LANDSCAPE-LEVEL INVESTIGATIONS OF AVIAN SPECIES AT FORT BENNING, GEORGIA

by

CLARK DAVID JONES

(Under the Direction of Robert J. Cooper)

ABSTRACT

The southeastern United States was once dominated by an estimated 60-90 million acres of longleaf pine savannas. Today only a fraction of this ecosystem remains as scattered, remnant patches primarily found on public lands. Strategies for restoring and maintaining these patches, and the animal species that depend on them, use a variety of habitat management approaches that occur at the ground-level, but less consideration has been given to approaches at a landscape level. Landscape-level processes can be critically important for maintaining metapopulation persistence and for providing context for patterns of species distribution. An understanding of patterns at the landscape level can also be used to evaluate the effectiveness of strategies for conservation. I investigate landscape-level patterns of distribution and movement of avian species at Fort Benning, GA using field surveys and experimental translocations, and compare inference about species-habitat relationships derived from multiple distribution modeling approaches. Additionally, I evaluate the use of the Red-cockaded Woodpecker (*Picoides borealis*) as an umbrella species for other avian species in decline throughout the Southeast.

My analyses suggest corridors are a useful tool for increasing habitat connectivity for Bachman's Sparrows (*Peucaea aestivalis*). Experimental translocations demonstrate that

Bachman's Sparrows preferentially use corridors when moving between patches of suitable habitat. I find that popular methods of presence-only species distribution modeling generate varying inferences for species-habitat relationships which has implications for improving our understanding of species distributions. In my evaluation of the Red-cockaded Woodpecker as an umbrella species, I find that areas closer to breeding clusters of this woodpecker are more likely to have higher densities of other species that share similar habitat characteristics, but that not all species exhibit a strong relationship. Additionally, this relationship varies across space. These findings can be used to inform large-scale conservation strategies to preserve and maintain avian species dependent on longleaf pine savannas in the Southeast.

INDEX WORDS: Red-cockaded Woodpecker, *Picoides borealis*, Bachman's Sparrow, *Peucaea aestivalis*, Brown-headed Nuthatch, *Sitta pusilla*, Field Sparrow, *Spizella Pusilla*, Northern Bobwhite, *Colinus virginanus*, Prairie Warbler, *Setophaga discolor*, umbrella species, species distribution modeling, Fort Benning, Maxent, Genetic algorithm for ruleset prediction, GARP, non-stationarity

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by

CLARK DAVID JONES

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by

CLARK DAVID JONES

Major Professor:	Robert J. Cooper
Committee:	Michael J. Conroy
	Lan Mu
	Nathan P. Nibbelink

Electronic Version Approved:

Maureen Grasso
Dean of the Graduate School
The University of Georgia
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DEDICATION

This project is dedicated to my parents

Winston and Barbara Jones

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CHAPTER 1

INTRODUCTION AND LITERATURE REVIEW

Longleaf pine (*Pinus palustris*) savannas were once the most dominant habitat in the southeastern United States, covering an estimated 60-90 million acres from Virginia through the Coastal Plain along the Atlantic Seaboard and westward into eastern Texas (Frost 1993, Outcalt 2000, Earley 2004, Frost 2006). Of its original extent, less than 3% remains of the longleaf pine forest (Frost 1993). Of old-growth longleaf pine, less than 0.00014% of the pre-settlement extent remains (Varner III and Kush 2004), despite its previous dominance across the southeastern landscape. The consequences of this loss to wildlife and ecosystem function are innumerable, and all remaining patches suffer from fragmentation and habitat degradation. Several strategies are used for promoting the conservation of the remaining pieces of this once vast ecosystem, many of which are used without empirical support for the assumptions that underlie their use. Three elements should be further evaluated to effectively implement conservation strategies going into the future: (1) examine the effects of connectivity and fragmentation in a landscape that currently exists as a collection of disparate patches, (2) evaluate the implicit paradigm that the Red-cockaded Woodpecker (*Picoides borealis*), an old-growth longleaf specialist, is serving as an umbrella species for the longleaf ecosystem, and (3) understand what current methods used to predict species distributions imply about species-habitat relationships, so remotely-sensed data can be used more effectively in conservation planning.

Across the former range of longleaf pine savannas, this habitat was historically maintained by frequent fire which occurred (naturally and anthropogenically) in most locations on a 3-5 year interval (Huffman 2006). These fires were typically not the catastrophic, stand-replacing fires that are common in other fire-dominated forests; rather, these disturbances cleared away the undergrowth on a regular basis which maintained the grassy understory that is typical of longleaf pine savannas (Garren 1943, Wahlenberg 1946, Van Lear et al. 2005, Frost 2006). The ease with which many loggers and settlers were able to travel through these southern “piney woods” was primarily due to these frequent fires that opened the understory and created a park-like savanna that was easily traversed (Bartram and Harper 1942). Consequently, it was once one of the most valuable and overexploited resources in the United States (Earley 2004).

The longleaf ecosystem is the most biologically diverse ecosystem north of the tropics (Early 2004). This high diversity may seem counterintuitive in a system dominated by a single tree species and with very little structural complexity in the sub-canopy; however, the groundcover vegetation is highly diverse and over 40 species of plants can be found within 1-m^2 in some locations (Walker and Peet 1984, Peet 2006). Within the southeastern Coastal Plain, approximately 6,000 species of vascular plants occur, representing nearly 25% of all plant species found in North America north of Mexico (Peet 2006). Many avian species, such as Bachman's Sparrow (*Peucaea aestivalis*), spend nearly all their time in this diverse groundcover which becomes too thick for nesting in the short-term when fire is excluded (Jones et al. 2013) and too sparse in the long-term when succession proceeds into a hardwood-dominated community that shades out all the undergrowth (Haggerty 1986).

Like many iconic forests in North America, the longleaf pine ecosystem was heavily logged and continues to be to this day. However, in addition to the heavy logging, the remaining longleaf pine forests have been plagued by a history of fire suppression that, in some cases, came in the form of federal government organizations attempting to reduce the amount of wildfire on the landscape (Earley 2004, Way 2011). This loss of fire and simultaneous destruction by logging reduced the extent and quality of the remaining habitat, much of which cannot be restored without intensive restoration that requires combinations of timber thinning, gradual reintroduction of fire, and herbicide application.

Benefits of fire

A myriad of species in southern pine savannas benefit from frequent fire (Means 1996, Van Lear et al. 2005, Means 2006). Frequent fire reduces understory growth by retarding encroachment of many woody species and maintaining a grass-dominated ecosystem. Additionally, it maintains an open canopy that allows sunlight to reach the forest floor (McGuire et al. 2001). The regular application of fire reduces competition among dominant species by setting back the system thus allowing other, less dominant species to grow in the understory. Although many eastern pine tree species, such as a loblolly pine (*Pinus taeda*), short-leaf pine (*Pinus echinata*), and slash pine (*Pinus elliotii*), are fire tolerant to varying degrees depending on soil moisture and other conditions, longleaf pine is far more tolerant and actually benefits from frequent fire when it is very young (Heyward 1939, Garren 1943, Grelen 1983, Waldrop et al. 1992).

Because of the benefits of frequent fire to many plant species (Waldrop et al. 1992), many vertebrate species (as well as invertebrate species) are also dependent on frequent fire (Means 2006). Southern pine savannas are home to more U.S. avian endemics than any other ecosystem in the United States. Two of these species, the Red-cockaded Woodpecker and Bachman's Sparrow, are almost entirely restricted to southern pine savannas (Jackson 1994, Dunning 2006). In fact, the current extent of the range of both Red-cockaded Woodpecker and Bachman's Sparrow closely matches the extent of the longleaf pine forest (Jackson 1994, Dunning 2006). Interestingly, fire tolerance for each of these two denizens of the longleaf pine forest is subtly different. For Bachman's Sparrows, fire every 2–5 years is required to clear areas for nesting and promote the growth of grasses and forbs (Dunning 2006, Jones et al. 2013), while Red-cockaded Woodpeckers are able to tolerate less frequent fire (Jackson 1994), so long as the fire return interval is sufficient to prevent the mid-story from nearing the height of their nest and roost cavities and maintains the dominance of the pine trees in the stand. Both of these species are often found in proximity to each other since their habitat preferences overlap to such a large degree (Conner et al. 2002, Dunning 2006).

Other declining avian species in the Southeast such as Brown-headed Nuthatch (*Sitta pusilla*, another U.S. endemic), Field Sparrow (*Spizella pusilla*), Northern Bobwhite (*Colinus virgnianus),* and Prairie Warbler (*Setophaga discolor*) also inhabit longleaf pine savannas and benefit from frequent disturbances similar to those that shaped the longleaf pine ecosystem. However, they also occur in a wider variety of habitats and ecosystems that extend beyond the current and historical range of longleaf (Stoddard 1931, Withgott and Smith. 1998, Brennan 1999, Nolan et al. 1999, Carey et al. 2008). Nonetheless, each of these species has exhibited drastic declines across their range, with some of the largest declines being in the southeastern United States (USGS 2013).

With the loss of both the extent of habitat and frequency of fire across the range of longleaf, many non-avian species have also declined in abundance. Numerous other vertebrates such as the federally endangered frosted flatwoods salamander (*Ambystoma cingulatum*) and the threatened reticulated flatwoods salamander (*Ambystoma bishopi*) have undergone drastic declines. Gopher tortoise (*Gopherus polyphemus*) is federally listed as threatened in portions of its range, and the eastern diamondback rattlesnake (*Crotolus adamanteus*) has been proposed for listing as well. In order to restore populations of these declining species, conserving and maintaining the remnants of this once dominant landscape has become one of the top priorities in the Southeast.

Fragmentation

One tactic for conservation of the remaining patches of the longleaf ecosystem is to promote efforts to increase connectivity between the remnant patches. The fragmented nature of the remaining pieces of the once vast longleaf pine ecosystem has undoubtedly contributed to the imperilment of many southeastern pineland specialists and continued habitat loss will further exacerbate this problem (Jackson 1994, Means 1996, Means et al. 1996, Earley 2004, Van Lear et al. 2005, Means 2006). However, little is understood about the importance of connectivity in the longleaf ecosystem and exploring measures to promote it for pine savanna species is of paramount importance to both management and conservation.

Habitat loss and fragmentation is one of the leading causes of species endangerment world-wide (Saunders et al. 1991, Foley et al. 2005). Fragmentation has contributed to the decline of many avian species occupying a wide variety of habitats across North America (Herkert 1994, Hagan et al. 1996). Due to edge effects, fragmentation can increase the rate of predation (Storaas et al. 1999), nest depredation (Small and Hunter 1988, Rolstad 1991, Berger 1997), and nest parasitism (Davis and Sealy 2000). Habitat fragmentation exposes species to increased risk of disease (Allan et al. 2003), negatively influences overall health of individuals (Niu 2007), and can even alter species morphology (Desrochers 2010). Additionally, fragmentation isolates local populations, alters immigration and emigration rates, and increases the risk of extinction (Hinsley et al. 1995, Fahrig 2003, Loehle 2007, Boscolo et al. 2008, Boscolo and Metzger 2011, Loehle and Eschenbach 2012).

Corridors, which are relatively narrow strips of suitable habitat that connect isolated patches, have been proposed as a conservation tool to help combat fragmentation. Corridors can be used to connect local populations, increase population size, and promote population stability (Simberloff et al. 1992, Beier and Noss 1998, Hanski 1998, Alderman et al. 2005). Connecting areas of suitable habitat can reduce the threats associated with stochastic events (Hinsley et al. 1995, Haddad and Baum 1999, Boscolo and Metzger 2011), promote gene flow (Keyghobadi 2007, Dixo et al. 2009, Wells et al. 2009), and support metapopulation persistence (Hanski 1994, Schooley and Branch 2011). The establishment of corridors is a proven conservation technique in many settings (Beier and Noss 1998, Haddad et al. 2003, Damschen and Brudvig 2012) that has facilitated the dispersal of numerous plant (Damschen and Brudvig 2012), insect (Haddad and Baum 1999, Haddad et al. 2000) and mammalian species (Mabry and Barrett 2002), as well as birds (Haas 1995, Clergeau and Burel 1997). However, promoting connectivity requires an understanding of how species move through their environment, of which little is known for many of the avian residents in the longleaf ecosystem.

Red-cockaded Woodpecker as an umbrella species

Another approach (which can be used in conjunction with efforts to increase connectivity) for conserving and managing habitat for many residents of the longleaf pine ecosystem is to manage for the Red-cockaded Woodpecker as an umbrella species. Multiple studies have shown that management for Red-cockaded Woodpeckers can be beneficial for several avian species that use the same habitat (Wilson et al. 1995, Plentovich 1998, Simberloff 1998, Conner et al. 2002, Cox and Jones 2007), and because of this it is often promoted as an umbrella species (Koenig and Dickinson 2004, Caro 2010). However, the benefits of single-species management (the context in which conservation of umbrella species is often implemented) are not without scrutiny (Roberge and Angelstam 2004).

In other systems species proposed as umbrella species were later discovered to have much more limited utility than was originally assumed (Berger 1997). Others have found that the umbrella species concept is particularly impotent if the species (or suite of species) chosen for protection are not complementary to the habitat requirements of the umbrella species (i.e., do not share similar habitat requirements or life history traits) and that the random selection of species may perform just as well in many instances (Andelman and Fagan 2000, Roberge and Angelstam 2004). The efficacy of any species as an umbrella species cannot be supported or rejected without quantitative evaluation (Roberge and Angelstam 2004). Because the Red-cockaded Woodpecker can tolerate varying conditions in the understory (including the open, manicured conditions typical of golf courses (USFWS 2002)) that many species cannot, it seems probable that not all species react in the same to way to Red-cockaded Woodpecker reintroductions and habitat restoration. Therefore, interpreting the utility of the Red-cockaded Woodpecker as an umbrella species is important because the degree to which it does or does not function as an umbrella warrants additional considerations for habitat management and restoration if an ecosystem approach to management is desired.

Planning for the future by understanding the present

Much of what is known about the location and distribution of many species across the extent of the longleaf pine ecosystem is limited to information derived from a local scale (i.e., plot level) and this knowledge is often difficult to extrapolate to a larger scale. When faced with the tasks of increasing connectivity between patches of existing habitat and using umbrella species as management tools, it is also invaluable to understand species-habitat relationships at a landscape scale (i.e., extrapolate beyond the plot level) so conservation benefits can extend beyond the local level. While the habitat preferences of species at the local scale are often considered in conservation planning, less attention has been given to preferences at the landscape scale, although many efforts are rapidly emerging (Grand et al. 2009).

Species distribution modeling is a valuable tool that has been used increasingly in recent years. This increase is—in large part—the result of the widespread availability of user-friendly software, particularly for presence-only data, that readily produces easily interpretable maps. However, many of these software packages provide limited information on how the model(s) are produced or how environmental variables are used to create the predictive map surface (Elith and Graham 2009). Furthermore, many of the most popular presence-only modeling methods (e.g., Maxent and GARP) provide little guidance on what data may be appropriate to use for a particular method (Yackulic et al. 2012). Understanding how environmental and bioclimatic data are used to create distribution maps derived from presence-only data with a given method is essential for informing landscape-scale conservation and land management decisions. Without a clear understanding of the model, the inference for such a model is limited. Therefore, investigating what these modeling approaches imply about species-habitat relationships of declining species in the longleaf pine ecosystem is particularly important for making effective decisions at a broad scale.

DISSERTATION OBJECTIVES AND STRUCTURE

In the second chapter of this dissertation, I explore the effects of fragmentation on two avian species found in longleaf forests: the neotropical migrant Prairie Warbler, and the resident Bachman's Sparrow. Specifically, I use experimental translocations to examine the permeability of different habitat patches for the two species. I also evaluate whether or not corridors may be useful in increasing habitat permeability for Bachman's Sparrows. Results of previous studies imply that connectivity may play a vital role in increasing dispersal between nearby patches of habitat (Dunning et al. 1995, Cox and Jones 2010) and several current conservation strategies in the longleaf pine ecosystem have focused on increasing habitat connectivity as part of landscape-scale conservation efforts (Grand et al. 2009, NFWF 2012). This effort represents one of the first such experimental translocation experiments used in the longleaf pine ecosystem to evaluate the importance of habitat connectivity to avian movement and likely has implications for dispersing individuals. It also illustrates that the effects of fragmentation may be more pronounced for some species that are non-migratory.

The third chapter examines the relationship between locations suitable for Red-cockaded Woodpeckers and the presence and abundance of five species that are classified as species of concern in Georgia: Bachman's Sparrow, Brown-headed Nuthatch, Prairie Warbler, Northern Bobwhite, and Field Sparrow. This chapter not only examines how proximity of a sampling point to a Red-cockaded Woodpecker influences the abundance of these species, it also explores how this influence changes across the landscape at the study area, Fort Benning Military Reservation. While ecologists and land managers are often interested in the average effect of a particular set of stand conditions they are striving for (which in this case is the result of single-species management), the spatially-varying effect of these actions is seldom considered. In this chapter I illustrate that some locations near Red-cockaded Woodpeckers on Fort Benning have a higher diversity (more species and higher abundance) of species of concern, but that in other locations the diversity is lower. These results are not intended to provide a causal mechanism for this relationship, rather they are intended to illustrate that ignoring spatial heterogeneity in these types of analyses can often lead to a misconception that the effect of such management is the same in all locations at all times.

In Chapter Four I explore the use of different species distribution modeling approaches using presence-only data (only known locations of species, not absences) for modeling upland and lowland species that are typically found within and near longleaf pine stands. Specifically, I examine how different presence-only modeling approaches differ in their inference about species-habitat relationships and what consequences this may have for understanding species-habitat relationships. Presence-only species distribution modeling is becoming commonplace and is used across a wide range of software packages, taxa, and expertise. I use data collected at Fort Benning, Georgia from 2008-2010 and widely available landcover data (from southeastern GAP data) to model simple relationships for several species of concern and then compare how the relationship of each species to each habitat type varied across three different species distribution modeling approaches. The purpose of this analysis is to draw attention to the fact that not only do many of these distribution modeling approaches differ in their ability to predict species locations, but they also differ in their modeling of the relationship of a species to different habitats, an extremely important component to understand if landscape-scale conservation planning efforts are to be designed and evaluated in a rigorous manner. Overall, the goals of these investigations are to reveal landscape-level patterns that influence declining species in longleaf pine savannas and to understand how existing methods to predict species distributions can be interpreted as we plan for the future.

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CHAPTER 2

EFFECTS OF FRAGMENTATION ON MOVEMENTS OF BACHMAN'S SPARROWS (*PEUCAEA AESTIVALIS*) AND PRAIRIE WARBLERS (*SETOPHAGA DISCOLOR*): OVER THE FIELD OR THROUGH THE WOODS?[1]

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[1] Jones, C. D., K. W. Stodola, M. Ward, J. Coombs, and R. J. Cooper. To be submitted to *The Auk*

ABSTRACT

Habitat fragmentation and loss of patch connectivity has led to the decline of many species. As habitats become more fragmented and patches become less connected, species are exposed to increased risks such as predation and parasitism that threaten population persistence. The longleaf pine savannas of the southeastern United States have experienced some of the highest rates of fragmentation and loss of connectivity of any ecosystem in North America. Consequently, they are home to many federally endangered and declining species across a wide variety of taxa. Corridors are one tool that can be used to alleviate some of the effects of fragmentation by increasing the connectivity between existing patches. We tested habitat permeability and corridor use in pine savannas in southern Georgia for Bachman's Sparrows (*Peucaea aestivalis*) and Prairie Warblers (*Setophaga discolor*) using displacement experiments and radio telemetry (Bachman's Sparrows only). Permeability was highest in unfragmented habitats for Bachman's Sparrows, while Prairie Warblers were less sensitive to the effects of fragmentation. Results from radio-telemetry indicated that Bachman's Sparrows used predicted corridors designed with the ArcGIS Corridor Designer Toolbox (Majka et al. 2006) on their return paths suggesting corridors are likely useful for conservation of Bachman's Sparrows in southern pine savannas. Efforts to increase connectivity of existing pine savannas in the Southeast will likely benefit habitat specialists in these settings.

INTRODUCTION

Habitat loss and fragmentation are the leading causes of species endangerment (Saunders et al. 1991, Foley et al. 2005). Fragmentation has contributed to the decline of many avian species occupying a wide variety of habitats across North America (e.g., Herkert 1994, Hagan et al. 1996). Fragmentation has been shown to increase the rate of predation (Storaas et al. 1999), nest depredation (Small and Hunter 1988, Rolstad 1991, Berger 1997), and nest parasitism

(Davis and Sealy 2000). Fragmented habitats can expose species to increased risk of disease (Allan et al. 2003), negatively influence overall health of individuals (Niu 2007), and can alter species morphology (Desrochers 2010). Additionally, fragmentation isolates local populations, alters immigration and emigration rates, and increases the risk of extinction (Hinsley et al. 1996, Fahrig 2003, Loehle 2007, Boscolo et al. 2008, Boscolo and Metzger 2011, Loehle and Eschenbach 2012).

Southeastern pine savannas are one of the most highly imperiled ecosystems in the United States due to their history of destruction and loss of natural disturbances necessary to maintain habitat quality (Jackson 1994, Landers et al. 1995, Earley 2004). Not only is there a dearth of existing habitat on the landscape (<1% of old growth longleaf pine savannas and less than 10% of the original estimated 60–90 million acres), but much of the remaining habitat exists as a highly fragmented mosaic of isolated forest patches (Earley 2004). The fragmented nature of the habitat has undoubtedly contributed to the imperilment of many southeastern pine savanna specialist species and continued habitat loss and fragmentation will further exacerbate this problem (Jackson 1994, Means 1996, Means et al. 1996, Earley 2004, Van Lear et al. 2005, Means 2006). Consequently, understanding the importance of connectivity and exploring measures to promote it for pine savanna species is of paramount importance to both management and conservation.

Corridors have been proposed as a conservation tool to help combat fragmentation. Corridors can be used to connect local populations, increase population size, and promote population stability (Simberloff et al. 1992, Beier and Noss 1998, Hanski 1998, Alderman et al. 2005). Connecting areas of suitable habitat can reduce the threats associated with stochastic events (Hinsley et al. 1995, Haddad and Baum 1999, Boscolo and Metzger 2011), promote gene flow (Keyghobadi 2007, Dixo et al. 2009, Wells et al. 2009), and support metapopulation persistence (Hanski 1994, Schooley and Branch 2011). The establishment of corridors is a proven conservation technique (Beier and Noss 1998, Haddad et al. 2003, Damschen and Brudvig 2012) that has facilitated the dispersal of numerous plant (Damschen and Brudvig 2012), insect (Haddad 1999, Haddad et al. 2000) and mammal species (Mabry and Barrett 2002), as well as birds (Haas 1995, Clergeau and Burel 1997). However, promoting connectivity requires an understanding of how species move through their environment.

Innate dispersal ability and the response of a species to the physical structure of its environment determines how a species responds to fragmentation and the value of a corridor (Bissonette and Storch 2003, Bennett et al. 2004, Fahrig 2007). Animal movement depends on the movement, perceptual, and gap-crossing abilities of the species in question (With et al. 1999). For instance, species that are habitat generalists are more likely to occupy and move through various habitat types (Gobeil and Villard 2008). Consequently, fragmentation may not be as detrimental to these species and promoting connectivity may be easier in comparison to habitat specialist species (Newbold et al. 2013). In addition, the vagility of a species influences how detrimental fragmentation will be (Robert et al. 2002), because movement ability dictates how easily a species can disperse to other suitable habitat. For instance, corridors appear to be more effective for less mobile taxa, presumably because highly mobile taxa can traverse more unsuitable habitat (Gilbert-Norton et al. 2010). Even within a highly mobile group such as birds, long-distance migratory species are less constrained by dispersal (Thorup 2006), potentially because they utilize highly fragmented landscapes during their migration (Packett and Dunning 2009).

Life-history characteristics of a species can determine the importance of fragmentation and the efficacy of corridor establishment. Species (or populations) that capitalize on natural disturbance events (such as fire, windthrow, insect damage, hurricanes, and floods), may be more robust to the effects of fragmentation because it is advantageous for them to colonize disparate patches of suddenly available habitat. High vagility, and other life history traits (e.g., diet, breeding season length, length of post-fledging period) may permit them to occupy landscapes with limited connectivity between patches of suitable habitat (Bélisle et al. 2007). In addition, species that are highly vagile may be less influenced by the effects of fragmentation because the effective fragmentation distance is decreased for these species. Therefore, species in southern pine savannas may not be sensitive to the effects of fragmentation because this habitat was historically burned at a high frequency (every 2-5 years; Huffman 2006), necessitating that many understory-dwelling species disperse in search of suitable habitat.

However, these presumptions may be misleading. For example, Jones (2008) found that Bachman's Sparrows (*Peucaea aestivalis*) — a species that inhabits regularly burned pine savannas — do not always abandon areas in longleaf pine savannas following fires, and instead remain near their original territories while the understory vegetation recovers. Bachman’s Sparrow is also less likely to colonize isolated patches of habitat, and densities of singing males are generally highest at distances ≤2 km from source populations (Dunning et al. 1995), indicating a possible threshold effect at this distance. Additionally, Northern Bobwhite (*Colinus virginianus*), which is a relatively immobile species, thrives in frequently burned pine savannas and typically lives within 1 km of its natal territory (Lehmann 1984, Dixon et al. 1996, Taylor et al. 1999). Thus, it is likely that connectivity plays an important role even for species that evolved in regions where disturbances were frequent and widespread. Because southern pine savannas require intensive management practices (e.g., frequent prescribed fire, thinning of timber) and there is such a dearth of existing habitat remaining, far more research has focused on habitat management strategies while largely ignoring issues of habitat connectivity.

Conservation of southeastern pine savannas is a multifaceted challenge that requires securing land for conservation and implementing management plans to ensure habitat quality. Few studies have examined the importance of connectivity for birds in southeastern pine savannas despite this area having some of the highest levels of avian endemism in the United States. Additionally, many of the endemics (e.g., Red-cockaded Woodpecker [*Picoides borealis*] and Bachman's Sparrow) have relatively poor dispersal capability. Furthermore, there are non-avian species currently federally listed under the endangered species act (e.g., frosted flatwoods salamander [*Ambystoma cingulatum*], reticulated flatwoods salamander [*Ambystoma bishopi*], gopher tortoise [*Gopherus polyphemus*]) or proposed for listing (e.g., eastern diamondback rattlesnake [*Crotalus adamanteus*]) that have low vagility and would likely benefit from increased connectivity of pine savannas, even at small scales.

We used displacement experiments to test the permeability of agricultural fields for two avian species: one that is a pine savanna habitat specialist and one that often occupies pine savannas, but is more of a habitat generalist. Specifically, we translocated territorial male Bachman's Sparrows (pine savanna specialist) and Prairie Warblers (*Setophaga discolor*, a habitat generalist) to test the effects of distance and habitat connectivity on the probability a displaced subject would return to its territory. Translocation is a proven, albeit underutilized, technique towards identifying how landscape characteristics influence species movement (e.g., Butler et al. 2005, Brown et al. 2009, Kennedy and Marra 2010, Ibarra-Macias et al. 2011, Tremblay and St. Clair 2011). We further explored the effects of fragmentation by investigating the specific movements of Bachman's Sparrow in relation to agricultural barriers using radio telemetry. Finally, we investigated whether habitat suitability and permeability were similar by testing the predictive ability of corridor models for translocated Bachman's Sparrow.

METHODS

Study species

Bachman's Sparrow.– Bachmann's Sparrow is a resident to short-distance migrant species that inhabits frequently burned (every 3–5 years) or disturbed pine savannas in the Southeast (Dunning 2006). Its population has declined >3% per year across most of its range since 1966 (Sauer et al. 2011). The dependency of this species on frequent fire is such that it will abandon habitats if the area has not been recently burned (≤3 year fire return interval). The species shows high site fidelity in well-maintained habitats (Cox and Jones 2007) and there is limited evidence for long-distance dispersal (Cox and Jones 2010) or seasonal migration (but see Dunning 2006). Habitat connectivity may be important (Dunning et al. 2009), but the effects of anthropogenically-induced fragmentation are unknown.

Prairie Warbler.– Prairie Warbler is a long-distance migratory species that often inhabits southeastern pine savannas with open canopies similar to Bachman's Sparrow. However, Prairie Warbler is more of a habitat generalist and is also found in abandoned fields, coastal dunes with a shrubby component, and swamp habitats (Nolan et al. 1999). Site fidelity in this species is similar to other migratory warblers (58–65%) and Bachman's Sparrow (Nolan et al. 1999). Like Bachman's Sparrow, the Prairie Warbler has declined dramatically across its range, presumably due to loss of suitable habitat (Nolan et al. 1999).

Study Area

Fort Benning is located near Columbus, GA and straddles the Upper Coastal Plain and Sandhills (which occupy the transition area between the Upper Coastal Plain and Piedmont) physiographic regions. It was established in 1920 on former plantation and agricultural land near the Chattahoochee River (Kane and Keeton 1998). Because of limited development prior to its establishment as a military base and large areas of restricted access, Fort Benning supports many denizens of the longleaf pine ecosystem that were once common across the Southeast, but are now in drastic decline elsewhere. Gopher tortoise, Bachman's Sparrow, and Red-cockaded Woodpecker are among declining, threatened and endangered species that are found on the fort (DoD 2009). Fort Benning contains approximately 90,000 acres (36,400 ha) of upland pine habitat, but also includes over 90,000 acres (36,400 ha) of other habitat types including ponds, wetlands, bottomland hardwoods, areas resembling agricultural pastures and urban areas.

Site selection

We selected two landscape types on Fort Benning to conduct translocation experiments: continuous and fragmented pine forests. The continuous pine forest site was located within a 500 ha patch of contiguous upland longleaf and loblolly pine habitat (Figure 2.1). The fragmented pine forest consisted primarily of longleaf and loblolly pine forest patches that were interrupted by two large fields (Figure 2.2) consisting predominantly of bahia grass (*Paspalum notatum*) and strips of wildlife plantings such as grain sorghum (*Sorghum* sp.). The combined area of the fields and forest patches was approximately 600 ha. One field was approximately 550–950 m by 1,400 m (hereafter large barrier) and the other was approximately 250 m by 1,500 m (hereafter small barrier).

Translocation Experiments

We used experimental translocations of Bachman's Sparrows and Prairie Warblers to examine effects of translocation distance and landscape permeability among and within forest patches maintained with prescribed fire on Fort Benning. Landscape permeability is the degree to which habitat or landscape features permit—or function as a barrier to—species movement. Landscapes with low permeability are traversed less often or with more difficulty, while high permeability permits movement in an unrestrictive manner. Male Bachman's Sparrows and Prairie Warblers were captured, color-banded, and released either ~1 km or ~2 km from their capture location and across either continuous (Figure 2.1; high habitat permeability) or fragmented (Figure 2.2; low habitat permeability) pine habitat. Time between capture and release was ≤30 minutes. All translocations occurred between 0700 and 1000. The distance and permeability category that an individual was assigned was primarily determined by its capture location and therefore was non-random. Territories were intensively surveyed every hour for four hours the day of release and beginning at 0630, for two days following translocation. These methods generally follow previous experimental translocation protocol used by Gobeil and Villard (2008). Although we continued to monitor the empty territories, we discontinued intensive monitoring after the 48-hour search period if the individual did not return within that time frame due to the limited number of field assistants required to monitor multiple territories while additional translocations were being conducted.

Assessment of return path

We attached 0.7 g radio transmitters (< 4% of body weight) to 14 Bachman's Sparrows using a thigh-harness (Rappole and Tipton 1991). Bachman's Sparrows with transmitters attached via a thigh-harness exhibit no adverse effects (e.g., Stober and Krementz 2006). After attaching the transmitters we released all sparrows back on their territories to allow them to become accustomed to the transmitter. We subsequently recaptured sparrows for translocation after a minimum period of 48 hrs. Time between initial capture and release — and recapture and displacement — was ≤30 minutes. We translocated all birds with transmitters into the fragmented pine forest to assess how Bachman's Sparrows respond to unsuitable habitat. Specifically, we were interested in the movement decisions of Bachman's Sparrows when faced with small (300–400 m wide) and large (600–1,000 m wide) patches of open fields dominated by bahia grass, a non-native perennial typically planted for forage. Five of the displacements were short-distance (~ 1 km) and across a small open field (Figure 2.1). Five subjects were short-distance (~1 km) displacements across a large open field (Figure 2.1). The last four subjects were long-distance displacements (~ 2 km) that required crossing or navigating around both fields (Figure 2.1).

Breeding Status Assessment

Because we suspected breeding status may influence the time it takes an individual to return, and many Bachman's Sparrows often exhibit no physical evidence of breeding (Tucker et al. 2006), we assessed breeding status of Bachman's Sparrow and Prairie Warbler using an indirect index similar to Vickery et al. (1992). We conducted breeding status assessments while attempting to catch adults prior to translocation and on follow-up visits when monitoring their return. We categorized breeding status as: (1) only a singing male was observed, (2) a singing male was paired with a female, (3) the adult male was seen carrying food, or (4) fledglings were present in the territory. Fledged Bachman's Sparrows give a distinctive call when they are being tended by adults and adults frequently emit a characteristic chip note when nestlings or fledglings are present.

Vegetation Measurements

We suspected territory quality may influence the amount of time it took an individual to return to its territory (Gobeil and Villard 2008). Therefore we collected vegetation measurements within a 0.04-ha area surrounding the capture location using modified methods of James and

Shugart (1970). Groundcover composition, which has been shown to influence nest site selection in Bachman's Sparrow (Jones et al. 2013), was estimated by recording the percentage of grass, herbaceous plants, woody plant cover, bare ground, and litter within a 1-m^2 frame. Woody shrub components — a habitat characteristic that has been shown to influence Bachman's Sparrow site preferences (Haggerty 1998, Jones et al. 2013) — were quantified by walking transects at each sampling location and recording the number of short-statured shrubs (0.5–1 m) and tall statured shrubs (>1 m) that occurred within a 1-m radius every two meters along a 20-m transect. All trees greater than 3 cm in DBH and within 25 m of the sampling point were also measured and the species recorded. A hardwood (all *Quercus* spp.) and pine (all *Pinus* spp.) basal area also was generated for each capture point. Groundcover and woody shrub components were summarized by averaging all values in each category for each point.

Corridor Design and Analysis

We were interested in examining how computer generated corridors matched the return paths of the sparrows that were displaced and tracked using radio telemetry to see if commonly held assumptions about corridor design were relevant to Bachman's Sparrow movements. We used the ArcGIS Corridor Designer Toolbox (Majka et al. 2006) to create digital representations of putative corridors between patches of habitat that were also capture and release locations in our experiment (Figure 2.3). We created a habitat suitability index based on southeastern GAP landcover data (USGS 2011) and expert opinion for Bachman's Sparrow habitat suitability values of different landcover types (Table 2.1). We set the minimum patch size to zero for our habitat patch map because of the relatively small size of our study area. A least-cost-path raster dataset was created based on this index and putative corridors were then generated. A least-cost-path raster dataset is a pixel-based model of the ability of an individual to move through a given area. As a subject moves from pixel to pixel, the “cost” of each pixel accumulates along the path. Pixels of higher habitat suitability (high permeability) have a lower cost, while pixels of lower habitat suitability (low permeability) have a higher cost. Thus, the shortest distance between two points may not always have the lowest cost.

We examined three different corridors for our experimental landscape: a corridor that was made up of the most permeable 1% of the landscape, a corridor made up of the most permeable 5%, and a corridor made up of the most permeable 10% (hereafter referred to as 1%, 5%, and 10% corridors). Different corridor percentages were examined to incorporate uncertainty in the corridor design (see Beier et al. 2008). We then analyzed the return paths of Bachman’s Sparrows relative to the putative corridors for which we had the best data on radio-transmitter return paths following displacement (*n*=9). Some individuals were not included in the analysis because portions of their return paths were ambiguous due to the speed at which the subject returned and the difficulty in maintaining a consistent signal.

Statistical Analysis

We used logistic regression analysis to determine the influence of landscape habitat permeability, breeding status, and territory vegetation characteristics on the probability that a Bachman’s Sparrow or Prairie Warbler returned within a 48-hour period. Bachman’s Sparrows and Prairie Warblers were analyzed separately. A global model containing all predictor variables was generated for each species and then subsets of the variables were used to construct candidate models (Table 2.2). An information-theoretic approach (Burnham and Anderson 2002) was used to create and assess the relative fit of each model. Fit of each model was determined using Akaike’s Information Criterion (AIC; Akaike 1973) with the small sample bias adjustment (AICc; Hurvich and Tsai 1989).

Model averaging was used to incorporate uncertainty in model selection into the parameter estimates. Model-averaged estimates of the coefficients and standard errors were calculated according to Burnham and Anderson (2002). Estimates of the regression coefficients and standard errors were weighted for each model according to their corresponding AICc weight and then used to compute a composite model. The composite model was comprised only of parameters contained within the confidence set of models. These were then used to assess the relative effect of the parameters on the probability that a subject returned within 48 hours of displacement. All model inferences were based on the resulting composite models. Precision of model-averaged coefficients was evaluated with 95% confidence intervals.

To assess whether or not there was an effect of the transmitters on the ability of the Bachman's sparrows to return to their territories, we used logistic regression to examine the factors influencing the probability an individual — those with and without transmitters — would return in the fragmented habitat. We built a set of candidate models incorporating variables for breeding status, whether or not an individual was wearing a transmitter, and the distance of the displacement (Table 2.2). An information-theoretic approach (Burnham and Anderson 2002) was used to create and assess the relative fit of each model. Fit of each model was determined using AIC with the small sample bias adjustment. The top models for this analysis included the model for displacement distance and the null model with a combined weight of 0.66 (Table 2.3). The parameter estimates indicated that only the effect of distance was significant (Table 2.4). Therefore, we felt justified in combining our data for subsequent analyses from both the birds that received transmitters and those that did not.

We used paired t-tests to compare the straight-line distance a subject traveled to the distance of their actual path of their return. We also used paired t-tests to compare the proportion of the subjects' return paths that were within the 1%, 5%, and 10% corridors against the proportions of the straight-line path that were within the 1%, 5%, and 10% corridors. A straight line comparison was used because these represent the optimal return paths if habitat was not a factor in the subjects' choice of their path of return following displacement. Therefore, if Bachman's Sparrows were selecting the corridors during their return, a higher proportion of their actual return path would fall within a corridor than it would if the return path was simply a straight line (the shortest possible distance) from the release location to the capture site.

RESULTS

Bachman's Sparrow translocation. – We translocated 51 Bachman's Sparrows, 23 were moved in the continuous pine forest (1 km translocations [n=10], 2 km translocations [n=13]) and 28 were moved in the fragmented pine forest (1 km translocations [n=18], 2 km translocations [n=10]), including those with transmitters (Table 2.5). Over three-quarters (18 of 23) returned within 48 hours in the continuous pine forest while just over half (15 of 28) returned in 48 hours in the fragmented pine forest.

The top model for predicting whether or not a Bachman's Sparrow returned following translocation only included the parameters Distance and Barrier (Table 2.6; $w_i = 0.74$). The parameter estimates for both the distance and fragmentation variables indicated that as the level of fragmentation and the distance an individual was displaced increased, the probability an individual would return within 48 hours was lower (Table 2.7).

Prairie Warbler translocation. – We translocated 25 Prairie Warblers, 11 were moved in the continuous pine forest (6 displaced ~1km, 5 displaced ~2km) and 14 were moved in the fragmented pine forest (7 displaced ~1km, 7 displaced ~2km). All of the Prairie Warblers translocated in continuous habitat (11 of 11) returned within 48 hours, while 12 of 14 translocated in the fragmented pine forest returned within 48 hours.

The top models predicting whether or not a Prairie Warbler returned to its territory following translocation were the model for pine basal area and the null model (Table 2.8). The two models combined carried 49% of the weight of all the models. However, the model-averaged parameter estimate (Table 2.9) for the influence of pine basal area on return probability indicated that the effect was not significant and very weak (odds ratio of 1.009), which can be interpreted that a 10% increase in pine basal area would increase the probability of return <1%.

Habitat specific movements

For Bachman's Sparrows that were affixed with radio transmitters, all long distance movements (>400 m) of birds occurred within an hour of sunrise or sunset. No radio-monitored birds made long distance movements during the middle of the day (1100–1930). Three out of five short-distance displacements directly crossed the narrow open field, while only one of five short-distance individuals crossed the large open field by first flying into a small fence-row of shrubs in the middle of the field. The remaining individuals either followed the shrubby edge surrounding the field (n=6), or remained near the release location for >48 hours (n=4).

Return paths of sparrows included higher proportions of the corridor ($\bar{x}$ = 0.51±0.14) than straight-line return paths ($\bar{x}$ = 0.31±0.26) when considered within the 10% corridor, $t_{8=2.34,\ p=0.04}$. Proportions of return paths in the 5% corridor (0.31±0.14 vs. 0.16±0.14) and the 1% corridor (0.13±0.16 vs. 0.02±0.03) were not significantly different from proportions that were derived from straight-line paths (p=0.11 and p=0.53, respectively). The actual return paths for the subjects ($\bar{x}$ = 1,748.6 m ± 694.2 m) were also significantly longer than straight-line distance ($\bar{x}$= 1007.6 m ± 183.1 m; $t_{8=3.14,p=0.01}$).

DISCUSSION

Fragmentation and displacement distance influenced the probability of Bachman's Sparrows returning to their territory within 48 hours, but did not influence Prairie Warblers. Bachman's Sparrows have a relatively sedentary nature (Cox and Jones 2011) which may make them less adept at traversing longer-distances in unsuitable habitat in comparison to more vagile species. Conversely, Prairie Warblers traverse >1000 km during migration (Nolan et al. 1999) and must utilize a variety of habitats during this process. Consequently, Prairie Warbler movement may not be as impeded by patches of unsuitable habitat in comparison to Bachman's Sparrow, which our data demonstrate. Fragmentation may be more problematic for sedentary species such as Bachman's Sparrow in comparison to migratory species such as Prairie Warbler because of each species' dispersal limitations. Seemingly appropriate and suitable habitat for Bachman's Sparrow is often unoccupied (Buckelew and Hall 1994), suggesting that dispersal limitation is prevalent in this species (Gaston 2009).Consequently, distance to the nearest source population is the primary cause for their absence in these cases. However, seemingly appropriate, yet unoccupied, habitat for Bachman's Sparrow is often occupied by Prairie Warblers in our study site (pers. obs.). Prairie Warblers are also much more widespread, not only in our study area (Fischer et al. 2011) but throughout eastern North America (Nolan et al. 1999). Although both species are exhibiting population declines, Bachman's Sparrow has been declining at a greater rate.

Fragmented landscapes may be more difficult to traverse for Bachman's Sparrow because unsuitable habitat creates a more impenetrable barrier to dispersal in comparison to more vagile species like Prairie Warbler. Unsuitable habitat rarely creates an impenetrable barrier to dispersal (Haddad 1999). However, we found that large agricultural fields were rarely traversed by Bachman's Sparrow, which instead moved around the edge of the field and through areas of suitable habitat. Bachman's Sparrow's reluctance to directly cross a large (600-1000 m wide), open field likely contributed to the decreased probability of its return in the fragmented landscape. Furthermore, return probability decreased with increasing distance, presumably because multiple barriers can impede the movement and the effect is cumulative even when the barriers are relatively narrow (Bélisle and Cassady-St Clair 2002). Thus, southeastern pine savannas that are highly fragmented may be difficult for Bachman's Sparrows to traverse, which only reinforces the importance of connectivity in this species (Dunning et al. 1995).

Southeastern pine savannas are highly ephemeral habitats that require frequent fires for proper ecosystem functioning. Species such as Bachman's Sparrow and Prairie Warbler that reside in highly ephemeral habitats should be better dispersers (Gadgil 1971, Paradis 1998, Travis and Dytham 1999 – from Fahrig 2007), and more robust to the effects of fragmentation because it is advantageous for them to colonize disparate patches of suddenly available habitat (Bélisle et al. 2007). However, our data suggest these presumptions may be misleading and that Bachman's Sparrow may be dispersal limited because of the fragmented nature of their habitat. Even though southeastern pine savannas require frequent fires, Bachman's Sparrows exhibit high rates of annual site fidelity (>60% of males remaining on the same or nearby territories year-to-year; Cox and Jones 2007) similar to (or greater than) other neotropical migrants. Therefore, this species may not move around as much as one would presume. In addition, dispersal distances are likely short for adults and the probability of an adult male emigrating following prescribed fire is low (Cox and Jones 2010). Bachman's Sparrows are also less likely to colonize isolated patches of habitat and densities of singing males are generally highest at distances ≤2 km from source populations (Dunning et al. 1995), further indicating dispersal limitation of the species in a fragmented landscape. Low dispersal ability in a fragmented landscape may be why Bachman's Sparrows do not always abandon areas in longleaf pine savannas immediately following fires, and instead remain near their original territories while the understory vegetation recovers (Jones 2008).

Corridors may be an effective means of combating fragmentation in southeastern pine savannahs because they can promote movement among habitat patches. Bachman’s Sparrows preferred moving through the predicted corridors on their return paths over the shortest possible distance. They also crossed small barriers more frequently than large ones indicating that they are capable of some movement across unsuitable habitat. Although our study took place at a relatively small scale, it demonstrates that habitat connectivity is still important in facilitating the movement of Bachman’s Sparrows even in a local landscape context. Some of our radioed birds spent several days beyond the 48 hour time period before they returned to their territories. Birds that spent more time before returning were primarily those released at the 2-km distance. The number of days that a bird remains in a release patch before returning to its territory has been used in other studies as a metric for measuring permeability (Castellón and Sieving 2006). We frequently observed subjects with radio transmitters moving laterally along field edges with daily movements in excess of 1km that typically resulted in the subject returning near its release location. Unfortunately, we did not have individuals with transmitters that were not displaced, so we were unable to make this direct comparison in our study. However, a concurrent study of radio-transmittered Bachman’s Sparrows in Florida found that average daily movements of many Bachman’s sparrows were >400 m (Brown 2012).

Conservation of southeastern pine savannas is a challenging endeavor and our data demonstrate that promoting connectivity can be a helpful means. Many declining southeastern pine savanna specialists are dispersal limited, including Red-cockaded woodpeckers, Northern Bobwhite, gopher tortoise, and flatwoods salamanders. Numerous programs have already been initiated to help combat this decline. For instance, the Department of Defense's Army Compatible Use Buffer (ACUB) program places lands adjacent to Army installations under easements to reduce conflicts with local urban areas and to preserve habitat for species (some of which are protected under the Endangered Species Act) the DoD is required to manage. If conservation decision makers face a choice between creating new habitat that is unconnected to existing habitat versus improving nearby habitat that may be colonized at a faster rate, the latter may be the more efficient option. Indeed, for species that are highly disturbance dependent such as Bachman's Sparrow, maintaining habitat connectivity is an important consideration for maintaining stable populations.

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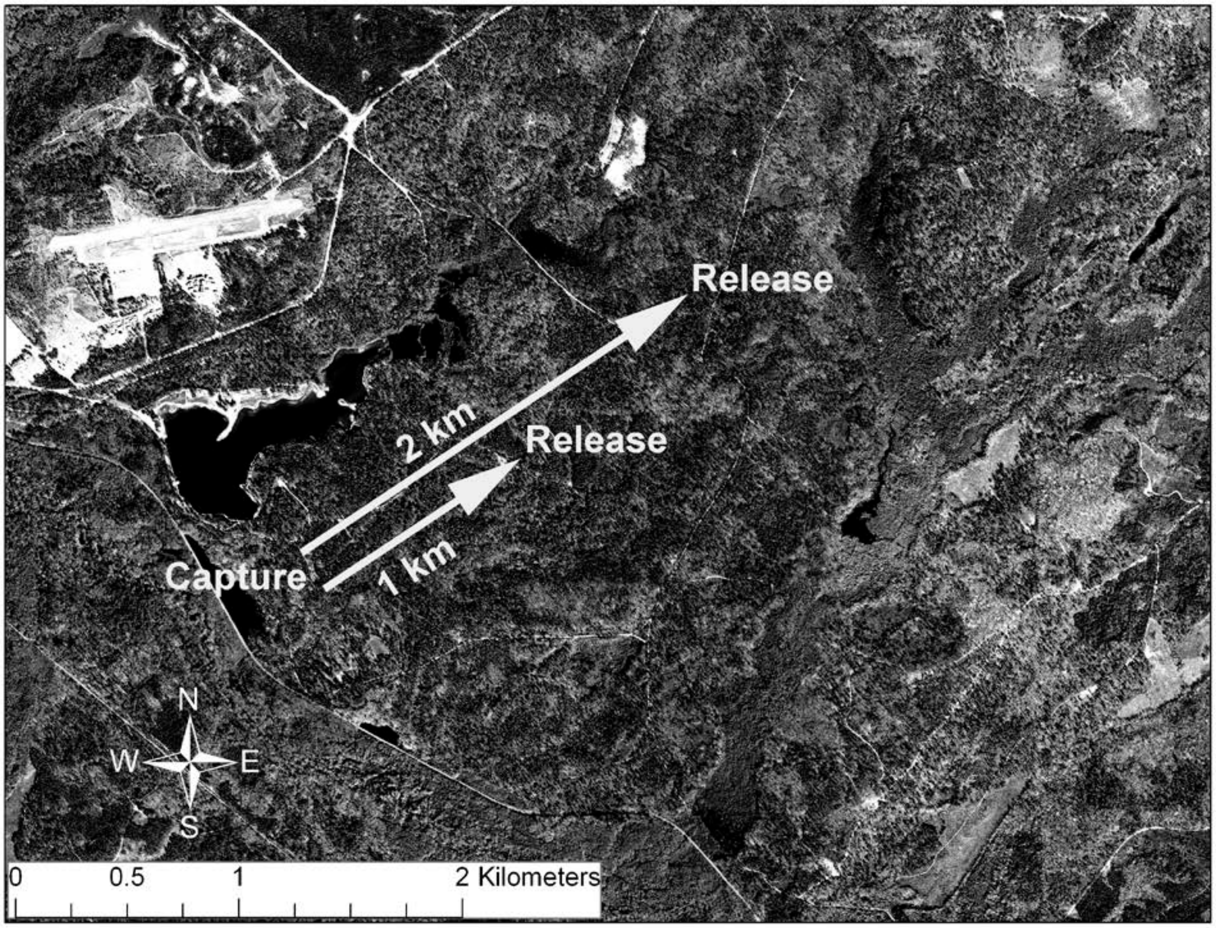

Figure 2.1. Example of landscape configuration with high permeability and experimental translocations. Darker areas indicate upland pine habitat (and water). Lighter areas indicate deciduous habitat. Entire location is forested primarily by upland longleaf pine with the exception of the lake and small development area in the upper left.

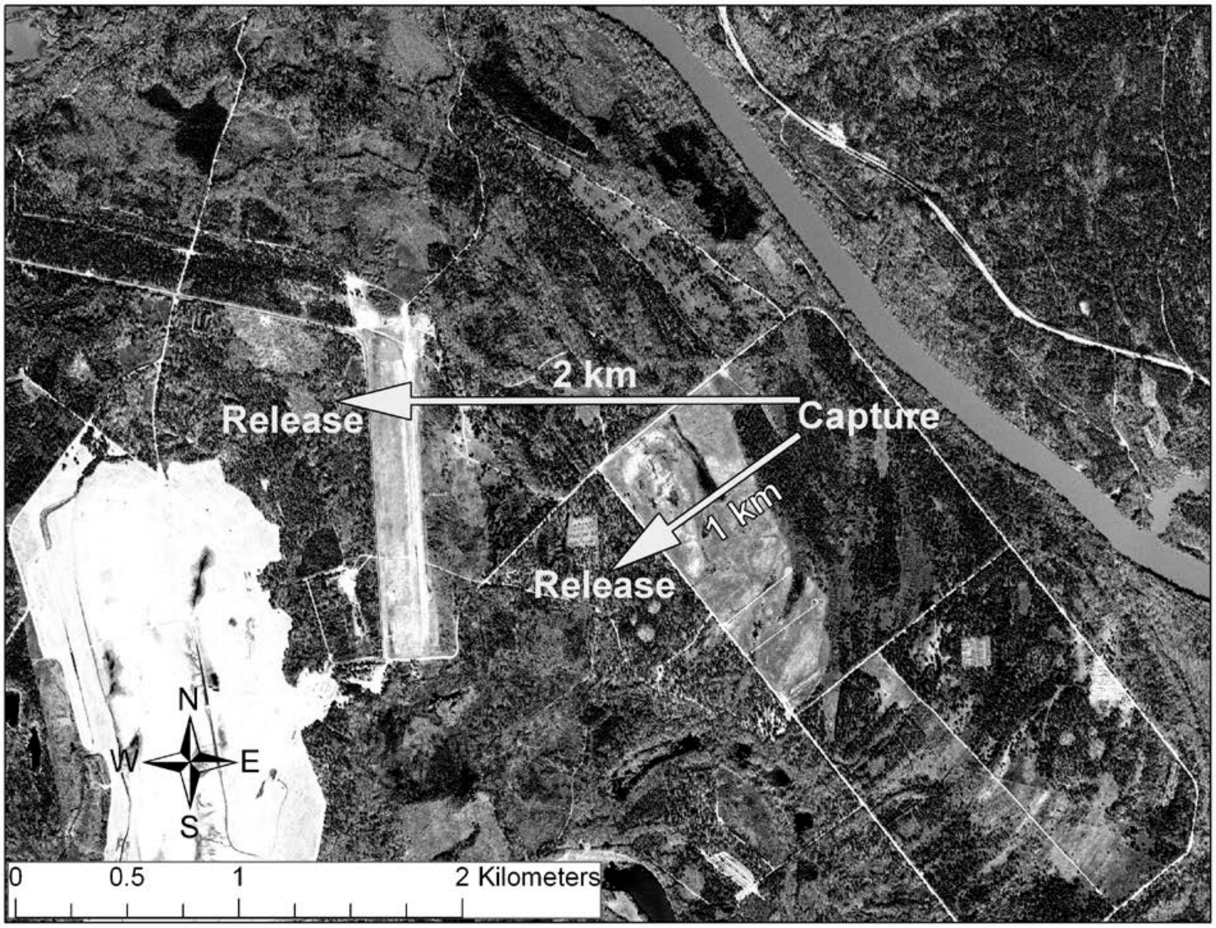

Figure 2.2. Example of landscape configuration with low permeability and experimental translocations. Darker areas represent forested locations while lighter areas indicate fields and deciduous habitat**.**

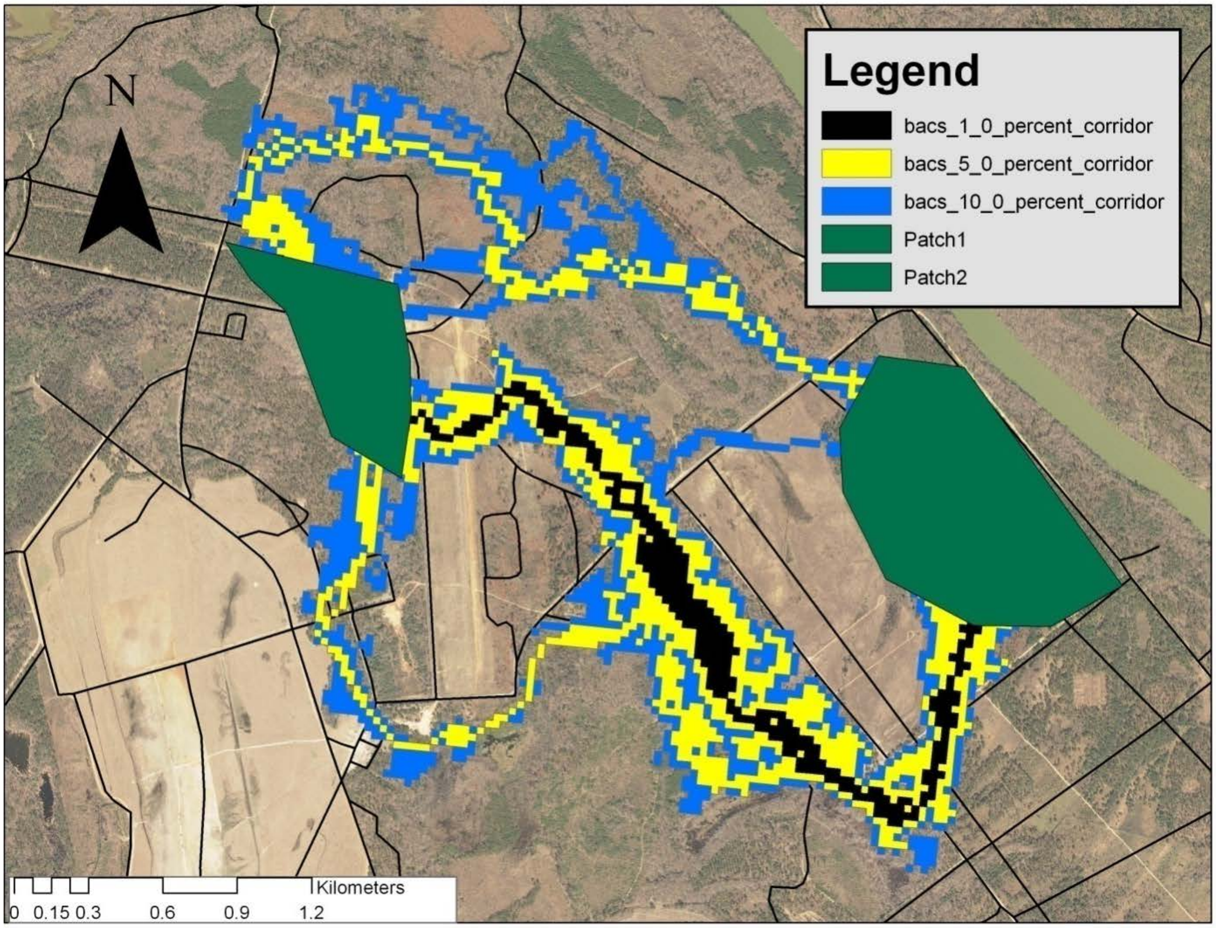

Figure 2.3. Putative corridors (10%=blue, 5% =yellow, 1% = black) generated using Corridor Design Tool in ArcGIS. Green polygons represent patches of Bachman's sparrow habitat.

Table 2.1. Habitat suitability values assigned to Southeastern GAP (USGS 2011) landcover National Vegetation Class (NVC) data in order to create putative corridors between patches of Bachman's sparrow habitat at Fort Benning, GA.

NVC Macro Class	**Suitability Value**
Longleaf pine and sand woodland	90
Longleaf pine and sand woodland	90
Longleaf pine and sand woodland	90
Southern Mixed Deciduous-Evergreen Broadleaf Forest	0
Southeastern N. American Ruderal Forest and Plantation	75
Southeastern N. American Ruderal Forest and Plantation	65
Southeastern N. American Ruderal Forest and Plantation	50
Southeastern N. American Ruderal Forest and Plantation	80
South-Central Oak-Hardwood & Pine Forest	50
Central Mesophytic Hardwood Forest	25
Southern Floodplain Hardwood Forest	0
Southern Floodplain Hardwood Forest	0
Southern Coastal Plain Evergreen Hardwood & Conifer Swamp	0
Southern Coastal Plain Evergreen Hardwood & Conifer Swamp	0
Southern Coastal Plain Basin Swamp	0
Wet Longleaf Pine and Southern Flatwoods	50
Atlantic Gulf Coastal Plain Bog and Fern	0
Herbaceous Agricultural Vegetation	0
Herbaceous Agricultural Vegetation	0
Recently Disturbed or Modified	0
Recently Disturbed or Modified	0
Recently Disturbed or Modified	0
Recently Disturbed or Modified	0
Open Water	0
Developed and Urban	0
Developed and Urban	0
Developed and Urban	0

Table 2.2. Hypotheses and candidate models for the influence of vegetation characteristics, breeding status, fragmentation, displacement distance, and transmitter effect.

Hypothesis	**Candidate Model**
None of the variables considered are important	Null
Return probability is primarily determined by territory quality as measured by vegetation characteristics	Groundcover composition + Shrub Structure and Prevalence + Canopy Cover + Pine Basal Area + Hardwood Basal Area
Return probability is influenced only by the pine forest basal area	Pine Basal Area
Return probability is influenced only by the pine forest basal area	Hardwood Basal Area
Return probability is influenced by breeding status, displacement distance, fragmentation, and presence of a radio transmitter	Breeding Status + Distance + Fragmentation + Radio
Return probability is influenced only by breeding status	Breeding Status
Return probability is influenced only by the distance that an individual was displaced	Distance
Return probability is influenced only by whether or not the landscape is fragmented.	Fragmentation
Return probability is influenced by both the distance an individual was displaced and the breeding status of the individual	Distance + Breeding Status
Return probability is influenced by both the distance an individual was displaced and habitat fragmentation	Distance + Fragmentation
Return probability is influenced by breeding status and fragmentation	Breeding Status + Fragmentation
Return probability is influenced solely by the presence of a radio transmitter	Radio

Table 2.3. Top models (ΔAICc ≤ 2), AICc, ΔAICc, and AICc weight (w_i) for predicting whether or not Bachman's Sparrows with and without radio transmitters in fragmented habitat returned within 48 hours of being displaced from their territories at two different distances (1 or 2 km).

Model	**AICc**	**ΔAICc**	**w_i**
Distance	37.31	0	0.48
null	39.26	1.94	0.18

Table 2.4. Parameter estimates and 95% confidence intervals (CI) for the top model predicting whether or not a Bachman's Sparrows with and without radio transmitters in fragmented habitat returned within 48 hours of being displaced from their territories at two different distances (1 or 2 km).

Parameter	Estimate	SE	Odds Ratio	95 % Lower CI	95% Upper CI
Distance_Cat	-1.72	0.87	0.18	0.03	0.98

Table 2.5. Summary of results of displacement experiments of Bachman's sparrows with radio transmitters.

Number of Bachman's Sparrows	Distance Category	Field Width	Number that crossed field	Number that returned w/in 48 hours
5	1 km	250 m	4	5
5	1 km	550-900 m	1	4
4	2 km	250 m and 550-900 m	0	0

Table 2.6. Top five models, AICc, ΔAICc, and AICc weight (wi) for predicting whether or not a Bachman's sparrow (including birds with a radio transmitter) returned within 48 hours of being displaced from its territory at two different distances (1 or 2 km) and across two landscape configurations (continuous or fragmented).

Model	AICc	ΔAICc	w_i
Distance + Barrier	57.56	0	0.74
Distance	61.56	4	0.1
Breeding Status + Distance + Barrier + Radio	62.21	4.65	0.07
Distance + Breeding Status	64.21	6.65	0.03
null	65.35	7.79	0.01

Table 2.7. Parameter estimates, odds ratio, and 95% confidence intervals (CI) for the top model predicting whether or not a Bachman's Sparrow returned within 48 hours of being displaced from its territory at two different distances (1 or 2 km) and across two landscape configurations (continuous or fragmented).

Parameter	Estimate	SE	Odds Ratio	95% Lower Odds Ratio CI	95% Upper Odds Ratio CI
Distance	-2.11	0.78	0.12	0.03	0.56
Barrier	-1.81	0.79	0.16	0.03	0.77

Table 2.8. Top models (ΔAICc ≤ 2), AICc, ΔAICc, and AICc weight (wi) for predicting whether or not a Prairie Warbler returned within 48 hours of being displaced from its territory at two different distances (1 or 2 km) and across two landscape configurations (continuous or fragmented).

Model	**AICc**	**ΔAICc**	**w_i**
Pine basal area	18.70	0	0.27
null	19.13	0.43	0.22

Table 2.9. Model-averaged parameter estimates and 95% confidence intervals (CI) for the top models (ΔAICc ≤ 2) predicting whether or not a Prairie Warbler returned within 48 hours of being displaced from its territory at two different distances (1 or 2 km) and across two landscape configurations (continuous or fragmented).

Parameter	**Estimate**	**SE**	**Odds Ratio**	**95% Lower Odds Ratio CI**	**95% Upper Odds Ratio CI**
Pine BA	0.009	0.013	1.01	0.98	1.04

CHAPTER 3

CONSIDERATION OF THE NON-STATIONARY EFFECTS OF THE RED-COCKADED WOODPECKER (*PICOIDES BOREALIS*) AS AN UMBRELLA FOR OTHER DECLINING AVIAN SPECIES

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[1] Jones, C. D., and R. J. Cooper. To be submitted to *Avian Conservation and Ecology*

ABSTRACT

Umbrella species can be a useful tool for the conservation of non-target species that share similar habitats and population trajectories. The influence that management actions have on non-target species is seldom evaluated with direct consideration for their non-stationary influence across the landscape. Examination of the spatially heterogeneous effects of management strategies can reveal patterns which can be used to improve model parameterization and identify locations where the umbrella is not working effectively. Geographically weighted regression is a tool that can be used to explore the non-stationary relationship between an umbrella species and those that are intended to receive secondary benefits from single-species management. This study investigated the non-stationary relationship between locations of Red-cockaded Woodpecker (*Picoides borealis*) clusters which are extensively managed to meet federal criteria and five non-target avian species (Bachman's Sparrow [*Peucaea aestivalis*], Brown-headed Nuthatch [*Sitta pusilla*], Field Sparrow [*Spizella pusilla*], Northern Bobwhite [*Colinus virginianus*], and Prairie Warbler [*Setophaga discolor*]), listed as species of management concern by the International Partners in Flight and the Georgia Department of Natural Resources. Results suggest that management for Red-cockaded Woodpeckers on Fort Benning, GA increases overall diversity of these non-target species, but this relationship is stronger in some areas compared to others. Non-stationary effects of management and species response should be considered when implementing population recovery strategies for the endangered Red-cockaded Woodpecker.

INTRODUCTION

Monitoring and managing all species within an ecosystem is a daunting task that can never be fully realized. Therefore, conservation strategies frequently focus on a few species or even a single species and direct activities aimed toward their preservation. Actions taken to conserve one species may not promote the sustainability of all other species within the community (Simberloff 2007, Simberloff 1998, Hunter 1994). In fact, the conservation of a single species should be balanced against the marginal detriment it may bring to other species who do not share the same resource requirements (Hunter 1994). In recent decades, conservation management activities have invoked strategies that aim to conserve a single species while simultaneously promoting biodiversity within the same habitats (Simberloff 1998). One such approach, the umbrella species concept, describes the strategy whereby the protection of a single species confers protection to many, but not necessarily all, species that occupy the same habitat.

The umbrella species concept has been invoked to promote the conservation of large habitat patches, particularly under the auspices of the Endangered Species Act (ESA). For example, grizzly bears (*Ursus arctos horribilis*) have been suggested to possess many of the characteristics that constitute an effective umbrella species and are currently listed as *Threatened* in the contiguous United States and are therefore granted protection under the ESA. Grizzly bears are considered effective umbrella species because they require large tracts of various habitat types and many other species are protected as a result of implementing protection for grizzly bears (Noss et al. 1996). Species that benefit from the preservation of grizzly bears include other large carnivores and ungulates such as gray wolf (*Canis lupus*), mountain lion (*Puma concolor*), moose (*Alces alces*), and Rocky Mountain elk (*Cervus canadensis*). However, it has been noted that not all species receive protection from conservation efforts aimed to protect grizzly bears, particularly reptiles and amphibians (Noss et al. 1996). Other species or suites of organisms may serve as more effective conservation tools that result in the preservation of more species in need of protection (Noss et al. 1996).

The Northern Spotted Owl (*Strix occidentalis*) is an example of the application of the umbrella species concept intended to protect the old-growth conifer forest communities of the Pacific Northwestern United States. Currently listed as *Threatened* under the ESA, the life history requirements of this species are thought to encompass many aspects of old-growth forest structure in the Pacific Northwest and that by protecting it, other smaller mammals and species at lower trophic levels that are negatively affected by logging would also be preserved (Dawson 1987). However, Northern Spotted Owl populations are continuing to decline and the relationship between old growth forests and the species' persistence suggests that a mosaic of older forest and other vegetation types may improve fitness (Franklin et al. 2000). The often complex relationships among species and the multiple unidentified factors driving wildlife populations complicate efforts to manage entire ecosystems, but single-species management is frequently the only means available to achieve this goal.

A proposed umbrella species, the Red-cockaded Woodpecker (*Picoides borealis*), is a longleaf pine (*Pinus palustris*) specialist that was formerly found across large expanses of the southeastern United States (Jackson 1994). Due to large-scale destruction of longleaf pine forests across the South over the past 150 years, the Red-cockaded Woodpecker is classified as *Endangered* by the United States Fish and Wildlife Service and therefore is afforded protection under the ESA. This species has been intensively studied with over 1,700 publications resulting from various inquiries into its habitat requirements and relationship to ecosystem health (Jackson 1994). Multiple studies have shown that management for Red-cockaded Woodpeckers can be beneficial for several avian species that use the same habitat (Wilson et al. 1995, Plentovich 1998, Simberloff 1998, Conner et al. 2002, Cox and Jones 2007), but these benefits are not without scrutiny.

Although single-species management is frequently employed because it often generates funding, criticism of the concept is wide-spread (Roberge and Angelstam 2004). For example, the black rhinoceros (*Diceros bicornis*) has been proposed as an umbrella species; however, changes in black rhino populations may not reflect changes in the populations of other species under the umbrella, suggesting that the black rhinoceros may be a relatively ineffective umbrella species (Berger 1997). Others have found that the umbrella species concept is particularly impotent if the species (or suite of species) chosen are not complimentary (i.e., do not share similar habitat requirements or life history traits) and that the random selection of species may perform just as well in many instances (Andelman and Fagan 2000, Roberge and Angelstam 2004).

Results of examinations of the proof of concept for umbrella species cannot be considered successes or failures until they are evaluated quantitatively (Roberge and Angelstam 2004). Additionally, the degree to which the umbrella species concept is effective undoubtedly varies over space, but is seldom examined. Therefore, in order to examine how and where it is effective, spatial non-stationarity should be considered. Non-stationarity is the heterogeneity in the relationship between predictors and a response over space. For example, it has been shown that Greater Prairie Chicken (*Tympanuchus cupido*) nest site characteristics share similarities in some locations across their range, but that many of the characteristics vary in different locations (Mcnew et al. 2013). Incorporating analyses that explore non-stationary influences can reveal spatial patterns that are unaccounted for with statistical methods that ignore spatial structure.

Techniques that account for spatial non-stationarity are sometimes employed when modeling species distributions because predictor variables inevitably vary across space and often show high levels of multicollinearity. For example, Osborne and Suárez-Seoane (2002) found that accounting for spatial non-stationarity resulted in higher receiver operating characteristic curve (ROC) values for several species in Spain. Similarly, predictive accuracy and model fit were improved in a study of North American songbirds when geographically weighted regression (GWR) was employed (Lieske and Bender 2009). For the examination of umbrella species, consideration of spatial non-stationarity is paramount to identify how spatially-varying landscape level influences may be altering the expected results of management actions.

The purpose of this study was to examine the non-stationary influence of Red-cockaded Woodpecker management on non-target avian species to evaluate the utility of Red-cockaded Woodpeckers as an umbrella species for upland birds classified as species of management concern (hereafter species of concern). Geographically weighted regression was used to examine the effect of Red-cockaded Woodpecker management on five species of concern as identified by the International Partners in Flight and Georgia Department of Natural Resources. These species occurred in the same or similar habitats and show range-wide declines throughout most of the southeastern United States. Because species respond to different habitat characteristics such as the amount of open canopy and constantly changing understory components that are common near some (but not all) Red-cockaded Woodpecker clusters, we predicted that some species would benefit more than others as proximity to the center of a cluster increased. Additionally, because of inherent habitat heterogeneity, some locations near Red-cockaded Woodpecker clusters would be more amenable to a higher diversity of species even when the proximity to a cluster was similar.

METHODS

Study Area

In 1920 Fort Benning was established as a U.S. Army military installation on former plantations and agricultural lands near the Chattahoochee River (Kane and Keeton 1998). It supports a large number of training facilities, with more than 20,000 troops training at this location annually. Prior to European settlement, this area was inhabited by Native Americans who created settlements along the Chattahoochee, practiced agriculture, and hunted the region (Kane and Keeton 1998). Because of the limited development prior to its establishment as a military base and large areas of restricted access, Fort Benning supports many denizens of the longleaf pine ecosystem that were once common across the Southeast, but are now in drastic decline. Among these are the gopher tortoise (*Gopherus polyphemus*), Bachman's Sparrow (*Peuceau aestivalis*), and Red-cockaded Woodpecker (*Picoides borealis*).

Currently, Fort Benning supports 262 potential breeding groups of Red-cockaded Woodpeckers as well as an additional 44 manageable clusters (DoD 2009; Figure 3.1) which are monitored by land management staff year-round. Due to the obligations of endangered species management, a substantial amount of land management activity is aimed at the recovery of Red-cockaded Woodpeckers on Fort Benning. These activities include, but are not limited to: prescribed fire, insertion of artificial cavities for nesting and recruitment, enhancement of foraging habitat by removal of hardwood midstory trees, and planting of longleaf pines for future habitat (DoD 2009). The present management goal is to expand the population to 361 active breeding clusters which is the minimum criteria for recovery of this species on Fort Benning as set by the U.S. Fish and Wildlife Service, *Focal Species*

Bachman's Sparrow.—Bachman’s Sparrow (*Peucaea aestivalis*), an endemic North American passerine, is among the many species associated with longleaf pine savannas and the frequent use of prescribed fire (Dunning 2006). The distribution of this ground-nesting species overlaps broadly with the former range of longleaf forests (Engstrom et al.1996), and preferred habitat conditions for this sparrow are described as open pine forests with few shrubs and a dense ground layer of grasses and forbs (Dunning 2006, Jones et al. 2013), largely overlapping with habitat preferences of Red-cockaded Woodpeckers (Plentovich et al. 1998, Jackson 1994).

Brown-headed Nuthatch.—Brown-headed Nuthatch (*Sitta pusilla*) is an endemic species that occupies pine forests of various age classes, but particularly mature pine forests, across the Southeast (Withgott and Smith 1998). Brown-headed Nuthatch is most common in mature, old-growth forest settings with an open understory, but can often be found in urban areas as well. Similar to the Red-cockaded Woodpecker, this nuthatch is a cavity nesting species that often breeds cooperatively in groups of >2 adults that help raise young (Walters et al. 1988, Cox and Slater 2007). Studies of the overlap between habitat conditions optimal for Brown-headed Nuthatch and Red-cockaded Woodpecker have yielded opposing results with some indications that efforts to promote Red-cockaded Woodpecker habitat enhance nuthatch habitat (Wilson et al. 1995, Plentovich et al. 1998), while others have documented that areas suitable for Red-cockaded Woodpeckers are not necessarily suitable for Brown-headed Nuthatch (Cox et al. 2012).

Field Sparrow.—Field Sparrow (*Spizella pusilla*) is a declining species that is most commonly found in abandoned fields and woodland openings with scattered woody vegetation (Carey et al. 2008). Because it benefits from frequent disturbances such as prescribed fire, it may benefit indirectly from habitat management for Red-cockaded Woodpecker even though it typically is found in areas with more of an open canopy. In some old-growth settings, such as the intact longleaf woodlands of the Red Hills of southern Georgia and north Florida where Red-cockaded Woodpeckers are widely distributed, Field Sparrows can often be found in the same setting (C. Jones, personal obs.).

Northern Bobwhite.—Northern Bobwhite (*Colinus virginianus*) is a ground-nesting game bird widely distributed throughout the eastern United States and Mexico. They prefer early successional habitats and can be found in agricultural fields, grasslands, open pine forests, and pine-hardwood forests (Brennan 1999). Across the Bobwhite's range, the Southeast has experienced the greatest level of population decline (5% per year since 1966) (Lee and Brennan 1994). Typically, the highest densities of this species are found in a mosaic of field patches, forests and low intensity agriculture, but populations often respond positively to management actions that promote habitat for Red-cockaded Woodpeckers (Wilson et al. 1995, Cram et al. 2002).

Prairie Warbler.—Prairie Warbler (*Setophaga discolor*) is a long-distance migratory species that often inhabits southeastern pine savannas with open canopies similar to Red-cockaded Woodpecker and Bachman's Sparrow. However, Prairie Warbler is more of a habitat generalist and is also found in abandoned fields, coastal dunes with a shrubby component, and swamp habitats (Nolan et al. 1999). Management strategies that promote suitable conditions for Red-cockaded Woodpeckers have been suggested to be beneficial for Prairie Warbler (Wilson et al. 1995).

Density Estimation

Density estimates for the five species of concern were derived using standardized point count surveys during the breeding seasons 2009-2010. A stratified random sampling scheme was used to place 280 points on the landscape using Hawth's Tools (Beyer 2004) in ArcMap 9.3 that were stratified by major habitat types. Points were minimum of 250 m apart. Because access is limited or restricted in many areas of Fort Benning, some points were relocated to facilitate sampling efforts and some areas were not sampled for safety reasons.

The point count protocol utilized distance sampling techniques (Buckland et al. 2001) whereby distance to each bird detected during a 5 minute point count was estimated by a trained observer. All points were visited at least three times during each year of sampling, except those points that were in restricted areas and required special permission to access (<10% of all points). Distance sampling techniques allow for the modeling of a detection function that represents the probability of detection as a function of distance. The proportion of objects missed during the survey can then be approximated to generate density estimates for each species. Program Distance (Thomas et al. 2009) was used to generate candidate models for the probability of detection of each species of concern. Half-normal and hazard rate key functions, as well as covariates for the effect of survey time, date, observer, temperature, wind, and weather were incorporated into models to account for probability of detection. Model selection was based on Akaike's Information Criterion (Akaike 1973) and density estimates were averaged across years by species. These methods generally follow those used by Grundel and Pavlovic (2007) to examine bird species in fire maintained landscapes in Indiana.

The density estimates for each individual species were then compiled for each point and a local diversity index (hereafter constrained Simpson Diversity) was computed using the reciprocal Simpson’s Diversity index (Simpson 1949). An index for diversity was computed instead of simple species richness (the total number of species present) because the index takes into account the number of species present as well as the density or abundance of each species. The reciprocal (instead of the raw index) Simpson’s Diversity was computed to ease interpretation of the influence of regression parameters on diversity at each point.

Landscape variables

Landscape variables were selected based on their potential to influence bird communities. Variables were selected based on potential influence on avian communities on Fort Benning (Olsen et al. 2005), personal experience, and the potential for military activities to affect bird communities (Table 3.1). These variables were placed into three categories: 1) habitat variables measuring landcover type and connectivity, 2) military impact variables, and 3) an endangered species management variable measured as the distance to a given survey point from the center of a Red-cockaded Woodpecker group. Distance to Red-cockaded Woodpecker group was chosen as the management variable because management actions are primarily focused on improving or maintaining habitat near woodpecker groups. Therefore, if the woodpeckers are functioning as an umbrella, their influence should be higher at locations closest to the group.

Contagion, edge density, and Euclidean nearest neighbor were calculated with program Fragstats (McGarigal et al. 2002) using a raster landcover dataset of Fort Benning and based on the National Vegetation Classification Standard (NVCS). Road density and distance metrics (measured in meters) were generated using the Spatial Analyst in ArcGIS 9.3. Road density was based on a moving window 100 ha in size, while edge density was based on a 150 m radius moving window since this was the typical radius for detection of birds during surveys. Raster grid files were generated for each variable and values were extracted to each survey point for inclusion in regression analysis.

Analysis

Linear regression was used to examine the influence of landscape variables (Table 3.1) on (1) the constrained Simpson Diversity index at each survey location and (2) the density of each individual species. For this analysis, we used only those points that were classified as longleaf pine (*n* = 119) by the National Vegetation Classification Standard. We reduced our analysis only to longleaf pine points since this is the primary NVCS habitat classification for Red-cockaded Woodpecker clusters at Fort Benning and some of the other species of concern (e.g., Prairie Warbler) are also found in other habitats that will never be potential Red-cockaded Woodpecker habitat.

Global models with all predictors were generated for each species and constrained diversity, and normality was assessed visually by examining quantile-quantile (QQ) plots and plots of residuals in the R statistical package version 2.10.0 (2009). Constrained Simpson Diversity was normally distributed; however, individual species models showed some evidence of non-normality. Data transformations did not improve normality, so the original values were used in subsequent species density analyses. Multicollinearity of predictors was evaluated using Pearson correlation coefficients calculated for each pair-wise combination of variables. Variables that were correlated ($r^2 > 0.3$) were not included together in candidate models.

An information-theoretic approach (Burnham and Anderson 2002) was used to assess the relative fit of each model. Akaike's Information Criterion (AIC) with small sample bias adjustment (AIC_c; Hurvich and Tsai 1989) was used to assess the fit of each model, and relative fit was determined by evaluating Akaike weights. A confidence set of models was created using models with a ΔAIC_c <2 of the best fitting model, and model averaging (Burnham and Anderson 2002) was used to incorporate uncertainty in model selection into parameter estimates. Estimates of the regression coefficients and standard errors were weighted for each model according to AIC_c weights and then used to assess the relative effect of each parameter used. Precision of model-averaged coefficients was evaluated with 95% confidence intervals.

We then tested the top models for the constrained diversity index and species density models for evidence of global spatial autocorrelation of residuals using the Moran's *I* statistic to determine if the residuals were not independent and showed evidence of spatial clustering. The Moran's *I* statistic indicated that residuals from the constrained diversity index model were not spatially independent and showed evidence of clustering ($p<0.01$). Additionally, three of the five density models (Bachman's Sparrow, Prairie Warbler, and Northern Bobwhite) showed evidence of spatial clustering in the residuals as well ($p<0.01$). Geographically weighted regression (GWR) was then employed to account for clustering of residuals in the linear regression models. GWR is a tool that can be used to examine spatial heterogeneity when modeled processes vary across a given area. We used the GWR tool in ArcGIS 9.3 with a fixed kernel type and the AICc bandwidth selection method. The Moran's *I* statistic was calculated again to determine if GWR was accounting for clustering that was present in the residuals in the original linear regression analysis. Geographically weighted regression eliminated the spatial dependence of the residuals in all the models that showed evidence of spatial dependency in the residuals of the original linear regression models except for the model for Prairie Warbler where the dependency was reduced, but Moran's *I* was still significant. A raster surface was then generated for the parameter of primary interest in our analysis, the effect of distance to Red-cockaded Woodpecker clusters on the constrained diversity index, so that variation in the effect of the parameter across the study area could be visualized. Isopleth lines were also generated by mapping those locations where the effect of the parameter was significant when $\alpha \leq 0.5$ and $\alpha \leq 0.1$. Additionally, an interpolated map was generated of the constrained Simpson diversity estimates within pine habitat so that areas of high diversity could be viewed in comparison to the parameter for the relationship between diversity and proximity to woodpecker clusters.

RESULTS

Bachman's Sparrows were detected >500 times during the two years of surveys, Field Sparrows were detected were detected only 77 times, Brown-headed nuthatches were detected >300 times, Northern Bobwhite were detected >400 times, while Prairie Warblers were detected >500 times. Models for the probability of detection of each species indicated that those models accounting for differences in observer were frequently ranked highest (Table 3.2). However, temperature and time effects were included in the top model during 2009 for Brown-headed Nuthatch and Field Sparrow. Prairie Warblers and Brown-headed Nuthatches had the highest densities in both years of surveying while Field Sparrows had the lowest (Table 3.3). Although density estimates varied by year for Bachman's Sparrow and Brown-headed Nuthatch, 95% confidence intervals around those estimates showed substantial overlap among years for each species (Table 3.3). Average density in pine habitat was 0.18 (SD = 0.17) for Bachman's Sparrow, 0.66 (SD = 0.5) for Brown-headed Nuthatch, 0.02 (SD = 0.05) for Field Sparrow, 0.05 (SD = 0.06) for Northern Bobwhite, and 0.61 (SD = 0.5) for Prairie Warbler.

The average constrained Simpson Diversity across all the points was 1.88 (SD = 0.74). The average constrained Simpson Diversity estimate across all points within 200 m ($n = 65$) of the center of a Red-cockaded Woodpecker cluster was 2.10 (SD = 0.66). The top model for predicting the constrained Simpson Diversity Index included only the variable for the distance to the center of a Red-cockaded Woodpecker cluster and comprised 69% of the AIC weight (Table 3.4). The confidence set of models for predicting Bachman's Sparrow density included the variables for the distance to the center of a Red-cockaded Woodpecker cluster, the distance to the nearest military practice range, and the distance to the nearest patch of upland pines. These top three models comprised 60% of the AIC weight for this set of models (Table 3.4). The confidence set of models for Brown-headed Nuthatch included distance to a Red-cockaded Woodpecker cluster and the null model. The null model comprised nearly the same weight (~20%) as the top model indicating that it is likely none of the variables we examined had a strong influence on density. For Field Sparrow, the confidence set included distance to the nearest pine patch and contagion (both are measures of habitat connectivity; combined weight of 59%). Four models were present in the confidence set for Northern Bobwhite and included the variables for distance to a Red-cockaded Woodpecker cluster, distance to cantonment (military development), the null model, and the distance to a military practice range. Finally, distance to cantonment was the only model present in the confidence set for Prairie Warbler and comprised 51% of the AIC weight.

For all model sets for which distance to Red-cockaded Woodpecker was in the confidence set or was the top model, parameter estimates indicated that as distance to a woodpecker cluster increased, there was subsequent decline in diversity or species density (Table 3.5). However, confidence intervals overlapped zero for Brown-headed Nuthatch and the null was present in the confidence set for Northern Bobwhite and Brown-headed Nuthatch. For Field Sparrow, the parameter estimates for contagion and distance to nearest pine patch had opposite signs, but confidence intervals overlapped zero for both parameters, indicating uncertainty in the effect of either parameter on Field Sparrow density (Table 3.5). The parameter estimate for distance to cantonment in the Prairie Warbler model indicated that densities of Prairie Warblers decreased as distance to military development increased, which is likely the product of edge effects (Table 3.5).

The raster surface for the GWR model for constrained Simpson Diversity illustrated that distance to a Red-cockaded Woodpecker group had the highest magnitude of effect in the north central portion of Fort Benning. In this region, constrained diversity was higher compared to other regions on the fort, and diversity increased at a faster rate as the proximity to a Red-cockaded Woodpecker decreases (thus, it also decreases at a faster rate as distance increases; Figure 3.2). This location corresponded to a hot-spot of high diversity on Fort Benning, but other locations also had similarly high diversity across the fort (Figure 3.3).

DISCUSSION

Red-cockaded Woodpecker management is known to enhance habitat for several avian species (Wilson et al. 1995, Plentovich 1998, Conner et al. 2002); however, the specific impact of management on diversity of multiple avian species of concern has received little attention. We found that our constrained estimate of Simpson Diversity was higher in areas closer to Red-cockaded Woodpecker clusters, but this effect varied across space (Figure 3.2) and across species (Table 3.4, Table 3.5). Foody (2004) found that relationships between environmental variables and species richness in sub-Saharan Africa were non-stationary and that these relationships were highly variable across space. Similarly, our results suggest that the relationship between management for an endangered species is heterogeneous across space and does not always benefit all species the same way in all locations.

From a single species perspective, only Bachman's Sparrow exhibited a clear relationship between proximity to woodpecker clusters and changes in density. This is likely because this species exhibits the closest overlap of habitat characteristics of Red-cockaded Woodpecker. However, this relationship also showed evidence of non-stationarity. It has also been illustrated on other DoD lands that not all locations managed for Red-cockaded Woodpeckers are suitable for Bachman's Sparrows (Plentovich et al. 1998). This is not surprising since the number of years a cluster has been managed likely influences the quality of the groundcover conditions that are suitable for Bachman's Sparrow (Plentovich et al. 1998), so not all locations would be expected to have the same relationship.

Similar to recent investigations of Brown-headed Nuthatch occupancy in central Florida (Cox et al. 2012), our top model did not carry much weight for the relationship between proximity to a woodpecker cluster and nuthatch density. Both our study and Cox et al. (2012) are somewhat at odds with previous studies (Conner et al. 1983, Conner et al. 2002) that found strong relationships between areas managed for Red-cockaded Woodpecker and abundance of Brown-headed Nuthatches. Cox et al. (2012) suggested that their results could be influenced by food resources, which are often lower in sandhill habitats. In our study area, many woodpecker clusters are found in sandhill habitats, so this could explain why the top model did not receive much weight.

The top models for Prairie Warblers and Field Sparrows did not contain the variables for proximity to a woodpecker cluster. Thus, these two species contributed very little to the patterns seen in the relationship between our constrained diversity estimate and proximity to a woodpecker cluster. As others have noted previously, it is unlikely that all species will respond in the same manner to single-species conservation (e.g., Simberloff 1998, Hunter et al. 1994), even in situations when habitat conditions for the umbrella would seem to benefit others with similar (though not identical) habitat requirements. Prairie Warblers were ubiquitous on our study site, but their relationship to military development was unexpected. This finding is likely a correlate with shrubby habitat surrounding development and not the development itself. Field Sparrows were uncommon on our study site in spite of the fact that they are frequently observed near Red-cockaded Woodpecker clusters in other settings in Georgia (C. Jones, pers. observation).

The use of GWR in this analysis revealed that the positive influence of Red-cockaded Woodpecker management was found to increase at a greater rate in the central portion of Fort Benning (Figure 3.2). The reasons for this are unclear, but this area has relatively large patches of continuous pine that are intersected by streams that may give rise to high habitat heterogeneity. Additionally, we did not consider whether clusters were composed primarily of naturally excavated cavities or artificial inserts (often used to create new colonies). Clusters with artificial cavities may be in areas that are of marginal benefit to the species we examined in our analysis. These results also suggest that including additional environmental parameters in the model, such as cluster age, cavity type (natural or artificial), soil type, and elevation is probably warranted.

Red-cockaded Woodpecker management on the southern portion of the base appears to either have a very wide-ranging influence on the diversity of species of concern that does not decay with distance or simply has very little influence at all. However, even though the effect of Red-cockaded Woodpecker management does not appear to be important in these locations, the secondary effect of burning locations that do not contain woodpecker groups is likely conferring benefit to some of these species of concern. It could be argued that without Red-cockaded Woodpeckers on Fort Benning, prescribed fire would not be used as a management tool at all, so the benefit in some locations may be difficult to measure with a simple metric such as distance to Red-cockaded Woodpecker cluster.

The scale of this study was limited to Fort Benning and by a single cell size in the final raster output. This may limit the interpretation of the results since an increased cell size could reveal different patterns that are occurring at a larger (or smaller) scale which may have been masked. A multi-scale approach may reveal that different patterns exist in different locations and could prove useful for the examination of how the extent of different management actions (e.g., prescribed fire, timber thinning, and herbicide application) influences diversity. Indeed, local distributions of birds have been found to have varying relationships with regional distributions when examined at multiple scales because the habitats at the regional scale often vary from those at a local scale (Gaston and Lawton 1990). This further reinforces the need for considering spatial non-stationarity and examining the effect of variables at multiple scales since regional habitat subtleties may enhance the habitat of some species while being marginal or of no use to others.

Few studies of avian taxa have considered the effect of autocorrelation and non-stationarity on inferences obtained from field studies. The importance of accounting for autocorrelation and non-stationarity in ecological models has been stressed (Legendre 1993, Lichstein et al. 2002), but infrequently implemented. Lieske and Bender (2009) examined North American Breeding Bird Survey data and concluded that utilizing GWR resulted in large reduction of spatial autocorrelation. Exploratory visualization of the change in the influence of environmental and management variables across the landscape (i.e., non-stationarity) permits the examination of location-specific influences. This is extremely important to consider if the population recovery of Red-cockaded Woodpeckers is assumed to have a certain effect on non-target species. By concentrating recovery strategies in locations that have the greatest benefit to all species, management scenarios will be more effective at the ecosystem level.

Umbrella species will continue to be used implicitly for the foreseeable future as long as endangered species management continues to generate funding. In our examination, it appears that the umbrella functions in some locations for some species, but not all. We also chose to examine a suite of species that should benefit from woodpecker management, but the effects were not always evident. In the end, depending on conservation goals, a suite of species (both avian and non-avian) are likely to provide a better indicator of ecosystem health than any single species that is used as an umbrella.

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Table 3.10. Landscape variables with potential influence on bird communities at Fort Benning.

Landscape Metrics
Habitat Variables
Contagion
Edge Density
Euclidean Nearest Neighbor of Similar Patch Type
Military Impact Variables
Distance to Military Development (cantonment)
Distance to Weapons Practice Range
Road Density
Endangered Species Management Variable
Distance to Red-cockaded Woodpecker Cluster

Table 3.11. Model selection for detection functions describing the probability of detecting five species, Bachman’s Sparrow, Northern Bobwhite, Brown-headed Nuthatch, Prairie Warbler, and Field Sparrow during the breeding seasons 2009-2010 using program Distance. K is the number of parameters in the specified model.

Bachman's Sparrow (*Peuceau aestivalis*)

Model	K	Δ AIC	AIC
2009			
HalfNorm+Cos(Observer)	4	0	604.06
Hazard+Cos(Observer)	5	16.62	620.68
HalfNorm+Cos(Time)	2	23.54	627.60
HalfNorm+Cos(Weather)	2	23.55	627.61
HalfNorm+Cos(Temperature)	2	23.74	627.80
2010			
Hazard+Cos(Observer)	5	0	448.97
HalfNorm+Cos	1	11.81	460.78
HalfNorm+Cos(Wind)	2	12.08	461.05
HalfNorm+Cos(Time)	2	12.13	461.10
HalfNorm+Cos(Date)	2	13.03	462.00

Northern Bobwhite (*Colinus virginianus*)

Model	K	Δ AIC	AIC
2009			
HalfNorm+Cos(Observer)	4	0	731.48
Hazard+Cos	2	3.29	734.76
Hazard+Cos (Weather)	3	3.74	735.21
HalfNorm+Cos	1	11.83	743.31
HalfNorm+Cos(Temperature)	2	12.02	743.49
2010			
Hazard+Cos (Observer)	5	0	388.36
Hazard+Cos	2	17.38	405.74
Hazard+Cos (Weather)	3	19.13	407.49
Hazard+Cos (Wind)	3	19.13	407.49
Hazard+Cos (Time)	3	19.24	407.61

Brown-headed Nuthatch (*Sitta pusilla*)

Model	K	Δ AIC	AIC
2009			
HalfNorm+Cos(Time)	2	0	408.47
Hazard+Cos	2	2.67	411.14
HalfNorm+Cos	1	3.78	412.25
Hazard+Cos(Weather)	3	3.92	412.38
HalfNorm+Cos(Weather)	2	5.27	413.74
2010			
HalfNorm+Cos (Observer)	5	0	445.25
HalfNorm+Cos(Wind)	2	13.75	459.00
HalfNorm+Cos (Temperature)	2	13.84	459.09
HalfNorm+Cos	2	14.45	459.70
HalfNorm+Cos (Weather)	2	20.92	466.17

Prairie Warbler (*Dendroica discolor*)

Model	K	Δ AIC	AIC
2009			
HalfNorm+Cos (Observer)	4	0	805.46
Hazard+Cos (Observer)	5	59.61	865.07
HalfNorm+Cos (Weather)	2	69.69	875.14
HalfNorm+Cos	1	69.77	875.23
HalfNorm+Cos (Date)	2	71.34	876.79
2010			
HalfNorm+Cos (Observer)	5	0	948.34
HalfNorm+Cos (Time)	2	30.70	979.05
HalfNorm+Cos	1	32.19	980.53
Hazard+Cos	2	32.46	980.80
HalfNorm+Cos (Wind)	2	34.09	982.43

Field Sparrow (*Spizella pusilla*)

Model	K	Δ AIC	AIC
2009			
HalfNorm+Cos (Temperature)	2	0	59.93
HalfNorm+Cos	1	0.02	59.94
Hazard+Cos	2	1.14	61.06
HalfNorm+Cos(Wind)	2	1.82	61.75
HalfNorm+Cos(Weather)	2	1.92	61.85
2010			
Hazard+Cos	2	0	66.16
Hazard+Cos(Weather)	3	1.07	67.24
HalfNorm+Cos(Observer)	5	1.21	67.38
Hazard+Cos(Wind)	3	2.02	68.18
Hazard+Cos(Temperature)	3	2.04	68.20

Table 3.12. Breeding season density estimates for 2009-2010 for five upland species of concern on Fort Benning, GA across all points (*n* = 280). Densities are reported as the number of birds per hectare.

Density Estimates 2009 - 2010 on Fort Benning, GA				
		Estimate	**Lower 95% CI**	**Upper 95% CI**
Bachman's Sparrow				
	2009	0.056	0.041	0.076
	2010	0.038	0.026	0.056
Field Sparrow				
	2009	0.023	0.010	0.053
	2010	0.020	0.011	0.037
Northern Bobwhite				
	2009	0.031	0.024	0.039
	2010	0.025	0.017	0.037
Brown-headed Nuthatch				
	2009	0.173	0.126	0.238
	2010	0.330	0.190	0.576
Prairie Warbler				
	2009	0.251	0.182	0.346
	2010	0.252	0.203	0.313

Table 3.13. AICc, ΔAICc and AIC weights for models of landscape variables affecting constrained Simpson diversity and density of five species of concern at Fort Benning, GA.

	AICc	ΔAIC	WT
Simpson Diversity			
Distance to RCWO cluster	259.85	0	0.69
BACS Density			
Distance to RCWO cluster	-46.48	0	0.27
Distance to military practice range	-45.84	0.64	0.2
Distance to nearest patch of pine habitat	-44.95	1.52	0.13
BHNU Density			
Distance to RCWO cluster	257.89	0	0.21
null	258.02	0.12	0.20
FISP Density			
Distance to nearest patch of pine habitat	-353.02	0	0.39
Contagion	-352.14	0.88	0.25
NOBO Density			
Distance to RCWO cluster	-318.10	0	0.29
Distance to military development	-316.69	1.41	0.14
null	-316.24	1.86	0.12
Distance to military practice range	-316.11	1.99	0.11
PRAW Density			
Distance to military development	176.88	0	0.51

Table 3.14. Parameter estimates for models of constrained Simpson diversity and density of species of concern on Fort Benning. Estimates and 95% confidence intervals are scaled from 1 m to 500 m. NA indicates inapplicable scale due to units of variable. ENN = Euclidean distance to nearest patch of pine.

	Estimate	**Scalar**	**Scaled Estimate**	**SE**	**Lower 95% CI**	**Upper 95% CI**	**Scaled Lower 95% CI**	**Scaled Upper 95% CI**
Simpson Diversity								
DISTTORCWO	-0.00043	500 m	-0.2146	0.0001	-0.0007	-0.0002	-0.3450	-0.0841
BACS Density								
DISTTORCWO	-0.00007	500 m	-0.0368	0.0000	-0.0001	0.0000	-0.0733	-0.0004
DISTTORANG	-0.00002	500 m	-0.0103	0.0000	0.0000	0.0000	-0.0215	0.0010
ENN	0.00022	500 m	0.1123	0.0003	-0.0003	0.0008	-0.1739	0.3984
BHNU Density								
Dist to RCWO	-0.00020	500 m	-0.0982	0.0001	-0.0005	0.0001	-0.2289	0.0325
FISP Density								
ENN	0.00059	500 m	0.2939	0.0003	-0.0001	0.0013	-0.0430	0.6309
Contagion	-0.00020	NA	NA	0.0001	-0.0004	0.0000	NA	NA
NOBO Density								
DISTTORCWO	-0.00002	500 m	-0.0117	0.0000	0.0000	0.0000	-0.0233	-0.0001
DISTTOCANT	0.00000	500 m	0.0008	0.0000	0.0000	0.0000	-0.0002	0.0017
DISTTORANG	-0.00001	500 m	-0.0026	0.0000	0.0000	0.0000	-0.0062	0.0011
PRAW Density								
DISTTOCANT	-0.00002	500 m	-0.0089	0.0000	0.0000	0.0000	-0.0166	-0.0012

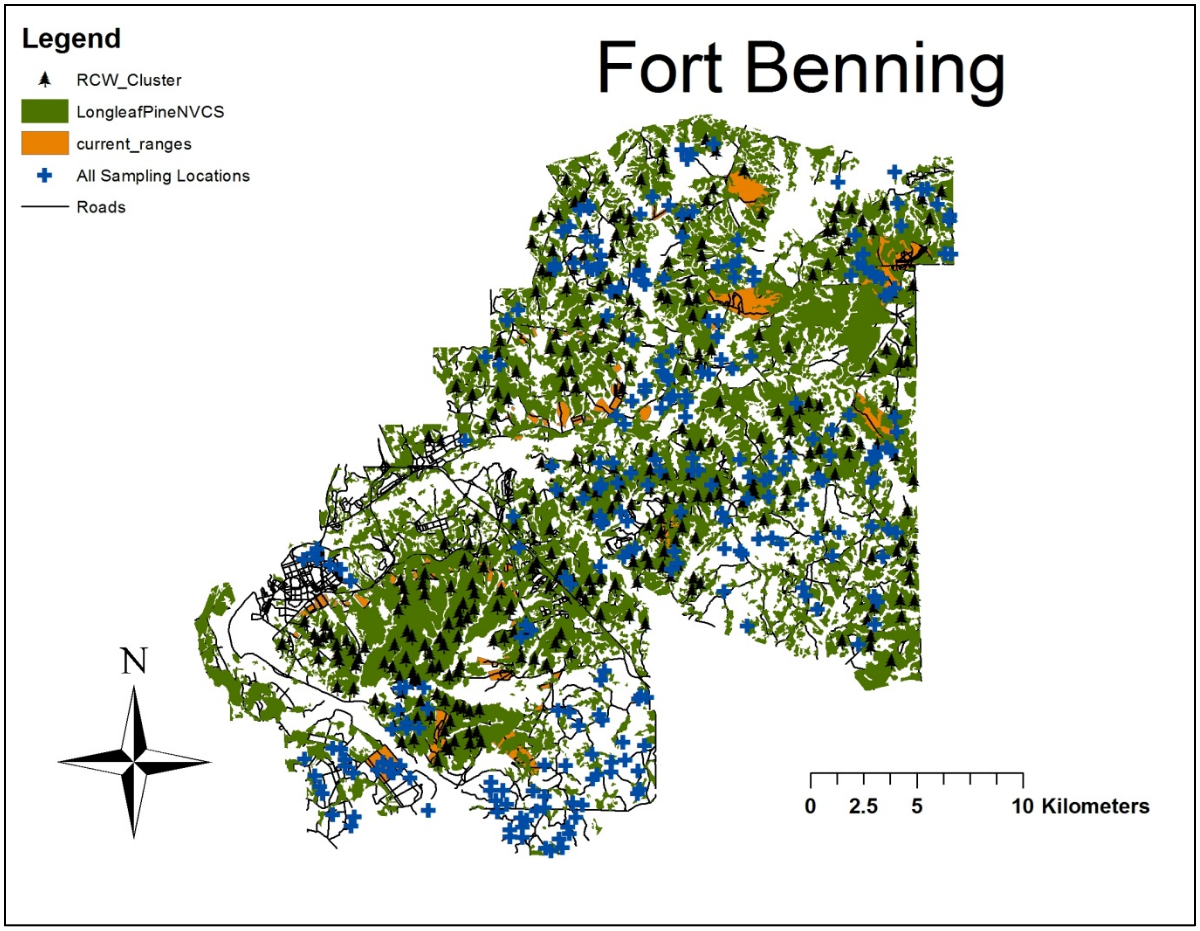

Figure 3.4. Location of Red-cockaded Woodpecker (*Picoides borealis*) groups, bird survey locations, roads, and current military ranges on Fort Benning, Georgia.

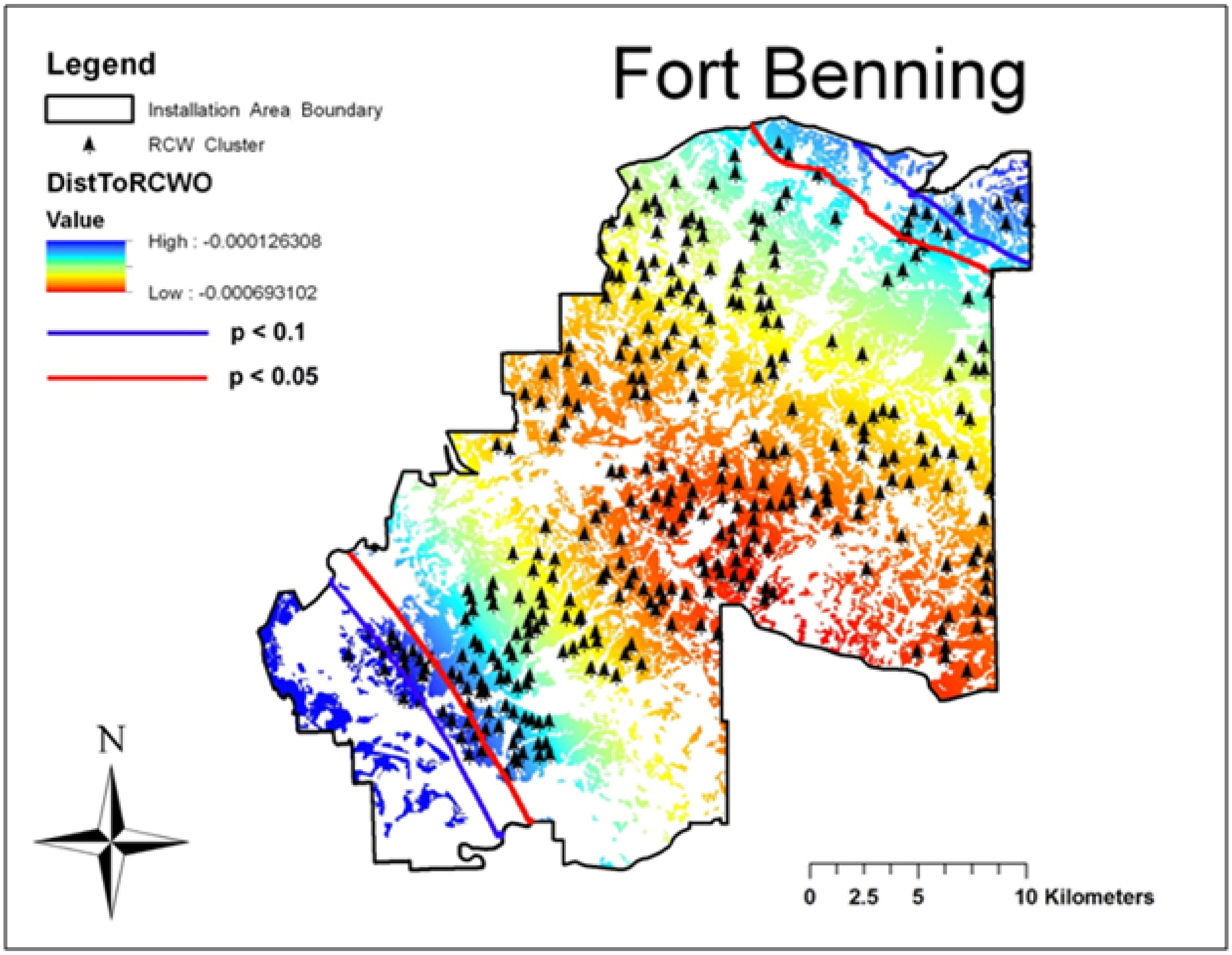

Figure 3.5. Geographically weighted regression output for influence of RCWO management on diversity of five species of concern (Bachman's Sparrow, Field Sparrow, Prairie Warbler, Northern Bobwhite, and Brown-headed Nuthatch) on Fort Benning. Red indicates locations where the parameter estimate for distance to RCWO had the greatest magnitude of influence (i.e., most negative values for the parameter estimates). Parameter values presented in meters. Red isopleth lines indicate boundary of parameter estimates at $\alpha \leq 0.05$. Blue lines indicate boundary of parameter estimates at $\alpha \leq 0.1$.

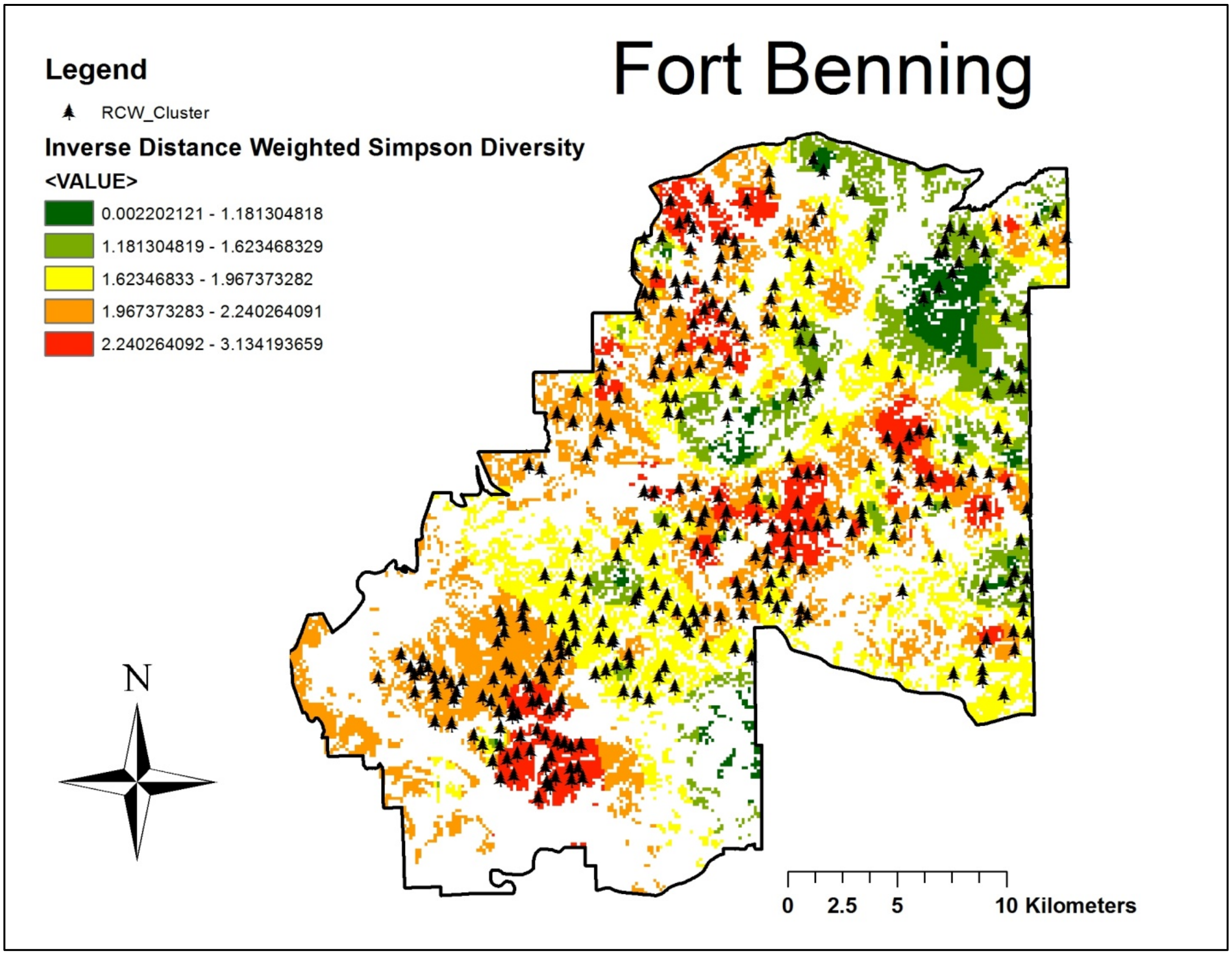

Figure 3.6. Interpolated (using inverse distance weighted method) constrained Simpson Diversity on Fort Benning, GA. Red indicates areas of highest constrained diversity while green indicates areas of lowest constrained diversity estimates.

CHAPTER 4

DIFFERENCES IN SPECIES-HABITAT RELATIONSHIPS DERIVED FROM MULTIPLE METHODS OF SPECIES DISTRIBUTION MODELING[1]

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[1] Jones, C. D., N. P. Nibbelink, and R. J. Cooper. To be submitted to *Diversity and Distributions*

ABSTRACT

Predicting species distributions where presence-only data are available is becoming a common exercise and holds great promise for conservation activities such as forecasting distribution shifts in response to climate change and large-scale conservation planning. Numerous presence-only methods for species distribution modeling exist and several lack transparency in their modeling approaches. Many comparisons for these different methods exist in the literature, but few have examined the inference for species-habitat relationships derived from different modeling approaches. We examined species-habitat relationships derived from presence-only data for Bachman's Sparrow (*Peucaea aestivalis*) and Prairie Warbler (*Setophaga discolor*) at Fort Benning, Georgia using three presence-only species distribution modeling methods: (1) GARP, (2) Maxent and (3) logistic regression. Species locations were derived from 280 randomly placed points across the ~180,000 acre study area. Models were constructed using environmental variables for habitat, elevation, and distance to streams as predictor variables. Our results indicate that inference about species-habitat relationships derived from each modeling approach differs greatly and choosing any single approach for conservation planning may be misleading. Additionally, some landscape variables improved prediction of models, but provided little information that related to the known habitat requirements of each species. We recommend multiple modeling approaches to investigate species-habitat relationships, the understanding of which is critical to making informed decisions for conservation planning.

INTRODUCTION

Species distribution modeling is a valuable tool that has been used increasingly in recent years. This increase is—in large part—the result of the widespread availability of user-friendly software that readily produces easily interpretable maps. However, many of these software packages provide limited information on how the model(s) are produced or how environmental variables are used to create the predictive map surface (Elith and Graham 2009). Furthermore, many of the most popular methods (e.g., Maxent [Phillips et al. 2006] and GARP [Stockwell and Peters 1999]), provide little guidance on what data may be appropriate to use for a particular method (Yackulic et al. 2012). Understanding how environmental and bioclimatic data are used to create distribution maps produced with a given method is essential for informing conservation and land management decisions. Without a clear understanding of the relationship of a species' distribution to variables used in a model, the inference for such a model is limited.

Various approaches have been used to examine and compare different methods of species distribution modeling. One approach is to use a simulated landscape with known species-environment associations so predictive output can be directly compared with the true underlying relationship. Elith and Graham (2009) found that Maxent, a presence-only modeling technique, reproduced mapped patterns of simulated species distributions better than four other popular methods (genetic algorithm for ruleset prediction [GARP], generalized linear models [GLM], random forests, and boosted regression trees[BRT]), but was outperformed by BRT when predicting frequency of occurrence. GARP—another frequently used presence-only modeling technique—performed poorly because it often assigns high values for areas that may only have limited suitability for a species when compared to other methods that produce gradations of suitability across a map surface (Elith and Graham 2009).

Another approach to evaluate different modeling methods is to examine a method's ability to predict the distribution of a particular species in an area or region that has not been sampled (i.e., transferability). Transferability is particularly useful for planning future investigations and making predictions about regions that are either too remote or too dangerous (e.g., U.S. Department of Defense training areas) to sample. Using Breeding Bird Survey data (BBS), Townsend Peterson et al. (2007) compared the performance of GARP and Maxent in their ability to transfer predictions to unsampled areas. Both approaches produced maps that coincided with the known distribution of a widespread species (Mourning Dove; *Zenaida Macroura*); however, GARP tended to over-predict areas of high suitability, whereas Maxent underpredicted. High predictive thresholds in Maxent may result in Maxent models failing to make general predictions, but this effect can be augmented when thresholds for prediction are lowered (Phillips et al. 2006, Townsend Peterson et al. 2007). So, while Maxent is relatively good at predicting distributions within the bounds of the sampling area, it lacks some ability to generalize these predictions beyond the sampling location (Townsend Peterson et al. 2007).

A third approach to comparing the performance of species distribution modeling techniques is to examine classification performance using the receiver operating characteristic (ROC) measured by the area under the curve (AUC). Generally, as the number of observations increase, the performance of many species distribution modeling methods increases (Hernandez et al. 2006). When confronted with limited data (5-25 occurrences) for rare species and small sample sizes, Maxent has been shown to have higher AUC and better prediction than many other presence-only modeling approaches when sample sizes are small (Hernandez et al. 2006). Similarly, Maxent often performs best (as measured by AUC) among presence-only modeling approaches when datasets are larger (~50 occurrences) and calibrated using training data at multiple scales (Giovanelli et al. 2010). A common observation among evaluations of species distribution model comparisons is that Maxent tends to under-represent the amount of area that a given individual may use, but has higher accuracy (measured by AUC), while GARP tends to over-estimate the amount of suitable habitat with lower accuracy.

In spite of all the comparisons of different species distribution methods using various evaluations of performance, oftentimes the basic information about the relationship between the species and the habitat predictors is ignored. Indeed, the majority of the studies published from 2008–2012 using Maxent failed to examine the relationship between the variables used to create the model and their influence on species probability of occurrence or index of suitability (Royle et al. 2012). However, one of the primary reasons for this shortcoming is that much of the modeling software itself does often does not provide a transparent method to examine how different predictors are used to create the model (Elith et al. 2005, Elith and Graham 2009). Some methods such as Maxent give the value and sign of coefficients for environmental predictors; however, because the resulting map is typically not a strict probability of occurrence, the interpretation of these coefficients is limited. Further, when multiple modeling approaches are compared among each other, the interpretation across multiple methods becomes even more difficult.

The goal of this exercise was not to find the best species distribution model for each species we examined. Numerous examples have covered that and similar topics (Manel et al. 1999, Stockwell and Peters 1999, Stockwell and Townsend Peterson 2002, Stockman et al. 2006, Townsend Peterson et al. 2007, Syphard and Franklin 2009). Rather, we sought to investigate: (1) how the output of each modeling approach differed in their predicted relationship to environmental data input into each model, and (2) what implications these results may have for understanding habitat relationships for species where fine-scale habitat information is often readily available, but landscape-level habitat associations are less understood.

METHODS

Study Area

Fort Benning is located near Columbus, GA and straddles the Upper Coastal Plain and Sandhill (which occupy the fall line between the Upper Coastal Plain and Piedmont) physiographic regions (Figure 4.1). It was established in 1920 on former plantation and agricultural land near the Chattahoochee River (Kane and Keeton 1998). Because of the limited development prior to its establishment as a military base and large areas of restricted access, Fort Benning supports many declining species including the two species used in this exercise: Bachman's Sparrow (*Peucaea aestivalis*) and Prairie Warbler (*Setophaga discolor*). Fort Benning contains approximately 90,000 acres of upland pine habitat, but also includes over 90,000 acres of other habitat types including ponds, wetlands, bottomland hardwoods, areas resembling agricultural pastures and urban areas.

Focal Species and Point Counts

Our analysis was restricted to two species which primarily occur in upland habitat in a range of understory and overstory conditions: Bachman's Sparrow (*Peucaea aestivalis*) and Prairie Warbler (*Setophaga discolor*). We chose these species because they are abundant on Fort Benning, and they represent two levels of habitat specificity on the fort: Bachman's Sparrow is an upland pine specialist that requires frequent fire and typically occurs in areas dominated by pines and areas that are frequently disturbed and is restricted primarily to the coastal plain phiyographic region (Dunning 2006); Prairie Warbler has similar but more general habitat preferences, inhabiting a wider geographical range that extends northward into southern Canada and utilizing a variety of open, shrubby (ruderal) habitat types (Nolan et al. 1999). Both of these species are recognized as species of concern by the conservation group Partners in Flight and Bachman's Sparrow is state-listed as rare in the state of Georgia.

We conducted general avian point counts at 280 sites across Fort Benning during the breeding season (May – June) in 2008 and 2009. Points were placed randomly and stratified by habitat type proportional to habitat availability; however, some areas were excluded due to inaccessibility (e.g., behind military practice ranges and explosive impact areas). Points were a minimum of 250 m from each adjacent point. Point counts were conducted for five minutes in each location for each visit and the distance to each individual bird of any species was estimated and recorded (Buckland et al. 2001). Each site was visited at least three times during the breeding season each year of sampling. We considered a species present at a particular point if was detected at least once and the estimated distance to the species was <100 m. Because the goal of this exercise was to examine differences generated from presence-only species-distribution modeling methods, we used only the presences in our dataset, and absences were ignored.

Data Layers

For our environmental variables, we used habitat classifications derived from GAP landcover data. GAP has been used to create over 2000 species distribution models including models for numerous federally listed species; for example, Florida Grasshopper Sparrow (*Ammodramus savannarum floridanus*) and Greater Sage Grouse (*Centrocercus urophasianus*) (USGS 2012). GAP landcover data (USGS 2012) has also been crosswalked with the National Vegetation Classification Standard (NVCS) which uses ecological associations that take into account physiographic regions when habitats are classified and are more meaningful for trying to infer habitat associations with species.

Our habitat layers were based on the NVCS macro habitat layer, and sampling points where species were present fell into the following classifications: (1) Longleaf pine and sand woodland (hereafter Longleaf), (2) Southern Mixed Deciduous-Evergreen (hereafter Broadleaf), (3) Southeastern Ruderal Forest and Plantation (hereafter Ruderal Forest and Plantation), (4) South-central Oak Hardwood and Pine Forest (hereafter Mixed hardwood-pine), (5) Southern Floodplain Hardwood Forest and Central Mesophytic Hardwood Forest (hereafter Bottomland Hardwood), and (6) Recently Disturbed or Modified (Table 4.2).

We then created binary habitat maps using ArcGIS 9.3 (ESRI 2011) for each class and computed a focal statistic for the number of cells of a given habitat within a circle with an area of 1 ha. This approach had the effect of "smoothing" the maps of the given layers and decreased the influence of edge effects on our models. It also prevented any single cell from belonging entirely to one class, but rather it is a range of values of all the cells within a 1 ha area surrounding a given cell.

We also used a digital elevation model with a 30 m grid cell size (https://data.georgiaspatial.org/) and created a distance to second- and third-order streams raster layer derived from a streams layer obtained from the Georgia GIS Data Clearinghouse (https://data.georgiaspatial.org/). Distance to stream was calculated as a Euclidian distance from a second- or third-order stream. We included this as a habitat variable in our analysis because some of the larger streams in our study area may affect groundcover conditions in a way that is not distinguishable by aerially derived landcover data. Focal statistics were not calculated for elevation or Distance to Stream layers.

Distribution Modeling

We used three presence-only species distribution modeling approaches: (1) GARP, (2) Maxent, and (3) logistic regression. We chose these three methods because one approach has been shown to perform poorly (GARP; Townsend Peterson et al. 2007), one has been shown to perform well when there are few observations (Maxent; Stockwell and Peterson 2002, Hernandez et al. 2006), and one has been widely applied in a number of settings (logistic regression (Romero and Real 1996, Bustamante 1997, Martínez et al. 2003) and is in many ways methodologically more transparent (Stockman et al. 2006). All logistic models were fit in the R statistical package (R team 2009).

For logistic regression and Maxent, we used the same 500 pseudo-absence background points that were randomly distributed across all of Fort Benning. No background points were supplied for GARP since this modeling approach does not allow users to input or control the number of background points used in the analysis. This (500) is fewer background points than the number used in some other analyses; however, our study site was much smaller than most other areas and contains fewer habitat types than other analyses (Stockwell and Townsend Peterson 2002). When we used more than 500 background points, it became apparent that a large proportion of the pseudo-absences were actually contaminated controls (Lancaster and Imbens 1996).

Because logistic regression classification is sensitive to the proportion of presences and absences in a sample, and an extremely disproportionate number of absences to presences causes logistic regression output to tend toward extreme values (Hosmer and Lemeshow1989), we employed the use of a favorability function (Real et al. 2006). A favorability (or "favourability") function is a modification of the logit equation that is independent of the ratio of presences to absences (or false absences in our study). Here the logistic probability (*P*) is expressed in terms of the favorability function (*F*):

$$F = \frac{\frac{P}{(1-P)}}{\frac{n_1}{n_0} + \frac{P}{(1-P)}}$$

where n_1 is the number of presences and n_0 is the number of absences (Real et al. 2006). The favorability function was implemented using the raster calculator in ArcGIS 9.2 (ESRI 2011). Hereafter we refer to the favorability as relative suitability.

Analysis

We created two model sets for each analysis and ran each separately for each modeling approach: one set included all the habitat-type variables in addition to the distance to stream variables and elevation, and one set included only the habitat variables. To compare how different environmental data were used in each the three different species distribution modeling approaches, we used evaluation strips (Elith et al. 2005, Elith and Graham 2009). Evaluation strips are columns of raster data inserted into the environmental layers outside the extent of the original environmental data. For each evaluation strip in each environmental layer the value of a given layer is varied over the entire range of the values and then held constant in all other layers. When the model is run and the prediction map is produced, the relationship between the environmental parameter of interest and species occurrence can then be examined. This approach permits the comparison of multiple modeling approaches in spite of the lack of the transparency for how the model was created in the approaches used by GARP and Maxent. We plotted the response of each variable in each approach against the relative suitability for the GARP, logistic regression and the Maxent relative suitability values. Additionally, as a measure of the models' predictive ability, we computed the receiver operating curve (ROC) and calculated the area under the curve (AUC) to examine the predictive ability across each method.

RESULTS

Our surveys detected 45 locations for Bachman's Sparrow and 110 locations for Prairie Warbler within 100 m of a sampling point across the two years of sampling. For the analysis using all predictor variables (habitat variables as well as elevation and distance to stream), the highest AUC was observed when Maxent was used for both species, followed by GARP, then the logistic model (Table 4.3). When only habitat variables were used, the highest AUC for both species was again observed using the Maxent models, but the logistic model outperformed GARP for Prairie Warbler (Table 4.3).

The evaluation strip plots revealed that many of the shapes and slopes of the relationships between the relative suitability of a model and the change in the value of a predictor variable (holding the values of all the other variables constant) were different among the approaches (Figures 4.1a–4.4c). When all predictors were used, both species exhibited changes in relative suitability values with changes in elevation (Figure 4.2a, Figure 4.3a). However, the shape of this relationship differed among all three modeling approaches for Bachman's Sparrow, but was similar for the Maxent and logistic models for Prairie Warbler (Figure 4.3a). Maxent was the only approach that modeled much of a relationship between distance to stream, area of longleaf pine, or mixed habitat area for Bachman's Sparrow when all habitat variables were included (Figure 4.2a-4.2c). GARP and logistic models were the only approaches that exhibited changes in relative suitability with increases in area of the ruderal plant habitat type for Prairie Warbler (Figure 4.3c).

When only habitat type was considered in the models (i.e., when elevation and distance to stream were not modeled with the other environmental variables; Figures 4.4a–4.5b), relative suitability for Bachman's Sparrow increased with increases in longleaf area for all three modeling approaches (Figure 4.4a), but only the logistic model indicated higher relative suitability in longleaf habitat. The Maxent and logistic models were the only two approaches where recently disturbed or modified habitat had much of any relationship to relative suitability for Bachman's Sparrow (Figure 4.4b). Additionally, Maxent was the only approach where no relationship was seen between changes in ruderal plant area and changes in Prairie Warbler relative suitability (Figure 4.5b). For both species, GARP exhibited the strongest relationship between ruderal plant area and relative suitability when only habitat variables were used in the analysis (Figure 4.3b, Figure 4.5b).

DISCUSSION

Relationships between species and environmental habitat layers varied dramatically among the three different species distribution modeling approaches. Syphard and Franklin (2009) compared the correlation of four different species distribution modeling method (classification trees, GLM, GAM, and random forests) and found varying correlation between predictions and across methods. They also found that variable importance differed across the different methods. To date, many species distribution modeling approaches have utilized ancillary species locations across broad geographic regions to predict the current (Milsom et al. 2000) and future (Bakkenes et al. 2002, Milanovich et al. 2010) distribution of species. Given that we have illustrated how many of the different approaches differ in the modeling of their relationships to habitat characteristics, and that many climate models have a high degree of uncertainty in forecasting changes in landcover and other bioclimatic variables (Feddema et al. 2005, Maurer 2007), it seems prudent to consider to what degree the modeling method alone is influencing these predictions.

We found that several of the modeling approaches were not concordant with commonly perceived habitat relationships for Bachman's Sparrow and Prairie Warbler when all habitat variables were used. This result likely has important implications for extrapolation of models to unsampled areas or to areas with few presence locations. For example, elevation had one of the strongest relationships with relative suitability for both species (Figure 4.1a, Figure 4.2a). Although elevation appears to be an important factor at Fort Benning, the entire range of both of these species extends across a large elevation gradient and this variable is unlikely to be important at the scale of the entire range of both of these species. In some respects this is unsurprising as map-derived habitat classifications have been shown to have good predictive ability for some species, but that field derived measurements can provide better information related to specific habitat requirements for others (Earnst and Holmes 2012). Additionally, some local landscape characteristics might be more important than they are at larger extents. It should be noted, however, that some approaches to species distribution modeling, such as Maxent, have gained widespread use for their ability to generate "useful" models with small sample sizes (5–10; Hernandez et al. 2006). Using a model across a wide geographic region with as few as five presence locations seems recklessly optimistic since even high numbers of locations from a restricted geographic extent may lead to misleading predictions about the importance of a particular habitat feature to a species' distribution.

We caution, as others have suggested (Royle et al. 2012), that because the sampling of geographical areas is often not probabilistically based for presence-only modeling and many predictive maps extend beyond known locations for these species, interpreting a landscape-level habitat association using any method of species distribution modeling should be done with caution in the absence of a well-defined sampling strategy. The data derived from our sampling strategy for this exercise was probabilistically based and more intensively collected compared to other presence-only distribution modeling efforts (Stockman et al. 2006), yet the relationships we found for our species may be of limited use for making inferences for conservation strategies. For a species such as Bachman's Sparrow, landscape-level characteristics may be far less important than conditions that can only be measured on the ground.

Understanding species distributions is essential to implementing effective strategies for conservation (Samways 2005). Thus, the relationships of modeled species distributions to landscape-level habitat characteristics are also equally important if we are striving to implement conservation schemes that enhance characteristics of existing and future habitat. Given that many of the current methods differ in the way that these relationships are modeled, there is a large amount of uncertainty associated with what factors—from a landscape-scale—are important for declining species. We suggest using multiple modeling approaches in any conservation planning efforts to incorporate uncertainty in species-habitat relationships, especially when sampling is not probabilistic and uses presence-only data.

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Table 4.1. Species used in distribution modeling comparison and their conservation priority scores, population estimates, and percentage of population breeding in the United States. Continental Concern Score ranges from 1 to 20, where 1 is of least concern and 20 is of highest concern.

Common Name	Global Pop Est.	Continental Concern Score	TNC	UCC	CBSD	UCS	%Pop US
Bachman's Sparrow	200,000	14	No	Yes	No	Yes	100
Prairie Warbler	3,500,000	13	No	Yes	Yes	Yes	100

TNC = Tri-national Concern Species, UCC = U.S. Canada Concern Species, Common Bird in Steep Decline, U.S. - Canada Stewardship Species

Table 4.2. Habitat classes from GAP data used as environmental layers in distribution models.

GAP Pixel Value(s)	Gap Class Name	New Class Name
9, 10, 12, 13, 17	Longleaf Pine and sand woodland	Longleaf
26	Southern Mixed Deciduous-Evergreen Broadleaf Forest	Broadleaf Forest
33, 34, 35, 36, 38	Southeastern Ruderal Forest and Plantation	Ruderal Forest and Plantation
103, 104, 109,112, 113	South-central Oak Hardwood and Pine Forest (mixed)	Mixed hardwood-pine forest
120, 216, 219, 220, 232	Central Mesophytic Hardwood Forest	Bottomland Hardwood
	Southern Floodplain Hardwood Forest	
567, 568, 574, 575	Recently Disturbed or modified	Recently Disturbed or Modified

Table 4.3. Area under the curve (AUC) for distribution models of Bachman's Sparrow and Prairie Warbler at Fort Benning, Georgia using three different modeling techniques.

All Predictors	**Species**	**Modeling Technique**	**AUC**
	BACS	GARP	0.79
		Maxent	0.84
		Logistic	0.76
	PRAW	GARP	0.69
		Maxent	0.78
		Logistic	0.67
Habitat Predictors Only	BACS	GARP	0.73
		Maxent	0.8
		Logistic	0.68
	PRAW	GARP	0.59
		Maxent	0.73
		Logistic	0.64

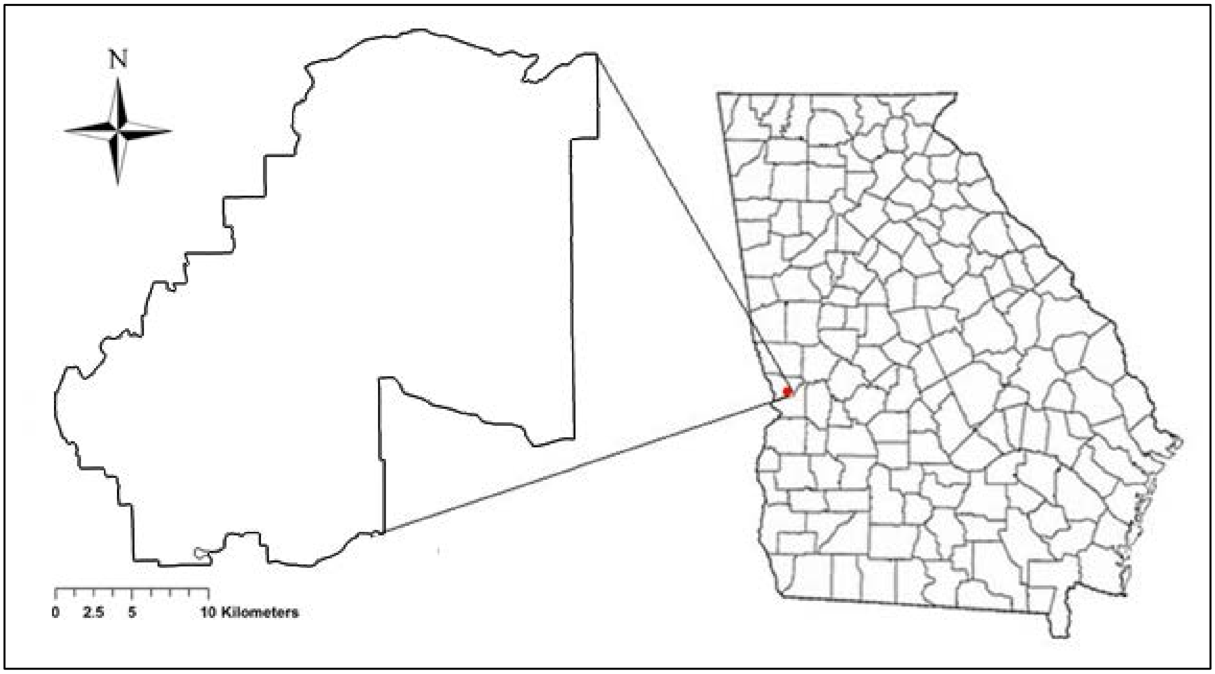


Figure 4.1. Outline map of Fort Benning and its approximate location within the state of Georgia.

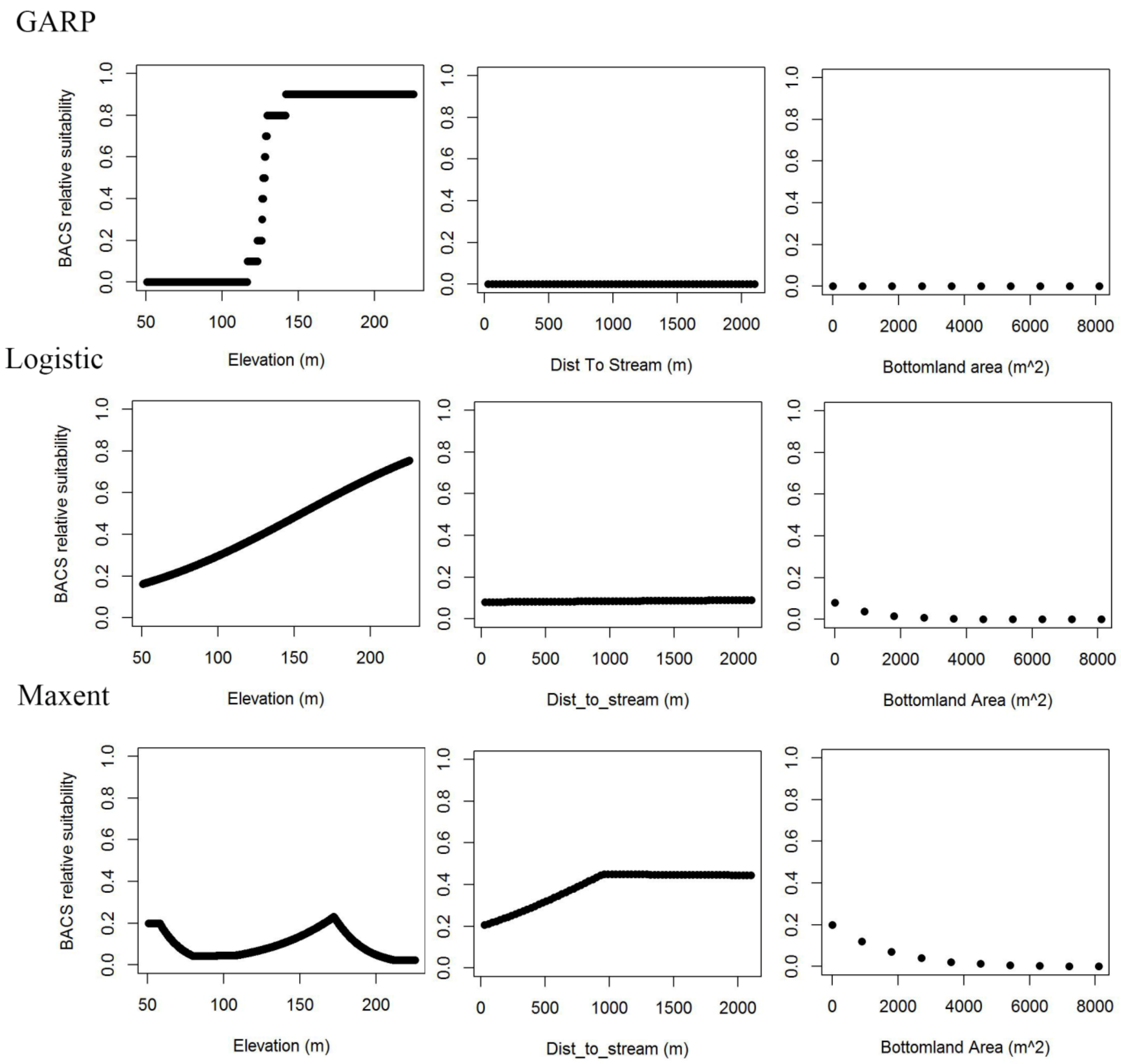


Figure 4.2a. Relationships of environmental variables included in models for the prediction of Bachman's Sparrow distribution at Fort Benning, GA.

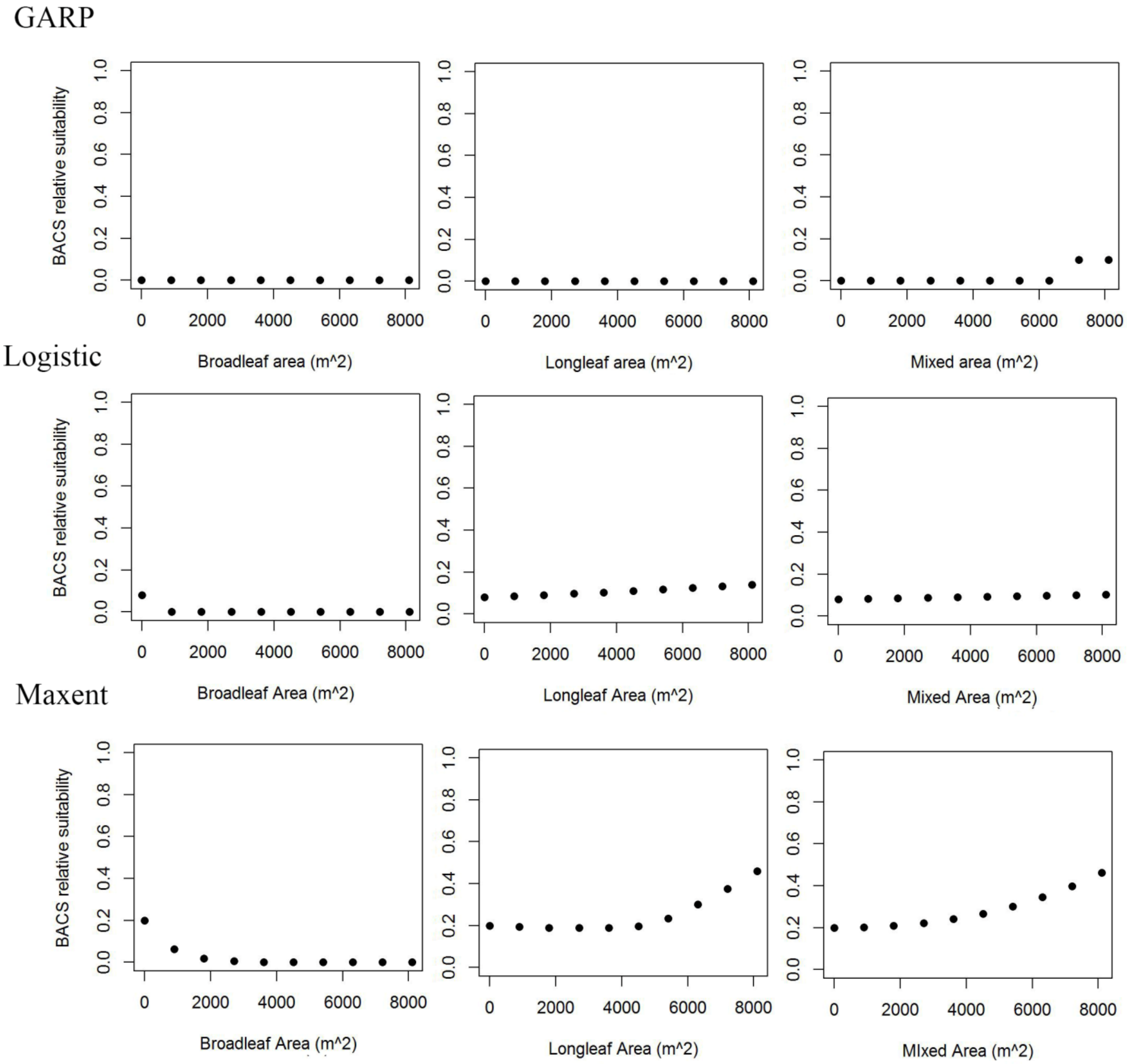


Figure 4.2b. Relationships of environmental variables included in models for the prediction of Bachman's Sparrow distribution at Fort Benning, GA.

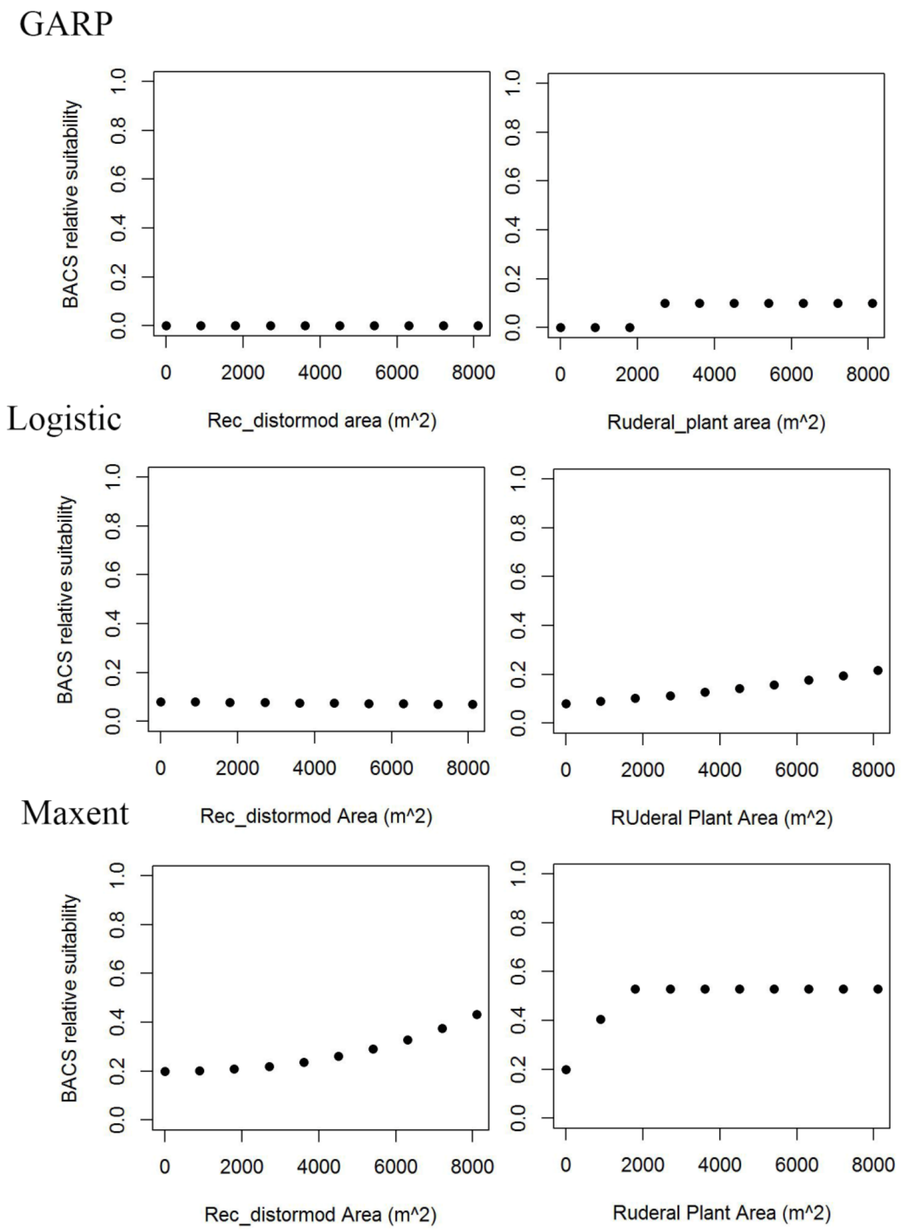


Figure 4.2c. Relationships of environmental variables included in models for the prediction of Bachman's Sparrow distribution at Fort Benning, GA.

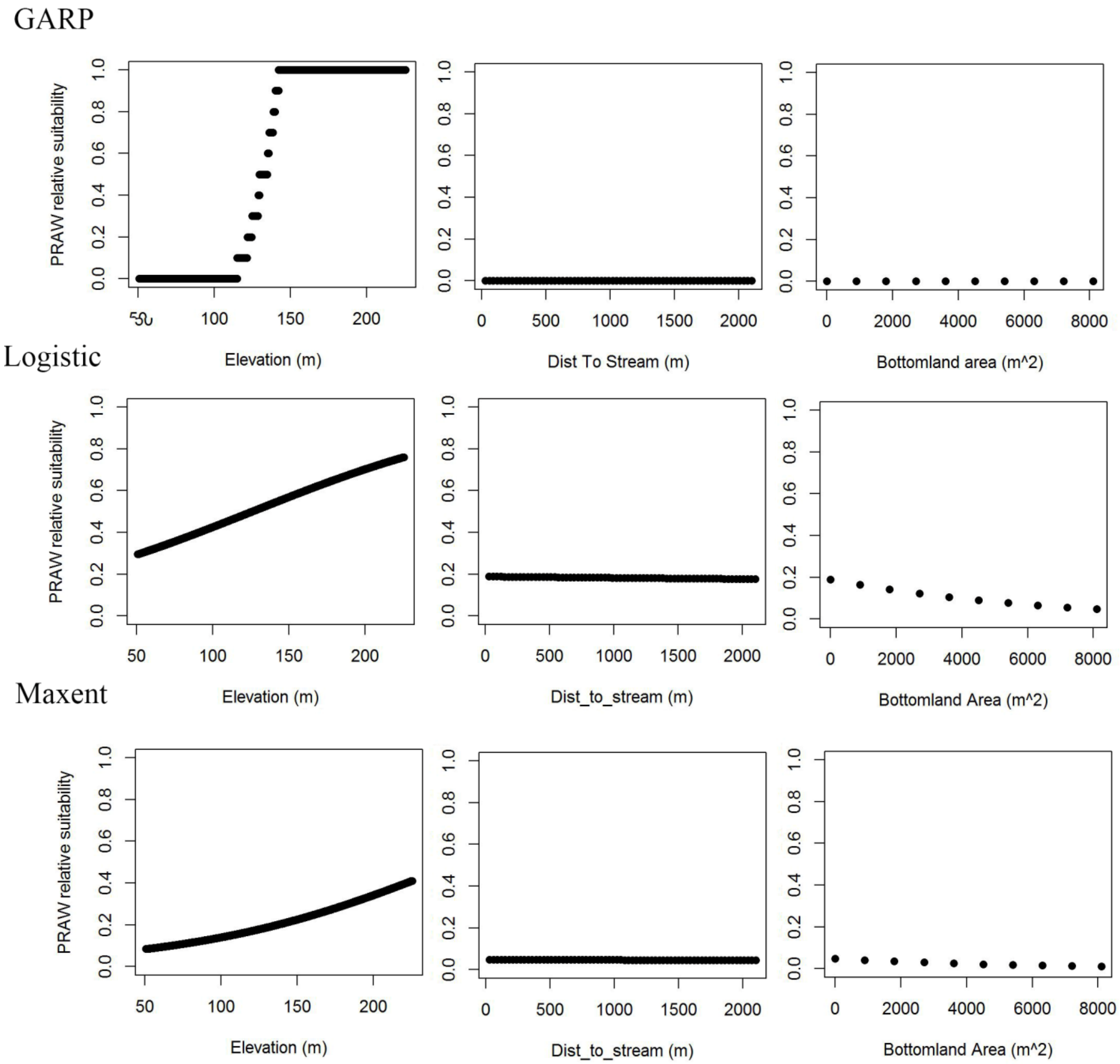


Figure 4.3a. Relationships of environmental variables included in models for the prediction of Prairie Warbler (*Setophaga discolor*) distribution at Fort Benning, GA.

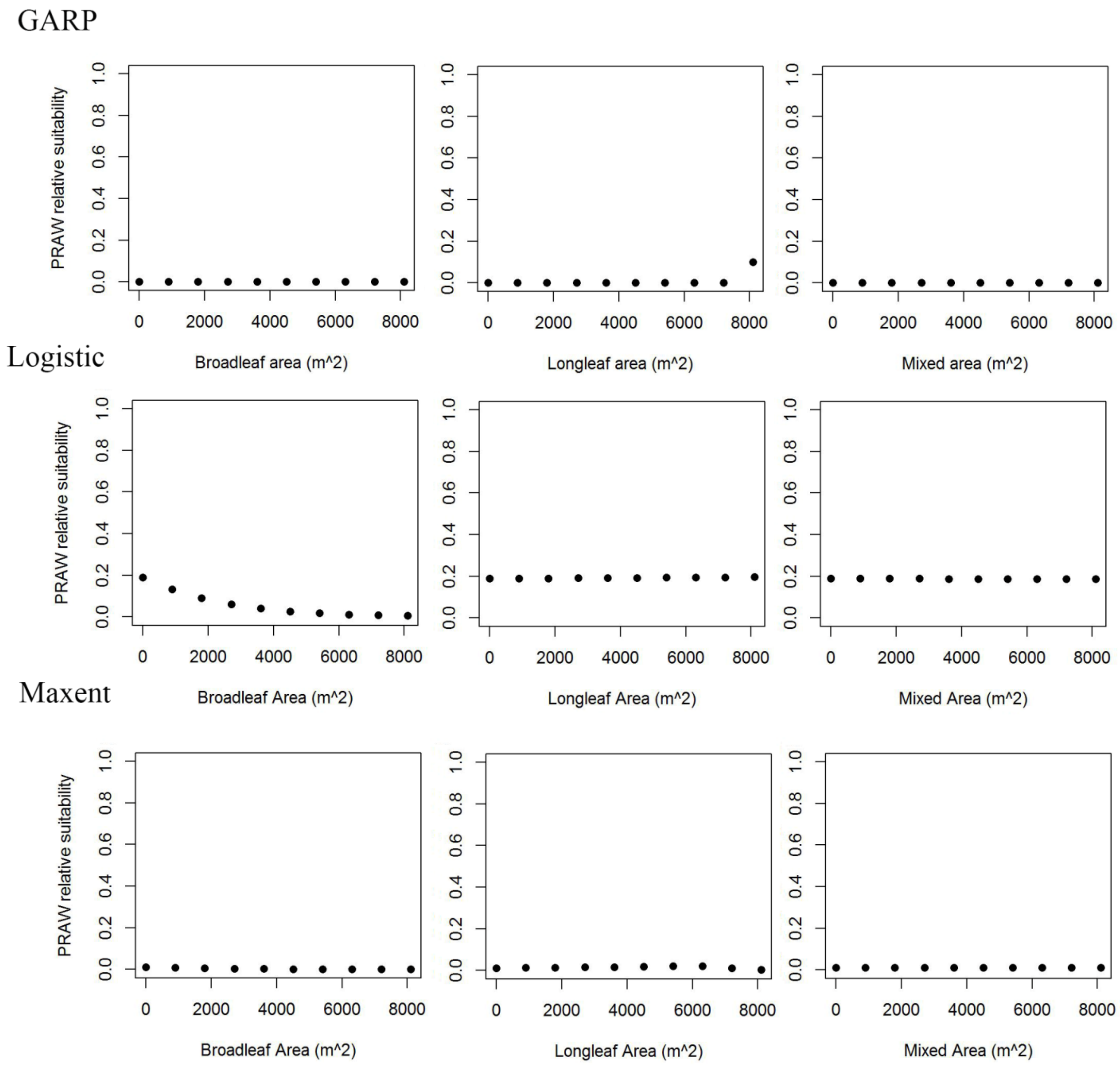


Figure 4.3b. Relationships of environmental variables included in models for the prediction of Prairie Warbler (*Setophaga discolor*) distribution at Fort Benning, GA.

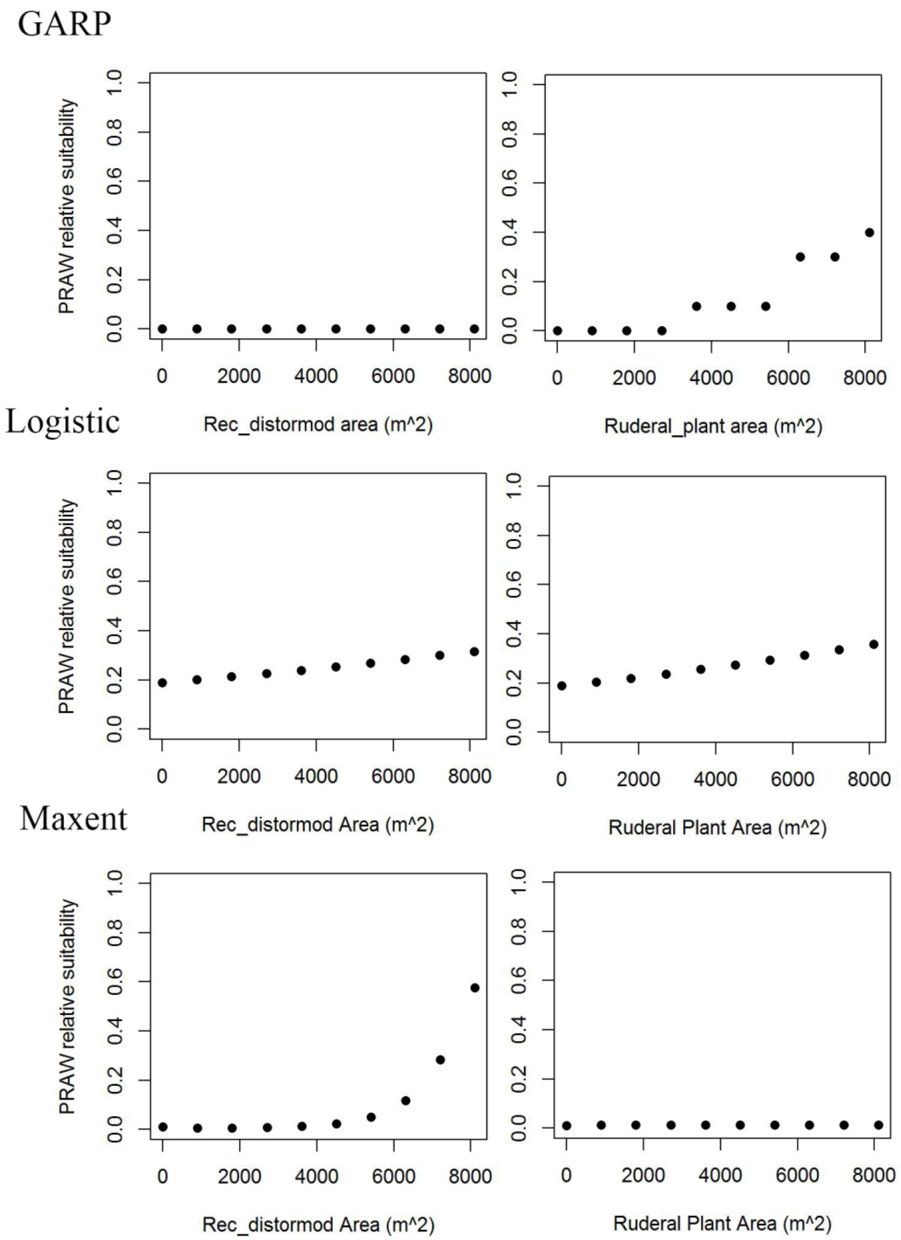


Figure 4.3c. Relationships of environmental variables included in models for the prediction of Prairie Warbler (*Setophaga discolor*) distribution at Fort Benning, GA.

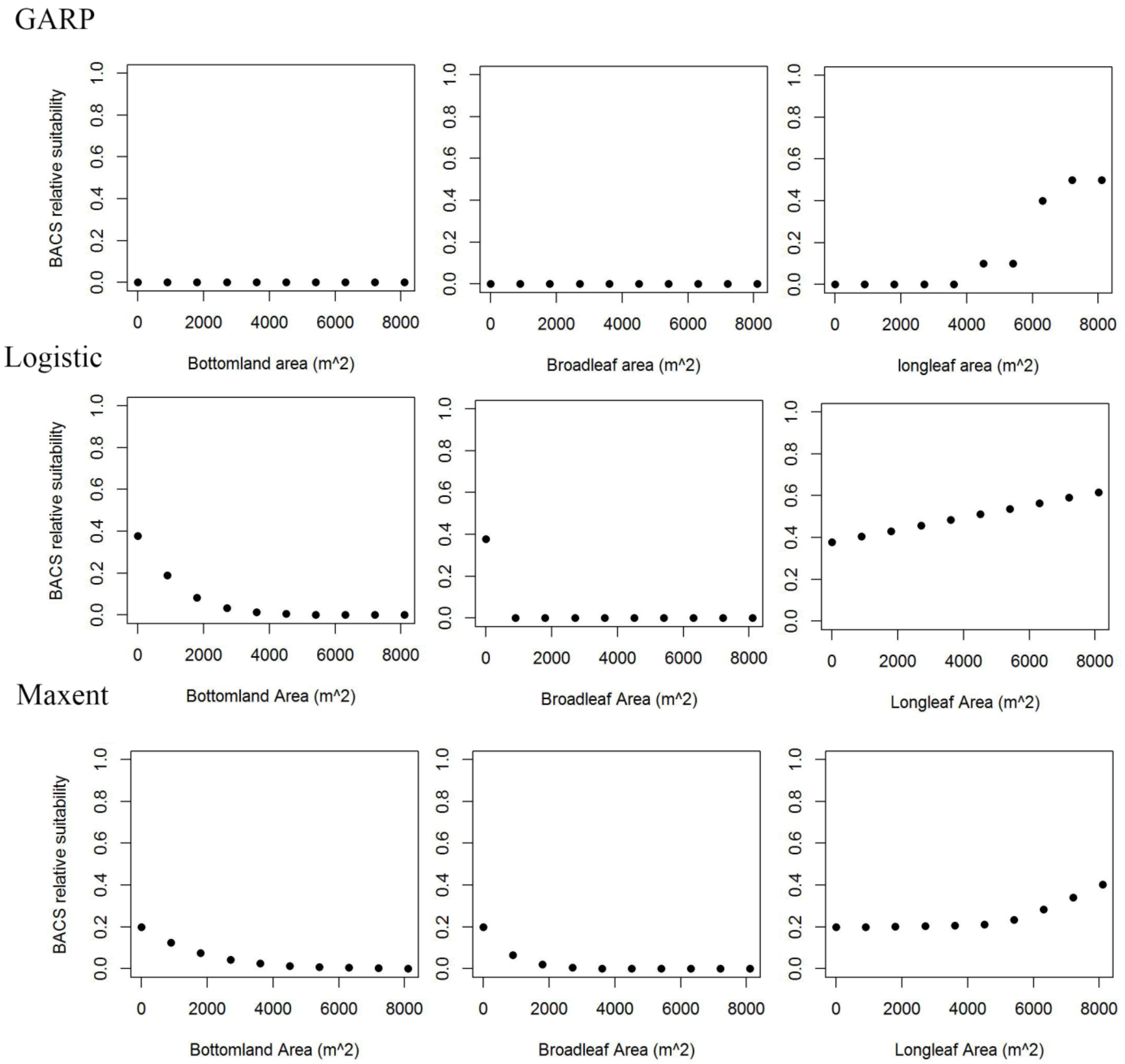


Figure 4.4a. Relationships of environmental variables (landcover habitat variables only) included in models for the prediction of Bachman's Sparrow (*Peucaea aestivalis*) distribution at Fort Benning, GA.

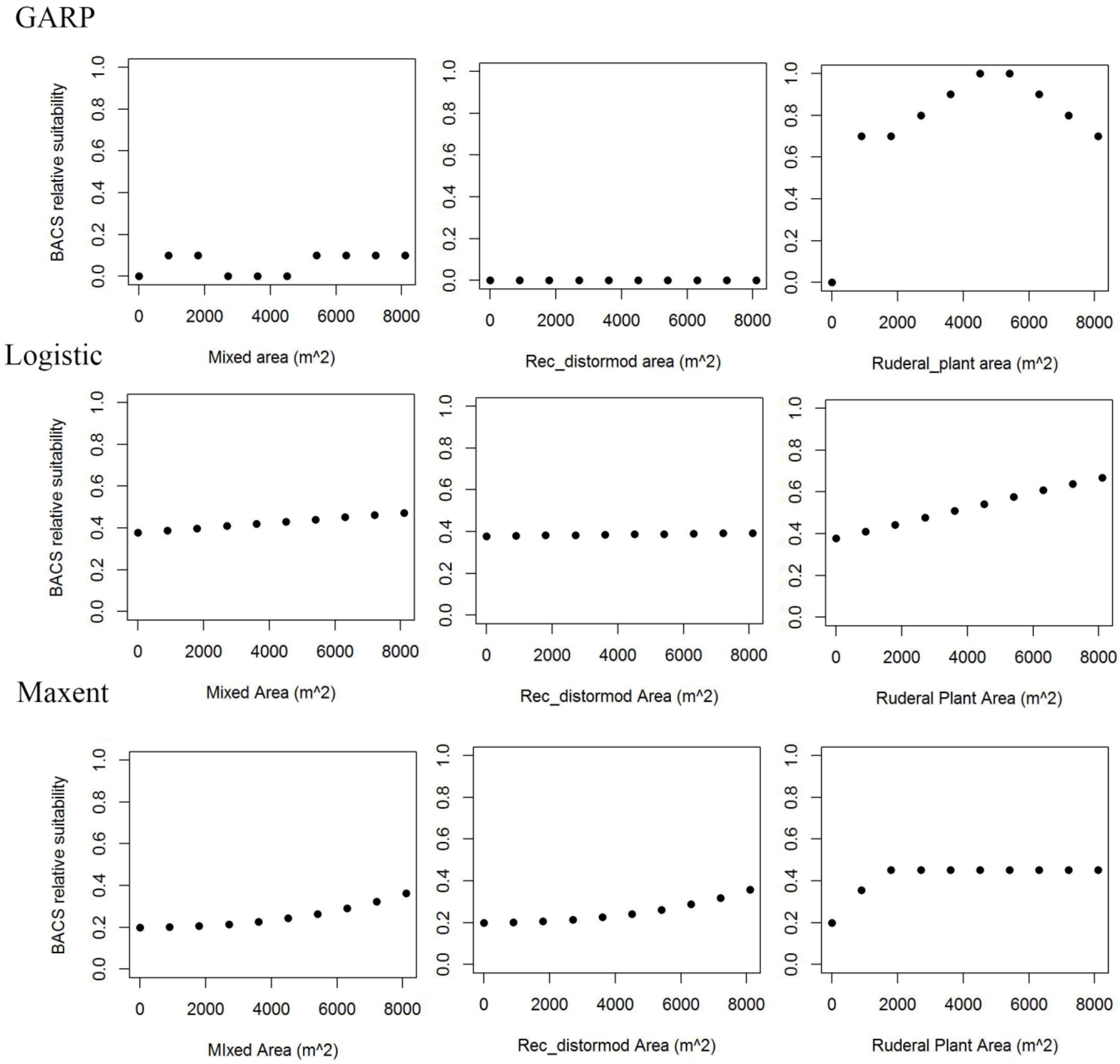
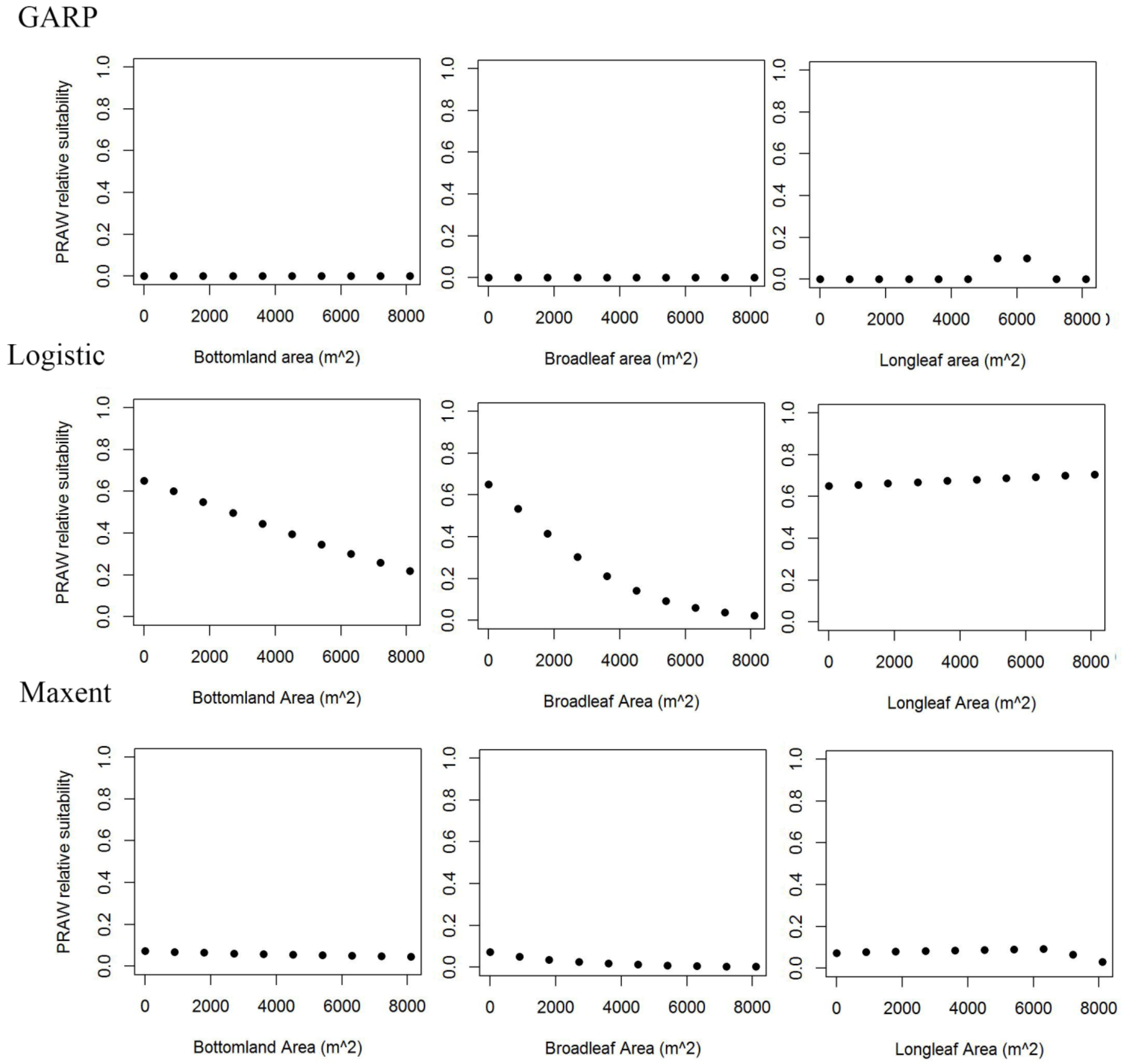


Figure 4.4b. Relationships of environmental variables (landcover habitat variables only) included in models for the prediction of Bachman's Sparrow (*Peucaea aestivalis*) distribution at Fort Benning, GA.


GARP

Logistic

Maxent

Figure 4.5a. Relationships of environmental variables (landcover habitat variables only) included in models for the prediction of Prairie Warbler (*Setophaga discolor*) distribution at Fort Benning, GA.

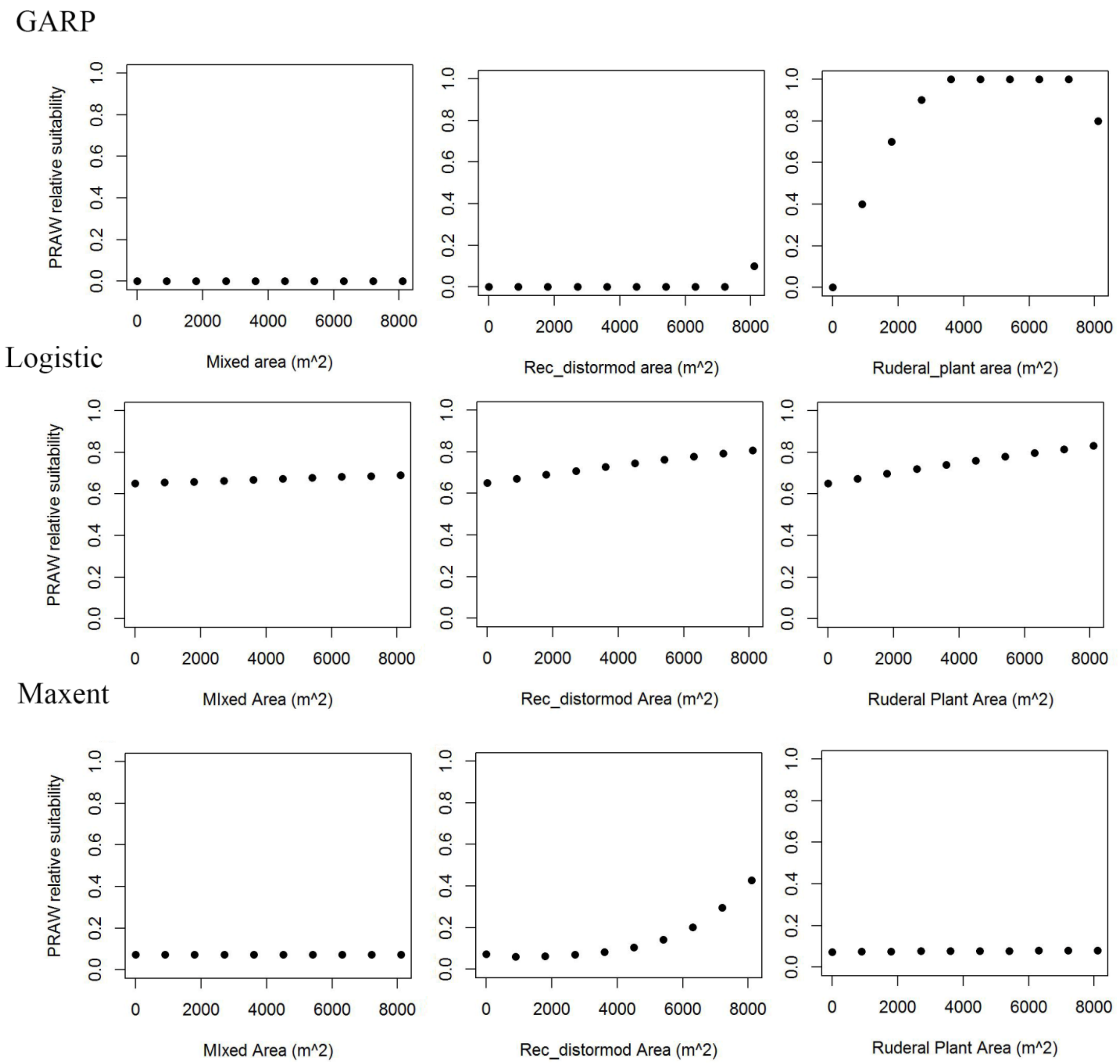


Figure 4.5b. Relationships of environmental variables (landcover habitat variables only) included in models for the prediction of Prairie Warbler (*Setophaga discolor*) distribution at Fort Benning, GA.

CHAPTER 5

CONCLUSION AND SYNTHESIS: CONSERVING THE FUTURE OF LONGLEAF PINE SAVANNAS BY UNDERSTANDING LANDSCAPE-LEVEL INFLUENCES

The aim of this dissertation is to understand how landscape-level characteristics affect members of the avian community in longleaf pine forests at Fort Benning, Georgia. Numerous members of the longleaf pine avian community have undergone population declines across their range (Jackson 1994, Means et al. 1996, Earley 2004, Dunning 2006, Means 2006). A number of factors have contributed to these declines— including loss of natural processes such as fire (Jackson 1994, Dunning 2006, Huffman 2006, Means 2006)—but the primary reason for these decreases is the loss of habitat (Means 1996). In addition to loss of habitat, secondary effects resulting from habitat fragmentation have also played a role in population declines. Fragmentation increases the rate of predation (Storaas et al. 1999), nest depredation (Small and Hunter 1988, Rolstad 1991, Berger 1997), and nest parasitism (Davis and Sealy 2000) in landscapes. Fragmented habitats expose species to increased risk of disease (Allan et al. 2003), negatively influence overall health of individuals (Niu 2007), and can alter species morphology (Desrochers 2010). Additionally, fragmentation isolates local populations, alters immigration and emigration rates, and increases the risk of extinction (Hinsley et al. 1996, Fahrig 2003, Loehle 2007, Boscolo et al. 2008, Boscolo and Metzger 2011, Loehle and Eschenbach 2012). Fort Benning is a remnant of the expansive longleaf pine savanna that previously dominated the southeastern landscape and provided an ideal setting in which to investigate strategies for longleaf conservation and landscape-level factors that influence avian species in longleaf savannas. Processes that were once common across the Southeast are still regular occurrences on the fort, and management strategies are similar to those applied across the remnant patches of longleaf scattered disparately across the Southeast.

ARE CORRIDORS USEFUL FOR CONSERVATION OF AVIAN SPECIES IN LONGLEAF PINE SAVANNAS?

Habitat loss and fragmentation is the leading cause of species endangerment (Saunders et al. 1991, Foley et al. 2005). Fragmentation has contributed to the decline of many avian species occupying a wide variety of habitats across North America (Herkert 1994, Hagan et al. 1996) and undoubtedly has had negative consequences for the longleaf pine ecosystem. Unfortunately, few studies have examined the effects of fragmentation within southeastern pine savannas for avian species (but see Dunning et al. 1995). In Chapter 2 I demonstrated that for the resident Bachman's Sparrow (*Peucaea aestivalis*), a species whose distribution is almost entirely restricted to pine savannas in the Southeast, movements across the landscape at a relatively small scale are influenced by different levels of habitat connectivity. These results likely explain why some patches of seemingly suitable habitat are unoccupied by Bachman's Sparrows in portions of the species' range (Buckelew and Hall 1994). By contrast, the neotropical migrant Prairie Warbler (*Setophaga discolor*) was not as sensitive to habitat connectivity. The life history of each species provides some clues for the patterns observed since Bachman's Sparrow is a resident species that undergoes little or no migration in this region (Dunning 2006, Cox and Jones 2009) while Prairie Warbler is a neotropical migrant that undergoes long annual migrations that traverse a myriad of habitat types. My results indicate that corridors are likely an effective tool to increase connectivity between patches of suitable habitat for Bachman's Sparrows.

There are currently multiple efforts on Department of Defense lands in the Southeast promoting connectivity in longleaf pine savannas and adjacent habitats as a conservation strategy (e.g., The Altamaha/Ocmulgee Corridor, The Lower Ogeechee/Ft. Stewart Corridor, Army Compatible Use Buffer program). My research shows that these efforts will likely lead to benefits for inhabitants of the longleaf ecosystem in spite of previous criticisms that resources may be better spent on acquiring additional habitat (Simberloff et al. 1992). Given the paucity of existing habitat and the isolated nature of much of it, slowly restoring and acquiring land in proximity to existing habitat with the goal of increasing connectivity will undoubtedly benefit species dependent on the longleaf pine habitat.

IS THE RED-COCKADED WOODPECKER FUNCTIONING AS AN AVIAN UMBRELLA SPECIES FOR OTHER DECLINING BIRDS?

Management for Red-cockaded Woodpeckers (*Picoides borealis*) on public lands is intensive and expensive. Invoking the Red-cockaded Woodpecker as an umbrella species is often used, in addition to requirements imposed by the endangered species act, as justification for single-species management. Although single-species management is frequently employed because it generates (or is a source of) funding, criticism of the concept is wide-spread (Roberge and Angelstam 2004). Multiple studies have shown that management for Red-cockaded Woodpeckers can be beneficial for several avian species that occupy similar habitats or benefit from similar land management actions (Wilson et al. 1995, Plentovich 1998, Conner et al. 2002, Cox and Jones 2009); however, other studies have found contrasting results that suggest optimal conditions for the Red-cockaded Woodpecker do not necessarily create optimal conditions for other avian inhabitants of longleaf pine savannas (Liu et al. 1995, Cox et al. 2012).

In Chapter 3 I demonstrated that patterns exist between locations of Red-cockaded Woodpecker clusters and occurrence of five declining species that share similar habitats (Brown-headed Nuthatch [*Sitta pusilla*], Bachman's Sparrow, Field Sparrow [*Spizella pusilla*], Northern Bobwhite [*Colinus virgianianus*]). These results suggest that for some species, especially Bachman's Sparrow, land management for Red-cockaded Woodpecker is conferring some benefit. However, I also illustrate that some locations have higher diversity (as measured by Simpson Diversity) of these five species than others. The goal of Chapter 3 was to illustrate that the effect of management for Red-cockaded Woodpeckers is variable across different locations; an outcome that is largely ignored when single-species management is implemented (but see Liu et al. 1995, Plentovich 1998). This result is intuitive as there are a number of factors that influence local and landscape-level abundance and occupancy of different species (some of which are suggested in Chapter 2), but examination of these patterns could prove useful in a single-species paradigm if they aid in the identification of areas (or factors) for re-introduction of Red-cockaded Woodpeckers that would confer benefit to the most species possible.

LOOKING INTO THE FUTURE BY UNDERSTANDING THE PRESENT: SPECIES DISTRIBUTION MODELS TELL DIFFERENT STORIES

Species distribution modeling is a valuable tool that has been used increasingly in recent years. This increase is—in large part—the result of the widespread availability of user-friendly software (e.g., Maxent, GARP, Open Modeller) that readily produces easily interpretable maps. However, many of these software packages provide limited information on how the model(s) are produced or how environmental variables are used to create the predictive map surface (Elith et al. 2005, Elith and Graham 2009). There are at least two useful inferences that can be derived from species distribution models: (1) a predictive map can be produced that provides information on areas where a species might be found, allowing managers to identify target areas for conservation and (2) species-environment relationships can be inferred. The former is arguably the most widespread application; the latter is often just as important, but frequently ignored (Royle et al. 2012). In Chapter 4 I used simple, presence-only distribution models to make predictions about the occurrence of Bachman's Sparrow and Prairie Warbler on Fort Benning. I illustrate that the inference for species-habitat relationships using each modeling method is highly variable and suggest that the variability of inference obtained from each method has important consequences for predicting beyond the extent of known occurrences. Additionally, I advocate the use of multiple species distribution modeling approaches when these tools are being used for conservation planning.

IMPLICATIONS FOR CONSERVATION OF LONGLEAF PINE SAVANNAS

There are numerous considerations for implementing effective conservation of longleaf pine savannas. Unlike the old-growth forests in the northwestern United States, the rain forests of Central and South America, or the tundra of the North Slope of Alaska, longleaf pine savannas cannot simply be set aside for conservation; they require active management (Jackson 1994, Means 1996, Earley 2004, Dunning 2006, Means 2006). Additionally, because the remaining patches of the ecosystem are disparate and isolated, a suite of approaches is necessary if effective conservation is sought. As I demonstrated, the fragmented nature of the remaining habitat requires explicit consideration for spatial context for the conservation of some species (such as Bachman's Sparrow). Linking patches of existing habitat using corridors will benefit some species in the longleaf ecosystem, but the list of declining species that are longleaf dependent is long, and there are many more considerations that have not been examined (e.g., corridor width, length, and juxtaposition to other landcover types). Single-species management does appear to play some role in promoting the diversity of declining species sharing similar habitat requirements, but as is the case with many conservation strategies, the effect is variable in different locations. Conservation efforts should focus at two scales: (1) at the scale of local management actions and (2) at the landscape level where these factors likely have top-down influences on the success or failure of local actions. Without a comprehensive plan, the effectiveness of many conservation strategies may be greatly reduced.

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