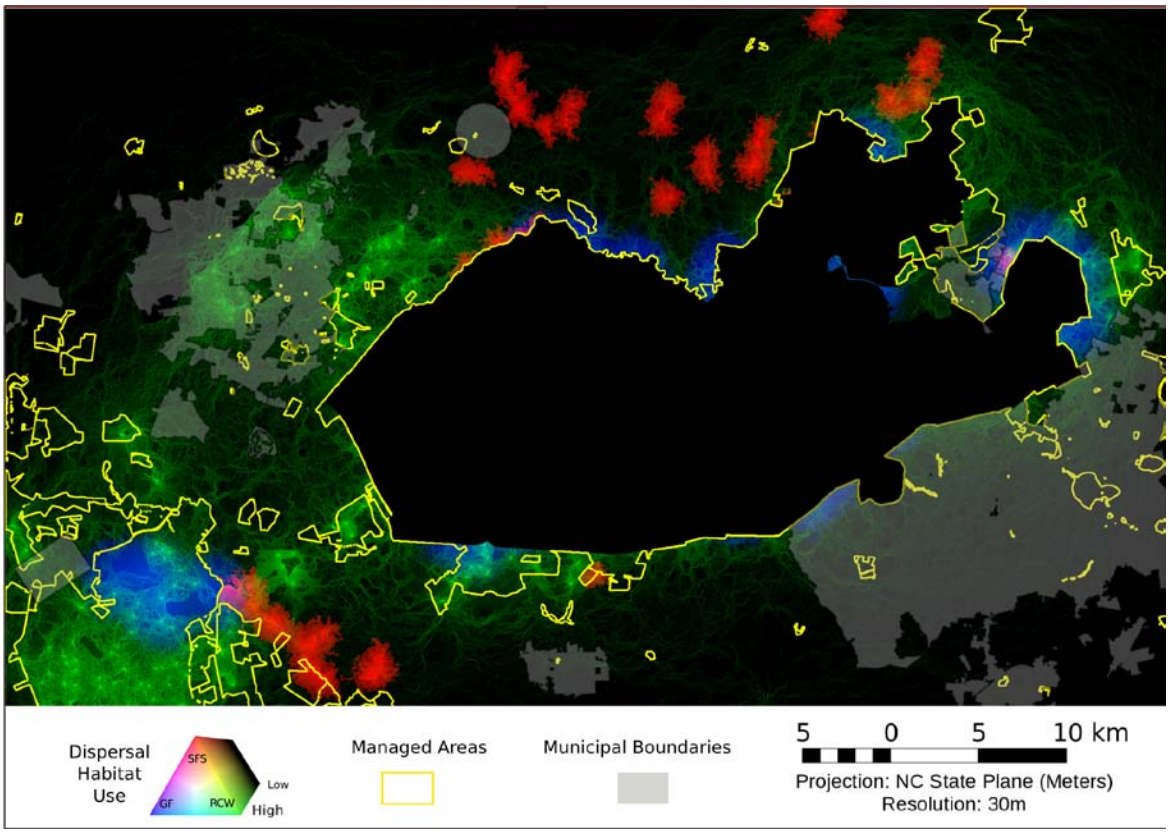

Figure 44: RGB composite of dispersal habitat off of Fort Bragg for our target organisms, Red-cockaded Woodpecker (RCW, green) Carolina Gopher Frog (GF, blue), and Saint Francis Satyr (SFS, red). High luminance (brighter color) represents relatively higher dispersal habitat use. Habitat use maps are based on the most sophisticated model for each species incorporating predicted, as well as known habitats and relaxed assumptions about dispersal times and distances. See text for additional details.

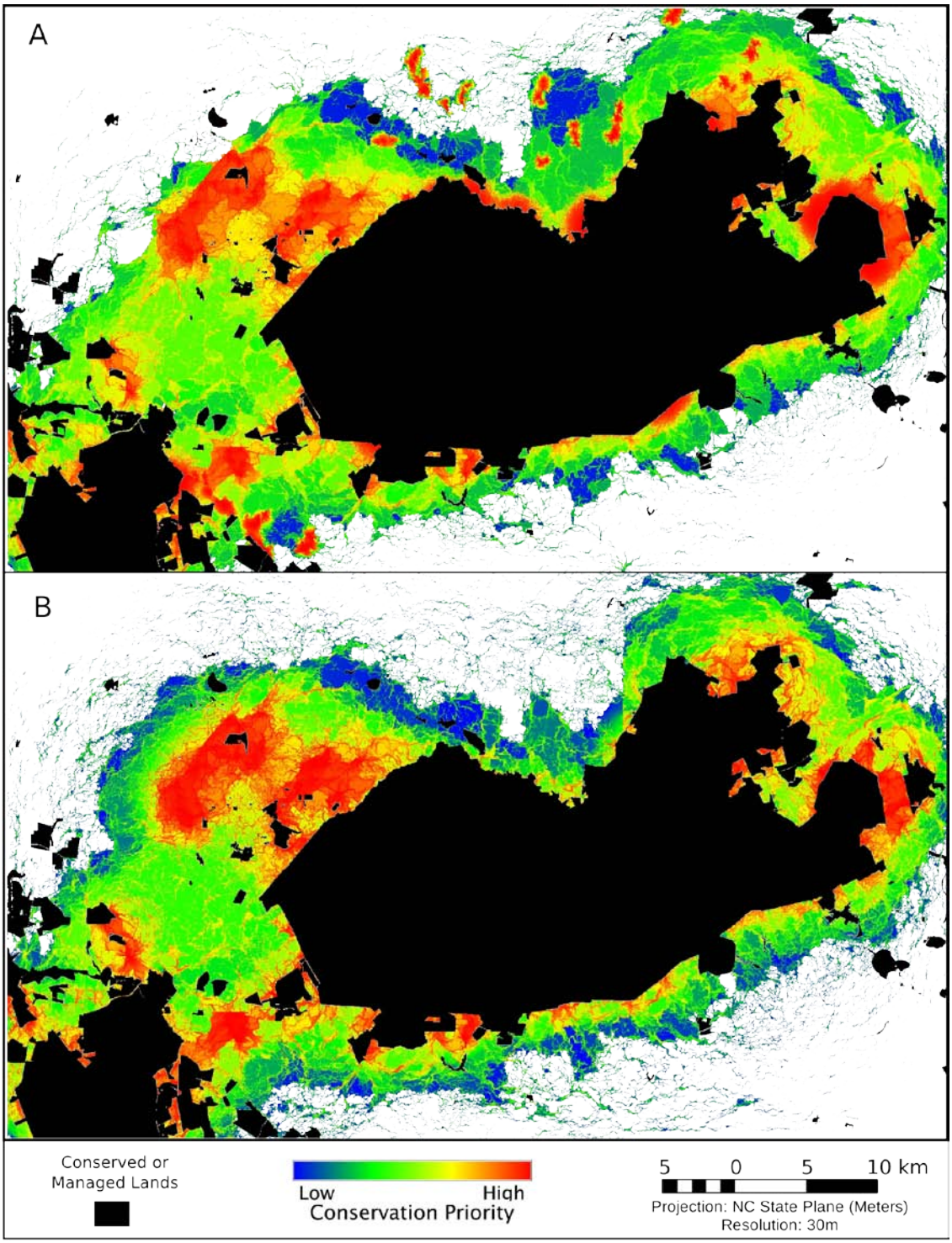

Figure 45: Zonation-based connectivity conservation priorities for all the species considered (A) and Red-cockaded Woodpecker only (B). Details in the text.

Because conservation land-acquisition efforts on private lands have historically targeted areas thought to be important for RCW dispersal, we wanted to see how including other species into connectivity assessments might change which private lands are considered the most important targets for connectivity conservation. Our dispersal models based on predicted habitat allow us to answer this question. Figure 45 compares Zonation-derived conservation priorities across all species (A) to conservation priorities for RCWs only (B) on private lands that are not managed explicitly for wildlife. The maps are similar, but a few key differences emerge when we compare the top ten percent of the landscape for the two scenarios (Figure 46). This shows that the RCW-only conservation priority map neglects riparian areas predicted to be SFS dispersal habitat along Drowning Creek and its tributaries, and drainages to the north of Fort Bragg, as well as some areas along the base boundary that are predicted to be dispersal habitat for amphibians, including several areas near the town of Spring Lake and suburban Fayetteville that are highly suitable for residential and commercial development (Figure 42 and 46).

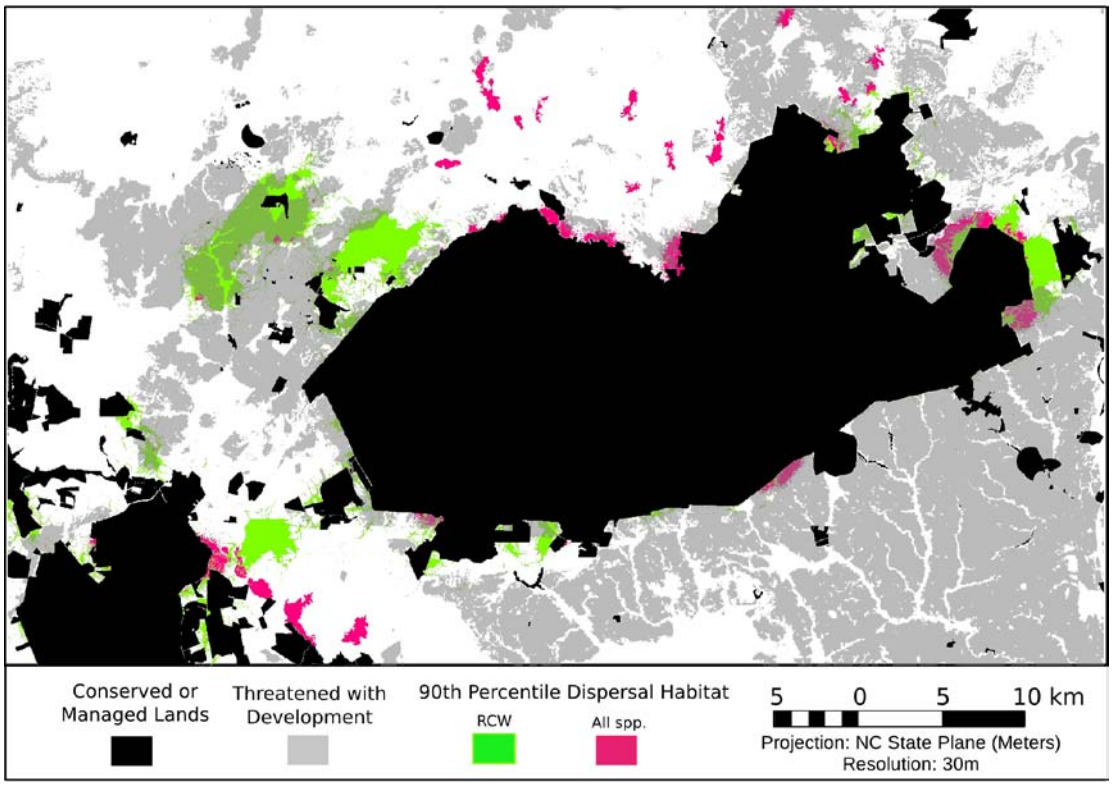

Figure 46: Highest-priority dispersal habitats on unprotected private lands for RCW-only (green), and the most important habitats across all species (pink). Highest priority areas are the top 10% of the landscape selected by Zonation. Light grey areas are at risk of urban or suburban development. See text for additional details.

4.7.5 Development Scenarios

The most important dispersal habitats on private lands occur in areas that are highly suitable for commercial residential and industrial development as well as areas that are less suitable, as judged by the Sustainable Sandhills land-use suitability model and a 2100 urban growth scenario (47). Low priority dispersal habitat was slightly more common on lands that are not at risk of

development, and high priority dispersal habitat was slightly more common on lands that are at risk. This is due to the fact that most RCW dispersal habitat is located away from floodplains that limit human development. The dividing line where threatened areas begin having higher areal density than non-threatened is approximately the 40th percentile of conservation priority. Areas that were above this 40th percentile and were in development-threatened areas are excellent candidates for future conservation land acquisitions.

Our analyses showed a marked difference between areas that were high conservation priority and areas that were suitable for development. Based on conservation priority alone, the connections between the southwestern corner of Fort Bragg and northeastern corner of Camp Mackall are important dispersal habitat, but this area is at lower threat of urban development due to its distance from existing infrastructure. Important connectivity habitat that is at a greater threat of urban development is much more frequent in the vicinity of Southern Pines / Pinehurst and Spring Lake / Fayetteville. Additionally there are two sites north of Fort Bragg that are important based on the simulation results. These areas are key SFS habitat whose predicted habitat is most abundant north of Fort Bragg.

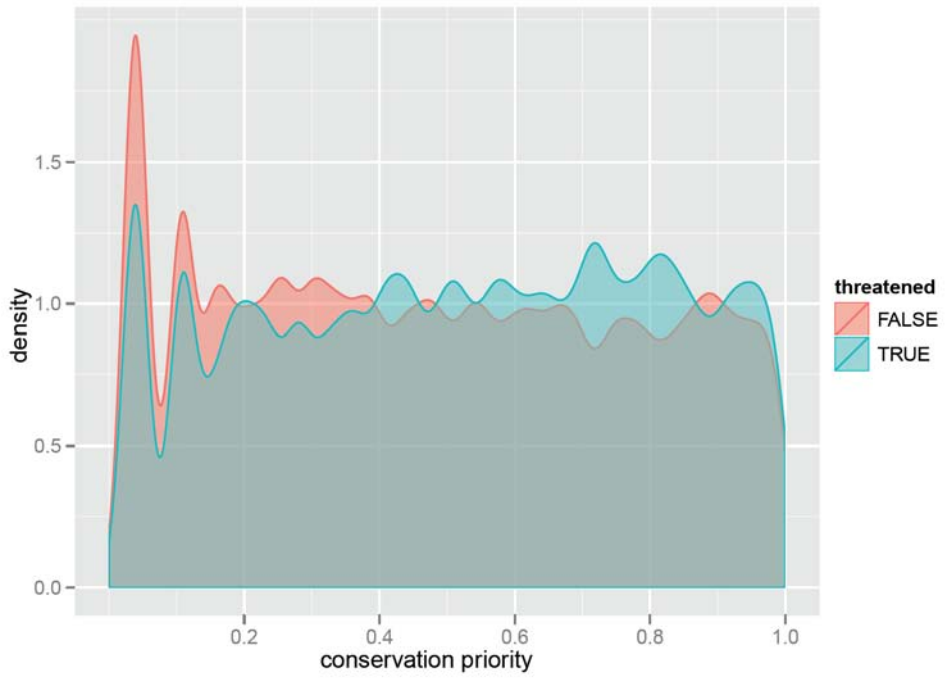

Figure 47: Density plot of conservation priority for areas predicted to be threatened and not threatened by urban development on private lands surrounding Fort Bragg and Camp Mackall. Conservation priorities are based on the full-extent uniformly weighted Zonation output using simulation models with relaxed assumptions.

4.7.6 ACCOUNTING FOR UNCERTAINTY

The dispersal models that we have generated for this project are subject to a variety of sources of uncertainty, and the model predictions reflect different underlying assumptions about the process of dispersal for the different organisms. Although a full accounting of uncertainties in the

empirical data, dispersal landscapes, model parameters, and model structure is not currently possible, we recognize that some of the largest uncertainties lie in the underlying distributional data and our assumptions about the maximum distances that organisms disperse during their lifespan. Because long-distance dispersal events occur infrequently, we are limited in our ability to make predictions about the process of long-distance dispersal from observations of routine dispersal events (Clark 1998). As an example, we can predict with some accuracy the territories to which juvenile RCWs are likely to disperse if they choose a destination territory within 6km of the source. Beyond 6km however, despite our new understanding of long-distance dispersal behavior resulting from the telemetry study, we are unable to predict the destination of dispersing RCWs from our models. Long-distance dispersers appear to be less affected by intervening landscape features, and we observed too few of them to be able to model their movements.

To deal with uncertainty in this analysis, we have developed two sets of dispersal models. One set relies on known populations of organisms and incorporates conservative assumptions about how far animals move. Another set of models relies on predicted habitats and incorporates relaxed assumptions about total dispersal distances and activity times. The differences in dispersal habitat use between these two sets of models give us some sense of how model uncertainty affects our major conclusions.

The "conservative" amphibian model, parameterized for the Carolina Gopher Frog, is based on known occurrences and assumes a total activity time of 30 days. The "conservative" SFS model is based on known occurrences and considers dispersal over 100 days with an activity time of six hours per day. The "conservative" RCW dispersal model, which is based on circuitscape, was constrained to a maximum dispersal distance of 6km. The "relaxed" amphibian model, parameterized for the Carolina Gopher Frog, is based on predicted occurrences and assumes a total activity time of 100 days. The "relaxed" SFS model assumes 10 hours of activity per day and no rest. The "relaxed" RCW model does not limit dispersal to 6km.

Figure 48 represents Zonation conservation priorities in the larger study area across all species. Dark colors represent areas with small absolute differences in rank between the conservative and relaxed scenario, while lighter colors represent areas with larger differences in rank, representing relatively greater uncertainty about their importance for preserving landscape connectivity across this suite of species. A high degree of uncertainty is present in areas where dispersal habitat use is hypothesized due to predicted occurrence of a single target species, such as predicted SFS habitat areas in drainages to the north of Fort Bragg.

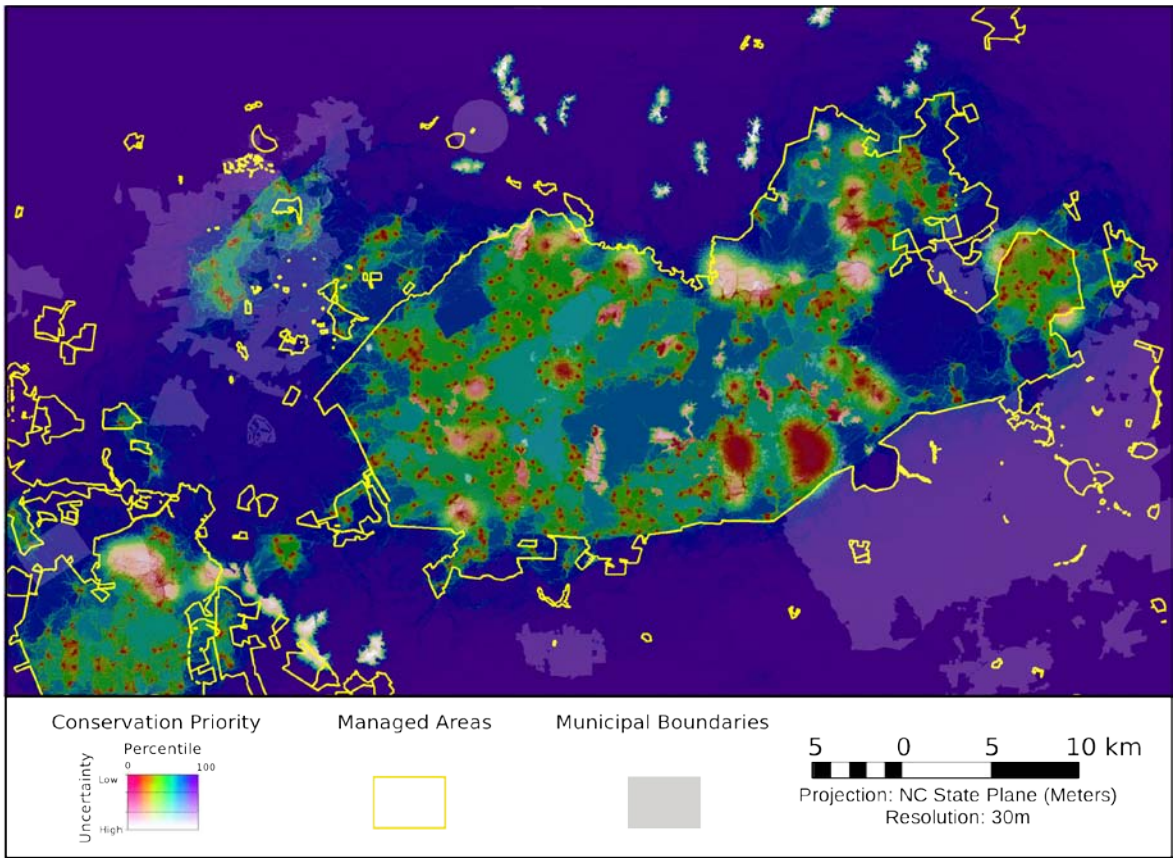

Figure 48: Connectivity conservation priority areas across all of our target species from a Zonation solution that uses our most sophisticated dispersal models with relaxed assumptions. Lighter colors represent areas with more uncertainty regarding dispersal habitat use (i.e. greater differences in conservation rank between predictions from conservative and relaxed dispersal models for each species. Details in the text.

4.8 THE CONNECT TOOLBOX

4.8.1 RATIONALE

As a major goal of this project, we aimed to provide wildlife managers with tools that they can use to better manage DoD lands for wildlife connectivity. The modeling strategies that we developed could be applied to imperiled species in many different contexts, however the potential barriers to implementing our most sophisticated dispersal models in new sites and new species are substantial: First, the individual-based dispersal models that we developed for this project are based on years of intensive field study and a large amount of data on both habitat requirements and movement behaviors of our target organisms. Wildlife managers need tools that they can apply based on the types of data that are more widely available. Second, our most complex models require substantial technical expertise to implement. In particular, because they are so flexible, individual-based models require users to directly program movement rules in software languages. Wildlife managers need tools that they can easily implement without specialized computing skills. Finally, these sophisticated models are often too computationally intensive to be run effectively on desktop computers in a reasonable amount of time. In order to

overcome these challenges, we sought to develop an alternative modeling strategy that addresses questions of interest to land managers and package it in a user-friendly decision support tool that could be used on and around DoD lands worldwide.

4.8.2 DEVELOPMENT

In order to be useful, any software tool must directly address the needs of its users. Because we wanted our tool to be useful to land managers and environmental planners on and around military bases, before beginning software development we held a series of meetings and workshops with members of the North Carolina Sandhills Conservation Partnership (NCSCP), a coalition of of public and private conservation stakeholders in the vicinity of Fort Bragg, North Carolina. NCSCP stakeholders included members of the Army Environmental Command, the Nature Conservancy, the US Fish and Wildlife Service, and others. During these sessions, held on January 20th and February 3rd 2010, we asked these stakeholders what questions the tool should address and how it could be used. According to our partners, the decision-support tool should:

- interface easily with ESRI ArcGIS, the dominant platform for processing geospatial data.
- provide a framework for prioritizing landscapes based on multiple criteria.
- allow planners to compare the impacts of alternative land-management scenarios.
- fit into an adaptive management framework that allows new data to be integrated as it becomes available.
- integrate with existing planning processes.

Early in project development, our team concluded that the individual-based modeling strategy that we were applying to our target species would be cumbersome to incorporate into a decision-support tool aimed at wildlife managers. To address the concerns of our stakeholders, we needed a computationally efficient strategy for modeling animal movements, a method for prioritizing landscapes based on connectivity value and other criteria, and a method for quantifying how changes to the landscape influence landscape connectivity that was comparable across species. After reviewing the existing literature we selected three existing modeling strategies that met our requirements. Circuit theory (McRae et al. 2006) provides a method to incorporate location data and habitat maps into simple, flexible models of animal movement. The Zonation algorithm (Moilanen et al. 2005) provides an elegant method to prioritize landscapes based on its value to multiple species while incorporating other criteria like development threat and acquisition cost. Lastly, network routing algorithms from graph theory (Urban and Keit 2001, Minor and Urban 2008) can be used to measure how changes in land use influence the overall connectivity of landscapes. We adapted and extended these existing tools (Figure 49) and incorporated them into a new geoprocessing toolbox for ArcGIS called CONNECT.

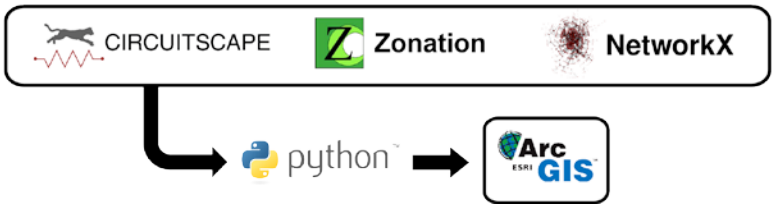

Figure 49: Existing software integrated into the CONNECT toolbox using the Python scripting language.

We have continued our close collaboration with SCP stakeholders throughout the development of CONNECT. The Nature Conservancy and AEC staff provided crucial feedback on early versions of the tools, and we are currently in the early stages of working with the Endangered Species Branch staff at Fort Bragg to implement the CONNECT tools for several other species of management concern outside of the target species.

4.8.3 THE CONNECT TOOLS

The overall work-flow of CONNECT is shown in Figure 50. The tools take as inputs geolocated records of a species occurrence and resistance maps that relate animal dispersal probabilities to land-cover information from forestry inventories or remotely sensed data. Resistance maps can be derived from animal behavior data in a variety of ways including statistical models of telemetry data, and / or expert opinion. Using this data and optional supplementary information, users can generate maps of relative dispersal density, combine these maps to prioritize landscapes for multiple species, and measure the effects of land-use change on landscape connectivity. Details of the operation of the CONNECT toolbox can be found in the CONNECT USER GUIDE and CONNECT TUTORIAL which are included in the appendices. Here we briefly describe the tools and some of the ways that the toolbox can be applied to problems of relevance to land management on and around DoD installations.

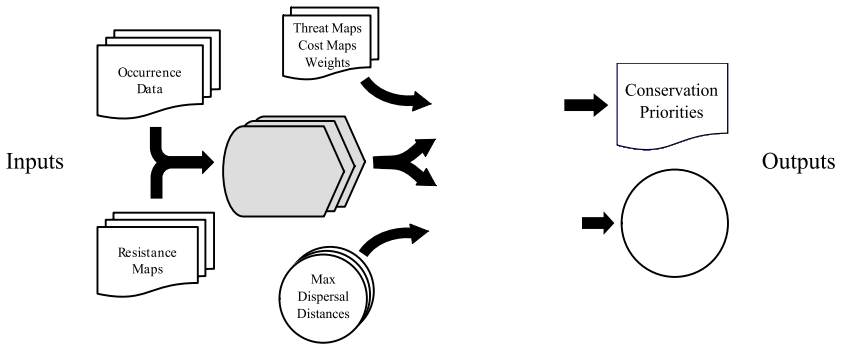

Figure 50: The CONNECT Tools

4.8.4 CREATE CONNECTIVITY MODEL TOOL

This tool models animal movements using Circuitscape, a Python package that implements circuit theory. Circuit-based dispersal models assume that dispersing organisms are analogous to

electrical current flowing over a landscape composed of conductors with various amounts of resistance, represented by a raster dataset. Circuit-based models can be considered an efficient analytical equivalent to simple individual-based models known as "biased random walk" models (McRae et al. 2008), and allow dispersal corridors and "pinch points", where animal movements are constricted to only a few possible paths, to be mapped quickly and effectively. These models also allow us to quantify the relative strength of connections between all habitat patches, based on their distance and the quality of intervening habitat. These assessments can be passed along to the Generate Landscape Network Tool for further analysis.

4.8.5 PRIORITIZE LANDSCAPE FEATURES TOOL

The Prioritize Landscape Features tool combines outputs from dispersal models for multiple species into a single landscape prioritization that ranks pixels or parcels according to their value across all species using the Zonation algorithm (Moilanen et al. 2005). Optionally, the tool also allows users to incorporate land acquisition costs and development threats into the prioritization.

4.8.6 GENERATE LANDSCAPE NETWORK TOOL

This tool uses network routing algorithms from graph theory (Minor and Urban 2008) to measure connectivity between habitat patches and evaluate the connectedness of landscapes for individual species. The tool connects each habitat patch to every other habitat patch with a connection (called an edge) that varies in strength according to the effective resistance between those two nodes. The tool then calculates the least cost path between all of the nodes. This path, often called the Minimum Spanning Tree, represents potentially important connections between habitat patches. The tool can also calculate summary statistics for each network that can be used to compare habitat management or development scenarios.

4.8.7 APPLYING THE CONNECT TOOLS

4.8.7.1 EFFECTIVE CONSERVATION

Our NCSCP partners recognize that using scarce conservation resources efficiently requires that we address four key considerations in prioritizing landscapes for the management of connectivity. First, decision-makers must base their decisions on robust assessments of the biological value of different parts of the landscape for target species. Effective conservation actions will address the parts of the landscape that are most valuable across all target species. Second, conservation goals can be achieved most efficiently when cost criteria are also included. Efficient conservation actions will target high-value areas that can be managed at the least cost. Third, threats to connectivity, including residential and infrastructure development, are higher in some areas than others. Conservation actions should target areas of rapid land-use change in order to protect important wildlife movement corridors. Finally, many conservation decisions, particularly voluntary land acquisitions, are by nature opportunistic. Any planning framework must allow decision-makers to take advantage of targets of opportunity. We are designing the CONNECT tools to incorporate biological value, cost, and threat criteria, and are promoting its use in an adaptive management framework.

Figure 51 shows how incorporating data on development threats can improve our ability to identify priority areas for the conservation of connectivity for multiple species. In the left-hand panel, parcels in part of the study area are ranked according to their connectivity value for all target species. The highest priority lands are large parcels between Fort Bragg (top-right) and

Camp Mackall (bottom-left). Incorporating a development suitability index from Sustainable Sandhills into the analysis shifts conservation priorities to adjacent parcels that are near existing areas of development (right-hand panel). These parcels have slightly lower connectivity value, but are under much greater risk of being developed for commercial or residential use than the parcels identified in the first analysis. Landscapes are dynamic, and we expect biological values, economic costs, and development threats to change over time. When using the CONNECT tools in the ArcGIS ModelBuilder framework, analysis can be saved and updated easily when new data on biological value, costs, or development threats become available.

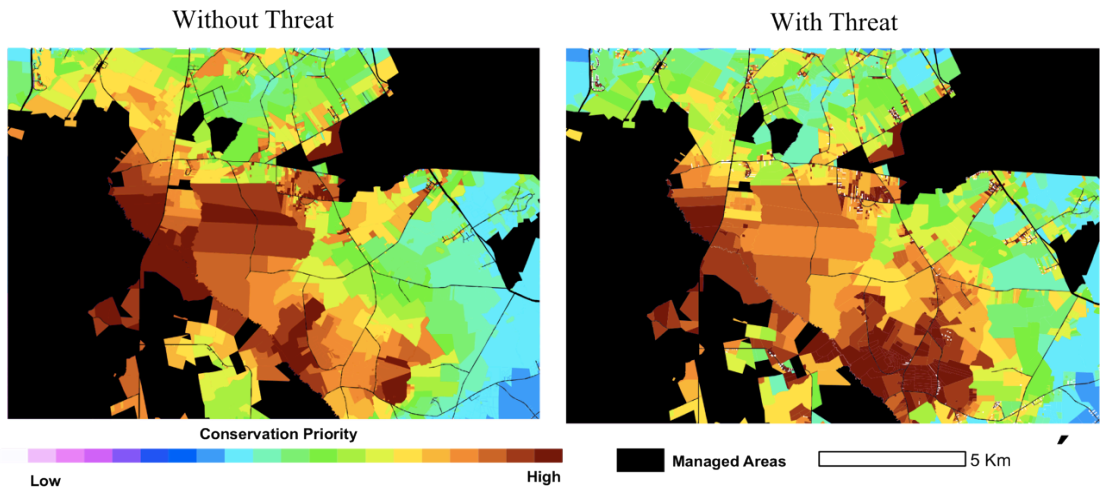

Figure 51: The influence of incorporating development threats into a prioritization of connectivity habitat for multiple species.

4.8.7.2 LAND-USE ALTERNATIVES

How would the development of new infrastructure projects impact landscape connectivity? How do we choose the habitat restoration projects that will most benefit our target species? Answering these two types of questions requires creating alternative dispersal models for each scenario that we wish to compare. In this example we show how the CONNECT tools can be used to compare the impact of two hypothetical sites for the development of an airfield on landscape connectivity for the federally endangered red-cockaded woodpecker (Figure 52).

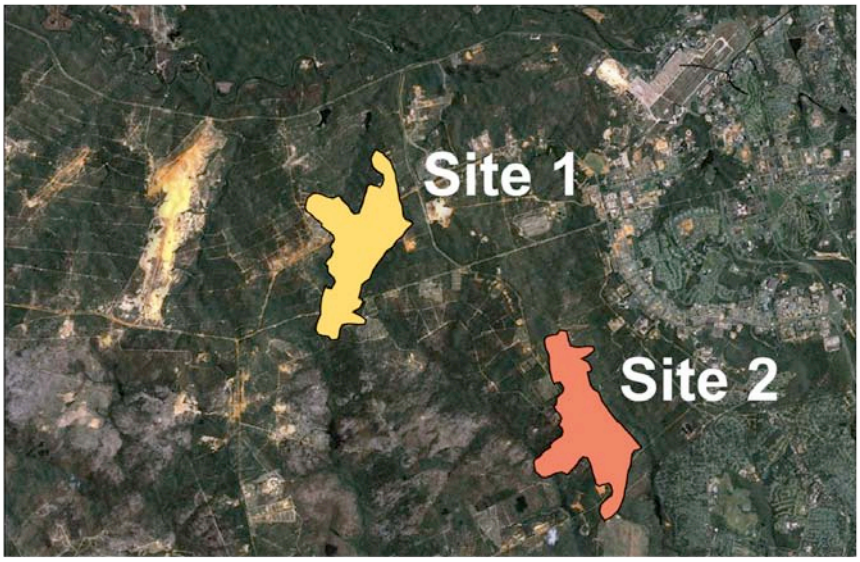

Figure 52: Hypothetical alternative airfield sites.

Our analysis (Figure 53) begins by developing a resistance map for each landscape scenario. Because the landscape already contains an airfield, we assume that the footprint and resistance values of the new airfield will be identical to the existing one. These three resistance maps (for the baseline, site 1 and site 2) are used to model dispersal in each scenario using the Create Connectivity Model tool. In the model output, we see that birds are expected to re-route around each potential airfield site, and are unlikely to cross it on a direct path. We then analyze the model output using the Generate Landscape Network tool. The connections in the lower three panels represent the MST of the habitat network, and their width represents the relative strength of the connections between them. The total resistance of the MST is lowest for Site 2, indicating that development at Site 2 will have less impact on connectivity than development at Site 1.

Note that CONNECT evaluates the effect of land use changes on population connectivity, not population performance. Population performance depends on population dynamics within habitat patches as well as the dynamics of movement between patches and effects of connectivity thereon. To evaluate the relative impact of the alternative airfield locations on population performance would require incorporating the dispersal dynamics represented by CONNECT into a Spatially Explicit Population Model (SEPM) for RCWs. This was accomplished as part of a related SERDP project (RC-1472, "A decision support system for identifying and ranking critical habitat parcels on and in the vicinity of Department of Defense installations"), as we discuss further below.

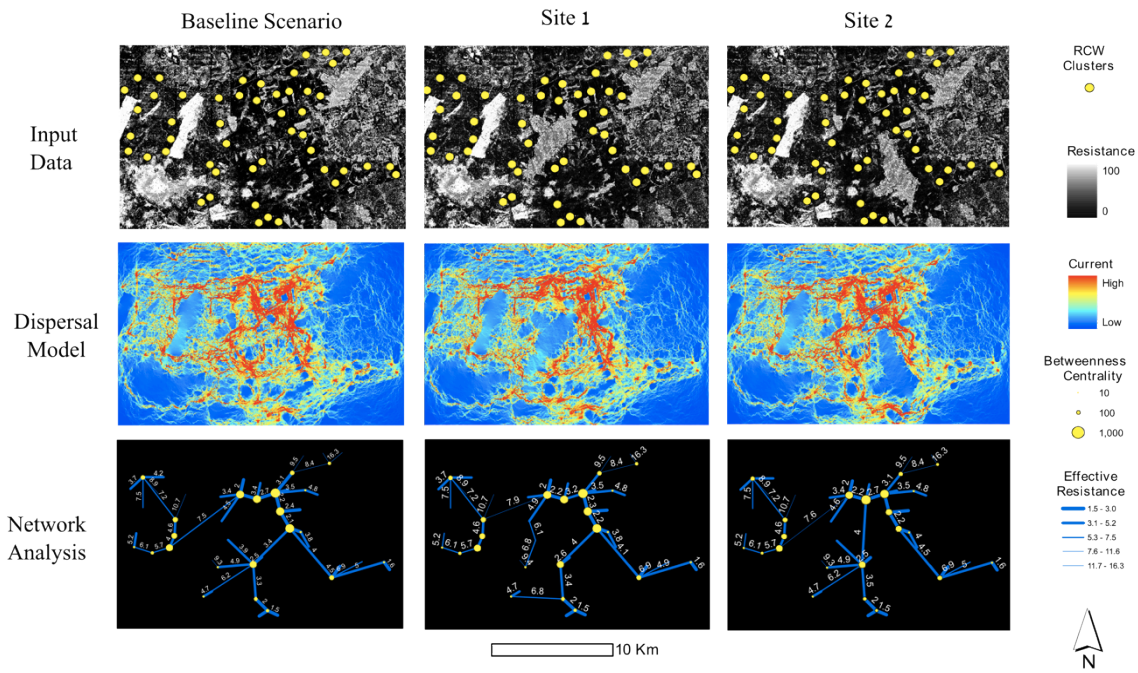

Figure 53: Impact of hypothetical development scenarios on habitat connectivity for the Red-cockaded Woodpecker on Fort Bragg, NC.

5 CONCLUSIONS AND IMPLICATIONS FOR FUTURE RESEARCH/IMPLEMENTATION

5.1 ACHIEVEMENT OF STUDY OBJECTIVES

Although technology transfer and development of habitat management scenarios is still in progress, this study has achieved its five major objectives.

5.1.1 DEVELOP A FRAMEWORK FOR EVALUATING FUNCTIONAL CONNECTIVITY OF LANDSCAPES FOR MULTIPLE SPECIES.

We have developed a unique framework for assessing functional landscape connectivity for multiple species which we believe is general enough to apply to many lands managed by the Department of Defense (Figure 54). Our process begins with selecting a set of target species of conservation concern because of issues of habitat isolation or continued fragmentation. **For each species, data on current animal distributions** and **animal dispersal at key life-history stages** must be collected using a combination of experimental and observational approaches. Next we **develop maps of landscape attributes** that that are important predictors of species presence and dispersal behavior, using the best available combination of remotely-sensed data and existing on-the-ground inventories. These environmental data becomes the **"dispersal landscape"** that abstracts key features of the environment that matter to wildlife dispersal. **If distributional data is incomplete, then we also use species distribution models** to find areas that are expected to be important habitats based on environmental covariates and known occurrences. A variety of statistical techniques are used to **translate empirical movement data into abstract rules** that govern how animals move across landscapes, including the amount of "resistance" that certain features pose to wildlife dispersal as well as movement times, jump lengths, and boundary behavior.

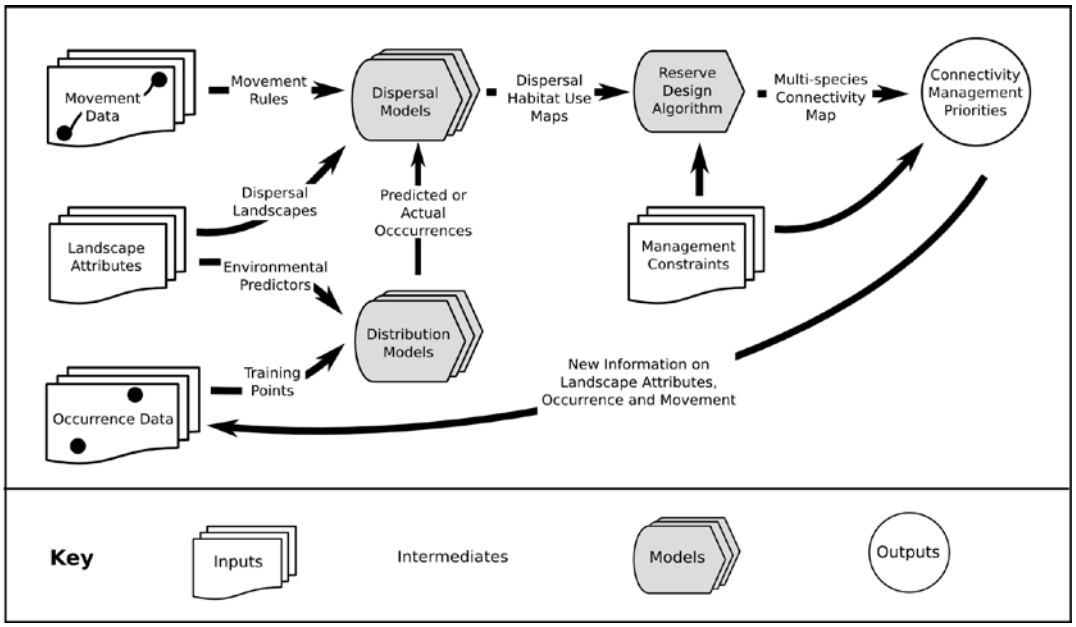

Figure 54: Framework for prioritizing lands for management of multi-species connectivity.

Once we have identified key habitat patches, developed the dispersal landscapes, and defined sets of movement rules that govern dispersal, we **develop and validate dispersal models for each species**. The outputs of these models represent the relative prevalence of dispersal habitat use for each species in a defined spatial window. In order to make model outputs comparable across species, **care should be taken that the models operate on landscapes with similar spatial grain and extent**. After creating maps of dispersal habitat use for each target species, we then use reserve design algorithms such as Zonation to combine dispersal habitat maps and **identify areas that are most important in maintaining connectivity across the entire suite of target species**. These algorithms also give use the opportunity to evaluate spatial synergies and tradeoffs in dispersal habitat use across species.

Each stage of the process generates information that is useful in managing landscapes for wildlife conservation. Collecting movement data itself can suggest management strategies because through release experiments and radio-tracking we learn which features of landscapes tend to promote dispersal, and which present impassable barriers. The compilation of occurrence data and extrapolation of these data using species distribution models can clarify the habitat requirements of each species and suggest areas where further survey work is required. The maps of dispersal habitat use for each species suggest core dispersal habitat areas that should be managed for different species separately, as well as areas of low dispersal where connectivity between habitat patches could be improved. **Multi-species connectivity maps output from a reserve design algorithm provide overall assessments of the connectivity value of lands across a suite of species.**

Ultimately, **we envision this process of multi-species connectivity assessment will exist in the context of adaptive management**. Habitat management actions, disturbance, and other changes

in land-cover and land-use alter the distributions of organisms as well as the underlying landscape attributes that affect dispersal. Experimental or quasi-experimental habitat management can also be used to generate new data on the habitat requirements of the target species as well as their movement behavior. It is critical that, over time, this new information is incorporated into dispersal models that can be updated to reflect current conditions or anticipate future conditions.

5.1.2 EVALUATE MODELING APPROACHES FOR LANDSCAPE CONNECTIVITY ACROSS SPECIES WITH DIVERGENT LIFE-HISTORY STRATEGIES AND HABITAT REQUIREMENTS

Evaluating potential modeling approaches for different species, we found that **the modeling framework and level of complexity that is appropriate for dispersal models varied depending on the available data and organism-specific attributes of dispersal behavior**. We found that simple models based on Euclidean distance reproduced the major patterns of dispersal for amphibian species that were present in the more complex individual-based models, while distance-based models performed less well for the Red-cockaded Woodpecker and Saint-Francis' Satyr. Moderately complex models, based on circuit theory, were most appropriate for RCWs because detailed data on dispersal paths were not available. Finally, individual-based simulations were most appropriate for modeling SFS dispersal because of their strong preferences for different habitats during dispersal, short activity times, and asymmetric boundary behavior.

5.1.3 IDENTIFY LANDS IMPORTANT FOR MULTI-SPECIES LANDSCAPE CONNECTIVITY

Because our movement models were created for identical spatial grains and extents, and represent similar dispersal timescales relative to the lifespan of our organisms, we were able to combine our best movement models for each species using a reserve-design algorithm to identify areas that contribute to landscape connectivity across all of our target species. Our major finding in this area is that **overlap in core dispersal habitats between the Red-cockaded Woodpecker, Saint-Francis Satyr, and our target amphibians probably only occurs in small areas on Fort Bragg itself**. A few areas outside those currently managed for wildlife have the potential to support long-distance dispersal of multiple species; however these results are highly uncertain.

5.1.4 EVALUATE THE ABILITY OF RED-COCKADED WOODPECKER TO BE A "CONNECTIVITY UMBRELLA" FOR THE OTHER SPECIES.

We found that RCW dispersal habitat is quite extensive on Fort Bragg, and a large proportion of the installation's total area is probably used by dispersing RCWs. By virtue of its extent, dispersal habitat for RCWs does overlap with some areas that are important for other species, however, we don't consider RCWs an adequate "connectivity umbrella" for dispersing SFS and amphibians because **the most important areas that promote RCW dispersal (the top 20th percentile dispersal habitats) show relatively little overlap with important areas for the other two species**. Our results suggest that widespread management of RCW dispersal habitat will facilitate dispersal of other longleaf-pine associated species, but focusing on the areas that are most important for RCW dispersal will likely neglect the dispersal needs of other organisms with divergent distributions, habitat requirements and dispersal biology.

5.1.5 DEVELOP STRATEGIES THAT ALLOW FOR EASY TESTING OF MULTIPLE HABITAT MANAGEMENT SCENARIOS.

The number of potential habitat management scenarios on and surrounding Fort Bragg is large, and our most sophisticated dispersal models are not well-suited to exploring large numbers of habitat management options because they are computationally intensive and require specialized expertise to implement. Because of these limitations **we have developed an alternative connectivity modeling strategy, and a piece of end-user software that implements it, called "CONNECT".** CONNECT is a GIS toolbox that allows wildlife managers to use limited data to assess the degree and spatial configuration of important dispersal habitats for multiple species. We are currently working with managers on Fort Bragg to develop alternative management scenarios for our target species and training them to use CONNECT to evaluate the influence of those management scenarios on landscape connectivity.

5.2 RECOMMENDATIONS FOR CONSERVATION

5.2.1 MULTI-SPECIES MANAGEMENT RECOMMENDATIONS

Except in small areas of overlapping dispersal habitat use, described above, we recommend that connectivity for Red-cockaded Woodpecker, Saint-Francis' Satyr, and the target amphibians should be managed independently. **Local actions that are taken to protect and restore connectivity within local networks of SFS and amphibian habitats are unlikely to either significantly hinder or promote landscape-scale connectivity for RCWs**. Conversely, management actions that are taken to promote connectivity between RCW breeding clusters, such as prescribed burns, longleaf pine restoration, or stand improvement, are unlikely to directly promote or adversely affect dispersal of SFS or amphibians unless they affect areas in the immediate vicinity (<~1.5 km) of breeding sites.

For the species with relatively poor dispersal ability (SFS and amphibians), rare dispersal between local networks will likely be due to a different type of dispersal process (e.g., storm winds for butterflies, flooding for amphibians) than is responsible for "routine" dispersal between colonies in the same network. Because such events are likely to be extremely rare, it is difficult to observe their mechanism or estimate their frequency. Basing a management strategy on such unpredictable events would be unwise. Instead, **we advocate a strategy of establishing new local networks between intervening ones in order to restore landscape-wide connectivity for dispersal-limited species**.

In contrast, managing current dispersal habitats at the landscape scale should suffice to maintain a high level of interconnectedness within the RCW population on Fort Bragg. Our work has shown that **the intervening landscape does hinder dispersal between Fort Bragg and surrounding populations in Southern Pines / Pinehurst, the Sandhills Gamelands, and between RCW clusters in the Overhills and Murchison Road areas on Fort Bragg**. These findings provide a mechanistic explanation of previously documented patterns of dispersal of RCWs between different parts of the Sandhills. Significant opportunities exist for conserving additional extant dispersal habitat in intervening areas, and restoring additional areas that promote dispersal for this species.

Much of DoD's efforts to promote off-installation wildlife habitat conservation in the landscape surrounding Fort Bragg and Camp Mackall have focused on securing breeding, foraging, and

dispersal habitats for RCWs. A central goal of our study was to evaluate whether RCW-centric evaluations of connectivity habitat also capture valuable dispersal habitats for other species. We have concluded that, **although there are some private lands important for promoting the dispersal of RCWs that might also be used by our other target species, the most important dispersal areas for these species on private lands would be neglected by focusing solely on RCWs**. In particular, areas north of the Fort Bragg boundary have the potential to be important habitats for threatened amphibians and SFS, but are probably not important for promoting RCW dispersal. Likewise areas along Drowning Creek are potential dispersal habitats for amphibians, but the hardwood forests on the floodplain of Drowning Creek probably constitute a mild, natural dispersal barrier for RCWs.

5.2.2 CONTRIBUTIONS TO KNOWLEDGE OF DISPERSAL BEHAVIOR FOR EACH SPECIES

Previously existing models depicting RCW population dynamics have included no information on the species response to landscape features, portraying dispersal as simple functions of distance (Letcher et al. 1998, Schiegg et al. 2002, Pasinelli et al. 2004, Schiegg et al. 2005). Our results show that RCW movement is strongly inhibited by open areas. We further found that RCW prospecting and dispersal movements were best explained by detailed forest structure features that closely corresponded to foraging habitat characteristics. Specifically, RCWs prefer to pass through forests stands with an average canopy height of approximately 20 m, and less than 20% midstory cover. RCW movements were also moderately reduced through forested areas with abundant midstory cover and developed areas. We were able to empirically estimate RCWs response to landscape features at a regional scale by combining radio-telemetry data during prospecting behavior and LiDAR data. With this greater understanding of RCW response to detailed landscape features we have greater confidence predicting the flux of individuals between territories and overall *P. borealis* connectivity. Avoidance of habitat gaps, the previously undescribed foraying behavior of juveniles and the also previously unknown long-distance jumping behavior of RCWs (Kesler et al. 2010) all were incorporated into an RCW SEPM as part of the companion project RC-1472. This resulted in a much improved, individual-based RCW population model that includes interaction with the landscape during dispersal.

Our studies of amphibian movement behavior demonstrated the importance of testing implicit assumptions of connectivity studies with field data. We showed that common species may not provide an appropriate surrogate for rare species, even when putative surrogate species are closely related. We also found that movements of species can be as strongly affected by understory vegetation as they are by canopy structure. Finally, we showed that the conditions experienced by amphibian larvae may have carryover effects on their movement behavior after they have completed metamorphosis. The influence of the spatial pattern of habitats on connectivity is especially important to investigate since habitat specific resistance values could be affected by the factors we investigated. While these findings highlight the need for sensitivity analyses, our studies suggest that rare amphibian populations in our study area are likely isolated from other suitable unoccupied habitat.

Little was known about SFS dispersal behavior before this study was initiated. Our release experiments with a surrogate species and movement modeling have highlighted important facets of SFS movement that can be used to guide management for this species. First, the connectivity between patches of SFS habitat (e.g. probability > 0.01 of a dispersing individual reaching

another habitat patch), is likely restricted to patches within a few hundred meters of each other. Surprisingly, we found that the most important habitats facilitating dispersal were upland areas where movement rates were rapid relative to breeding habitat (wetlands). Open areas appear to be strong barriers to dispersal. Overall our results indicate that management or restoration of connectivity for this species should be focused on increasing the number of local networks of habitat patches near existing breeding populations.

5.3 CONTRIBUTIONS TO MULTI-SPECIES CONNECTIVITY THEORY

Our study outlines the differences between structural and functional connectivity (sensu Tischendorf and Fahrig 2000). A standard structural approach is to develop a map that considers discrete habitat patches surrounded by a matrix of non-habitat and evaluate connectivity using the Euclidean distance between habitat patches (Minor and Urban 2008). Often, patches are divided into local networks based on a distance criterion that represents the maximum distance likely to be traversed by the least vagile species of concern (Hall 2008). This leads to a focus on dispersal between local habitat patches and gives little information about how the intervening matrix between those patches is used by dispersing organisms and provides little basis for suggesting how these intervening dispersal habitats should be managed. A multi-species approach that follows our framework will allow wildlife managers to identify dispersal habitats that are important for different suites of species, and manage the matrix appropriately.

Multi-species habitat assessment and conservation planning has generally followed one of two approaches: analyses of "biodiversity hot spots" or identification of "umbrella species". Biodiversity hotspot studies attempt to identify areas that are inhabited by multiple species of conservation concern, generally endemic species, rare species, or those that are threatened by human activity (Reid 1998, Meyers et al. 2000). These analyses rarely incorporate connectivity between habitats (but see Lehtomäki et al. 2009) and thus may miss dispersal corridors that are important for maintaining population persistence. Our approach builds on this existing framework and identifies "dispersal hotspots" that may not provide primary habitat for many species, but nonetheless permit their dispersal through patches of such habitat in fragmented landscapes.

Studies that identify umbrella species (Fleishman et al. 2000, Roberge and Angelstam 2004) attempt to find a single species, or a small set of species, whose needs can be used to guide management for a larger group of species for which there is less information. Central to the umbrella species concept is that the most important habitats for potential "umbrellas" also provide good habitat for other species. Generally, umbrella species have been selected based on rarity (Nieme et al. 1997), patterns of co-occurrence (Fleishman et al. 2000), or presumed key roles in important ecosystem processes. We wanted to see if red-cockaded woodpeckers, often considered an umbrella species for conservation in this region, provide a good umbrella for the management of key dispersal habitats for longleaf-pine associated species with divergent life histories and dispersal biology. Although current SERDP research elsewhere indicates that RCWs are an effective habitat umbrella for promoting avian diversity in longleaf systems (Defense Coastal / Estuarine Research Program, Research Project T-2), our assessment shows that RCWs do not provide an adequate "dispersal umbrella" for the suite of species considered in this study. However, the methodology that we have developed could be used to empirically evaluate whether any given species could serve that role.

5.4 Limitations and Next Steps

Although we envision that using our framework will allow for empirical evaluation of functional connectivity for multiple species and will be useful in guiding connectivity management around Fort Bragg and elsewhere, we have identified several key limitations of our work.

First, our analysis has been focused on dispersal through the matrix between primary habitats, not on the primary habitats themselves. The relative importance of primary or "core" habitat areas and dispersal habitats in promoting population persistence depends on both dispersal dynamics between core habitats and population dynamics within core habitats (Theodorou et al. 2009). Our most sophisticated dispersal models do not incorporate population dynamics, and thus are inadequate for answering these types of questions. Incorporation of detailed dispersal dynamics into Spatially Explicit Population Models (SEPMs) could allow researchers to investigate the population-dynamic consequences of limited dispersal and evaluate the influence of different habitat management options on population persistence and recovery. This has been done previously for RCWs in the Fort Bragg landscape, but the SPM employed did not include effects of the landscape on movement, but rather portrayed dispersal as a simple function of distance (Walters and Crowder 2002, Scheigg and Walters 2005). The detailed dispersal dynamics we documented for RCWs were incorporated into this SEPM as part of RC-1472. However, insufficient demographic data currently exist to parameterize this type of model for the other species that we considered in this study. We consider linking empirically-parameterized dispersal models with SEPMs a primary avenue for future research.

Second, our simulations omitted some biological details for which we lacked data. For example, for SFS we assumed that the mortality rate of butterflies was not influenced by the habitat in which they were located; we assumed all had the life expectancy we had estimated for butterflies in their breeding habitat (wetlands) using capture-mark-recapture data. Butterflies in open, sunny habitats may have a higher mortality rate than we estimated, which may render open habitat an even more impervious barrier to dispersal than our simulation results would suggest. Ethical considerations preclude direct measurement of mortality rates for threatened SFS in non-breeding habitat, but comparing mortality of SFS and ABB in wetlands and of ABB in other habitats, and then extrapolating the species difference from wetlands to other habitats represents one possible way forward. Our simulations for SFS and the amphibians also omit more subtle movement responses to habitat characteristics (such as tree cover or abundance of downed logs), because we treated all habitat in each type (such as upland forest) as homogeneous. With additional movement data and finer-scale landscape information, more sophisticated movement models may someday be constructed.

Third, the dispersal events with the largest biogeographic, genetic and evolutionary consequences are likely to be rare, long-distance events. These events may not share a common mechanism with the "routine" dispersal events that we used to parameterize spatially explicit dispersal models for each species (Nathan 2006). Indeed we documented that in RCWs they do not, as long-distance dispersers engaged in jumping differ in behavior and their reaction to the landscape from short-distance dispersers engaged in forays. Our models are biased towards dispersal behavior that is common enough to observe directly. Long-distance dispersal events between local networks of amphibian breeding ponds and SFS wetland habitats may occur infrequently due to extreme events or other mechanisms that promote long-distance dispersal.

Although challenges to direct measurement of these long-distance dispersal events are extreme, there is some potential to estimate long-term rates of immigration and emigration between isolated populations using landscape genetic analyses (Lowe and Allendorf 2010).

Much of our work has focused on collecting empirical data on wildlife dispersal, developing environmental datasets that map aspects of the landscape relevant to dispersing organisms, parameterizing dispersal models for a variety of different species, and showing how key dispersal areas for each species relate to each other spatially. We see testing a variety of land-use change scenarios as a key next step in this project. A thorough analysis would incorporate both on-installation habitat management and off-installation landscape change. For example, there is some ambiguity about whether longleaf pine restoration efforts associated with Long Valley Farm and Carver's Creek State Park will be sufficient to counter reductions in connectivity caused by continued rapid urban growth in greater Fayetteville. Using our connectivity modeling toolbox, we will incorporate restoration plans for Long Valley Farm, Carver's Falls, and an urban growth model (Jantz et al. 2010) to establish anticipated connectivity trends with and without restoration and suggest areas where further restoration of longleaf pine communities can best benefit habitat connectivity for RCWs.

Many of our overall conclusions are contingent on the species that we selected for study. A different suite of organisms might lead us to a different set of conclusions. There is some latitude to broaden taxonomic scope of the analysis in the future and incorporate other longleaf-pine associated species of management importance such as Bachmann's sparrow (*Aimophila aestivalis*) and pine snake (*Pituophis melanoleucus*) as well as species of recreational importance such as bobwhite quail (*Colinus virginianus*).

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APPENDIX A

ADDITIONAL/SUPPORTING MATERIALS

I. CONNECT

This report is bundled with a public beta version of the CONNECT toolbox. CONNECT is a set of GIS tools that helps researchers and conservation planners model landscape connectivity for multiple wildlife species in complex heterogeneous landscapes. CONNECT also allows users to combine single-species models of animal movement to identify areas of the landscape that facilitate the movement of multiple species. CONNECT can be used to support the design of nature reserves, facilitate land management, or examine the effects of land-use change on animal movements.

CONNECT packages three cutting-edge connectivity modeling and conservation planning tools, Circuitscape (McRae et al. 2008), NetworkX (Hagberg et al. 2009), and Zonation (Moilanen et al. 2008) into a user-friendly geoprocessing toolbox for ESRI ArcGIS 9.3. Using the CONNECT tools in the ArcGIS ModelBuilder environment allows users to incorporate animal movement models into larger workflows and use the tools iteratively to assess the impact of model assumptions and evaluate multiple conservation scenarios.

The CONNECT Toolbox contains four major tools:

- *Standardize Datasets*. This tool takes a group of raster datasets or feature classes and converts them to ASCII rasters, all with the same extent and cell-size. This tool is used to easily prepare inputs for use in the other tools.

- *Create Connectivity Model*. This tool creates animal movement models using Circuitscape. In mapping mode, this tool takes habitat locations and a map of the landscape's resistance to animal movement and generates a map of likely dispersal corridors between habitat patches. In modeling mode, this tool takes the same inputs, but instead of generating a map of dispersal corridors, the tool outputs pairwise calculations of the resistance distance between all habitat patches. These calculations are later used to generate a graph of habitat patches using the Generate Landscape Network tool.

- *Generate Landscape Network*. This tool takes pairwise calculations of resistance distance created by the Create Connectivity Model Tool and creates a landscape network using NetworkX. Various statistics are computed for the network, including the graph diameter, minimum spanning tree, and betweenness centrality of each node. Feature classes representing nodes and edges are output to a geodatabase from this tool, and graph statistics are output to a text file.

- *Prioritize Landscape Features*. This tool combines dispersal corridor maps for multiple species into a single landscape prioritization using the Zonation algorithm.

Optionally, the user can input maps representing planning units, economic costs, or conservation threats into the analysis. The output from this tool is a map of conservation priority rankings, either by pixel or by planning unit / parcel.

A user-guide and tutorial, along with sample datasets, are also included with CONNECT.

II. MAPS

Raster-based maps of dispersal habitat use and multi-species habitat priorities that were created for this project are attached in an ASCII raster format that can be imported into most desktop GIS programs. These datasets cover the two spatial extents displayed in Figure 2. The following datasets are included:

Table i: Maps of simulated dispersal habitat use delivered with the SERDP-RC 1471 final report.

Fort Bragg Extent, Recorded Occurrences (file path "dispersal_maps\ft_bragg")	
Dataset name	**Details**
gfusematftbragg10kN100t30days.asc	Average of 100 replicate runs of a gopher frog simulation with a travel time of 30 days.
gfusematftbragg10kN100t100days.asc	Average of 100 replicate runs of a gopher frog simulation with a travel time of 100 days.
ocfusematbragg10kN100t30days.asc	Average of 100 replicate runs of an ornate chorus frog simulation with a travel time of 30 days.
ocfusematftbragg10kN100t100days.asc	Average of 100 replicate runs of an ornate chorus frog simulation with a travel time of 100 days.
RCW_circ6kmthresh_ftbragg.asc	RCW Circuitscape model with a maximum dispersal distance of 6km.
sfsDispersalSimulationFtBragg.asc	Dispersal simulation for SFS on Fort Bragg.
tsusematftbragg10kN100t100days.asc	Average of 100 replicate runs of a tiger salamander simulation with a travel time of 100 days.
tsusematftbragg10kN100t30days.asc	Average of 100 replicate runs of a tiger salamander simulation with a travel time of 30 days.

Full Study Extent, Modeled Occurences (file path "dispersal_maps\full_extent")	
Dataset name	**Details**
GF_usemat100_v4.asc	Gopher frog simulation with an activity time of 100 days.
GF_usemat300_v4.asc	Gopher frog simulation with an activity time of 300 days.
RCW_circuitscape_6km_thresh.asc	RCW Circuitscape model with a maximum dispersal distance of 6km.
SFS_usemapNR285_v4.asc	Extreme SFS dispersal simulation with 10 hours of activity time per day and no rest.

Table II: Maps of dispersal habitat conservation priorities delivered with the SERDP-SI 1471 final report.

Dataset name	Details
ftbragg_zonation_allspp.asc	Zonation conservation priority map for Fort Bragg that weights dispersal habitat maps for RCW, SFS, and Gopher Frog equally. Units are percentile rank (e.g., 0.90 is a cell that is ranked higher than 90% of the other cells.
fullextent_zonation_allspp_protectedmask.asc	Zonation conservation priority map for the full study extent that masks currently protected lands. Inputs to zonation are dispersal simulations with relaxed dispersal assumptions.
fullextent_zonation_conservative_existingpops.asc	Zonation conservation priority map for the full study extent. Inputs to Zonation are dispersal simulations based on existing population with conservative assumptions.
fullextent_zonation_rcw_protectedmask.asc	Zonation dispersal habitat priorities on unprotected private lands for RCW-only.
fullextent_zonation_relaxed_modeledpops.asc	Zonation conservation priority map for the full study extent. Inputs to Zonation are dispersal simulations based on modeled populations with relaxed dispersal assumptions.

APPENDIX B

LIST OF SCIENTIFIC/TECHNICAL PUBLICATIONS

PEER REVIEWED PUBLICATIONS

Hudgens B.R., W.F. Morris, N. M. Haddad, W. Fields, J.W. Wilson and R.T. Jobe. How complex do models need to be to predict dispersal of threatened species through matrix habitats? *In preparation for Ecological Applications.*

Kesler, D. C., J. R. Walters and J. J. Kappes, Jr. 2010. Social influences on dispersal and the fat-tailed dispersal distribution in red-cockaded woodpeckers. *Behavioral Ecology* 21:1337-1343.

Kuefler, D., B. Hudgens, N. M. Haddad, W. F. Morris and N. Thurgate. 2010. The conflicting role of matrix habitats as conduits and barriers for dispersal. *Ecology* 91:944-250.

Trainor A. M., J. R. Walters, W. F. Morris, J. Sexton, and A. Moody. Empirically estimating and validating resistance surfaces for Red-cockaded Woodpecker prospecting behavior. *In preparation for Ecological Applications.*

Trainor A. M., J. R. Walters, W. F. Morris, and A. Moody. Environmental and conspecific cues influencing Red-cockaded Woodpecker prospecting behavior. *In preparation for Ecology.*

Trainor A. M., D. L. Urban, J. R. Walters, and A. Moody. Quantifying and validating connectivity of Red-cockaded woodpecker populations. *In preparation for Landscape Ecology*.

CONFERENCE ABSTRACTS

Breckheimer, I. K. and A. Milt. CONNECT: New GIS tools support management of habitat connectivity for wildlife. Partners in Environmental Technology Technical Symposium & Workshop. 2010.

Hudgens, B. R., Haddad N.M., Fields W., Thurgate N., Frock C., Morris W. F., Jobe R. T., Kuefler, D. C. 2010. Using movement behaviors to assess dispersal routes in complex landscapes. Society for Conservation Biology Annual Meetings 2010.

Hudgens, B. R., Haddad N.M., Fields W., Thurgate N., Frock C., Morris W. F., Jobe R. T., Kuefler, D. C. 2009. Using movement behaviors to determine connectivity in complex landscapes. Partners in Environmental Technology Technical Symposium & Workshop. 2009.

Kuefler, D., Hudgens, B., Haddad, N.M., Morris, W.F. and Thurgate, N. 2009. A behavioral approach to mapping connectivity for rare butterflies on military installations. Ecological Society of America Annual Meetings 2009.

Kuefler, D. Haddad,N.M. and Hudgens, B. 2007. Using movement behaviors to predict connectivity for rare animals. (2007). International Association for Landscape Ecology Annual Meetings 2007.