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Landcover Change And Population Dynamics Of Florida Scrub-jays And Florida Grasshopper Sparrows

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LANDCOVER CHANGE AND POPULATION DYNAMICS OF FLORIDA SCRUB-JAYS AND FLORIDA GRASSHOPPER SPARROWS

by

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A dissertation submitted in partial fulfillment of the requirements
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ABSTRACT

I confronted empirical habitat data (1994-2004) and population data (1988-2005) with ecological theory on habitat dynamics, recruitment, survival, and dispersal to develop predictive relationships between landcover variation and population dynamics. I focus on Florida Scrub-Jays, although one chapter presents a model for the potential influence of habitat restoration on viability of the Florida Grasshopper Sparrow. Both species are unique to Florida landscapes that are dominated by shrubs and grasses and maintained by frequent fires. Both species are declining, even in protected areas, despite their protected status.

I mapped habitat for both species using grid polygon cells to quantify population potential and habitat quality. A grid cell was the average territory size and the landcover unit in which habitat-specific recruitment and survival occurred. I measured habitat-specific recruitment and survival of Florida Scrub-Jays from 1988-2008. Data analyses included multistate analysis, which was developed for capture-recapture data but is useful for analyzing many ecological processes, such as habitat change. I relied on publications by other investigators for empirical Florida Grasshopper Sparrow data.

The amount of potential habitat was greatly underestimated by landcover mapping not specific to Florida Scrub-Jays. Overlaying east central Florida with grid polygons was an efficient method to map potential habitat and monitor habitat quality directly related to recruitment, survival, and management needs. Most habitats for both species were degraded by anthropogenic reductions in fire frequency. Degradation occurred across large areas. Florida Scrub-Jay recruitment and survival were most influenced by shrub height states. Multistate modeling of shrub heights showed that state transitions were influenced by vegetation composition, edges, and habitat management. Measured population declines of 4% per year corroborated habitat-specific modeling predictions. Habitat quality improved over the study period but not enough to recover precariously small populations.

The degree of landcover fragmentation influenced mean Florida Scrub-Jay dispersal distances but not the number of occupied territories between natal and breeding territories. There was little exchange between populations, which were usually further apart than mean dispersal distances. Florida Scrub-Jays bred or delayed breeding depending on age, sex, and breeding opportunities.

I show an urgent need also for Florida Grasshopper Sparrow habitat restoration given that the endangered bird has declined to only two sizeable populations and there is a high likelihood for continued large decline. A major effect of habitat fragmentation identified in this dissertation that should apply to many organisms in disturbance prone systems is that fragmentation disrupts natural processes, reducing habitat quality across large areas. Humans have managed wildland fire for > 40,000 years, so it should be possible to manage habitat for many endangered species that make Florida’s biodiversity unique. This dissertation provides methods to quantify landscape units into potential source and sink territories and provides a basis for applying adaptive management to reach population and conservation goals.

I dedicate this to my family, Vanessa, Robbie, Daniel, and Joshua.

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INTRODUCTION

Understanding and managing how landcover change influences population dynamics are necessary for conservation (Noss and Cooperider 1994, Dale et al 2000, Groves 2002). Dynamic models of habitat and populations have much potential for making such predictions, but serious data gaps usually exist (Karieva 1990, Hanski 1999, Breininger et al. 2002). Comparisons between population abundance and landcover data can fill those gaps, but abundance data are often subject to measurement bias, poor precision, and misleading relationships between abundance and habitat quality (Van Horne 1983, Johnson et al. 2006). Abundance is usually the result of many interacting factors and by itself offers little understanding (Hanski 1999). Quantifying habitat-specific reproductive survival, recruitment, and dispersal are critical information needs to overcome these gaps (Pulliam 1988) and much more work needs to be done confronting such data with alternative ecological models (Burnham and Anderson 2002, Williams et al. 2002). Most of this dissertation focuses on confronting necessary empirical habitat and population data with ecological theory about habitat dynamics and its influence on recruitment, survival, and dispersal. Florida Scrub-Jays and Florida Grasshopper Sparrow are species unique to Florida shrublands and savannas and are at risk of extinction due to habitat loss, fragmentation, and degradation (Stith et al 1996, Root 1998, Breininger et al. 1999, Perkins et al. 2008).

General goals

This dissertation focuses on how landcover influences species with emphases on fragmentation, particularly when fire flow across landscapes is disrupted and large natural areas remain. Such disruption in natural processes is common across the world but has been rarely studied. Two chapters broadly quantify relationships between landcover on habitat quality using empirical data or population modeling. Remaining chapters examine several details of habitat dynamics, survival, and dispersal using methods applicable to many species. Together these seek to quantify the significance of fragmentation effects and provide methods that can be used to monitor the efficacy of management to conserve populations in the remaining fragments.

General goals will be briefly introduced in this first chapter followed by a brief background of relevant topics about habitat and population dynamics. The second chapter quantifies the amount, quality and dynamics of Florida Scrub-Jay populations in habitat fragments comprising a large metapopulation. The chapter introduces a grid polygon mapping approach to characterizing habitat potential and quality that is influenced by fire, management actions, and vegetation recovery from fire. This chapter also quantifies how recruitment relative to apparent breeder deaths is specific to different measures of habitat quality. The third chapter focuses on applying grid polygons and multistate models as a new approach to quantify how habitat quality states are influenced by covariates related to intrinsic habitat factors (e.g., oak cover), habitat management (number of fires, mechanical cutting) and edges that disrupt natural fires. The third chapter also shows relations between capture-recapture models and Markov models, which are often used to describe habitat, vegetation, land cover, and ecosystem dynamics. The chapter shows how multistate capture-recapture models not only quantify transition probabilities of a system in relation to covariates but also quantify the variances of linear model coefficients and real parameters (e.g., transitions) in a model selection framework.

The fourth chapter uses 18 years of colorbanding data and multistate capture-recapture methods to test whether detection probabilities and survival are influenced by habitat. The fourth chapter also tests whether bird habitat state transitions between years are the result of habitat preferences or habitat state transitions that occur independent of bird territory boundaries. A fifth chapter uses an information theoretic approach and modern model selection techniques to investigate factors that influence whether non-breeding Florida Scrub-Jays choose to remain non-breeders or disperse elsewhere to become breeders.

A sixth chapter focuses on habitat mapping using grid polygons and population modeling of Florida Grasshopper Sparrows to make predictions to compare alternative habitat restoration actions. These predictions should be useful in making recommendations for achieving recovery objectives and exploring ecological uncertainties relevant for structured decision making. The seventh chapter summarizes conclusions, conservation applications, and future research needs of all sections with an emphasis on population recovery topics related to habitat fragmentation and degradation resulting from human-altered fire regimes.

Science background

Florida Scrub-Jays are described in many evolutionary, behavioral, and ecology textbooks because of their long-term study and cooperative breeding system where young delay breeding sometimes for many years after hatching (Woolfenden and Fitzpatrick 1984, 1991, 1996). Florida Scrub-Jays are the only species of bird unique to Florida and are a threatened species under the federal Endangered Species Act. Florida Scrub-Jays are generally described as being restricted to well-drained oak scrub (Woolfenden and Fitzpatrick 1984; Stith et al. 1996). Landcover and vegetation maps usually use soils maps to separate oak scrub from pine flatwoods because spectral signatures of many xeric and mesic plants are difficult to distinguish (Breininger et al. 1991). Pine flatwoods once represented the dominant native landcover in the southeastern U.S. coastal plain (Platt 1999), but most flatwoods are not considered suitable for Florida Scrub-Jays. Pine flatwoods, oak scrub, and dry prairie are among the most endangered ecosystems in North America (Noss et al. 1995, 1997).

The Florida Grasshopper Sparrow (*Ammodramus savannarum floridanus*) is an endangered species endemic to Florida dry prairie. More than 80% of the native prairie has been destroyed or converted to agriculture and most remaining habitat has been degraded by altered fire regimes (Shriver and Vickery 1999). The Florida Grasshopper Sparrow has declined to <5 known breeding subpopulations and all but 2 are near extinction (Delany et al. 1985, 1999, Delany and Cox 1986, Perkins et al. 2008, Tucker and Bowman 2008). Fire frequency and edge effects greatly influence Florida

Grasshopper Sparrow habitat use and nest success (Walsh et al. 1995, Shriver 1996, Shriver et al. 1996, Perkins et al. 1998, Perkins 1999).

I describe habitat potential and quality as being species specific and separate from landcover or vegetation, although the latter are used to describe species distributions in many coarse grained multi-species applications (Scott et al. 1993). Coarse-grained applications that rely on landcover classification might have limited use for species with specific habitat requirements (Bellis et al. 2008). Most landcover maps that describe species distributions rely on habitat features larger than 2-40 ha (Paine 1981, Scott et al. 1993). Breininger and Oddy (2004) demonstrated that Florida Scrub-Jays occupied territories in pine flatwoods having small scrub oak ridges (<0.4 ha) on soils mapped as poorly drained. Such scrub ridges on poorly drained soils have often been excluded from scrub ecosystem delineations (Schmalzer et al. 1999) and conservation reserve designs (Root 1998). Detailed mapping of habitats can be difficult across large areas when spectral signatures are not distinct and habitat heterogeneity is great (Breininger et al. 1991, 1998; Duncan et al. 1995). Pine flatwoods with small scrub ridges could supplement Florida Scrub-Jay populations residing in xeric oak scrub and are important because they propagate critical natural processes into oak scrub (i.e., fire; Breininger et al. 2002, Breininger and Oddy 2004).

Mapping Florida Grasshopper Sparrow habitat also seems to have many problems. For example, large areas of dry prairie habitat seem to have been excluded from recent mapping performed by Delaney et al. (2006). A promising mapping approach across large geographic areas is to grid landscapes into cells the size of potential territories (Breininger and Oddy 2004, Carter et al. 2006). Classifying grid cell by attributes is faster and allows tracking habitat changes over time.

Mapping Florida Scrub-Jay and Florida Grasshopper Sparrow habitat quality is confounded by habitat structural transitions that vary temporally because of frequent fire, habitat destruction, and fragmentation. Habitat transitions and the factors that influence them are rarely quantified. Many habitat fragmentation studies focus on habitat fragmentation effects without distinguishing impacts that are additive to habitat loss effects (Fahrig 2003). Harrison and Bruna (1999) argue that fragmentation magnifies impacts from habitat loss but empirical evidence is often anecdotal, except for edge effects (e.g., Mumme et al. 2002). Edge effects are a concern because Florida Scrub-Jay population territories often coincide with human-dominated edges (Stith 1999). Mortality exceeds recruitment in suburbs and along edges, but studies have not controlled for negative habitat quality associated with the anthropogenic disruption of natural fire regimes (Breininger 1999, Mumme et al. 2002). Edges of dry prairie habitat also appear to be population sinks for Florida Grasshopper Sparrows (Perkins et al. 2003).

Habitat fragmentation disrupts natural processes that maintain habitat quality, but such secondary effects are rarely quantified even though the indirect effects of habitat fragmentation might exceed the direct loss of habitat (Noss and Cooperider 1994, Groves 2002). Small changes in land cover that alter natural processes can influence ecosystems across large areas (Weier et al. 2000, Ross et al. 2003, Gallant et al. 2003, Pressey et al. 2003). Using fire behavior models and historical landcover sequences, Duncan and Schmalzer (2004) demonstrated that average fire sizes decrease by 50%

when only 10% of the landscape is converted to human land cover types. These results are consistent with declining habitat quality that began 50 years ago in east central Florida when human densities increased as a result of military and civilian space programs (Duncan et al. 1999).

Population modeling predicts that Florida Scrub-Jay and Florida Grasshopper Sparrow populations decline steeply when subject to infrequent fire even without additional habitat loss (Root 1998, Breininger et al. 1999, Perkins et al. 2008). Reductions in fire frequency result in the extinction of many other plant and animal species endemic to scrub and flatwoods (e.g., Quintana-Ascencio and Menges 1996, Hokit et al. 1999, Menges 2001). Altered fire regimes have caused tall shrubs and trees to invade Florida Grasshopper Sparrow habitat, not only decreasing habitat extent but also reducing nest success hundreds of meters into otherwise suitable dry prairie habitat (Perkins et al. 2003, 2008). Although rarely studied, the reduction of fire frequency caused by fragmentation has impacted plant species richness and habitat quality worldwide (Leach and Givnish 1996, Kemper et al. 1999, Ross et al. 2002, Pringle et al. 2003).

Dispersal can link habitat fragments together but is difficult to measure (Koenig et al. 1994, Wiens 1997, Cooper et al. 2008). Most studies focus on individual study areas and little has been done to quantify dispersal and exchanges among populations (e.g., Nichols and Kendall 1995, Harrison and Taylor 1997, Leturque and Rousset 2002). Most studies of population dynamics occur in areas with the greatest population densities and not in populations below carrying capacity (Greene and Stamps 2001). Florida Scrub-Jays and Florida Grasshopper Sparrows are site tenacious and have relatively low dispersal capabilities (Woolfenden and Fitzpatrick 1984, Perkins et al. 2008). Florida Scrub-Jay dispersal distances are greater in highly fragmented landscapes when compared to landscapes with many dozens of contiguous Florida Scrub-Jay families (Woolfenden and Fitzpatrick 1984, Thaxton and Hingtgen 1996, Breininger 1999, Breininger and Carter 2003). Larger populations might not necessarily supply individuals to small fragments, because dispersing jays perceive larger populations as having greater breeding opportunities (Breininger 1999). Complications in source-sink dynamics can occur because it is adaptive for animals in small populations to have greater exchange than animals in larger ones (McPeek and Holt 1992, Doncaster et al. 1997, Diffendorfer 1998). Perkins et al. (2008), in their population models, assumed that dispersing Florida Grasshopper Sparrows would be attracted to larger populations (Perkins et al. 2008).

Source-sink theory has many conservation applications but empirical verification needs to confront complications (Diffendorfer 1998, Runge et al. 2006). Source-sink theory often emphasizes metapopulation dynamics (Harrison and Taylor 1997), but can be useful to describe dynamics within landscapes (Howe et al. 1991, Mumme et al. 2001, Breininger and Carter 2003, Breininger and Oddy 2004). As considered here, sources have recruitment that exceeds mortality and export jays to sinks; sinks have mortality exceeding recruitment and must import jays to remain occupied. Subdividing landscapes into potential source and sink territories supports conservation because enough recruits must be produced in optimal territories to offset an excess of mortality in poor-quality territories (Breininger and Oddy 2004). Territory quality transitions supplement source-sink movements because optimal territories can produce an excess of potential breeders and then later transition to a sink condition (Breininger and Carter 2003). The proportions of sinks that can be sustained by sources is often predicted using population viability models, because stage-based vital rates, environmental and demographic stochasticity, density dependence, dispersal propensities, catastrophes, and changing habitat conditions complicate simple analytical calculations (Burgman et al. 1992, Breininger et al. 2002).

Although Florida Scrub-Jays are often stated to be one of the best studied birds in the world, there are no published studies that apply modern methods of mark-recapture analyses (e.g., Williams et al. 2002). Multistate models that consider re-sighting probabilities have many applications to measure how habitat quality and arrangement influence survival and breeding transitions (Kendal and Nichols 1995, Nichols and Kendal 1995, Spendelow et al. 1995). Studies across large geographical areas that overlap private lands are unable to colorband and census all birds and must confront detection probabilities and permanent emigration that goes undetected.

Modern information-theoretic and model selection applications are also relatively new to Florida Scrub-Jay and Florida Grasshopper Sparrow studies, with a few exceptions (Breininger et al. 2006, Carter et al. 2006). This new paradigm of model-based inference replaces null hypothesis testing and is useful where there are many interacting factors. From a philosophy of science perspective, model selection relies on extensive *a priori* thinking to generate sets of multiple working hypotheses represented by many models (Burnham and Anderson 2002, Williams et al. 2002). These models are parsimoniously ranked by their information using Akaike's link between Kullback-Leibler information (a cornerstone of information theory) and the maximized log-likelihood (a cornerstone of mathematical statistics; Anderson 2008). Evidence ratios for models can be constructed, as well as model averaging and rankings of important predictor variables (Burnham and Anderson 2002).

LANDCOVER CHARACTERIZATIONS AND FLORIDA SCRUB-JAY POPULATION DYNAMICS

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Introduction

Managing land cover change is paramount for conservation and requires mapping (Dale et al. 2000). Conserving biological diversity also requires approaches to sustain natural processes (Pressey et al. 2003). Landcover maps usually distinguish only general habitat features larger than 2-40 ha (Scott et al. 1993), but many species respond to habitat arrangement and small or specialized habitat features (Rouget 2003).

Florida Scrub-Jays (*Aphelocoma coerulescens)* are threatened with extinction and are an indicator species for scrub, which is an endangered ecosystem (Noss et al. 1997). Well drained scrub ridges are used to identify Scrub-Jay habitat (Stith et al. 1996) and their identification usually relies on soils mapped as well drained to separate them from pine flatwoods, but these approaches identify only large ridges (Breininger et al. 1991). Pine flatwoods mapped as poorly-drained are rarely considered suitable for Florida Scrub-Jays. In a small study area, we demonstrated that Florida Scrub-Jays occupied territories in pine flatwoods that had small scrub oak ridges (<0.4 ha; Breininger and Oddy 2004). Pine flatwoods are important for propagating fires in scrub

(Breininger et al. 2002) and pine flatwoods with small scrub ridges might supplement Scrub-Jay population size in fragmented landscapes.

Edge effects provide the most direct empirical evidence that habitat fragmentation effects can exceed habitat loss (Harrison and Bruna 1999). Examples include Florida Scrub-Jay studies that show poor demography in suburbs and along roadsides (Breininger 1999, Mumme et al. 2000). Habitat degradation caused by fragmentation is not restricted to edges and might have consequences across landscapes (Leach and Givnish 1996). Using fire behavior models and landcover sequences, Duncan and Schmalzer (2004) demonstrated that fire sizes decreased by 50% when only 10% of scrub and flatwoods landscapes became comprised of less flammable human land cover types.

An optimal Florida Scrub-Jay territory is a mosaic of medium-height oaks (1.2-1.7 m) and shorter scrub with open sandy areas (Woolfenden and Fitzpatrick 1984). Medium-height patches are often 10-20 years post-fire and provide acorns, nest areas, and predator-escape cover (Duncan et al. 1995). Mosaics of frequent burns provide open sandy areas, which persist only a few years post fire and are important to Scrub-Jays and many scrub specialists (Schmalzer and Hinkle 1992). Scrub >1.7 m averages 20 years post fire and reduces habitat quality (Breininger and Carter 2003) and is difficult to restore (Schmalzer and Boyle 1998).

Habitat quality, demography, and dispersal have been characterized at the scale of Florida Scrub-Jay territories to describe how habitat features influence source-sink dynamics within landscapes (Mumme et al. 2000, Breininger and Carter 2003, Breininger and Oddy 2004). Sources had recruitment that exceeded mortality and exported jays to sinks; sinks had mortality exceeding recruitment and were net importers. Subdividing landscapes into potential source and sink territories supports conservation planning because enough recruits must be produced in optimal territories to offset excess mortality in poor-quality territories.

Here, we compare traditional landcover mapping that identifies only large scrub ridges with specialized mapping that additionally identifies smaller scrub ridges in an otherwise unsuitable matrix. We quantify territory quality and changes in population size to investigate population modeling results that predicted population declines because of disrupted fire regimes (Root 1998). This study differs from previous empirical studies because of the large geographical extent of our study area and because we investigate how territory quality and demography vary along edges. Previous studies of jays along edges didn’t distinguish differences between optimal and suboptimal habitat quality associated with fire history (e.g., Breininger 1999, Mumme et al. 2000, Bowman and Woolfenden 2001). We also quantify dispersal among populations and landcover categories. These empirical investigations are needed to resolve whether habitat fragmentation actually magnifies the effects of habitat loss (Harrison and Bruna 1999). The disruption of natural processes by fragmentation is probably common in systems that require natural disturbance to sustain biological diversity, but requires empirical demonstration (Noss et al. 1997).

Methods

Study areas

We quantify habitat and population dynamics of three Florida Scrub-Jay metapopulations along central Florida's Atlantic coast (Figure 1). These are remnants of a scrub ecosystem that was contiguous for hundreds of kilometers (Schmalzer et al. 1999).

Although Florida Scrub-Jays residing in the study area are described as 3 metapopulations (e.g., Stith et al. 1996, Root 1998), we refer to them as "the population" because potential habitat remains between them. The population was subject to an exemplary conservation plan rejected by politicians resistant to government regulation (Noss et al. 1997). Despite rejection, conservation measures were implemented by voter referendums. Enough habitat has been acquired to protect 200 territories, or 1/4 the potential population size.

Schmalzer et al. (1999) describe that oak scrub occurs on ridges, marshes in troughs, and pine flatwoods in intermediate areas. Fires and Florida Scrub-Jay territories often range across habitat types (Breininger et al. 2002). Scrub oaks (*Quercus myrtifolia*, *Q. geminata*) dominate ridges. Marshes (e.g., *Spartina bakerii*, *Andropogon* spp.) are embedded within flatwoods. Flammable shrubs (saw palmetto [*Serenoa repens*], shiny lyonia [*Lyonia lucida*]) and grasses (e.g., wiregrass [*Aristida stricta*]) dominate pine flatwoods.

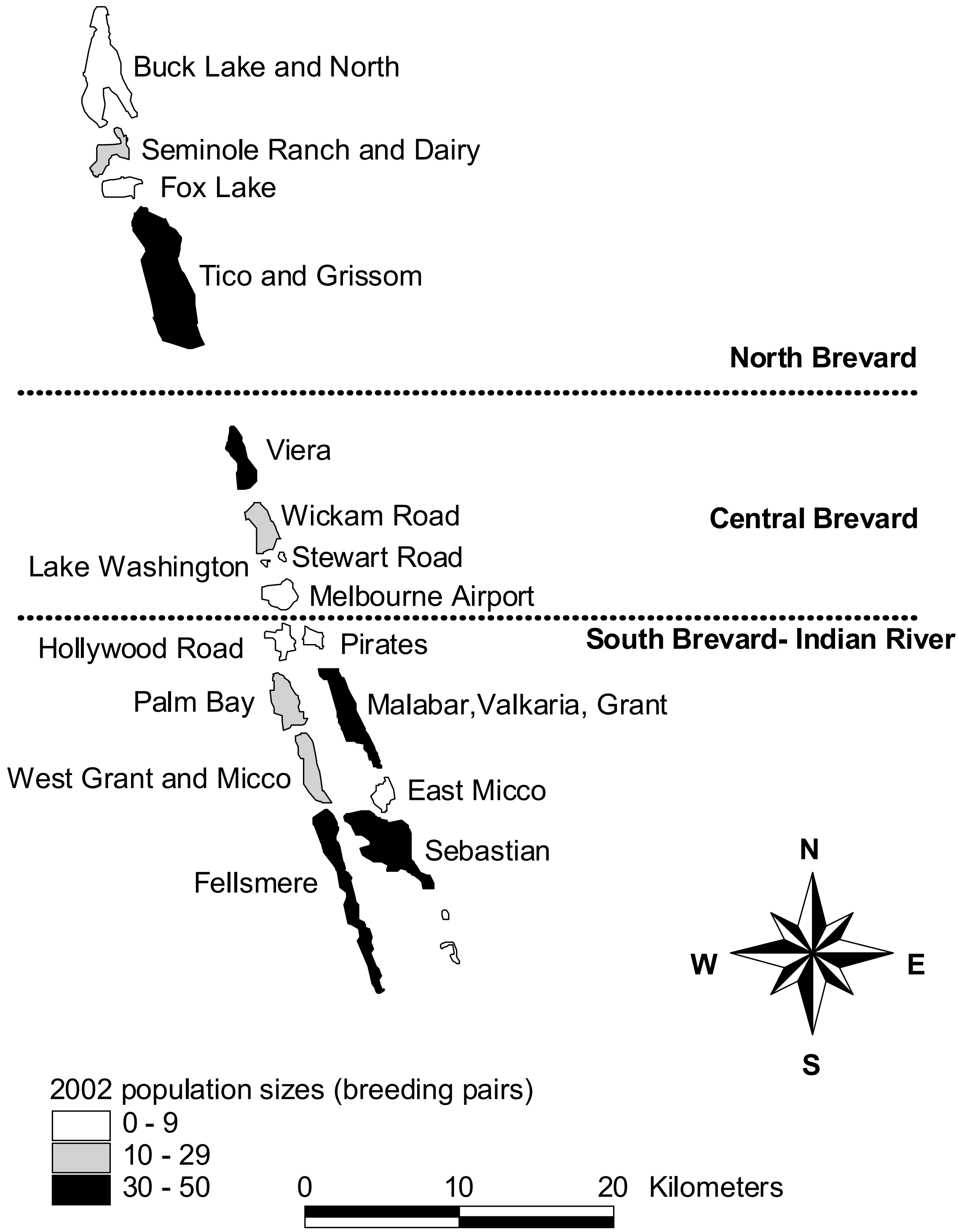

Figure 1. Florida Scrub-Jay territory clusters and 2002 population sizes along the mainland of central Florida's Atlantic coast. Horizontal lines separate the three Florida Scrub-Jay metapopulations identified by Stith et al. (1996) and Root (1998).

Grasses and shrubs sprout rapidly after fire so that composition changes little in frequently burned areas (Schmalzer 2003). The pines are resilient to most fires, except for sand pines that produce serotinous cones. Fire return intervals are 3-20 years for oak scrub and 2-8 years for pine flatwoods (Breininger et al. 2002), which can become forests in 20-40 years without fire (Duncan et al. 1999).

Habitat mapping

All geographical information analyses (GIS) used Arc/Info (ESRI 1999). We mapped 1994 and 1999 habitat using 1.0 m resolution digital orthophoto quads (DOQs). Boundaries between habitat patches were within 1-10 meters from actual locations. We used 1943 historical landcover maps (Duncan et al. 2004) to determine whether forests were suitable Florida Scrub-Jay habitat before anthropogenic reductions in the fire regime (Duncan et al. 1999). We used two approaches to identify habitat recognizing that mapping all scrub oak is not feasible across large geographic areas (Breininger et al. 1991). First, potential habitat polygons were explicitly mapped as oak ($\geq$50 % scrub oak cover) or palmetto-oak (1 – 49 % scrub oak cover) using a minimum mapping unit of 0.4 ha. Oak coincided with well drained soils (Huckle et al. 1974) and scrub on most landcover maps (Duncan et al. 2004). The distribution of palmetto-oak differed from other pine flatwoods polygons by having embedded scrub oak patches >20 m^2 on soils mapped as poorly drained. Palmetto-oak was compared with independent scrub habitat maps produced by the Brevard County Natural Resources Management Office.

Discrepancies in palmetto-oak were studied in the field and maps were updated accordingly.

A second mapping approach used 10-ha grid cells, which represented average territory size at carrying capacity (Carter et al. 2008). Grid cells were identified as primary if they intersected well drained scrub. Grid cells intersecting palmetto-oak were coded as secondary if they intersected scrub ridges >0.4 ha, which were readily identified but had boundaries difficult to map (Breininger and Oddy 2004). Tertiary grid cells had patches of oak scrub <0.4 ha.

We identified contiguous natural landscapes having >10 ha of oak and palmetto-oak as potential reserve units (PRUs). Oak and palmetto-oak polygons that were <0.67 km apart and connected by marshes or pine flatwoods were classified as the same PRU. PRUs excluded small (<10 ha) habitat fragments categorized as “suburban territories” that had poor long-term viability (Stith, 1999). We quantified habitat destruction by calculating the area of oak and palmetto-oak destroyed between 1994 - 1999 by overlaying the PRUs with 1999 DOQs. We used 1999 DOQs to map tree cover in PRUs because tree cover measured how habitat quality was influenced by fire history (Breininger et al., 1995). Tree cover was mapped as savanna (<15% pine canopy cover), woodland (16–65 % pine canopy cover), or forest (>65 % pine canopy cover).

Population distribution

Surveys using playbacks of Florida Scrub-Jay territorial calls were used to describe Scrub-Jay distributions in 1992 (Fitzpatrick et al. 1991, Stith et al. 1996).

Errors in population size were estimated as <10% (Root 1998). We repeated these techniques 1-4 times per year for >85% of the population from 2001-2002.

We defined "territory clusters" to compare 1992 and 2002 data because territory locations shifted. We described territory clusters as PRUs, smaller habitat remnants, and habitats permeable to dispersal in areas occupied by Florida Scrub-Jays. We delineated territory clusters by extending outward from known occupied areas into contiguous suitable habitat. Contiguity referred to non-forested (<65% tree canopy) oak and palmetto-oak patches within 0.67 km of each other, providing the matrix was suitable for dispersal. A suitable dispersal matrix included non-forested flatwoods, ruderal grassland, and marshes (Stith 1999). Territory clusters were larger than PRUs because they included human landcover types that jays foraged in and readily flew across.

Habitat-specific demography and dispersal

Color banding studies began in December 1996. Demographic procedures included monthly censuses of these easily observed, permanently territorial birds (Woolfenden and Fitzpatrick 1984). Juveniles were tallied among territories and were defined as young Florida Scrub-Jays present in July. We identified nonbreeders in territories, which occurred because Florida Scrub-Jays usually delay breeding and remain in their natal territories for >1 year, until they find a breeding vacancy (Woolfenden and Fitzpatrick 1984). Territory mapping was conducted from April through May.

We distinguished territory quality categories that might correspond to source-sink dynamics and that were easily delineated on 1994 and 1999 aerial photographs with annual ground-verification (Breininger and Carter 2003, Breininger and Oddy 2004). Territory quality categories were directly related to habitat potential (i.e., scrub oak cover), edge effects (i.e., houses, roads), and disrupted fire regimes (i.e., shrub heights, tree cover). Each territory was classified as primary, secondary, and tertiary as described for grid cells above. Four categories described the context of territories to human-dominated landscapes. Territories not within or adjacent to human landscapes (e.g., suburbs) or roads were “core.” Territories within contiguous natural communities were “house edge” if they were adjacent to human landscapes but not roads and were “road edge” if they intersected or were adjacent to roads where traffic exceeded 56 km/hour. Territories were “suburbs” if their habitat patches were <10 ha and they intersected roads and houses. Territories were classified into shrub heights that described source-sink dynamics (Breininger and Carter 2003, Breininger and Oddy 2004). Short territories had scrub oaks <1.2 m tall. Optimal territories were a mix of short and medium-height oaks (1.2-1.7 m). Tall mix territories included tall oaks (>1.7 m) and shorter oaks. Tall territories had scrub that was all >1.7 m. Territories were classified into savanna, woodland, and forest using the mapping criteria described above.

We used likelihood ratio chi-square tests (SPSS 2003) to cross-tabulate counts of territory quality categories of a variable (e.g., scrub ridge type: primary, secondary, tertiary) with categories of other variables (e.g., shrub height arrangements: short, optimal, tall mix, tall) to study relationships among habitat variables.

Demographic analyses

Individual demographic study years ranged from 1 April to 31 March. Birds were assumed dead if they were not seen anytime and anywhere after an annual survival period ending date (Woolfenden and Fitzpatrick 1984). Mark-recapture analyses were not used because detection probabilities for each visit exceeded 94%. We assumed that few dispersing Florida Scrub-Jays became breeders without our detection because they are philopatric (Fitzpatrick et al. 1999) and we regularly surveyed ≥85% of the population.

Demographic performance per pair was calculated for every year in every territory by subtracting the number of breeders that died from the yearlings recruited (Breininger and Carter 2003). Yearlings can breed and their recruitment is an important metric even if yearlings do not breed because non-breeding adults buffer short-term changes in the breeding population and enhance breeder demography by helping raise future generations, defending territories, and spotting predators (Woolfenden and Fitzpatrick, 1984). We assumed yearling production best represented recruitment because factors outside the territory (i.e., breeding opportunities) influenced delayed breeding (Breininger 1999). Negative demographic performance per pair suggested a territory quality category was a sink, whereas positive performance suggested the category was a source.

We used general linear models (GLM; SPSS 2003) to investigate which territory quality variable or combinations of variables had the greatest influence on demographic performance. We combined categories of scrub ridge, edge, and height to reduce the number of possible combinations of variables. There were no occupied territories in forests resulting in only two tree categories. We combined primary and secondary territories because both could be sources depending on fire patterns and we kept tertiary territories separate because they almost always were sinks (Breininger and Oddy 2004). Except in the landcover models below, we combined house edge, road edge, and suburbs into one edge category, separate from core territories. We combined suboptimal height categories (short, tall mix, and tall) because these were usually sinks (Breininger and Carter 2003). Fixed explanatory variables for each territory included scrub ridge category (primary or secondary, tertiary), height (optimal, suboptimal), edge (core, road or house edge or suburb), and tree (savanna, woodland). We constructed a global model that included all territory quality variables and two-way interactions and subsequently removed sources of variation (i.e., variables, two-way interactions) according to specific hypotheses to develop a series of models ranging from complex to simple.

We included 3 landcover models that addressed land acquisition and fire management questions by combining combinations of territory quality variables into similar categories. We combined all tertiary territories together because many combinations had low sample sizes and they were usually sinks regardless of height (Breininger and Oddy 2004). We combined all suburb territories because they almost always had suboptimal heights and because fire management of suburb territories would seldom be practical. One landcover model included eight categories that were: optimal core, suboptimal core, tertiary, optimal house edge, suboptimal house edge, optimal road edge, suboptimal road edge, and suburb. Optimal referred to optimal-height primary and secondary territories that were savannas and suboptimal referred to woodland or suboptimal-height primary and secondary territories. A second landcover model included only 6 categories because it combined road and house categories. The third landcover model comprised 4 categories (optimal primary or secondary, suboptimal primary or secondary, tertiary, suburb) because house and road edge territories were not distinguished from core territories.

We used Akaike's Information Criteria (AIC_c, Burnham and Anderson 2002) to rank the GLM models. We calculated the difference between AIC_c values among models (Δ_i) and ranked models in order of Δ_i values. We calculated Akaike weights (ω_i) to determine the best model.

We calculated juvenile production/pair, yearling production/pair, demographic performance/pair, and breeder survival for each category to test which demographic variables were influenced by landcover categories according to the best AIC model above. We used ANOVA (SPSS 2003) to test whether means varied among landcover categories. Differences in breeder survival of individual birds among landcover categories were tested using likelihood ratio chi-square tests (SPSS 2003) by pooling across years.

Dispersal analyses

We used two measures to describe dispersal distances. We measured the distance from the center of the territory a bird hatched in to the center of the territory that the bird first became a breeder. We also tabulated the number of territories between natal territories and the territory of first breeding (Woolfenden and Fitzpatrick 1984). If the jays inherited the natal territory, the number of territories traversed was zero. We cross-tabulated exchanges of natal dispersers among the categories of the best model to determine whether jays actively dispersed between categories.

Results

Habitat and population trends

The amount and contiguity of habitat increased greatly when palmetto-oak was considered (Figure 2). In 1994, 30% of the oak and palmetto-oak occurred in patches <10 ha within suburbs and therefore outside PRUs. Five % of the oak and palmetto-oak within PRUs was destroyed between 1994 and 1999. Oak and palmetto-oak respectively comprised 3541 ha and 4823 ha within PRUs during 1999. The number of primary, secondary, and tertiary grid cells within PRUs was respectively 470, 304, and 244.

Figure 2. Potential Florida Scrub-Jay habitat between Malabar and Fellsmere, which provides the core of the South Brevard-Indian River metapopulation.

The proportions of well drained oak that were savanna (optimal tree cover), woodland (marginal tree cover), and forest (unsuitable) respectively were 0.18, 0.39, and 0.43. The proportions of palmetto-oak scrub that were savanna, woodland, and forest respectively were 0.32, 0.37, and 0.31.

By 2001, >75% of Florida Scrub-Jays were color banded in the study population. Florida Scrub-Jay population surveys were conducted in nearly all areas during 1992 and 2002. A few areas were not surveyed in 1992 because they did not intersect well drained scrub and a few areas were not surveyed in 2002 because access was prohibited. The respective number of pairs in 1992 and 2002 was 343 and 222, when we excluded areas not surveyed in 1992 or 2002. The average annual growth rate was $222/343^{(1/10)} = 0.96$, which was an average decline of 4% per year. By 2000, we observed 45 pairs outside areas surveyed in 1992 because of the limited habitat search image. Assuming these jays declined by similar rates, there could have been 64 pairs not counted because of a limited search image. This would have been 16% of the total population for 1992.

Nearly all territory clusters were <50% of carrying capacity (Figure 3). Palmetto-oak was often occupied when well drained oak was not and much unoccupied scrub became occupied after habitat restoration (Figure 4). No occupied territories were forest although half the scrub had become forest since the 1940s (Duncan and Breininger, unpublished data). Secondary and core territories had the greatest proportion of optimal-height territories (Figure 5). Most optimal-height territories were savannas. Road edge and suburb territories almost always had suboptimal tree cover and shrub heights.

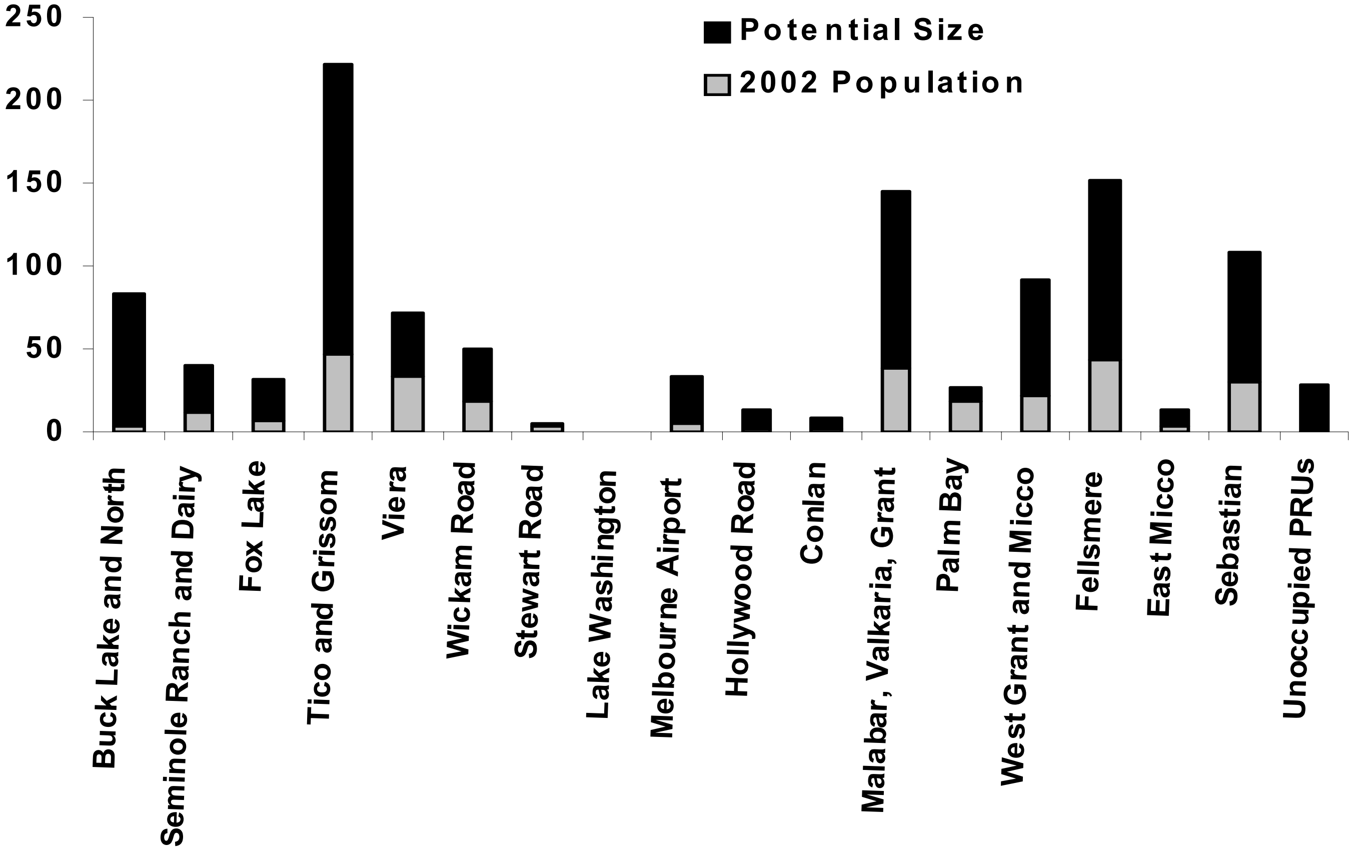

Figure 3. Population size (breeding pairs) of territory clusters in 2002 relative to the total potential population size in the cluster. The dark part of the bar represented the number of unoccupied territories in the cluster. The numbers of unoccupied territories within all unoccupied territory clusters were totaled into one bar.

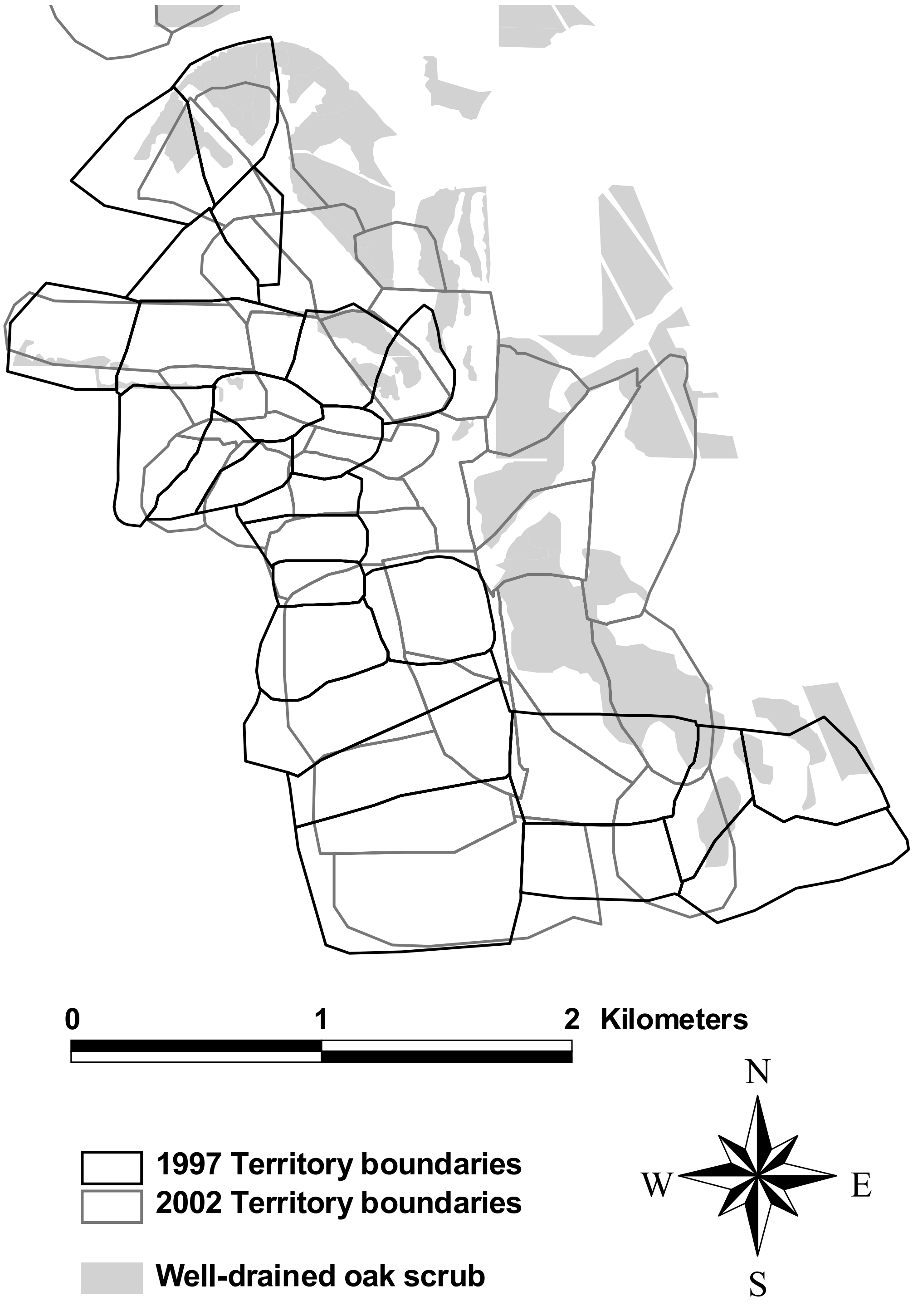

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Figure 4. Florida Scrub-Jay territory dynamics in relation to well drained oak scrub (traditional habitat) at Valkaria, Florida.

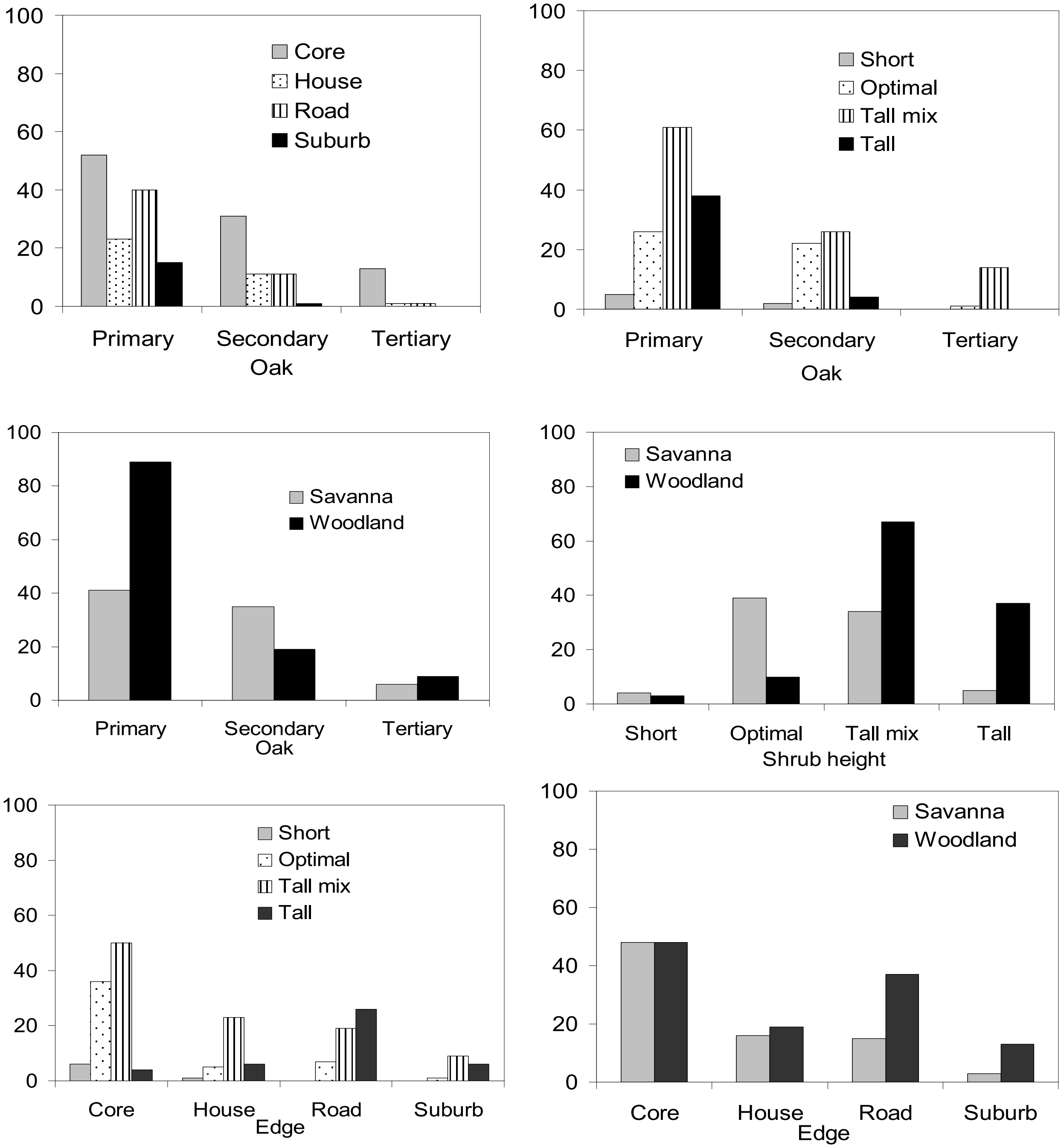

Figure 5. Two-way cross-tabulations of all combinations of territory quality categories. The y-axis is the count of territories. Territories were pooled for 1997-2002. Likelihood ratio chi-square tests were significant ($p < 0.001$) for all two-way combinations indicating discrepancies between the observed cell counts and the expected.

Demography

Height produced the greatest effect on demography among territory quality variables (Figure 6).

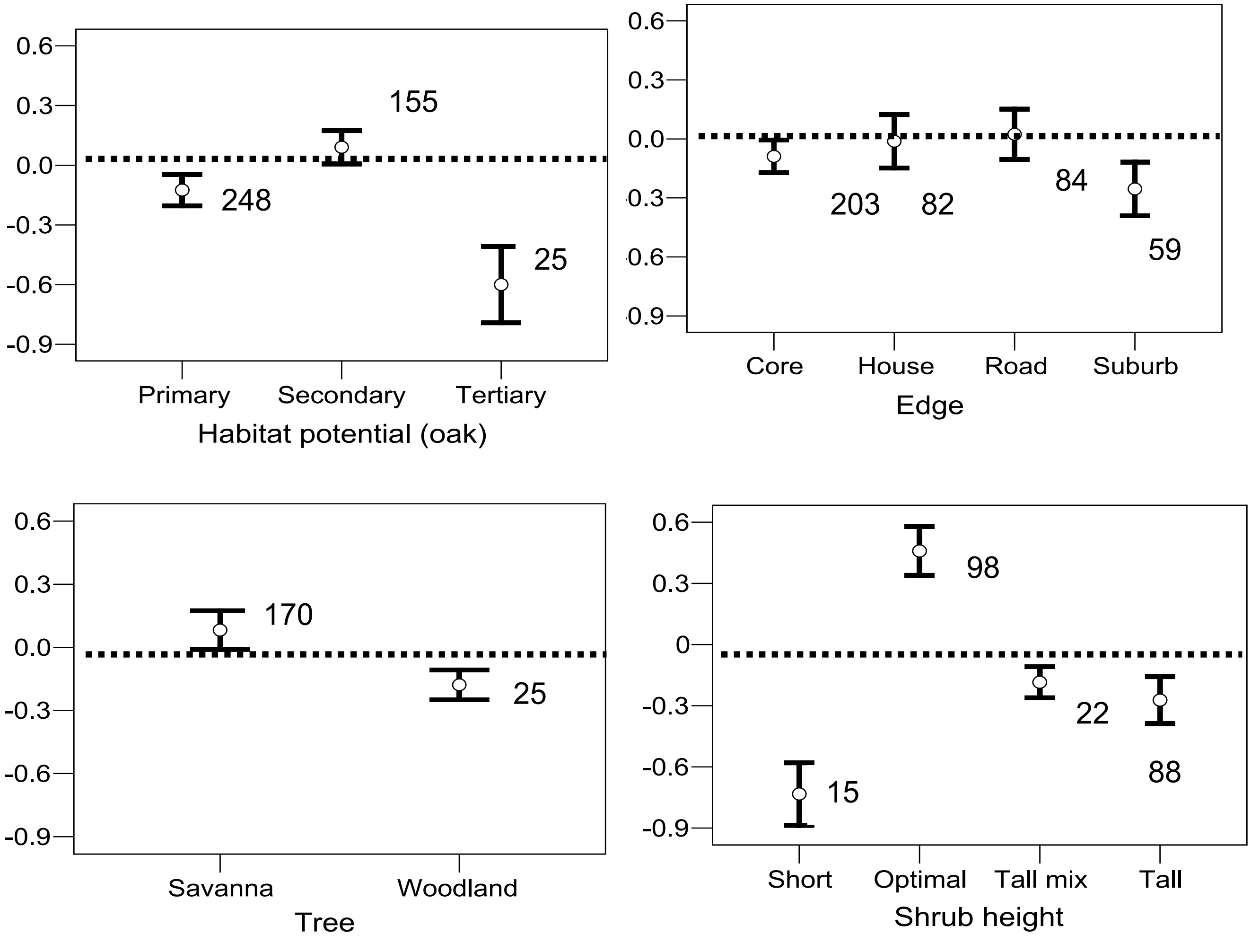

Figure 6. Mean + 1 SE demographic performance/pair/year (y-axis) for territory quality categories. Mortality matches recruitment along the dotted lines. Numbers right of error bars represent sample sizes.

The 8 category landcover model showed that optimal-height primary and secondary territories along houses and roads often had recruitment that exceeded mortality (Figure 7). The best AIC model was the 4 category landcover model (Table 1). Tertiary territories had the worst reproductive success and suburbs had the worst breeder survival (Table 2).

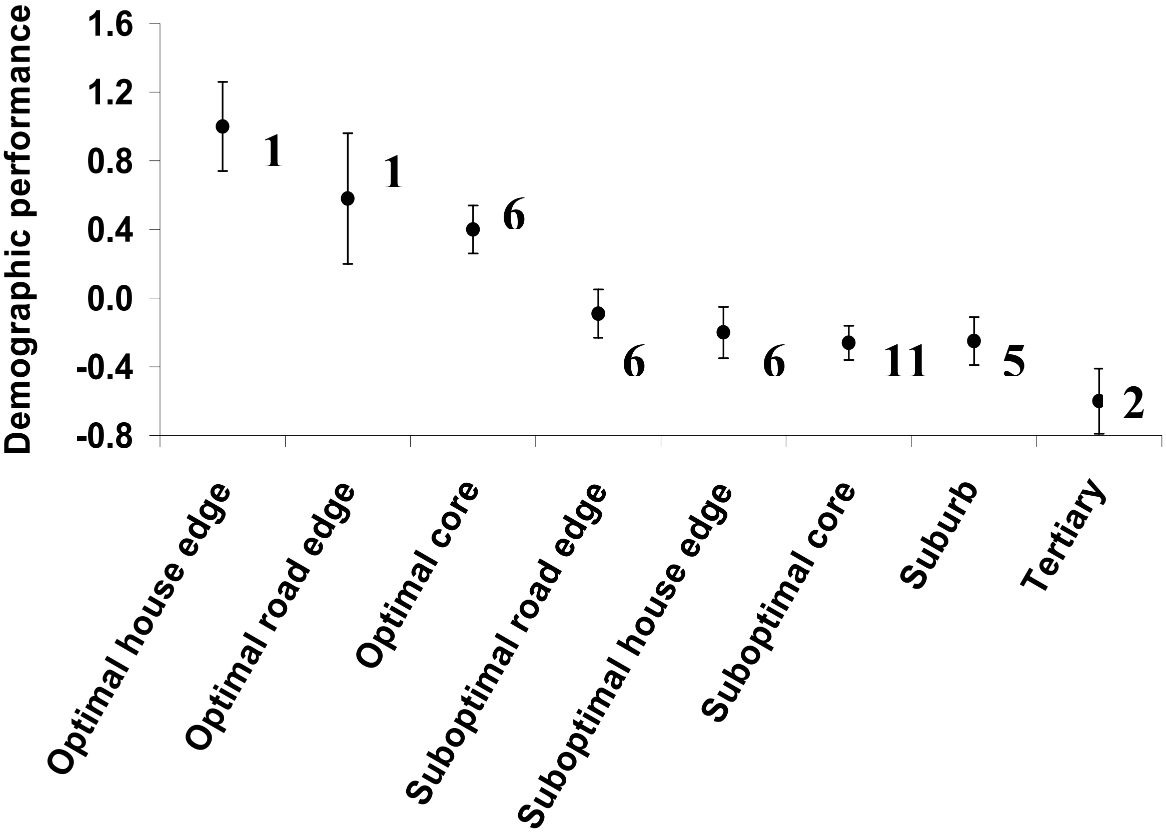

Figure 7. Mean + 1 SE demographic performance/pair/year for the 8 category landcover model where road and house edge effects are separated. Optimal referred to primary and secondary territories with optimal shrub heights and tree canopies within reserves. Mortality matches recruitment along the dotted lines. Numbers right of error bars represent sample sizes.

Table 1. Comparing alternative models describing relationships between Florida Scrub-Jay demographic performance ((recruitment – mortality)/pair/year) and territory quality/landcover variables using information theoretic methods (n = 428; Burnham and Anderson 2002).

Model	Estimable parameters (*K*)	Maximized log-likelihood log(£)	Akaike Information Criterion AIC_c	Difference in AIC_c (Δ_i)	Akaike weights ω
Landcover with no edge effects (4 categories)	5	-45.74	101.63	0.00	0.41
All main effects (oak, edge, height, tree) and 2-way interactions	12	-39.60	103.95	2.32	0.13
Landcover with house and road edge combined (6 categories)	7	-44.93	104.14	2.51	0.11
Height only (2 categories)	3	-49.35	104.75	3.12	0.09
Dynamic habitat (height, tree, interaction)	5	-47.35	104.85	3.22	0.08
All main effects (oak, edge, height, tree) without interactions	6	-46.95	106.10	4.47	0.05
Landcover (8 categories)	9	-44.12	106.67	5.05	0.04
Dynamic habitat (height, tree)	4	-49.35	106.79	5.16	0.03
Tree only (2 categories)	3	-62.44	130.93	29.30	0.00
Stable habitat (oak, edge)	4	-62.06	132.22	30.59	0.00
Oak only (2 categories)	3	-63.55	133.17	31.54	0.00
Edge only (2 categories)	3	-65.04	136.13	34.50	0.00
Stable habitat (oak, edge, and interactions)	5	-63.55	137.25	35.62	0.00

Table 2. Demography among landcover categories along central Florida's Atlantic Coast (1997-2003). Columns show mean demographic rates per pair + 1 SE (n), except for breeder survival, which represented individual survival rates. Within columns, different subscripts indicate significant differences between treatments as identified by Tukey's tests when variances were equal and Games-Howell tests when variances were unequal. A likelihood ratio chi-square test not ANOVA was performed on breeder survival so that the test statistic for "F" in the breeder survival value was a likelihood ratio chi-square test statistic.

	Juvenile production	Yearling production	Demographic performance	Breeder survival
Optimal primary and secondary	1.21 ± 0.13 (123)^{a}	0.87 ± 0.12 (111)^{a}	0.64 ± 0.13 (80)^{a}	0.86 ± 0.03 (188)
Suboptimal primary and secondary	0.65 ± 0.05 (484)^{b}	0.34 ± 0.04 (438)^{b}	-0.20 + 0.07 (264)^{b}	0.74 ± 0.02 (614)
Tertiary	0.39 ± 0.11 (46)^{b}	0.18 ± 0.07 (45)^{b}	-0.60 ± 0.19 (25)^{b}	0.73 ± 0.06 (56)
Suburb	0.57 ± 0.08 (148)^{b}	0.33 ± 0.07 (141)^{b}	-0.25 ± 0.14 (59)^{b}	0.69 ± 0.04 (171)
P	<0.001	<0.001	<0.001	0.008

Dispersal

Mean natal dispersal distances were 2.8 km and 1.6 km, respectively, for females (*n* = 83) and males (*n* = 87). This difference was significant (*p* = 0.044, *F* = 7.215, *df* = 1, 168). The destination for half of all natal dispersers was the territory closest to the natal territory (Figure 8).

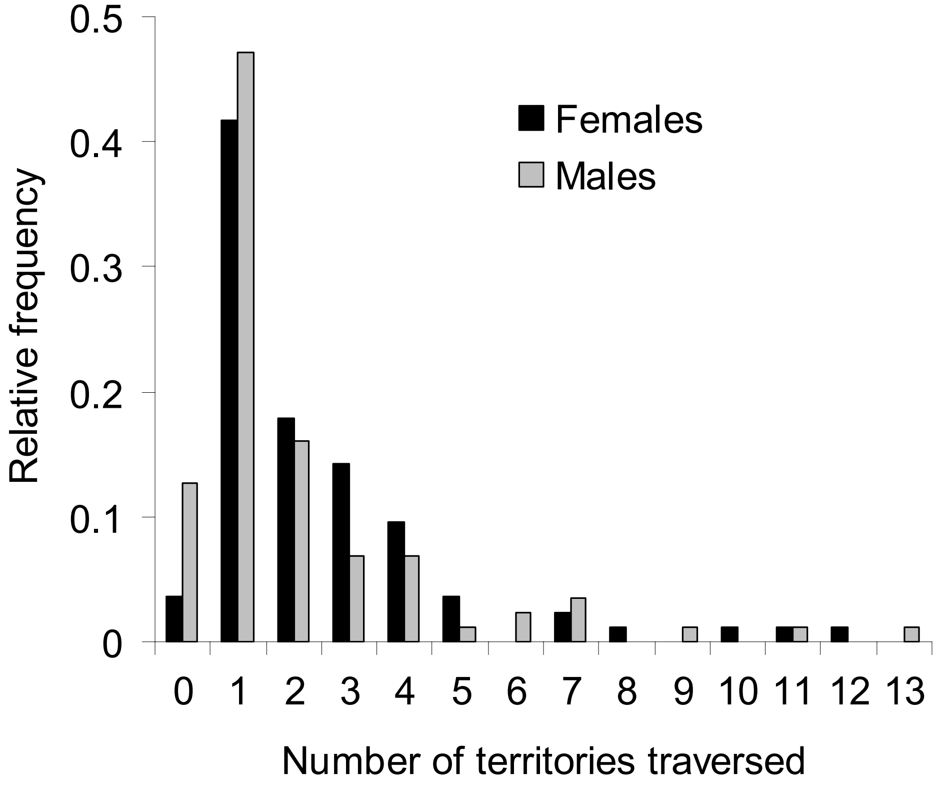

Figure 8. Natal dispersal distances of Florida Scrub-Jays excluding one female that traversed 24 territories. The number of territories traversed was equal to the actual number of territories that occurred between the natal and destination territory.

Eighty-seven % of natal dispersers remained within the natal territory cluster. Only 30% of the natal dispersers that occurred outside a territory cluster were males. We identified the total number of "breeding vacancies filled" during the study as the number of breeder deaths filled by a replacement breeder + twice the number of unoccupied territories colonized. Unbanded Scrub-Jays from unknown locations filled 10% of the vacancies. Color banded Scrub-Jays that immigrated from another cluster filled 8% of the vacancies. Therefore, Florida Scrub-Jays from the same territory cluster filled 82-92% of all breeding vacancies because unbanded birds occurred in most study areas and filled many vacancies.

Landcover categories having recruitment exceeding mortality were net importers, whereas categories with mortality exceeding recruitment were net importers (Table 3). Although suburbs exported no known natal dispersers to other categories, several jays with unknown breeding experience did disperse from suburbs to reserves (authors' unpublished data).

Discussion

Habitat potential

We estimated that the number of Florida Scrub-Jay pairs not detected in 1992, because of the limited habitat search image, was only 16% of the 1992 population. More undetected pairs would have occurred if most secondary and tertiary territories were not contiguous with primary territories. The relative number of underestimated of pairs caused by the limited habitat search image was much less than the relative number of estimated potential territories (see below) because most habitat was unoccupied and because Scrub-Jays selected areas with greater oak cover (Breininger and Oddy 2004).

Our estimate of maximum potential population size based only on large, well drained scrub oak ridges was 354 primary territories when we divided oak scrub by 10 ha. This was nearly identical to previous estimates (Root 1998, Stith et al. 1996). Our estimate of 470 primary territories, using grid cells, was more realistic than dividing the areal extent of well drained oak scrub by 10 ha because most occupied primary territories include much flatwoods adjacent to well drained scrub (Breininger and Oddy 2004). There were 304 secondary territories suggesting that the maximum population size of potential source territories was 774. Primary and secondary territories are usually occupied and function as sources when in optimal condition (Breininger and Oddy 2004). There were at least 244 potential tertiary territories but we never observed more than 13 occupied tertiary territories during any year. This contrasted with a previous study where most tertiary territories were occupied because primary and secondary territories supplied many breeders to them (Breininger and Oddy 2004). Most tertiary territories may have been unoccupied because new recruits preferred to disperse into primary or secondary territories and because the population was declining and far below carrying capacity allowing most jays to find breeding vacancies in preferred oak-dominated habitat. In the previous study area with high Florida Scrub-Jay population densities, Florida Scrub-Jays from primary and secondary territories often needed to emigrate or disperse into tertiary territories to breed. Although we observed tertiary territories to be population sinks, as expected, they could contribute to population viability by providing individuals to better quality territories during low population sizes (Breininger and Oddy 2004). Population sizes in sinks are complicated by the amount of sink habitat, the rates of population decline in sinks, productivity rates in sources, spatial proximities of sources and sinks, and dispersal behaviors (Dias 1996). Estimating maximum potential population size that might occur after habitat restoration is uncertain given the abundance of tertiary territories and our limited understanding about how dispersal is influenced by varying habitat quality and population density in fragmented populations.

Including flatwoods adjacent to well drained scrub and secondary ridges to increase potential population size would be important because >80% of all reserves comprised of only well drained oak could support <10 pairs, and these potential reserves were further apart than 80-90% of Florida Scrub-Jay dispersals. Populations <10 pairs have high extinction probabilities (Fitzpatrick et al. 1991). Small scrub ridges are often excluded from scrub ecosystem delineations and conservation reserve designs (Root 1998, Schmalzer et al., 1999). Increasing local population size and contiguity is critical for species like Florida Scrub-Jays that have limited dispersal and fecundity (Drechsler and Wissel, 1998, Walters et al. 1999, Cox and Engstrom 2001).

Primary territories have greater oak cover than secondary territories, which should have caused primary territories to have greater demographic success if other habitat quality variables were optimal (Burgman et al. 2001). Shrubs were usually too tall and trees too dense in primary territories explaining why they didn’t have greatest demographic success. Secondary territories had more optimal shrub heights and tree cover than primary territories because they were more flammable in the infrequently burned landscapes (Breininger et al. 2002). In a frequently-burned landscape elsewhere, primary territories usually had optimal shrub heights and secondary territories were often too short (Breininger and Oddy 2004). Maximizing territory numbers and having territories with varying flammability could help keep optimal-height territories somewhere within the reserve, given that fires vary in frequency and intensity.

Mapping boundaries of habitat features that are heterogeneous in small geographic areas using remotely-sensed data is difficult (Saveraid et al. 2001). We showed that it was not necessary to explicitly map all habitat features (e.g., scrub ridges) because features could be characterized as attributes within polygons. Mapping beyond coarse landcover information is especially important for some species that need specific habitat features in fragmented and heterogeneous habitats (Rouget 2003).

We showed that mapping habitat at the territory scale by overlaying grid cells on aerial photographs provided additional population information, such as the numbers of source and sink territories. Classifying attributes of grid cells at the territory scale took 8% of the time needed to produce maps that depicted habitat boundaries. We confirmed that categorizing shrub heights and other attributes within actual jay territories was useful to describe how demographic success varied with fire. Grid cells, Markov Chains, and population models could be further applied to address larger population processes, monitor restoration progress, and evaluate alternative land use practices. Grid cells are routinely used to incorporate detailed habitat information and provide a rapid alternative to mapping when existing land cover maps poorly represent habitat needs of many habitat specialists or habitat generalists vulnerable to edges (Roy and Tomar 2000,Joly and Myers 2001; Gavashelishvili 2004; Carter et al. 2006).

Scrub conservation requires a broader landscape approach than just including well drained ridges for reasons additional to maximizing Scrub-Jay numbers. Nearly all scrub endemics require frequent or occasional fires (Quintana-Ascencio and Menges 1996, Hokit et al. 1999). Mesic flatwoods and imbedded swale marshes are important for spreading frequent fires into large scrub ridges, which are difficult to ignite

(Schmalzer and Boyle, 1998, Yahr et al. 2000). Embedded and often ephemeral marshes are necessary breeding areas for many amphibians, which are important prey that reside in uplands (Moler and Franz 1987, Hermann et al. 2005). Isolated wetlands are another important habitat feature smaller than most minimum mapping units (Groves 2003). In contrast to our study, broad-scale data can overestimate habitat if identified habitat does have the necessary focal features (Krauss et al. 2004, Linderman et al. 2005).

Effects of reduced fire frequencies

Most territories had poor habitat quality because of reduced fire frequency. Rapid increases in human population growth by the 1960s resulted in reductions in fire frequency causing poor habitat quality for decades (Duncan et al. 1999, Duncan and Schmalzer 2004). We observed that areas with suboptimal shrub heights and tree cover had mortality that greatly exceeded recruitment. The rate of Florida Scrub-Jay population declines verified population model predictions using independent demographic data from other infrequently burned areas (Root 1998, Breininger et al. 1999). Habitat destruction alone did not explain the 34% population decline/decade because most habitat was unoccupied and habitat destruction rates within most potential reserves were <5%. Spatially explicit models suggested low extinction probabilities if habitat within most potential reserves was optimal (Root 1998, Stith 1999).

Infrequent fire resulting from habitat fragmentation caused mortality to exceed recruitment far beyond edges. This was expected because human landscapes (e.g., roads) disrupt fire propagation even when a small portion of the landscape is destroyed (Duncan and Schmalzer 2004). Fahrig (2003) suggests two categories of habitat fragmentation effects. The first is that patches become too small to sustain populations over time, especially for species that disperse poorly between patches. Edge effects are the second fragmentation effect (Stephens et al. 2003). We argue that the disruption of natural processes is third major habitat fragmentation effect that can exceed impacts of direct habitat loss and edge effects. Reductions in fire frequency result in the extinction of many other scrub endemics (e.g., Quintana-Ascencio and Menges, 1996; Menges and Hawkes, 1998, Hokit et al. 1999). Reduction in biological diversity resulting from reduced fire regimes caused by fragmentation is not unique to Florida scrub and is increasingly identified worldwide in grasslands, savannahs, shrublands, and even some wet tropical forests (e.g., Leach and Givnish 1996, Noss et al. 1997, Kemper et al. 1999; Ross et al., 2002; Gibb and Hochuli, 2002; Yates and Broadhurst 2002, Pringle et al. 2003). In contrast, fragmentation can increase fire frequency with negative impacts in some systems (e.g., Latta et al., 2000). Prescribed fire is necessary to maintain habitat quality in fragmented ecosystems that need fire to sustain biological diversity. Management must generate a greater proportion of territories in optimal condition to recover populations by better addressing shrub height arrangements at the territory scale (Breininger and Carter 2003). We observed population increases and recruitment rates that exceeded mortality rates in many optimally restored areas, especially when adjacent to a source of colonists.

Edge effects

Suburb territories had mortality exceeding recruitment, as expected (Breininger 1999). Edge territories had particularly poor habitat quality because they burned poorly (Duncan and Schmalzer 2004), which largely accounted for their reduced demographic success. Sochat et al. (2005) also found that incorporating fire history into edge studies was important. We unexpectedly did not observe reduced demographic success in edge territories that had optimal height and tree cover, but there were only a few study sites that had edge territories with optimal height and tree cover. Our results regarding edges must be treated cautiously, because edges with different configurations may vary (With and King 2001, Saarinen et al. 2005). There are negative factors associated with edges, such as road mortality (Mumme et al. 2000). Supplemental feeding can cause jays to nest prematurely before insects needed by nestlings are available (Bowman and Woolfenden 2001). Domestic cats and fish crows are predators along edges; but natural nest predators such as snakes can be less abundant along edges of human landscapes (Rudolph et al. 1999, Breininger et al. 2004).

Territories that directly border human landscapes now dominate most Florida Scrub-Jay populations (Stith 1999), emphasizing the need to specify relationships among edges and demography. Our results suggested that territories in reserves that border roads and houses were not necessarily sinks and could contribute to increases in population size. Attention should be given to managing shrub heights and tree cover along edges to enhance demographic success because some edge function as sources when in optimal condition.

Dispersal and population exchanges

Mean dispersal distances were greater than those in unfragmented landscapes (Woolfenden and Fitzpatrick 1984), as expected (Thaxton and Hingtgen 1996). The median number of occupied territories traversed between natal territories and breeding destinations was nearly identical to unfragmented landscapes, as expected (Fitzpatrick et al. 1999). Florida Scrub-Jays most often disperse into an adjacent territory even if it is not contiguous, because their dispersal tactics involve monitoring the immediate neighborhood for breeding vacancies while relying on the natal territory for residency (Fitzpatrick et al. 1999).

We observed exchanges between Central Brevard and South Brevard-Indian River metapopulations but none between Central Brevard and North Brevard. Potential habitat suggested all metapopulations could be recovered to one by restoring scrub that became unsuitable. Our results indicated that exchange occurs among many territory clusters, but more study is needed to understand implications. We observed dozens of territories, recently restored to optimal, that remained unoccupied for many years when they were not adjacent to territories with nonbreeders that were not directly related (i.e., siblings).

Optimal territories were net exporters and jays from them often dispersed into most types of suboptimal territories, which were net importers. Florida Scrub-Jays do not regularly disperse into all marginal territory types, as evident by unoccupied tertiary or forested grid cells. Other investigators observed that Florida Scrub-Jays residing in optimal habitat avoid dispersing into excessively overgrown scrub and suburbs (Woolfenden and Fitzpatrick 1991). Florida Scrub-Jays sometimes occupy marginal territories because of “territory quality transitions,” where optimal territories become marginal (Breininger and Carter 2003).

More analyses are needed to investigate net imports and exports among landcover categories and territory clusters. Understanding breeding choices is complicated by cooperative breeding, territory quality, population size, and the arrangement of territory vacancies (Leturque and Rousset 2002). These are poorly understood topics for species in fragmented populations below carrying capacity because most studies focus on optimal and densely inhabited areas (Greene and Stamps 2001).

Conclusions

Including pine flatwoods with small scrub ridges almost doubled the number of potential source territories (primary and secondary) that would otherwise be identified by typical landcover maps, which distinguished only large, well drained ridges. Errors in demarcating habitat are likely for many species that rely on focal patches in an otherwise unsuitable matrix. Uncertainty in maximum population size occurred because there were many potential tertiary territories, which would probably function as sinks if populations recovered enough to supply colonists into them. Secondary and tertiary territories were predominately pine flatwoods that increased flammability and decreased the need for mechanical treatments to initiate fire in scrub ridges that are otherwise difficult to ignite (Schmalzer and Boyle 1998). We advocated a broader approach to mapping that not only incorporated important population information (e.g., potential population size, source-sink territory locations) but that also considered natural processes (i.e., fire). Mapping endangered ecosystems for conservation not only requires delineating features that make them unique but also identifying features that sustain processes, such as fire and prey production (Noss et al. 1997).

Identifying potential habitat that could function as a source was more important than identifying only occupied habitat because there were large areas of potentially optimal, unoccupied habitat because of disrupted fire regimes. Mapping potential habitat and restoring its habitat quality is often important to maximize population size, exchange rates among populations, and resilience to catastrophes (Komdeur and Pels 2005, Powell et al. 2005). We showed that the most influential declines in habitat quality that resulted from habitat fragmentation were not restricted to edges because habitat loss disrupted fire propagation far beyond edges (Duncan and Schmalzer 2004). The disruption of natural processes caused by fragmentation greatly magnified the impacts of habitat loss and required greater recognition; these impacts needed mitigation using prescribed fire.

INFERENCES FROM MULTISTATE MODELING ABOUT HOW FIRES, VEGETATION AND EDGES INFLUENCE HABITAT TRANSITIONS

Introduction

Ecology concerns the distribution and abundance of organisms across the landscape (Elton 1927, Andrewartha and Birch 1954, Krebs 2001). Such landscape features as landcover, vegetation, and habitat are frequently viewed as primary determinants of both the distribution (e.g., Scott et al. 2002) and abundance (e.g., Van Horne 1983) of animal populations. Indeed, analyses relating habitat covariates to animal occurrence retain a prominent place in current ecological literature (Scott et al. 2002). For some classes of question this view of landscape features and animal populations as static entities is adequate, but many other questions focus instead on dynamics.

Examples of topics requiring a dynamical view include climate change, ecological succession, and wildlife management. Successional dynamics are important determinants of the dynamics and persistence of animal populations inhabiting such habitats (Amarasekare and Possingham 2001, Ellner and Fussmann 2003). For animal populations and communities associated with transitional habitats (habitats that do not represent endpoints of succession, or climax), habitat management frequently involves efforts to mimic disturbance and retain habitats in transitional stages (e.g., Breininger et al. in press, Johnson et al. in review). Investigations of these topics focus on dynamics and transitions of habitat stages and of the animal populations and communities that inhabit them. Topics such as these require models that do not simply project pattern (e.g., of animals, given habitat distribution), but also the dynamical processes associated with change in pattern.

A variety of approaches has been used to model habitat dynamics (Baker 1989). In cases where relevant landscape and habitat features can be adequately characterized by discrete stages or states, Markov models provide a useful framework for considering and modeling dynamics (e.g., Waggoner and Stephens 1970, Usher 1979, Augustin et al. 2001). In such models, state of the system at one point in time is written as a function of state of the system at a previous time with a set of state transition probabilities representing the different possible types of habitat change.

The key inferential step in the use of Markov models is estimation of the transition probabilities that govern change. In some cases, values for transition probabilities have been based on expert opinion (Fonnesbeck 2006). In other cases, output from more detailed models of dynamic processes (e.g., regeneration and mortality of individual trees) occurring within sites can be aggregated to draw inferences about the "state" of the sites (e.g., Acevedo et al. 1996). In many cases, transition probabilities can be estimated directly from data on the number of sample sites with habitat state recorded at each site at multiple periods of time.

Although there are multiple ways to estimate transition probabilities from such data (e.g., Augustin et al. 2001, Yemshanov and Perera 2002, Rutherford et al. 2007), here we use multistate capture-recapture models (Arnason 1972, Hestbeck et al. 1991, Brownie et al. 1993, Schwarz et al. 1993) as they can be readily implemented with existing software. These models were developed to estimate survival, detection, and transition probabilities for individual animals that are marked but not necessarily detected during sampling efforts. In this paper, we show the relationship between multistate capture-recapture models and Markov models for habitat dynamics. In particular, we show how to impose suitable constraints to capture-recapture model parameters in order to fit habitat dynamics models. The models are similar to those advocated by Augustin et al. (2001) and are readily implemented with available software. We also show how to model hypotheses about process stationarity, covariates associated with spatial and/or temporal variation in transition probabilities, and management effects on transition probabilities. These types of hypotheses can be represented as competing models and investigated using model selection (Burnham and Anderson 2002). In addition, capture-recapture software readily accommodates complications to the observation process (e.g., habitat state data are collected at some periods during an interval of interest but not at others) and loss of sample sites (e.g., to an absorbing state) during the study period.

Here we apply multistate models to dynamics of Florida scrub and flatwoods habitat. Specifically, we estimate habitat transition probabilities and draw inferences about the factors that influence transitions. Understanding how environmental factors and management actions influence these transitions is important because scrub and flatwoods have been greatly degraded by anthropogenic reductions in natural fire regimes, and restoring and managing scrub are important to conserving many unique plant and animal populations (Duncan et al. 1999, Duncan and Schmalzer 2004, Quintana-Ascencio and Menges 1996, Breininger et al. 2006, Menges et al. 2008). The habitat states we use in this modeling directly influence recruitment, survival, and source-sink dynamics of Florida Scrub-Jay populations (Breininger and Carter 2003, Breininger and Oddy 2004, Breininger et al. in press). In addition to being of great interest as a threatened species under the Endangered Species Act, the Florida Scrub-Jay is often considered an indicator and flagship species of scrub habitat (Noss et al. 1997).

Background and hypotheses

Study areas

We studied areas managed by controlled fires at Kennedy Space Center/Merritt Island National Wildlife Refuge located along central Florida's Atlantic coast (Breininger and Carter 2003). Most fires were the result of controlled fires used to reduce dangerous fuels and to manage for species of conservation concern, such as Florida Scrub-Jays. Scrub occurs on ancient dunes and is dominated by less flammable scrub oaks (*Quercus myrtifolia*, *Q. geminata*) that are intermixed and adjacent to very flammable flatwoods vegetation, such as palmetto [*Serenoa repens*], shiny lyonia [*Lyonia lucida*]) and wiregrass [*Aristida stricta*]; Breininger et al. 2002). Recently burned habitat has an open tree canopy of slash pine (*P. elliottii*) that is resilient to most fires. Grasses and shrubs sprout rapidly after fire so that composition changes little in frequently burned areas (Schmalzer et al. 2003). Fire return intervals in managed areas are 3-15 years for oak scrub and 2-8 years for pine flatwoods (Breininger et al. 2002).

Habitat states

Scrubby flatwoods is a fire maintained ecosystem that is often mapped as oak scrub and mesic flatwoods plant associations. We study habitat dynamics at the scale of 10 ha grid cells, which represent average Florida Scrub-Jay territory size. Changes in habitat structure occur because fires kill the above-ground stems and leaves of dominant plants, which sprout back because most of their biomass is underground. Territories usually include vegetation that is at different ages since the last fire. The short state (denote state as *Sh*) refers to territories that have scrub oaks <1.2 m tall because they are <3 years post-fire; short territories lack both cover for nesting and escaping predators, and adequate acorn production. The optimal state (with respect to Scrub Jay fitness; denote as *Op*) is a mix of short and medium-height oaks (1.2-1.7 m). Medium-height patches are 3-20 years post-fire and provide optimal acorn production, nesting cover, and predator-escape cover. A mixture of short and medium-height scrub results from mosaic fires that provide open sandy areas used for hunting prey and caching acorns (Woolfenden and Fitzpatrick 1984). Open sandy areas persist a few years post fire and are important to many unique scrub plants and animals (Schmalzer 2003, Menges et al. 2008). The tall mix state (*Tm*) includes tall scrub (>1.7 m) among shorter oaks because of recent mosaic fires within tall scrub. The tall state is entirely comprised of tall scrub and is avoided by Florida Scrub-Jays (Woolfenden and Fitzpatrick 1984). Tall scrub (*Ts*) is suboptimal because it reduces the ability to detect predators. Tall scrub is unburned for >20 years and results from fire suppression and habitat fragmentation that prevents fires from burning across landscapes (Duncan and Schmalzer 2004, Breininger et al. 2006).

Modeling habitat dynamics

Markov models of habitat dynamics are similar to projection models for population dynamics (e.g., Caswell 2001) and Markov models for occupancy dynamics of metapopulations (e.g., Martin et al. 2009). For a system of sites, define a variable of interest as the number of those sites in each possible habitat state ($n_i^{Sh}, n_i^{Op}, n_i^{Tm}, n_i^{Ts}$) in a given time period, *i*. Define transition probabilities as Equation 1:

$$\psi_i^{rs} = \text{probability that a site in state } r \text{ at time i is in state } s \text{ at time } i\text{+1} \qquad (1)$$

A projection model for habitat dynamics can then be written as Equation 2:

$$\begin{bmatrix} n_{i+1}^{Sh} \\ n_{i+1}^{Op} \\ n_{i+1}^{Tm} \\ n_{i+1}^{Ts} \end{bmatrix} = \begin{bmatrix} \psi_i^{ShSh} & \psi_i^{OpSh} & \psi_i^{TmSh} & \psi_i^{TsSh} \\ \psi_i^{ShOp} & \psi_i^{OpOp} & \psi_i^{TmOp} & \psi_i^{TsOp} \\ \psi_i^{ShTm} & \psi_i^{OpTm} & \psi_i^{TmTm} & \psi_i^{TsTm} \\ \psi_i^{ShTs} & \psi_i^{OpTs} & \psi_i^{TmTs} & \psi_i^{TsTs} \end{bmatrix} \begin{bmatrix} n_i^{Sh} \\ n_i^{Op} \\ n_i^{Tm} \\ n_i^{Ts} \end{bmatrix}, \qquad (2)$$

or, in matrix notation, as Equation 3:

$$\mathrm{n}_{\mathbf{i+1}} = \Psi_{\mathbf{i}}\, \mathrm{n}_{\mathbf{i}}. \qquad (3)$$

Thus, we can project the number of sites in each habitat state in one period as a function of the number of sites in each state the previous period and the transition matrix defining the state dynamics. Just as the study of population dynamics focuses on the vital rates (rates of birth, death, and migration) that define such dynamics, the study of habitat dynamics should focus on the transition probabilities ($\mathbf{\Psi}_i$) that constitute the vital rates of these dynamics (Boughton and Malvadkar 2002).

Factors influencing habitat dynamics

Transition probabilities might be most parsimoniously modeled as functions of single factors or certain combinations of factors (Table 3, first column). One of the simplest models is that transitions between habitat states are dependent only on the presence/absence of fire during the interval between transitions. Changes in habitat structure occur when fires kill the above ground stems and leaves of dominant plants, which sprout back because most of their biomass is underground (Schmalzer and Hinkle 1992). A second model includes not only fire but also the presence/absence of mechanical cutting (“cutting”) to enhance fire spread because habitat that has been degraded by long periods of reduced fire frequency burns poorly (Schmalzer and Boyle 1998, Duncan et al. 1999). Other factors that influence fire spread, and therefore might influence transitions, include vegetation composition (oak), edge effects (edge), and presence/absence of fire in previous time steps (history).

Table 3. Models represent competing habitat dynamics hypotheses and their support based on information-theoretic approaches (i.e., Burnham and Anderson 2002).

Model	AIC_c	ΔAIC_c	AIC_c Weights	No. Parameters	Deviance
oak x fire + oak x cutting + edge	2126.37	0.00	1.00	32	2061.21
oak x fire + cutting + edge	2139.66	13.28	0.00	30	2080.70
oak + cutting + edge + history	2148.36	21.99	0.00	24	2099.71
oak + cutting + edge	2171.64	45.27	0.00	23	2125.04
fire + cutting	2186.89	60.51	0.00	15	2156.63
oak + cutting + edge + history	2191.64	65.27	0.00	23	2145.04
oak + cutting + edge	2205.13	78.76	0.00	22	2160.58
oak + fire + edge	2211.61	85.24	0.00	24	2162.95
oak * fire + oak * cutting	2213.40	87.03	0.00	28	2156.51
oak * fire + cutting	2230.59	104.22	0.00	26	2177.82
oak + edge + history	2236.63	110.25	0.00	24	2187.97
oak x fire + edge + history	2238.09	111.72	0.00	29	2179.14
oak x fire + cutting + edge + history	2244.15	117.78	0.00	29	2185.20
oak x fire + edge + history	2254.67	128.29	0.00	26	2201.90
oak + time + edge	2265.48	139.10	0.00	26	2212.71
oak + edge	2273.87	147.50	0.00	22	2229.32
oak x fire	2315.38	189.01	0.00	23	2268.78
oak + fire	2319.63	193.26	0.00	21	2277.12
fire	2349.79	223.41	0.00	12	2325.62
oak + time	2369.55	243.17	0.00	22	2324.99
oak	2374.62	248.25	0.00	18	2338.25
time dependent only	2403.58	277.21	0.00	13	2377.38
time constant only	2497.04	370.67	0.00	8	2480.96

Notes: Abbreviations; + = additive models; x = specifies that fire and cutting covariates were specific to either scrub or flatwoods similar to an interaction model.

Oak scrub has a longer fire return interval and is less flammable than flatwoods, which have plants that promote fire spread (Breininger et al. 2002). Forests, human-dominated landcover types, and water bodies disrupt fire propagation across landscapes so that edge reduces fire propagation (Duncan et al. 1999) and may be useful for describing spatial variation in transition probabilities.

Methods

Data collection

All potential Florida Scrub-Jay habitat was divided into 10 ha grid cells (Breininger et al. 2006, Carter et al. 2006). Each of the 3 sampled years, we classified every grid cell (n = 914) into one of 4 habitat states (Breininger and Carter 2003; Breininger and Oddy 2004). The short state (<1.2 m tall) was identified by grid cells being burned completely within 3 years and having open sand visible between individual oak shrubs. The optimal state had an abundance of open sandy areas among medium height patches of oak scrub (1.2-1.7 m tall) that were > 0.4 ha in size. Medium height patches had interlocking shrub canopies and a smooth texture on 1.0 m resolution aerial photography. The tall mix state had short or medium height scrub patches among patches of tall oaks (>1.7 m tall) greater than 0.4 ha in size. Tall oaks had rough texture on 1.0 m resolution aerial photography. The tall state lacked short and medium height oaks and usually lacked open sand, except along man-made clearings. The habitat quality state of these grid cells was classified using 1.0 m resolution digital orthophoto quads available in 1994, 1999, and 2004 (Breininger et al. 2006, Carter et al. 2006).

Grid cells were also classified based on environmental factors that were predicted to influence transition probabilities. The first environmental factor termed “oak” distinguished grid cells based on whether they were intersected with well drained oak scrub or were dominated by flatwoods on poorly-drained soils using Brevard County soils maps (Breininger et al. 1991). The 2nd factor termed “fire” distinguished whether grid cells burned during the interval or not. A 3rd factor termed “cutting” distinguished grid cells that had been subject to mechanical cutting of trees and shrubs (Schmalzer and Boyle 1988). A 4th factor termed “history” identified whether the grid cell burned during the prior 5-year interval. Burning was determined using habitat management records and remote sensing applications (Shao and Duncan 2007). Burning or cutting was deisgnated when at least ¼ of the grid cells was burned or cut. A final factor termed “edge” distinguished grid cells that occurred along human landcover types (e.g., roads), open water, and forests from interior grid cells.

General modeling approach.

We used multistate capture-recapture models to estimate habitat-state transition probabilities and to quantify how they are influenced by environmental factors. Multistate models use longitudinal data from K sampling occasions (Nichols et al. 1994, Nichols and Kendall 1995). The basic Arnason-Schwarz model (Arnason 1972, 1973; Brownie et al. 1993; Schwarz et al. 1993) assumes that state transitions from one sampling occasion to the next represent a first-order Markov process, in that the probability of making a specified transition between occasions i and $i + 1$ depends only on the state at time i. The basic parameters for this model defined in the capture-recapture context are as Equations 4 and 5:

ϕ^{rs}_i = the probability that an organism alive in state r at time i is alive and in state s at time $i + 1$, (4)

p^{s}_i = the probability that a marked organism alive in state s at time i is recaptured or resighted on that sampling occasion. (5)

Because ϕ^{rs}_i reflects the probability of both surviving and making a specified state transition, it is often of interest to compute the following derived parameters (Hestbeck et al., 1991; Brownie et al., 1993; Schwarz et al., 1993) using Equations 6 and 7:

$S^{r}_i = \sum \phi^{rs}_i$ = the probability that an organism alive in state r at time i survives (and does not permanently emigrate from the study locations) until the time $i + 1$. (6)

$\psi^{rs}_i = \phi^{rs}_i / S^{r}_i$ = the probability of being in state s at time $i + 1$ for organisms that were alive in state r at time i and survived until $i + 1$. (7)

If survival between i and $i + 1$ depends only on state at time i (and not on state at time $i + 1$), then the ψ^{rs}_i can be viewed as conditional (on survival) state transition probabilities and used to provide inferences about the state transition process. In such cases, it is reasonable to parameterize the multistate models in terms of S^{r}_i and ψ^{rs}_i shown in Equation 8:

$$\phi^{rs}_i = S^{r}_i \, \psi^{rs}_i \qquad (8)$$

This parameterization permits direct estimation of S^{r}_i and ψ^{rs}_i and permits tests of hypotheses specific to these separate parameters using constrained models where certain parameters (e.g., time-specific parameters) can be set equal to each other.

Multistate habitat modeling with Program MARK

Data used to develop habitat models are the site-specific habitat states of each of the 914 10-ha grid cells for each of three years, 1994, 1999, and 2004. The relevant data for each cell were written as a detection history. For example, consider the following detection history: Sh Op Tm. In 1994 this site was classified as being in the short (Sh) state, in 1999 as Optimal (Op) and in 2004 as tall mix (Tm). The first decision in modeling the data is about the relevant time scale. As the data are from three specific years spaced at 5-year intervals, it is natural to estimate 5-year transition probabilities corresponding to the interval between samples. That is the approach taken in this paper, although elsewhere we show how to draw inferences about average annual transition probabilities from such data (Breininger et al. in press). For this application we constrained detection probabilities to be 1, reflecting our ability to classify each site for each of the three years of the study (Equation 9):

$$p_{94} = p_{99} = p_{04} = 1. \tag{9}$$

For different applications, for example estimation of year-specific transition probabilities, detection parameters can be modeled differently (Breininger et al. in press).

Habitat state dynamics are potentially associated with two kinds of parameters, S and ψ. The “survival” parameter, S, actually refers to a site or grid cell. In the case of the 914 sites included in our study, all sites remained in one of the four habitat states. However, if development (e.g., shopping center construction) essentially removed a site from the set of sites at which natural habitat change was possible, then we might be interested in estimates of S, the probability that a site did not enter this absorbing state. Because none of our sites was removed from consideration in this manner, we constrained site survival to be Equation 10:

$$S_i = 1, \text{ for all years, } i. \qquad (10)$$

Inferences about habitat dynamics were based primarily on the conditional transition parameters, ψ_i^{rs}. For all sites in each possible state r at time i, the probability that the site would be in any of the 4 states (s) at time i+1 followed a multinomial distribution (also see Augustin et al. 2001). Because our data on habitat state of sites were available for 3 specific years, our inferences about time-specificity of transition probabilities were limited. Specifically, we are able to estimate 5-year transition probabilities for the first 5-year period (1994-1999; denote as ψ_{94}^{rs}) and the second 5-year period (1999-2004; denote as ψ_{99}^{rs}) for all habitat states r and s. The resulting estimated transition probabilities can be combined into transition matrices and used to project habitat change following Equations 11 and 12:

$$n_{1999} = \Psi_{94}\, n_{1994}, \qquad (11)$$

$$n_{2004} = \Psi_{99}\, n_{1999.} \qquad (12)$$

The hypothesis of time-specificity for these two periods, 1994-1999 and 1999-2004, was tested by comparing this model with two transition probabilities against a model in which transitions were constrained to be equal for the 2 time periods,

$\psi_{94}^{rs} = \psi_{99}^{rs}$. We assess stationarity using evidence ratios that represent a common model selection approach in capture-recapture analyses (Burnham and Anderson 2002, Anderson 2008). Evidence ratios (wi / wj) give the relative likelihood of model i to model j, and provide a measure of relative support of the data for model i compared with model j. Model weights (w_i) provide a measure of relative model appropriateness, given the other models in the *a priori* set (Burnham and Anderson 2002).

In addition to providing estimates of habitat state transition probabilities, our modeling approach permits inference about covariates that might influence these probabilities. For example, if x_{ij} indicates a covariate associated with time period i and site j, then we can model the corresponding transition probabilities as Equation 13:

$$\psi_{ij}^{rs} = \frac{e^{(\beta_0+\beta_1 x_{ij})}}{1+e^{(\beta_0+\beta_1 x_{ij})}} \text{ ,} \qquad (13)$$

where β_0 and β_1 are parameters of the model and are estimated directly. Our models of habitat state are based on the multinomial distribution, thus the transition probabilities from any state of origin to all other possible states sum to 1 as in Equation 14:

$$\sum_s \psi_i^{rs} = 1. \qquad (14)$$

We always obtained one of the transition probability estimates by subtraction, specifically Equation 15:

$$\hat{\psi}_i^{rr} = 1 - \sum_{s \neq r} \hat{\psi}_i^{rs} \text{ .} \qquad (15)$$

For some applications, it may be desirable to use the multinomial logit, and this can also be readily implemented in program MARK. We used program MARK (version

5.1, White & Burnham, 1999) to compute maximum likelihood estimates of the transition probabilities and the parameters associated with covariate relationships.

Multi-state modeling requires the estimation of many parameters, sometimes resulting in numerical estimation problems, for example when data are sparse and when some transitions occur infrequently. Approaches to avoid numerical estimation problems include constraining transitions to 0.0 when they do not occur in the data and modeling transitions with few covariates where data are sparse. We constrained short to tall, optimal to tall, and tall to optimal transitions to 0.0 because they were not plausible within 5-year intervals. We included all possible covariates in the most general models only for tall mix to short and tall mix to optimal, because only these transitions had abundant data across all covariate values (Figure 9).

We only distinguished scrub and flatwoods and used no other covariates for short to tall mix, optimal to tall mix, tall mix to tall, tall to short, and tall to tall mix transitions because these transitions were rare. For short to optimal and optimal to short transitions we excluded covariates if there were ≤ 3 cases of a transition for each covariate condition. For the short to optimal transition, we only included fire, oak, and edge in the most general models. We exclude fire for the optimal to short transitions, because there were no occurrences of this transition when Op did not burn. Subsequent multistate modeling has great potential to become more useful for future analyses, as it should be possible to consider interactions between covariates and time.

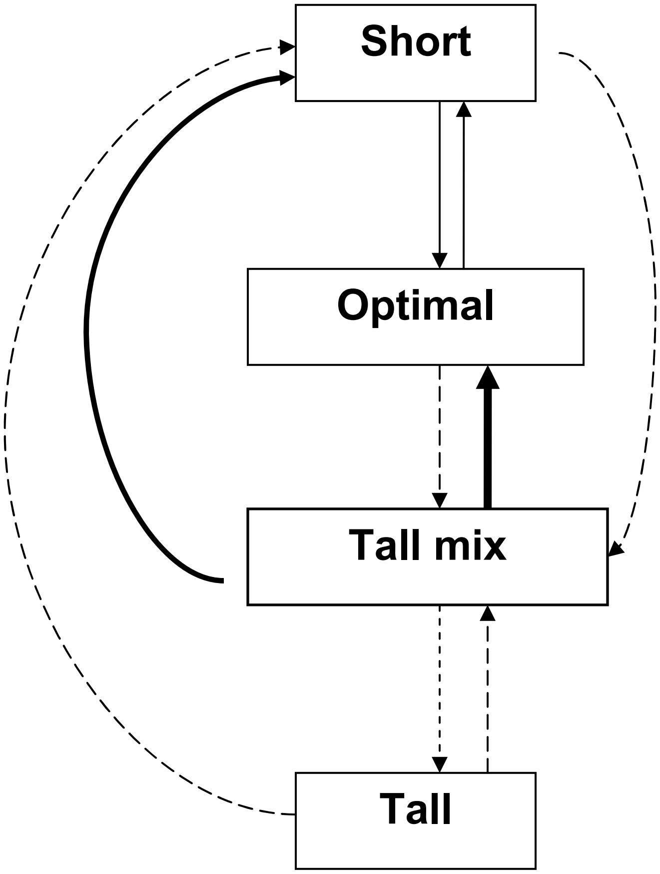

Figure 9. Transitions estimated by multistate modeling. Transitions depicted by heavy solid lines had adequate sample sizes for models including all covariates. Transitions depicted by thin sold lines occurred infrequently and were modeled using fewer covariates. Transitions with dotted lines had few occurrences and were modeled only using the covariate oak. Transitions from short to tall, optimal to tall, and tall to optimal, never occurred and were constrained to zero to aid numerical estimation. Transitions involving states that remained the same were estimated by subtraction.

Results of our analyses were used for two purposes. The first was to evaluate hypotheses about the influence of covariates on habitat transition probabilities. We not only made *a priori* predictions about which covariates would influence transitions, but we made *a priori* predictions about whether they would increase or decrease transition probabilities (i.e., we predicted whether the β coefficients would be positive or negative for particular transitions). Model selection statistics provided information about the relative importance of the different covariates, and the signs and magnitudes of the estimated β parameters provided more detailed information about the specific nature of these effects. We also noted whether the estimated approximate 95% confidence intervals for the β parameters covered 0.

The second use of our results was for projection of future habitat dynamics. We considered a vector of 1000 grid cells with the same relative abundances of habitat states found in 2004 as the basis for projection. We specified the time frame of each projection as the number of 5-year intervals (denote as m) into the future. Using 2004 as a basis, the expression used to project dynamics is Equation 2 modified to deal with time intervals >1 shown in Equation 16:

$$n_{04+m} = \Psi_i^m n_{04}. \tag{16}$$

Thus, if m = 2, then we are projecting the habitat states of the 1000 cells for the year 2014 [2004 + 2(5)], $\mathbf{n}_{14}$. We focused on such dynamics separately for the following states and transitions: burned scrub, burned and burned and mechanically cut scrub, unburned and uncut scrub, burned flatwoods, burned and burned and mechanically cut flatwoods, unburned and uncut flatwoods. For these projections, transition matrices remained constant, thus reflecting the repeated application of the rates corresponding to one of the above scenarios.

If m becomes sufficiently large in the above projection, the vector expressing the number of sites in each habitat class ($\mathbf{n}_{04+m}$) stabilizes and becomes a constant.

Following this stabilization, the vector represents the stable distribution of habitat states (analogous to a stable age distribution in population projection, Caswell 2001) defined by the repeated application of the transition matrix. This asymptotic distribution of habitat states can also be obtained directly as the right eigenvector associated with the dominant eigenvalue (which will equal 1) of the transition probability matrix. We were most interested in results that projected only into the near future because we did not envision habitat management practices remaining constant. Indeed, transient dynamics are receiving increased interest in population dynamics (e.g., Caswell 2007), and we believe they are likely important to habitat dynamics as well.

Results

Oak, fire, edge, cutting, but not history, were in the model that received virtually all support (Table 3). The model without time had no support compared to the model with only time. Models that specified an interaction between scrub/flatwoods and both fire and cutting were best supported. Signs of all $\hat{\beta}_j$ (+-) were consistent with *a priori* predictions for all environmental factors that had CIs that did not overlap zero (Table 4). Models that substituted time without fire and cutting had no support. The distributions of fires and mechanical cutting were a major cause for time variation, though they alone might not explain all time variation. Sample size was not large enough to make fire and cutting time-specific without numerical estimation problems.

Table 4. Results of *a priori* Beta Predictions

Betas	Ψ	Beta	Lower CI	Upper CI	Predict	Explanations
Flatwoods not scrub	ShOp	0.32	-1.04	1.69	-	Flatwoods grow faster but burn more extensively
Flatwoods not scrub	ShTm	-0.37	-2.35	1.62	-	Flatwoods grow faster
Fire versus no fire in scrub	ShOp	-0.45	-1.71	0.81	-	Scrub that burns less likely to increase height
Fire versus no fire in flatwoods	ShOp	-1.95	-2.91	-0.98	-	Flatwoods that burn less likely to increase height
Edge versus no edge	ShOp	1.16	0.44	1.88	+	Edges more likely to transition from short to optimal because less extensive fire
Flatwoods not scrub	OpSh	0.68	0.02	1.35	+	Flatwoods more likely than oak to go short because burn better
Flatwoods not scrub	OpTm	1.12	0.28	1.97	+	Flatwoods more likely than oak to go tall mix because grow faster
Edge versus no edge	OpSh	-0.33	-0.98	0.33	-	Edges less likely to burn completely
Flatwoods not scrub	TmSh	0.73	-1.50	2.95	+	Flatwoods burn better
Fire versus no fire in scrub	TmSh	2.44	0.42	4.46	+	Tall mix that burns more likely to transition
Fire versus no fire in flatwoods	TmSh	1.09	0.01	2.18	+	Tall mix that burns more likely to transition
Cutting versus no cutting in scrub	TmSh	0.66	0.07	1.25	+	Cut areas more likely to transition
Cutting versus no cutting in flatwoods	TmSh	2.39	1.80	2.97	+	Cut areas more likely to transition
Edge versus no edge	TmSh	-2.07	-2.56	-1.58	-	Edges likely to keep some tall
Flatwoods not scrub	TmOp	0.86	-1.30	3.03	+	Flatwoods burn better
Fire versus no fire in scrub	TmOp	2.16	0.15	4.17	+	Tall mix that burns more likely to transition
Fire versus no fire in flatwoods	TmOp	0.10	-0.95	1.15	+	Tall mix that burns more likely to transition
Cutting versus no cutting in scrub	TmOp	0.83	0.23	1.43	+	Cut areas more likely to transition
Cutting versus no cutting in flatwoods	TmOp	1.11	0.16	2.06	+	Cut areas more likely to transition
Edge versus no edge	TmOp	-0.86	-1.49	-0.23	-	Edges likely to keep some tall scrub
Flatwoods not scrub	TmTa	1.14	-0.39	2.68	+	Flatwoods grows faster
Flatwoods not scrub	TaSh	-0.15	-2.94	2.64	-	Flatwoods burn better
Flatwoods not scrub	TaTm	0.84	0.08	1.60	+	Flatwoods burn better

Notes: Individual Betas in table represent covariates (e.g., edge) specific to particular transitions. Fire and cutting Betas were specific to either scrub or flatwoods where subscripts were identified.

Transition probabilities between states were greatest for short and optimal (Table 5). Fire had a greater influence on the short to optimal, optimal to short, and optimal to tall mix transition probabilities in the more flammable flatwoods, when compared to oak scrub. However, fire had a much greater influence on tall mix to short and tall mix to optimal in scrub than flatwoods. Cutting greatly increased transition probabilities from tall mix to short or optimal for both scrub and flatwoods. Tall scrub was targeted for mechanical cutting, which explained relatively high transition probabilities from tall scrub to tall mix. Grid cells that were tall mix tended to remain tall mix regardless of management actions in flatwoods, in contrast to scrub where management activities had a greater influence.

Projections of habitat dynamics were made using transition probabilities separate for both scrub and flatwoods and 3 management actions (no management, burning only, burning and mechanical cutting). In the absence of burning or mechanical cutting, the relative abundances were likely to change slowly for scrub (Figure 10). Mechanical cutting in flatwoods resulted in a much greater increase in the short flatwoods state relative to scrub.

Discussion

Multistate modeling was useful not only because it provided estimates of transition probabilities and associated measures of precision, but also because it allowed testing alternative models that represented different hypotheses about the

Table 5. Transition probabilities for burned, unburned, and mechanically cut scrub and flatwoods.

Transition	Estimate	LCI	UCI	Groups
Short to short	0.45	0.29	0.61	Burned scrub
Short to short	0.34	0.07	0.61	Unburned scrub
Short to short	0.73	0.61	0.85	Burned flatwoods
Short to short	0.28	0.12	0.44	Unburned flatwoods
Short to optimal	0.52	0.36	0.67	Burned scrub
Short to optimal	0.63	0.34	0.85	Unburned scrub
Short to optimal	0.25	0.16	0.37	Burned flatwoods
Short to optimal	0.70	0.51	0.84	Unburned flatwoods
Short to tall mix	0.03	0.01	0.11	Scrub
Short to tall mix	0.02	0.01	0.08	Flatwoods
Optimal to short	0.11	0.07	0.18	Scrub
Optimal to short	0.20	0.13	0.30	Flatwoods
Optimal to optimal	0.83	0.77	0.89	Scrub
Optimal to optimal	0.63	0.53	0.73	Flatwoods
Optimal to tall mix	0.06	0.03	0.11	Scrub
Optimal to tall mix	0.17	0.11	0.25	Flatwoods
Tall mix to short	0.11	0.08	0.15	Scrub burned but not mechanically treated
Tall mix to short	0.01	0.00	0.07	Scrub not burned or mechanically treated
Tall mix to short	0.19	0.13	0.27	Scrub mechanically cut and burned
Tall mix to short	0.06	0.04	0.09	Flatwoods burned but not mechanically treated
Tall mix to short	0.02	0.01	0.06	Flatwoods not burned or mechanically treated
Tall mix to short	0.41	0.32	0.52	Flatwoods mechanically cut and burned
Tall mix to optimal	0.09	0.07	0.13	Scrub burned but not mechanically treated
Tall mix to optimal	0.01	0.00	0.08	Scrub not burned or mechanically treated
Tall mix to optimal	0.19	0.13	0.27	Scrub mechanically cut and burned
Tall mix to optimal	0.03	0.02	0.05	Flatwoods burned but not mechanically treated
Tall mix to optimal	0.03	0.01	0.06	Flatwoods not burned or mechanically treated
Tall mix to optimal	0.09	0.04	0.17	Flatwoods mechanically cut and burned
Tall mix to tall mix	0.79	0.75	0.83	Scrub burned but not mechanically treated
Tall mix to tall mix	0.97	0.93	1.01	Scrub not burned or mechanically treated
Tall mix to tall mix	0.62	0.54	0.70	Scrub mechanically cut and burned
Tall mix to tall mix	0.90	0.88	0.92	Flatwoods burned but not mechanically treated
Tall mix to tall mix	0.94	0.90	0.98	Flatwoods not burned or mechanically treated
Tall mix to tall mix	0.49	0.39	0.59	Flatwoods mechanically cut and burned
Tall mix to tall	0.00	0.00	0.02	Scrub
Tall mix to tall	0.01	0.01	0.02	Flatwoods
Tall to short	0.01	0.00	0.10	Scrub
Tall to short	0.01	0.00	0.08	Flatwoods
Tall to tall mix	0.19	0.11	0.30	Scrub
Tall to tall mix	0.35	0.25	0.46	Flatwoods
Tall to tall	0.80	0.70	0.90	Scrub
Tall to tall	0.64	0.54	0.74	Flatwoods

relevance of environmental factors to habitat transitions. Both intrinsic landscape features (i.e., oak and edge) and management activities (i.e., fires and cutting) were important influences on habitat transition probabilities. The interaction of site features and management have also been important in other ecosystems (McClanahan et al. 2002, Henkin et al. 2007, Wondzell et al. 2007).

The factor oak described vegetation composition differences associated with soils and topography not influenced by human activities. Edges influenced transition probabilities and mostly resulted from habitat fragmentation either directly (e.g., roads) or indirectly (i.e., forests). Even small amounts of roads began reducing fire spread and altering habitat more than 50 years ago (Duncan et al. 1999, Duncan and Schmalzer 2004). Forests were rare prior to anthropogenic reductions in natural fire frequency but now dominate many landscapes because scrub, flatwoods, and marshes converted to forests (Duncan et al. 1999, 2004; Duncan and Schmalzer 2002). Forests burn poorly and cause fire shadows downwind (Breininger et al. 2002).

Our results showed that most scrub and flatwoods sites were dominated by a tall mix state, which is associated with declining Florida Scrub-Jay populations through much of central Florida’s Atlantic coast (Breininger et al. 2006) and probably across much of the species extant range in peninsular Florida (Stith et al. 1996). The degraded tall mix state largely resulted from anthropogenic influences and moving from this condition depended greatly on cutting and not just fire (Duncan et al. 1999). High resiliency is often a desirable ecosystem state for natural habitats (Pascual and Guichard 2005), but seems not to apply to degraded Florida Scrub-Jay habitat, which takes considerable management effort to change (Schmalzer and Boyle 1998).

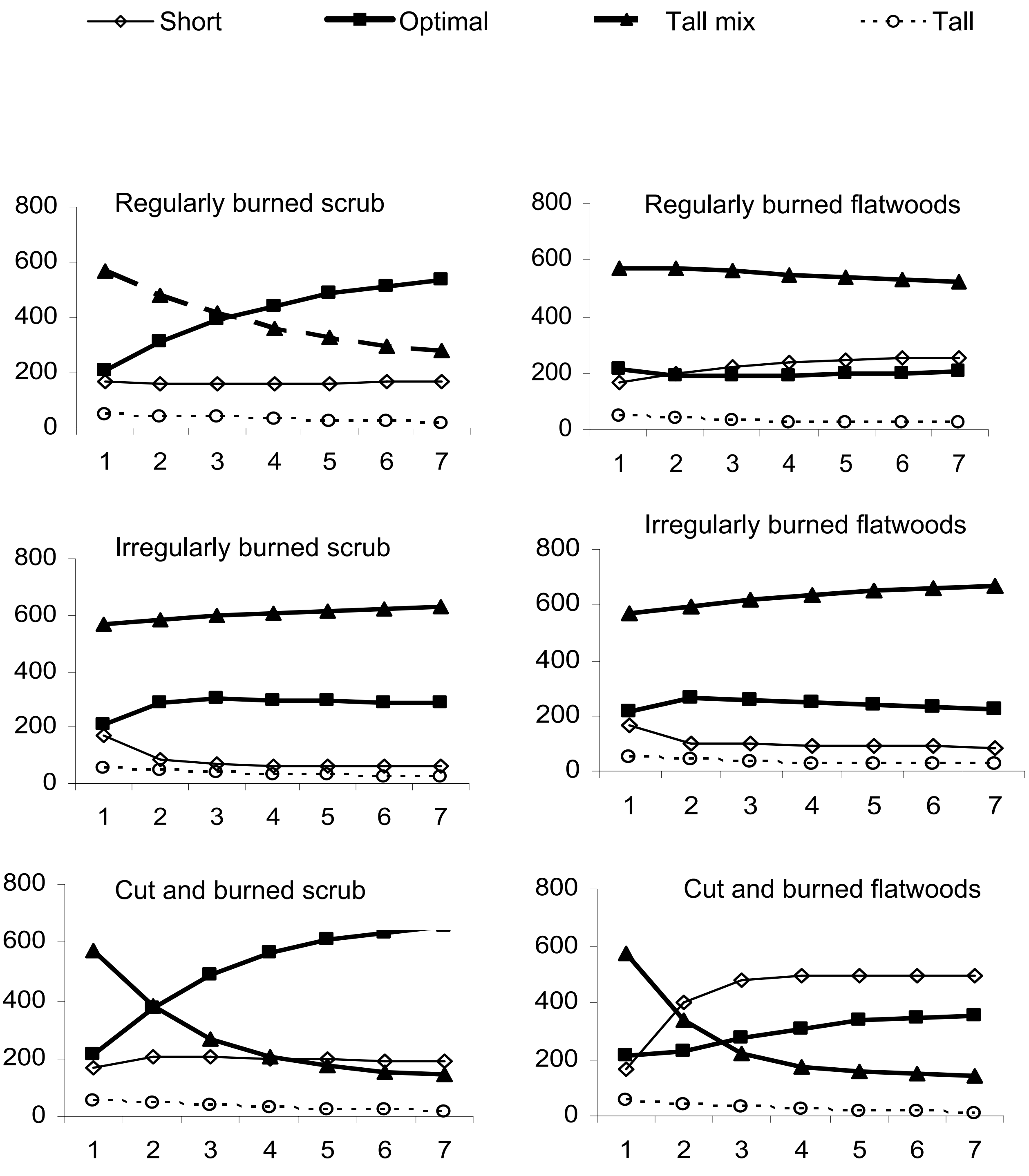

Figure 10. Projection of management actions across time using transition matrices produced from multistate models using data from Merritt Island Florida for 1994, 1999, and 2004. The y axis is the number of grid cells and x axis is the number of 5-year intervals.

Mechanical cutting is an expensive management tool and usually has been applied selectively to the tallest vegetation, rather than extensively across large areas (Schmalzer and Boyle 1998).

Our application of projection matrices using empirically derived transition probabilities to predict future conditions showed the relevance of these differences to habitat dynamics. Projections of fires without mechanical cutting resulted in increases in optimal state that were slower than the rates desired for recovery of Florida Scrub-Jay populations, especially within small populations (Breininger et al. 2006). Only the optimal habitat state results in Florida Scrub-Jay recruitment rates that exceed mortality rates (Breininger and Oddy 2004). Many Florida Scrub-Jay populations have become extremely small and isolated, such that preventing their extinction requires expedited management to achieve optimal habitat conditions (Stith et al. 1996; Root 1998; Breininger et al. 1999, 2006).

Fire history might not have been an important factor because we were only able to model its effects for tall mix to short and tall mix to optimal transitions because of limited samples for other transitions that would have created numerical estimation problems. We and our colleague (P. Schmalzer personal communication) believe that scrub recovers from short to optimal more quickly after one fire following a long period without fire compared to recovery times following many fires with short intervals. We did not consider time interactions with many covariates because we only had data for 3 time periods and small sample sizes for some transitions. Sample sizes for many transitions will improve because short and optimal states are increasing in abundance.

This modeling will become useful over time because time can be represented by trends or environmental covariates, such as drought that should influence flammability and growth (Breininger et al. 2002).

More generally, we believe that multistate modeling using capture-recapture software provides an easily implemented approach to the modeling of habitat dynamics data. It provides maximum likelihood estimates of habitat transition probabilities from the types of habitat data that are likely to be available for such inference. This type of modeling (also see Augustin et al. 2001) permits investigation of various hypotheses about the factors affecting habitat dynamics. In our case, we investigated the combined influence of factors associated with both landscape features and management actions. Estimated transition probabilities can be used to parameterize habitat models for use in investigating consequences of different management or environmental scenarios for future habitat dynamics. If the same transition matrix is applied repeatedly, then the resulting stable habitat distribution can be readily computed.

The transition matrices associated with different management levels can be used directly in efforts to develop habitat management strategies that are optimal with respect to specific management objectives (e.g., Florida Scrub-Jay fitness). In contrast to our simplified examples, projections need not use transition probabilities from only one matrix but could use different transition probabilities depending on environmental factors, much like population models, or particular matrices associated with decisions predicted to be optimal for particular habitat or population states (Nichols and Williams 2006, McCarthy and Possingham 2008).

Capture-recapture software readily accommodates complications to the observation process (e.g., habitat state data are collected at some periods during an interval of interest but not at others; Breininger et al. in press) and loss of sample sites (e.g., to an absorbing state) during the study period. In summary, we recommend this approach and its associated software for studies of habitat dynamics as multistate modeling has many possible applications and is underutilized (White et al. 2006).

HABITAT-SPECIFIC BREEDER SURVIVAL OF FLORIDA SCRUB-JAYS: INFERENCES FROM MULTISTATE MODELS

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Introduction

Habitat-specific survival is critical for understanding many ecological relationships (Van Horne 1983, Pulliam 1988, Armstrong 2004), but is rarely estimated in ways that account for the potentially confounding effects of detection probabilities (Conroy 1993, Conroy et al. 1996, Diffendorfer 1998, Anders and Marshall 2005). Estimating habitat-specific survival becomes even more difficult when habitat transitions between states over time.

Habitat-specific demography is especially important in the face of changes in habitat, as both individual fitness and population dynamics are expected to change when habitat transitions between states over time. Patchy, successional habitats can be characterized at any point in time by a mosaic of successional states. The nature of the successional process is an important determinant of the dynamics and persistence of metapopulations that inhabit them (Ellner and Fussmann 2003). For example, the rate of succession and the frequency of habitat disturbance are important determinants of metapopulation dynamics for species that prefer early successional or transitional habitat states (Amarasekare and Possingham 2001). Management of species is strongly dependent on the nature of the successional process, the manner in which this process can be influenced by management, and the responses of species vital rates to the different habitats (e.g., Johnson et al. in review).

Florida Scrub-Jays prefer transitional habitat states and exhibit greatest fitness in an intermediate successional state (Breininger and Carter 2003, Breininger and Oddy 2004). Florida Scrub-Jays are good candidates for habitat-specific survival studies because they vigorously defend territories year-round, which provide all necessary life requisites (Woolfenden and Fitzpatrick 1984). Florida Scrub-Jays are cooperative breeders that usually disperse once to breed within 2 kilometers from where they hatched (Woolfenden and Fitzpatrick 1984, Breininger et al. 2006). Habitat quality, demography, and dispersal have been characterized at the scale of Florida Scrub-Jay territories to describe how habitat features influence demographic success, but no published studies have applied modern mark recapture techniques (Mumme et al. 2000, Breininger and Carter 2003, Breininger and Oddy 2004). Here we use multistate capture-recapture models to test whether habitat quality within territories influences survival and detection probability and to estimate bird transition probabilities between territory quality states. We also develop Markov models for estimating habitat transition probabilities using grid cells at the size of average territories. These probabilities represent how birds would passively transition between habitat states. Passive transitions occur not because of bird movement, but because habitat in a bird’s territory changes state. The ratio of bird transition probabilities from one territory quality state to another, to these passive habitat transition probabilities provides a metric reflecting the degree of habitat selection. Testing *a priori* hypotheses about habitat-specific survival and transition probabilities will provide insights into habitat-specific variation in fitness, habitat-specific population dynamics, and management of metapopulations inhabiting successional habitat mosaics.

Predictions

We characterize habitat using territory quality states that depend on the time since the last fire and its extent (short, optimal, tall mix, tall; Breininger and Carter 2003; Breininger and Oddy 2004). These territory quality states do not refer to vegetation composition but instead to habitat structure that influences Florida Scrub-Jay reproductive success. Florida Scrub-Jays defend larger territories than necessary to meet immediate life requisites, probably as an evolutionary response to frequent fire regimes and the necessity to have some habitat in optimal condition (Woolfenden and Fitzpatrick 1984). The optimal state not only has open sandy areas that persist for a few years after fire and are used for caching acorns and hunting prey, but also medium-height oaks (1.2-1.7 m) that are 3-20 years post-fire and provide acorn production, nesting cover, and predator-escape cover. The optimal state lacks tall scrub, which is suboptimal because it reduces the ability to detect predators. Tall scrub is unburned for >20 years and usually results from fire suppression and habitat fragmentation that prevents fires from burning across landscapes (Duncan and Schmalzer 2004, Breininger et al. 2006).

We predict that detection probabilities do not vary with sex, but decrease with increasing vegetation height in the following order of territory quality states: short, optimal, tall mix, tall. Florida Scrub-Jay family members usually stay close together, and all family members usually fly to investigators for peanut bits when investigators enter Florida Scrub-Jay territories (Woolfenden and Fitzpatrick 1984). Peanut bits are used to lure Florida Scrub-Jays into traps for initial banding and then to briefly attract family members to the observers so that their unique color band sequences can be recorded. Florida Scrub-Jays are vulnerable to aerial predators (e.g., Cooper's hawk *Accipiter cooperii*) and are wary in tall, dense habitat where accipiters are difficult to detect (Breininger et al. 1996). Studies that do not account for detection probabilities can underestimate survival and improperly order the quality of territory quality states (e.g., Williams et al. 2002, MacKenzie et al. 2006).

Florida Scrub-Jays tend to remain in the same territories, and breeding dispersal is relatively rare (Woolfenden and Fitzpatrick 1984). There are 2 mechanisms that produce bird territory quality transitions. First, birds may actually shift territories to different locations, as jays may select certain habitat patches by slight adjustments in territory boundaries (e.g., Breininger and Carter 2003). Second, habitat at a territory location may change via disturbance (e.g., fire) or succession. Because of the site fidelity of Florida Scrub-Jays, we predict that most territory quality transitions will be associated with habitat structural changes at a territory location rather than bird movement. However, in situations where movement and active habitat selection are involved, we predict higher probabilities of movement to habitat states conferring higher fitness and lower probabilities of movement to states with reduced fitness.

We also predict that breeder survival rates are nearly the same among sexes (Woolfenden and Fitzpatrick 1984, Breininger et al. 1996) and are consistently high for breeding birds, except during rare die-offs associated with mosquito-borne arbovirus outbreaks (i.e., 1979, 1997; Woolfenden and Fitzpatrick 1984, Breininger 1999, Garvin et al. 2004). Life history parameters that most influence population growth and fitness usually vary little with environmental conditions (Gaillard et al. 1998, Pfister 1998).

We predict that habitat-specific survival is ordered, from highest to lowest, as follows: optimal, tall mix, tall, and short (Breininger and Carter 2003, Breininger et al. 2006). We evaluate these predictions about habitat-specific survival of Florida Scrub-Jays because previous studies did not deal with imperfect detection (all marked birds alive at any sampling occasion are not detected with probability 1.0), whereas detection probabilities are specifically incorporated into our analyses.

Methods

Study areas

Our study areas include 20 existing and proposed conservation areas along central Florida’s Atlantic coast (Figure 11; Breininger and Carter 2003, Breininger et al. 2006). The study areas are remnants of an ecosystem that is fragmented by urban areas and that has become marginal for Florida Scrub-Jays in many areas because of anthropogenic reductions in the fire frequency (Stith et al. 1996, Duncan et al. 2004, Duncan and Schmalzer 2004).

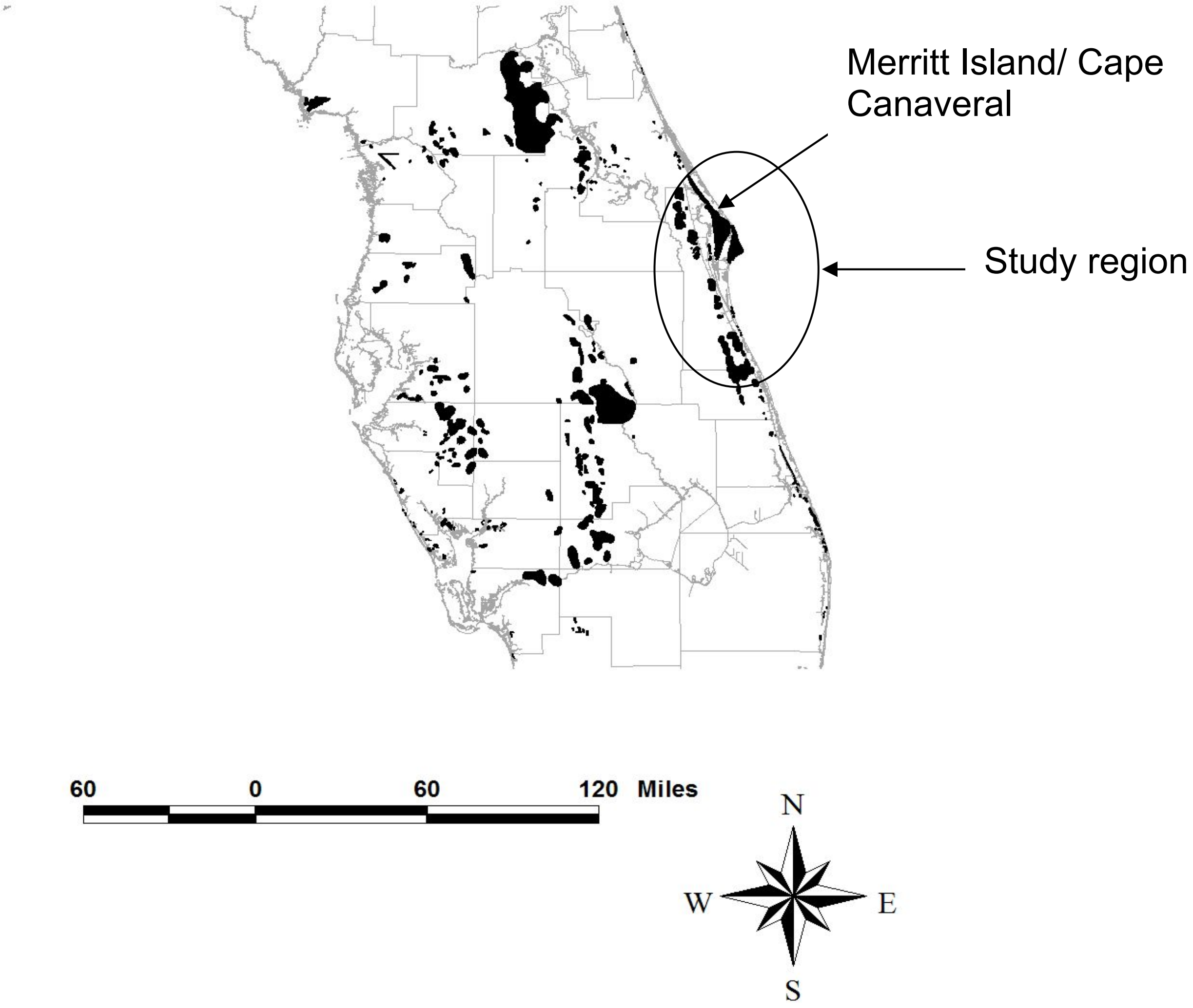

Figure 11. Map of study region and the range of the Florida Scrub-Jay, based on Stith et al. (1996). We estimated Florida Scrub-Jay life history parameters within most black areas in the study region except for Merritt Island/Cape Canaveral, where our studies sites represented <1/4 of the total area occupied by a Florida Scrub-Jays. The gray lines represent Florida county and shoreline boundaries.

Scrub occurs on ancient dunes and is dominated by less flammable scrub oaks (*Quercus myrtifolia*, *Q. geminata*) that are intermixed and adjacent to very flammable flatwoods vegetation, such as palmetto [*Serenoa repens*], shiny lyonia [*Lyonia lucida*]) and wiregrass [*Aristida stricta*]; Breininger et al. 2002). Recently burned habitat has an open tree canopy of longleaf pine (*Pinus palustris*), slash pine (*P. elliotii*), or sand pine (*P. clausa*). Grasses and shrubs sprout rapidly after fire so that composition changes little in frequently burned areas (Schmalzer et al. 2003). The pines are resilient to most fires, except for sand pines that produce serotinous cones. Fire return intervals in managed areas are 3-15 years for oak scrub and 2-8 years for pine flatwoods (Breininger et al. 2002). Tall scrub burns poorly and often needs mechanical cutting to completely reduce its extent (Schmalzer and Boyle 1998, Duncan et al. 1999, Schmalzer et al. 2003).

Data collection

From 1988 – 2005 we attempted to uniquely color band all individuals within our study areas using a numbered aluminum band and 2-3 colorbands. We captured birds using baited Potter traps, drop traps, and mist nets. Florida Scrub-Jays were often curious towards humans and familiar with human handouts because most populations occur near or within human-dominated landscapes (Stith et al. 1996, Bowman and Woolfenden 2001). We were unable to capture about 10% of the individuals and excluded them from survival analyses. We identified breeding status and family composition by performing monthly surveys (Woolfenden and Fitzpatrick 1984, Breininger et al. 2006). Breeders were distinguished by pair bond behaviors; non-breeders were nearly always young of one or both of the breeders that delayed breeding for at least one nesting season after they hatched. Females were identified by a unique hiccup call. We conducted territory mapping from April through May by observing disputes between families and instigating territory boundary display using playback of territorial calls.

Each year, we classified every Florida Scrub-Jay territory (n = 1719) into one of the 4 territory quality states. The short territory state (<1.2 m tall) was identified by territories being burned completely within 3 years and having open sand visible between individual oak shrubs. The optimal state had an abundance of open sandy areas among medium height patches of oak scrub (1.2-1.7 m tall) that were > 0.4 ha in size. Medium height patches had interlocking shrub canopies forming a smooth texture on 1.0 m resolution aerial photography. The tall mix state had short or medium height scrub patches among patches of tall oaks (>1.7 m tall) greater than 0.4 ha in size. Tall oaks produce shadows and tones that create a coarse texture on 1.0 m resolution aerial photography (Paine 1981). The tall state lacked short and medium height oaks and usually lacked open sand, except along man-made clearings. Habitat quality in study areas was also classified within 1450 grid cells using exactly the same habitat quality states as used for the birds themselves. These data were used to model habitat dynamics in order to compare bird territory quality transitions with habitat quality transitions that did not result from bird habitat selection. Each grid cell was 10 ha, which represented average territory size at carrying capacity (Woolfenden and Fitzpatrick 1984). The habitat quality state of these grid cells was classified using 1.0 m resolution digital orthophoto quads available in 1994, 1999, and 2004 (Breininger et al. 2006, Carter et al. 2006).

Capture – recapture

General modeling approach

We used multistate capture recapture models to estimate survival rates of Florida Scrub-Jays stratified by territory quality state and to test the predictions of our hypotheses. Multistate models use capture-recapture or re-sighting data from *K* sampling occasions (Nichols et al. 1994, Nichols and Kendall 1995). The basic Arnason-Schwarz model (Arnason 1972, 1973; Brownie et al. 1993; Schwarz et al. 1993) assumes that state transitions from one sampling occasion to the next represent a first-order Markov process in that the probability of making a specified transition between occasions *i* and *i* + 1 depends only on the state at time *i*. The basic parameters for this model are as follows in Equations 17 and 18:

ϕ^{rs}_i = the probability that an organism alive in state *r* at time *i* is alive and in state *s* at time *i* + 1, (17)

p^{s}_i = the probability that a marked organism alive in state *s* at time *i* is recaptured or resighted on that sampling occasion. (18)

Because ϕ^{rs}_i reflects the probability of both surviving and making a specified state transition, it is often of interest to compute the following derived parameters (Hestbeck et al., 1991; Brownie et al., 1993; Schwarz et al., 1993) shown is Equations 19 and 20:

$S^r_i = \sum \phi^{rs}_i$ = the probability that an organism alive in state *r* at time *i* survives (and does not permanently emigrate from the study locations) until time *i* + 1. (19)

$\psi^{rs}_i = \phi^{rs}_i / S^r_i$ = the probability of being in state *s* at time *i* + 1 for organisms that were alive in state *r* at time *i* and survived until *i* + 1. (20)

If survival between *i* and *i* + 1 depends only on state at time *i* (and not on state at time *i* + 1), then the ψ^{rs}_i can be viewed as conditional (on survival) state transition probabilities and used to provide inferences about the state transition process. In such cases, it is reasonable to parameterize the multistate models in terms of S^r_i and ψ^{rs}_i shown in Equation 21:

$$\phi^{rs}_i = S^r_i \, \psi^{rs}_i \qquad (21)$$

This parameterization permits direct estimation of S^r_i and ψ^{rs}_i and permits tests of hypotheses specific to these separate parameters using constrained models where certain parameters (e.g., time-specific parameters) can be set equal to each other. We performed multistate mark-recapture analyses to draw inferences about *p, S*, and ψ using Program MARK (version 5.1, White and Burnham, 1999), which implements model selection based on Akaike's Information Criterion as described by Burnham and Anderson (2002).

Florida Scrub-Jay data

We used resightings data for individual birds from the late May monthly census, which was the end of the nesting season. We began by assessing fit of our most general (global) model, in which all model parameters (*p*, ψ and *s*) were modeled as time (year)-dependent. We assessed fit of the most general model using the U-CARE software (Choquet et al. 2003, Pradel et al. 2003). The goodness of fit test statistic resulted in $\hat{c} < 1$, providing no evidence of a need for the overdispersion parameter, *c*, in the model selection process. We then developed reduced-parameter models to reflect different hypotheses about sources of variation in model parameters. The multinomial-logit link function was used to model territory quality transitions as a function of covariates. Model selection was based on a modified version of Akaike's Information Criterion that included corrections for small sample size (AIC_c,). Model weights were computed to reflect the relative (to members of the model set) appropriateness of each model (Buckland et al. 1997, Burnham and Anderson 2002).

We modeled *p*, ψ , and *S* in sequence using *a priori* model sets in order to maintain a manageable set of models (e.g., Franklin et al. 2004). For example, we focused on the modeling of *p* using a model set in which survival and transition probabilities were modeled very generally. Survival was modeled as a function of habitat x sex x time and transition parameters were modeled as a function of habitat x time, where x refers to inclusion of interactions. The most parsimonious model(s) for detection probabilities was then used in all subsequent models developed for ψ and *S*.

In the model set focusing on ψ, survival was again modeled as a function of habitat x sex x time. We focused on survival last, because it was the parameter of most interest. The survival modeling was based on the models for *p* and ψ that had been selected based on the previous modeling steps. Models constrained $\psi's$ to 0.0 for transitions that never occurred to aid in numerical estimation. Transitions between territory quality states that were constrained to 0.0 were: short to tall, optimal to tall, tall to short, and tall to optimal. Modeling for the focal parameters included both additive and interactive covariate models. Models for survival included some that replaced time with “epidemic”, which distinguished epidemic years from non-epidemic years. Epidemic years represented rare die-offs in study sites across central Florida and are believed to be years of mosquito-borne arbovirus outbreaks (i.e., 1979, 1997; Woolfenden and Fitzpatrick 1984, Breininger 1999, Garvin et al. 2004).

Habitat data

We investigated habitat dynamics by estimating habitat transition probabilities for the 10 ha grid cells in study sites. We used capture-recapture software MARK (White and Burnham 1999) as a convenient way to fit Markov models of multistate dynamics to habitat state data with missing years. Specifically, we estimated habitat transition probabilities (ψ_i^{rs}, where i denotes time and r and s denote habitat states) in MARK by fixing detection probabilities to 1.0 for 1994, 1999, 2004 (the years for which habitat classification data existed) and 0.0 for all intervening years, and by fixing “survival” to 1 for all years (all cells remained in the study for the 10 year period). We constrained annual transition probability parameters to be constant over time $\psi_i^{rs} = \psi^{rs}$, in order to estimate a single set of parameters corresponding to the average annual habitat transition probabilities over the entire period. The estimated transition probabilities were used to form a 4x4 habitat transition matrix. We estimated the asymptotic distribution of habitat states by computing the right eigenvector associated with the dominant eigenvalue of this habitat transition matrix.

Habitat selection metric

Finally, a matrix was computed to reflect the degree to which bird territory quality transitions reflected passive changes in habitat states within a location versus active selection by birds of particular habitats and avoidance of others. Habitat quality was ordered from best to worst (optimal, tall mix, tall, short) based on preliminary inferences from earlier studies (e.g., Breininger et al. 2006). Each entry in the matrix is viewed as a bird selection ratio and was computed as Equation 22:

$$\hat{\theta}^{rs} = \hat{\psi}_b^{rs} / \hat{\psi}_h^{rs}, \qquad (22)$$

the ratio of the time-constant transition probability for breeding birds (denoted with subscript b) to that for habitat (subscript h). Values of $\hat{\theta}^{rs}$ near 1.0 represent no selection by birds (territory habitat transitions reflected passive habitat change), whereas $\hat{\theta}^{rs}$ >1 represents selection of habitat state s and $\hat{\theta}^{rs}$ < 1 reflects movement away from habitat state s. We predicted $\hat{\theta}^{rs}$ >1 when the new habitat state (s) is of higher quality than the old habitat state (r), and $\hat{\theta}^{rs} < 1$ when the new habitat state is of poorer quality than the old habitat state. The variance of this bird selection ratio was computed as (e.g., Mood et al. 1974) shown by Equation 23:

$$\mathrm{v\hat{a}r}(\hat{\theta}^{rs}) = (\hat{\theta}^{rs})^2 \left[\frac{\mathrm{v\hat{a}r}(\hat{\psi}_b^{rs})}{(\hat{\psi}_b^{rs})^2} + \frac{\mathrm{v\hat{a}r}(\hat{\psi}_h^{rs})}{(\hat{\psi}_h^{rs})^2} \right] \quad . \qquad (23)$$

Approximate 95% confidence intervals were computed for the bird selection ratios as Equation 24:

$$\hat{\theta}^{rs} \pm 1.96 \sqrt{\mathrm{v\hat{a}r}(\hat{\theta}^{rs})} \; . \qquad (24)$$

Results

Model selection

The capture histories involved 1214 Florida Scrub-Jay breeders. The most parsimonious model for detection probability was specific to habitat but did not vary by time or sex (Table 6). Transition probabilities were best described as a function of habitat + time (Table 7). The best survival model was habitat + time specific (Table 8). Models with habitat and time interactions had little support, and neither did models that substituted epidemics for annual variation.

Table 6. Model selection rankings of detection probability models for Florida Scrub-Jays banded and captured along Florida's Atlantic coast 1988-2005.

Model						
S	ψ	*p*	Δ AIC$_c$	AIC$_c$ Weights	Deviance	No. parameters
h x s x t	h x t	h	0.00	0.63	2600.21	280
h x s x t	h x t	h + s	1.97	0.24	2599.81	281
h x s x t	h x t	h + t	4.77	0.06	2569.24	295
h x s x t	h x t	h x s	5.36	0.04	2596.08	284
h x s x t	h x t	h + s + t	6.73	0.02	2568.82	296
h x s x t	h x t	t x s	8.34	0.01	2594.30	286
h x s x t	h x t	.	28.76	<0.01	2636.08	277
h x s x t	h x t	h x t	29.80	<0.01	2533.95	320
h x s x t	h x t	s	31.05	<0.01	2636.00	278
h x s x t	h x t	t	31.79	<0.01	2603.44	292
h x s x t	h x t	s + t	34.07	<0.01	2603.33	293
h x s x t	h x t	h x s x t	157.70	<0.01	2492.76	388

Notes: Abbreviations: h (habitat), s (sex), t (time); + = additive; x = (interactions). No entry indicates that the parameter was treated as a constant.

Table 7. Model selection rankings of transition probability models for Florida Scrub-Jays banded and captured along Florida's Atlantic coast 1988-2005.

Model						
S	*p*	ψ	Δ AIC$_c$	AIC$_c$ weights	Deviance	No. parameters
h x s x t	h	h + t	0.00	1.00	2737.14	212
h x s x t	h	h x t	92.71	<0.01	2600.21	280
h x s x t	h	h	118.85	<0.01	2998.59	148

Notes: Abbreviations: h (habitat), s (sex), t (time), + (additive) x (interactions). No entry indicates that the parameter was treated as a constant.

Table 8. Final model selection table for survival of Florida Scrub-Jays banded and captured along Florida’s Atlantic coast 1988-2005.

Model						
S	*p*	ψ	Δ AIC$_c$	AIC$_c$ weights	Deviance	No. parameters
h + t	h	h + t	0.00	0.71	2862.96	96
h + s + t	h	h + t	1.81	0.29	2862.65	97
h x e	h	h + t	10.31	0.00	2898.59	84
h + e	h	h + t	14.13	0.00	2908.71	81
h + s + e	h	h + t	15.89	0.00	2908.37	82
t	h	h + t	15.97	0.00	2885.28	93
s + t	h	h + t	17.78	0.00	2884.97	94
h x s x e	h	h + t	17.97	0.00	2895.72	89
h	h	h + t	25.53	0.00	2922.21	80
h + s	h	h + t	31.58	0.00	2921.96	83
h x s	h	h + t	32.19	0.00	2920.47	84
e	h	h + t	33.06	0.00	2933.93	78
e + s	h	h + t	34.84	0.00	2933.61	79
t x s	h	h + t	35.93	0.00	2869.13	110
e x s	h	h + t	36.39	0.00	2933.07	80
.	h	h + t	44.35	0.00	2947.31	77
s	h	h + t	46.21	0.00	2947.07	78
h x t	h	h + t	46.93	0.00	2806.78	144
h x s x t	h	h + t	128.61	0.00	2737.14	212

*Note*s: Abbreviations: h (habitat), s (sex), t (time), e (epidemic) + = additive x = interactions). No entry indicates that the parameter was treated as a constant.

Parameter estimates

Detection probabilities did not exactly match *a priori* predictions because the short state did not have the highest detection probabilities (Figure 12). As predicted, the estimated β parameters reflecting sex effects on detection probability had little influence compared to those associated with habitat under the less supported model *S* (habitat + sex + time) *p* (habitat + sex) ψ (habitat + time).

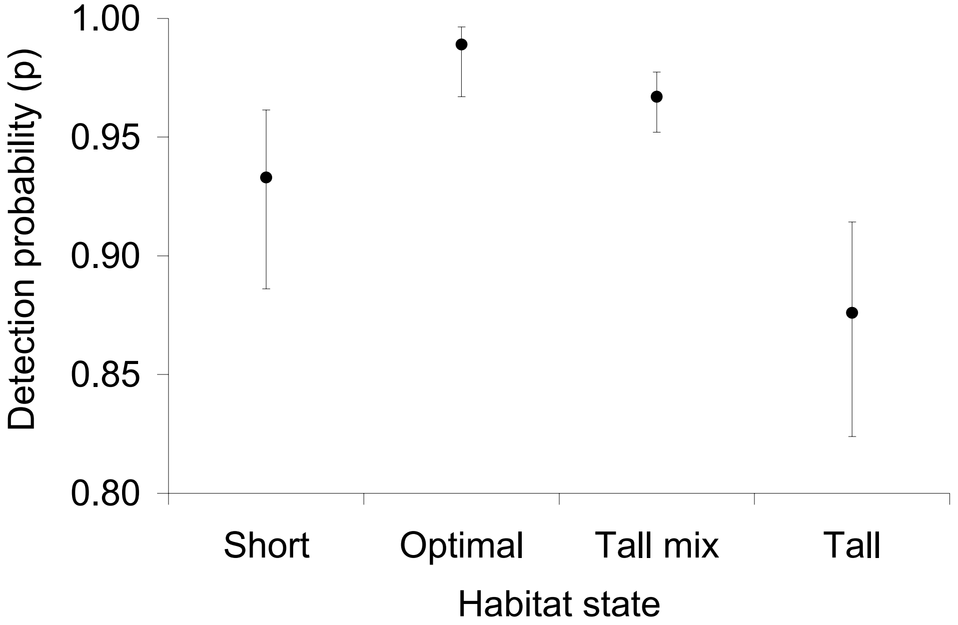

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Figure 12. Real parameter estimates ± 95% CI for detection probabilities under the best model.

Most states remained the same between years for birds and grid cells (Table 9). The greatest annual variation in transition probabilities for birds occurred within short and optimal states. Transitions from optimal to short were high during years of extensive wildfires or prescribed burns that killed nearly all above ground shrubs. The least annual variation occurred among tall mix transitions because territories in that state usually stayed in that state.

Table 9. Comparison of bird territory quality and habitat transition probabilities (with SE in parentheses for ψ and 95% CI for b/h habitat selection metrics). Habitat transition probabilities were mapped independently of bird territories using 10 ha grid cells.

Transition	Bird ψ (b)	Habitat ψ (h)	Habitat selection metric (b/h ratio)	Expected (b/h) under habitat selection
Short to Short	0.740 (0.024)	0.798 (0.018)	0.94 (0.55-1.33)	<1
Short to Optimal	0.234 (0.023)	0.168 (0.017)	1.40 (0.00-3.39)	>1
Short to Tall mix	0.021 (0.008)	0.044 (0.089)	0.47 (0.00-1.94)	>1
Optimal to Short	0.13 (0.013)	0.044 (0.008)	2.97 (0.38-5.56)	<1
Optimal to Optimal	0.785 (0.016)	0.932 (0.008)	0.84 (0.00-2.13)	>1
Optimal to Tall mix	0.084 (0.011)	0.025 (0.004)	3.45 (0.97-5.93)	<1
Tall mix to Short	0.025 (0.004)	0.038 (0.003)	0.67 (0.00-2.14)	<1
Tall mix to Optimal	0.040 (0.005)	0.007 (0.002)	5.46 (2.31-8.61)	>1
Tall mix to Tall mix	0.919 (0.007)	0.947 (0.002)	0.97 (0.00-2.19)	<1
Tall mix to Tall	0.016 (0.003)	0.008 (0.001)	1.93 (0.21-3.65)	<1
Tall to Tall mix	0.109 (0.017)	0.036 (0.003)	3.02 (1.35-4.69)	>1
Tall to Tall	0.891 (0.017)	0.960 (0.003)	0.93 (0.12-1.74)	<1

Notes: Bird transitions are time-constant estimates from multistate capture-recapture models. Habitat transitions are estimated from a time-constant habitat transition model.

Tall states transitioned to tall mix most often when restoration activities cut much tall scrub while keeping some tall scrub intact to serve as cover for resident Florida Scrub-Jays (Schmalzer and Boyle 1998).

The relative percentages of grid cells in the short, optimal, tall mix and tall states in 2004 were respectively, 12, 18, 50, and 20. The asymptotic distribution of habitat states among grid cells was 13, 27, 43, and 17, based on average transition probabilities. Quantifying how fire frequency, mechanical cutting, and other covariates influence transitions between habitat states of grid cells is the subject of an ongoing study. Although, the asymptotic distribution of habitat states is particular to the studied set of years and their specific fire frequencies and management activities, it is important that the percentage of optimal territories was low and likely to remain low.

Differences between time-constant transition probabilities among habitat states for bird territories and grid cells were usually small (Table 9), yielding habitat selection metrics near 1.0. This general result is consistent with our basic prediction of most changes in territory state occurring because of habitat change rather than bird movement.

Habitat selection metrics that differed from 1.0 were consistent with those expected based on our predictions about habitat preference or avoidance for only 7 of the 12 transitions. The CIs for most habitat selection metrics overlapped 1.0, providing little evidence for habitat preference or avoidance and instead supporting the basic conclusion that most change in territory quality was associated with habitat dynamics rather than bird movement. The only 2 habitat selection metrics that did not overlap 1.0 (corresponding to the transitions from tall mix to optimal, and tall to tall mix) were both >1.0 as predicted.

A model that included sex (*S* (habitat + time + sex)) had some support, but differences in point estimates of survival between sexes were nearly identical and differences were smaller than standard errors.

The model that assumed annual time variation had much greater support than models that substituted epidemics for time, though survival was lowest during the epidemic in 1997 (Table 10). We used a time-constant survival model to provide a useful summary of habitat-specific survival estimates; the means (1 SE) of the annual survival estimates were 0.71 (0.02), 0.82 (0.01) 0.75 (0.01), 0.73 (0.02) respectively for short, optimal, tall mix, and tall, and were consistent with a priori predictions.

Table 10. Florida Scrub-Jay breeder survival estimates (with SE in parentheses) for the most parsimonious model *S* (habitat + time) *p* (habitat) ψ (habitat + time).

Year	Short	Optimal	Tall mix	Tall
1988	0.80 (0.08)	0.88 (0.05)	0.83 (0.06)	0.82 (0.07)
1989	0.81 (0.06)	0.89 (0.04)	0.84 (0.05)	0.83 (0.05)
1990	0.71 (0.05)	0.82 (0.04)	0.75 (0.05)	0.74 (0.05)
1991	0.71 (0.05)	0.82 (0.04)	0.75 (0.05)	0.73 (0.05)
1992	0.85 (0.04)	0.92 (0.02)	0.88 (0.03)	0.87 (0.04)
1993	0.70 (0.05)	0.81 (0.03)	0.75 (0.04)	0.73 (0.04)
1994	0.74 (0.05)	0.84 (0.03)	0.78 (0.04)	0.77 (0.04)
1995	0.63 (0.04)	0.76 (0.04)	0.68 (0.04)	0.65 (0.04)
1996	0.83 (0.04)	0.90 (0.02)	0.86 (0.03)	0.85 (0.04)
1997	0.58 (0.04)	0.72 (0.03)	0.64 (0.03)	0.61 (0.04)
1998	0.73 (0.04)	0.83 (0.03)	0.77 (0.03)	0.75 (0.04)
1999	0.67 (0.04)	0.79 (0.03)	0.72 (0.03)	0.69 (0.04)
2000	0.67 (0.03)	0.79 (0.03)	0.72 (0.03)	0.70 (0.03)
2001	0.75 (0.03)	0.85 (0.02)	0.79 (0.02)	0.78 (0.03)
2002	0.63 (0.04)	0.76 (0.03)	0.68 (0.03)	0.66 (0.04)
2003	0.75 (0.03)	0.84 (0.02)	0.79 (0.02)	0.77 (0.03)
2004	0.74 (0.03)	0.84 (0.02)	0.78 (0.03)	0.77 (0.03)

Discussion

Detection probabilities

Florida Scrub-Jay detection probabilities approached 1.0 for tall mix, which was the most abundant territory quality state, and optimal, which was the desired state for population recovery. The tall state had the lowest detection probability, as expected, because this was the densest habitat having the lowest visibility for the investigators. Florida Scrub-Jays have an effective sentinel system for detection of predators in the optimal state that is less effective in the tall state resulting in wary behavior (McGowan and Woolfenden 1989). Detection probabilities were intermediate for the short state, which had sparse cover. This unexpected result might have been because jays were wary in the short state because they had little cover to escape predators, such as Cooper's Hawks. It may also be that territorial behavior is a function of territory quality, being most pronounced (and leading to higher detection probability) for birds in the optimal state.

Transition probabilities

Bird and habitat transition probabilities were similar, indicating that most bird territory quality transitions resulted from habitat dynamics rather than bird movement. Florida Scrub-Jays had limited opportunity to adjust their territory boundaries to select better habitat conditions. For example, Florida Scrub-Jays residing in optimal territories often transitioned to short because of extensive fires. In extensively burned areas it was difficult or impossible to incorporate medium-height scrub into their territories, because such scrub did not exist or was defended by other families. Transition from optimal to tall mix often occurred in landscapes where fires did not occur often enough, resulting in territory quality transitions occurring via succession for these sedentary breeders. Many tall mix-to-tall transitions occurred in habitat fragments outside managed areas where scrub remained unburned and where vegetation grew taller.

Bird and habitat transitions between short and optimal occurred naturally as vegetation recovered from fires (Breininger and Oddy 2004). Tall and tall mix territories were likely to remain in their same state because scrub >1.7 m tall is difficult to ignite and often needs mechanical cutting or hot fires to return it to a fire maintained community (Schmalzer and Boyle 1998, Duncan et al. 1999). The abundance of tall scrub and its resistance to burning explain why most territories are suboptimal and likely to remain in that condition.

Survival

Separating the epidemic year from other years did not result in a better survival model, because there was substantial annual survival variation across years when range wide epidemics were not observed. Frequent, but small, disease outbreaks might cause variation in Florida Scrub-Jay survival. The presence of positive arbovirus exposure in the blood of sentinel chickens frequently has a patchy temporal and spatial distribution (unpublished data, Brevard County Health Department). Other factors causing variation in survival might result from fluctuations in predation. Breeder disappearances (presumed mortality) are highest during months of high snake activity and accipiter migration and are rare during periods of lowest food availability (Woolfenden and Fitzpatrick 1984, Breininger et al. 1996). The differences in point estimates in male and female breeder survival were small relative to precision estimates. The direction of the differences was consistent with an explanation of female susceptibility to mortality while incubating or brooding, particularly from snakes (Carter et al. 2007).

Birds in the optimal territory quality state had the greatest survival, as expected. This is an important result, as strong inferences about habitat-specificity of survival are rare for mobile vertebrates, despite the widespread belief in the importance of habitat to fitness components. The survival differences we observed between optimal and other territory quality states would be very influential when applied to Florida Scrub-Jay population models (Root 1998, Breininger et al. 1999). For relatively long-lived species, survival generally is one of the most important factors determining population growth rates and fitness (e.g., Gaillard et al. 1998, Pfister 1998, Sandercock 2006). One reason that habitat-specific survival inferences are seldom published is the difficulty in distinguishing the effects of detection probability, movement, and survival on raw detection history data (Conroy et al. 1996). We believe our estimates of apparent survival are nearly identical to true survival because Florida Scrub-Jays nearly always remain in the same territory for life once they become breeders.

Most Florida Scrub-Jay populations were likely to continue their decline because of poor habitat-specific survival, relative to fecundity needed to sustain populations (Breininger et al. 2006), even though the proportion of optimal habitat has been increasing slightly in recent years. These improvements could be reversed if management efforts were curtailed; the extirpation of Florida Scrub-Jays in unburned habitat fragments has long been established (Woolfenden and Fitzpatrick 1984, Stith et al. 1996). Differences observed in survival between short and tall mix have management implications. In contrast to slower population declines observed for populations dominated by tall mix states, we often observe steep population declines in Florida Scrub-Jay populations subjected to extensive fire (e.g., Breininger and Carter 2003, Breininger and Oddy 2004, Breininger et al. 2006). These declines last a few years before the population recovers when the populations are large and widely distributed, but recovery frequently does not occur in small, fragmented populations (authors, unpublished data).

Occasional, extensive fire might be beneficial because it can eliminate tall scrub or keep tall scrub from accumulating (Breininger et al. 2002); the decision to attempt extensive fire might be made depending on habitat and population state. Results of this study present the manager with an interesting, yet not uncommon, problem. For Florida Scrub-Jays and other species that prefer intermediate transitional states, difficulties arise because succession eventually moves habitat away from preferred states, and the primary management action and cause of disturbance (fire) can move the habitat into a different suboptimal state. Wise management in such situations represents a nontrivial problem in dynamic optimization (Nichols and Williams 2006, Johnson et al. in review).

A MODEL SELECTION APPROACH TO PREDICTING WHETHER FLORIDA SCRUB-JAYS HELP OR BREED

Cooperative breeding in birds broadly refers to 3 or more individuals cooperating in the care of young, and commonly involves delayed dispersal by offspring participating in such care (helping). There is a rich history of debate about the ordering of fitness trade-offs that have led to the evolution of cooperative breeding in various species (Koenig and Dickinson 2004). These debates often focus on constraints, such as habitat saturation, that keep less experienced birds from obtaining breeding status (Emlen 1982, 1991; Brown 1987). Others argue for benefits of philopatry, where delayed dispersal in a natal territory enhances survival and fitness and is thought to be better than having offspring be evicted into unfamiliar habitat with high predation risk (Stacey & Ligon 1987). Most authors acknowledge that it is difficult to identify a single evolutionary variable that first led to cooperative breeding in particular taxa (Koenig et al. 1994, Ekman et al 2004). For example, a species may initially have evolved cooperative breeding in response to habitat saturation, while the benefits to group living may later have been strengthened by evolutionary forces. High survival might have led to the initial habitat saturation, or it may have come about as a consequence of delayed dispersal.

Most studies of cooperative breeding have compared the evolutionary history of cooperative breeding among taxa or long-term fitness consequences of delayed dispersal in single populations (Koenig et al. 1994, Ekman et al 2004, Ekman and Ericson 2006). Anthropogenic change has greatly altered the habitats of many cooperative breeders with unknown effects on the benefits and costs of cooperative breeding. Science and conservation should not only focus on recovering such populations, but also on sustaining cooperative breeding behavior (Walters et al. 2004). Here, we seek the most important variables that annually predict whether non-breeding Florida Scrub-Jays delay dispersal within their natal territory or disperse to breed. Our study differs from most cooperative breeding studies in that we focused on the proximate (ecological) rather than ultimate (evolutionary) causes of delayed dispersal. We used a model selection approach to investigate which of several variables together explained whether an individual delayed dispersal within 3 recently fragmented metapopulations that represented a single genetic unit (Stith et al. 1996, Breininger et al. 2006, Coulon et al. 2008). Understanding which variables predict delayed dispersal is important for parameterizing population models used to guide conservation efforts (Root 1998, Breininger et al. 1999, Stith 1999, South et al. 2002).

Background to predictions

Florida Scrub-Jays are well known cooperative breeders that have one breeding pair/territory and generally mate and occupy a single territory for life (Woolfenden and Fitzpatrick 1984, 1996). Not only do Florida Scrub-Jays that delay dispersal help raise future generations and defend territory boundaries, but they also participate in a highly effective sentinel system to detect predators (McGowan and Woolfenden 1989).

Florida Scrub-Jays are relatively weak fliers among birds and use a “delay and foray” dispersal strategy by relying on their natal territory as a safe haven to monitor breeding opportunities within the closest territories, in contrast to a floating strategy where nonbreeders leave their natal territory for long periods (Fitzpatrick et al. 1999, Stith 1999). Nonbreeders are rarely observed far from their natal territories until they become breeders or permanently disappear and presumably die. Few studies have observed floating outside a natal territory in philopatric birds (Kesler and Haig 2007).

Woolfenden and Fitzpatrick's (1984) classic long-term study of Florida Scrub-Jay cooperative breeding, dispersal, and demography involved optimal habitat saturated with a relatively stable population growth rate. In contrast, our studies involve a broad range of habitat quality, population densities, and population growth rates (e.g., Breininger and Carter 2003, Breininger and Oddy 2004, Breininger et al 2006). The optimal habitat quality and population stability associated with Woolfenden and Fitzpatrick's classic long-term study in optimal habitat has become rare within the species range because of habitat fragmentation and degradation (Stith et al. 1996, Stith 1999, Breininger et al. 2006).

We begin with the general philosophy that the goal of ecological science is to produce and evaluate hypotheses that explain how given ecological systems work (Nichols 1991). One of the best ways to achieve this goal is by comparing the support for models representing the alternative hypotheses given the data, a method referred to as information-theoretic model selection (Burnham and Anderson 2002, Hobbs and Hilborn 2006). Implementing these methods includes the development and ranking of models that represent individual variables and combinations of variables that influence whether jays delay dispersal. We briefly review each variable that might explain why a Scrub-Jay would choose to delay dispersal based on Scrub-Jay biology, cooperative breeding theory, and commonly proposed variables that might cause an animal to leave its natal area (e.g., Andreassen et al. 2002, South et al. 2002). We introduce these variables by broadly dividing them into 3 major categories: 1) individual characteristics, 2) breeding opportunities, and 3) habitat quality.

We use age, sex, and the number of breeding parents in a helper's territory as individual characteristics. We predict that younger birds, males, and young whose parents remain breeders the following nesting season are more likely to delay dispersal than older birds, females, and birds residing in a territory with a change in breeders. Woolfenden and Fitzpatrick (1984) reported that Florida Scrub-Jays of either sex usually do not breed during the first breeding season after hatching. Delaying breeding for at least one year represents a benefit to philopatry where younger birds are more likely to survive by remaining helpers in their natal territories until a breeding vacancy develops nearby than to be forced out of their natal territory (Woolfenden and Fitzpatrick 1984). Females disperse earlier and often at greater distances than males, perhaps because males are more dominant and likely to inherit their natal territories (Woolfenden and Fitzpatrick 1984). Helping parents is related to kinship benefits that enhance genetic lineages. Parentage is relevant also because breeders that replace parents are not always tolerant of progeny that are not their own.

We predict that opportunities to breed increase in years with many breeder deaths, low population densities, low densities of same-sex competitors, and high densities of potential mates. These measures of breeding opportunities might be important predictors of delayed dispersal, given that the habitat saturation hypothesis predicts that staying home might be better than floating when breeding opportunities are constrained (Brown 1987, Woolfenden and Fitzpatrick 1984). Many cooperative breeders, including Florida Scrub-Jays, avoid incest so that the opportunities to breed may also depend on the availability of suitable mates in their surroundings, particularly in fragmented populations.

We predict that Florida Scrub-Jays living in optimal habitat quality (source) territories, where recruitment exceeds mortality, are more likely to delay dispersal than Scrub-Jays living in poor habitat quality (sink) territories, where mortality exceeds recruitment. Steep gradients in habitat quality are an expansion of the habitat saturation hypothesis referred to as the “marginal habitat hypothesis” (Koenig and Pitelka 1981). Florida Scrub-Jays avoid habitats that are not optimal in Woolfenden’ and Fitzpatrick’s (1884) study area, whereas sink habitats dominate our study areas and Florida Scrub-Jays regularly disperse into them (Breininger and Carter 2003, Breininger and Oddy 2004, Breininger et al. 2006). In our study areas, sink territories have too little oak cover or have marginal shrub heights. Florida Scrub-Jay territories sometimes shift between source and sink types because of vegetation recovery from fire, and slight shifts in territory boundaries.

We consider another habitat category that describes suburbs, where Florida Scrub-Jays often breed during the first nesting season after their hatching (Breininger 1999). We predict that jays in suburbs have lower propensities to delay dispersal than jays residing in sink territories within conservation reserves. Florida Scrub-Jays in suburbs have almost no chance of having their territory transition into a source condition in contrast to conservation areas. Competing models provided below include single variables described above and combinations of these variables.

Methods

Study areas

We studied Florida-Scrub Jays in 20 local populations occurring for a 130 km length of mainland along central Florida's Atlantic coast (Breininger et al. 2006). Most habitat in these local populations was within existing or proposed conservation areas although a few populations occurred in suburbs. These populations were remnants of a scrub ecosystem that was contiguous for hundreds of kilometers (Schmalzer et al. 1999). Fire spread was greatly reduced beginning 60 years ago because human landcover features reduced fire spread causing long-term habitat degradation (Duncan et al. 1999, Duncan and Schmalzer 2004). Populations in most fragments declined greatly because of poor habitat-specific recruitment and survival related to degraded habitat, although populations have started to increase in some conservation areas where management has restored habitat quality using controlled burns (Breininger et al. 2006).

Florida-Scrub Jays occupy oak scrub (*Quercus myrtifolia*, *Q. geminata*) interspersed by pine flatwoods. Flammable shrubs (saw palmetto [*Serenoa repens*], shiny lyonia [*Lyonia lucida*]) and grasses (e.g., wiregrass [*Aristida stricta*]) dominate pine flatwoods. Recently burned scrub and flatwoods have an open tree canopy of longleaf pine (*Pinus palustris*), slash pine (*P. elliottii*), or sand pine (*P. clausa*). Grasses and shrubs sprout rapidly after fire so that composition changes little in frequently burned areas (Schmalzer 2003). The pines are resilient to most fires, except for sand pines that produce serotinous cones. Fire return intervals are 3-20 years for oak scrub and 2-8 years for pine flatwoods (Breininger et al. 2002).

Field procedures

We performed color banding studies from 1997– 2005 by uniquely banding individuals with a numbered aluminum band and 2-3 colorbands. We captured birds using baited Potter traps, drop traps, and mist nets. Florida Scrub-Jays were often curious towards humans and familiar with human handouts because populations occurred within human-dominated landscapes (Breininger et al. 2006). Breeders were distinguished by pair bond behaviors; non-breeders were nearly always young of one or both of the breeders that delayed dispersal for at least one nesting season after they hatched. Females were identified by a unique hiccup call. We conducted territory mapping from April through May by observing disputes between families and instigating territory boundary display using playback of territorial calls. We began colorbanding and regular monitoring of the youngest non-breeders by July when they approached nutritional independence. These procedures allowed us to track age, sex, breeding status, parentage, and territory quality (Woolfenden and Fitzpatrick 1984, 1996; Breininger et al. 2006).

Data analysis and inference

We formulated an *a priori* set of hypotheses offering alternative explanations of how variables influenced the probability that a Florida-Scrub Jay delayed breeding. Each alternative hypothesis was formulated as a model relating the binary response variable (delay breeding or disperse to breed) with a set of predictor variables. The relative support for each model, given the data, was evaluated based on relative Kullback-Leibler information distance of that model, measured by the adjusted Akaike Information Criteria or AICc (Burnham and Anderson 2002). Models were formulated as generalized linear models with a logit link and binomial random component (i.e., the traditional logistic regression model). This model structure was chosen for the problem because it constrained the response variable appropriately (i.e., the predicted probability that a jay will delay dispersal from 0 and 1; Agresti 1996).

The response variable was coded as to whether the jay remained a helper in the natal territory the following year (1) or bred in another territory (0). Each data record was based on a uniquely color-banded adult or juvenile that did not breed during the nesting season (April/May) of a given year, provided it survived to the following nesting season long enough to determine whether it helped or bred. We excluded 326 juveniles and 134 adult nonbreeders that permanently disappeared, 6 jays that disappeared for 1-2 years, and 5 jays that were unpaired but did not occupy their natal territory throughout the nesting season. We also excluded 14 jays that became breeders by inheriting their natal territory following the disappearance of their parents because these birds did not have a clear active choice in staying to help or dispersing to breed. The remaining birds used in the analyses were 659. This numbers excluded about 10% of the metapopulations that we were unable to capture.

We believe that few Florida Scrub-Jays emigrated because Florida Scrub-Jay dispersal distances were usually short, exchanges among populations were few, and we regularly surveyed >85% of the habitat (Breininger et al. 2006). We couldn't access several private lands where subsequent studies confirmed only a few Florida Scrub-Jay families in each. The lowest detection probabilities for breeding adults were 0.88 for tall, overgrown habitats that jays avoid when possible; detection probabilities were $\geq$0.97 in habitats occupied by most individuals (Breininger et al. in press). We later plan to use multistate capture-recapture models to better quantify helper survival and movements (Williams et al. 2002). We did not use capture-recapture models in this exploratory analysis given that multistate models rapidly accumulate parameters creating many numerical estimation problems and we wanted to investigate a large number of covariates related to delayed dispersal.

Explanatory variables measured characteristics of the bird (age, sex, parent), local populations (e.g., breeding opportunities), and habitat of the natal territory. We measured three variables describing bird characteristics. Age was a binary variable that recorded whether the bird was greater or less than one year of age. We did not distinguish birds two or more years after hatching because most bred in the study population by two years since hatching. Sex was a categorical variable with two levels: male and female. Parent was a categorical variable with four levels that recorded the number of breeders that were parents (none, dad only, mom only, both).

We defined local populations as nearly contiguous territories (<600 m apart) separated from other groupings of territories by unsuitable habitat (Breininger et al. 2006). Local populations were much further apart from other local populations than average dispersal distance and were separated by habitat that was not conducive to dispersal or survival (Stith 1999). Within these local populations we measured five variables related to breeding opportunities. Population density (labeled “density”) was calculated as the number of breeding pairs / the number of potential territories within a local population. We identified potential territories using 10-ha grid cells, which was average territory size at carrying capacity (Woolfenden and Fitzpatrick 1984, Breininger et al. 2006, Carter et al. 2006). Population size was the number of breeding pairs in each local population. Breeder deaths per pair were the number of breeders in a local population that disappeared during a particular year divided by local population size. Competitors per pair were calculated as the number of same sex helpers in local populations divided by local population size. Mates per pair were calculated as the number of opposite sex helpers that were not siblings divided by local population size.

Two variables (habitat quality, suburb) measured habitat characteristics of the natal territory. Habitat quality was a categorical variable with two levels. Optimal habitat had average recruitment that exceeded mortality (habitat quality = 1) and marginal habitat had mortality that exceeded recruitment (habitat quality = 0). Optimal habitat occurred on large scrub oak ridges (>0.4 ha) having a mix of short and medium-height oaks (1.2-1.7 m). Marginal habitat lacked large scrub oak ridges or had only short scrub oaks (<1.2 m tall) or patches of tall oaks (>1.7 m; Breininger and Carter 2003, Breininger and Oddy 2004, Breininger et al 2006). Suburb coded whether jay resided within a suburb, defined as territories that were intercepted by houses and roads (suburb = 1) versus territories within existing and proposed conservation areas (suburb = 0).

Model selection

Evidence evaluating support for models in the *a priori* set was evaluated based on the relative adjusted Akaike weight (w_i), the model probability, also called model weight (w_i), and the evidence ratios, calculated as follows (Burnham and Anderson 2002) in Equations 25-29:

$$\mathrm{AICc}_i = -2 * \log_e (\text{Likelihood of model i given the data}) + 2*K + 2*K*(K+1)/(n-K-1)$$

where K = the number of parameters estimated and n = the sample size. (25)

$$\mathrm{AICc}_{\min} = \text{AICc for the model with the lowest AICc value} \quad (26)$$

$$\Delta_i = \mathrm{AICc}_i - \mathrm{AICc}_{\min} \quad (27)$$

$$w_i = \exp(-1/2 * \Delta_i) \Big/ \sum_{r=1}^{n} \exp(-1/2*\Delta_i) \quad (28)$$

$$\text{evidence ratio of model i to model j} = w_i / w_j \quad (29)$$

Model weights (w_i) can be interpreted as the likelihood that model i is the best model in the *a priori* set (Burnham and Anderson 2002). Evidence ratios (w_i / w_j) give the relative likelihood (or likelihood ratio) of model i to model j, and represent the relative support of the data for model i compared with model j. Models were considered for interpretation of their parameters if they had: 1) ΔAIC_c of less than 10.0, 2) were included in the set of best supported models with combined Akaike weights of 0.95 (95% confidence set) and 3) had an evidence ratio relative to the best supported model greater than 0.135 (Burnham and Anderson 2002).

Logistic regression models were fit using R version 2.5.0 (R Development Core Team 2007). Following model selection, model fitting diagnostics were performed on the full model (i.e. a model with all main effects and interaction terms included in any of the *a priori* models) and all models considered for further interpretation, following tests in Hosmer and Lemshow (2000). Univariate logistic regression models were fit to ensure that there was a relationship between each explanatory variable included in the model, and the response variable. The fit of models were examined using Nagelkerke R^2 described in Hosmer et al. (1997) and implemented in the Design package in R (Harrell 2001). We calculated Receiver Operating Characteristic (ROC) curves for both the global model and the best supported *a priori* model using the ROCR package in R (Sing et. al. 2005). Diagnostics identified nonlinear effects we did not consider in our *a priori* model set. We compared model support for additional nonlinear models relative to our best *a priori* models in *post hoc* analyses.

We used relative variable importance to compare variables that predicted whether Florida Scrub-Jays helped or bred. This involved summing model probabilities (w_i) across all models in which a variable occurred (Burnham and Anderson 2002). One caveat was that each variable should have been represented in the same number of models to allow a fair opportunity to accumulate importance (Burnham and Anderson

2002). Because this was not true for models in our *a priori* set, we substituted all of the possible additive models using combinations of the ten predictor variables (e.g. all 1023 model combinations) as a new model set for calculating each variable's relative importance. This model set was not used to select models for inference, but to calculate relative variable importance and model-averaged parameter estimates. We wrote visual basic programs in Access 2003 (Microsoft Corporation 2003) which created model specifications for all 1023 additive models, fit each model in R, then returned information regarding the model fit (e.g. deviance, parameter estimates, standard errors) to tables in Access. Once the information was recorded in Access, we used spreadsheets to conduct necessary calculations.

We graphed the β *'s* for the best supported *a priori* model as a nomogram using the Design package in R (Harrell 2001). We used nomograms to graphically show how models and their variables influenced whether Florida Scrub-Jays delayed dispersal or dispersed to breed because interpretations of logistic model parameters (β) were not directly intuitive, being on the logit scale. We compared predictions on the predicted probability of helping using different combinations of variables for the best *a priori models* and best *post hoc models* in spreadsheets.

Results

The top 13 models in the *a priori* model set had a combined Akaike weight of 0.95 (Table 11). The best supported model had 6 variables: age, sex, parents, breeder deaths per pair, mates per pair, and suburb. The 3 next best supported models added one or both of the interactions age*sex and age*parents. Four variables (age, sex, parents, and breeder deaths per pair) were included in all of the top 13 models.

Table 11. Information-theoretic selection model selection results for 65 a priori models relating the probability of a Florida-Scrub Jay remaining in its natal territory (help) to ten explanatory variables. ag = age, s = sex, pa = parents, su = suburb, bd = breeder deaths per pair, ma = mates per pair, co = competitors per pair, dn = density (pairs/ha), hq = habitat quality, ps = population size, The first thirteen models have 95% of the weight, and all contain: age, sex, parents, breeder deaths, and mates.

Model	k	-2loglikelihood^a	Δ_i AICc	w_i
ag + s + pa + su + bd + ma	9	702.21	0.00	0.29
ag + s + pa + su + bd + ma + s * pa	12	696.33	0.33	0.24
ag + s + pa + su + bd + ma + ag * s	10	702.21	2.06	0.10
ag + s + pa + su + bd + ma + ag * s + s * pa	13	696.32	2.41	0.09
ag + s + pa + bd + ma + co	9	706.01	3.80	0.04
ag + s + hq + pa + bd + ma	9	706.11	3.90	0.04
ag + s + hq + pa + bd + ma + s * pa	12	700.10	4.10	0.04
ag + s + pa + bd + ma + co + s * pa	12	700.11	4.11	0.04
ag + s + pa + bd + ma + co + ag * s	10	706.01	5.86	0.02
ag + s + hq + pa + bd + ma + ag * s	10	706.11	5.96	0.01
ag + s + pa + bd + ma + co +ag * s + s * pa	13	700.06	6.14	0.01
ag + s + hq + pa + bd + ma + ag * s + s * pa	13	700.09	6.18	0.01
ag + s + pa + bd	7	712.64	6.32	0.01
ag + s + hq + pa + su + bd + ma + dn + co + ps	13	700.83	6.91	0.01
ag + s + pa + bd + s * pa	10	707.29	7.14	0.01
ag + s + hq + pa + su + bd + ma + dn + co + ps + s * pa	16	694.86	7.24	0.01
ag + s + hq + pa + bd	8	712.55	8.28	0.00
ag + s + pa + bd + ag * s	8	712.62	8.35	0.00
ag + s + hq + pa + su + bd + ma + dn + co + ps + ag * s	14	700.83	9.00	0.00
ag + s + hq + pa + bd + s * pa	11	707.18	9.10	0.00
ag + s + pa + bd + ag * s + s * pa	11	707.21	9.13	0.00
ag + s + hq + pa + su + bd + ma + dn + co + ps + ag * s + s * pa	17	694.82	9.31	0.00
ag + s + hq + pa + bd + ag * s	9	712.54	10.33	0.00
ag + s + hq + pa + bd + ag * s + s * pa	12	707.10	11.10	0.00
ag + pa + su + bd	7	721.30	14.98	0.00
ag + pa + bd	6	723.39	15.03	0.00
ag + s + pa	6	724.71	16.34	0.00
ag + hq + pa + su + bd	8	721.23	16.96	0.00

ag + pa + bd + dn	7	723.29	16.97	0.00
hq + bd + pa + ag	7	723.38	17.06	0.00
ag + hq + s + pa + su	8	721.89	17.62	0.00
ag + s + su + bd + ma + co	7	724.37	18.04	0.00
ag + s + pa + ag * s	7	724.59	18.27	0.00
ag + s + pa + s * pa	9	720.87	18.65	0.00
su + hq + ag + s + pa + ag * s	9	721.77	19.56	0.00
su + hq + ag + s + pa + s * pa	11	718.17	20.09	0.00
su + ag + s + ag * s + bd + co + ma	8	724.36	20.09	0.00
ag + s + pa + ag * s + s * pa	10	720.57	20.42	0.00
hq + ag + s + bd + co + ma	7	726.91	20.59	0.00
su + hq + ag + s + pa + ag * s + s * pa	12	717.88	21.88	0.00
hq + ag + s + ag * s + bd + co + ma	8	726.91	22.64	0.00
bd + ma + pa	6	735.11	26.74	0.00
hq + bd + co + ma + pa + dn	9	734.72	32.51	0.00
pa	4	747.87	35.43	0.00
ag + s	3	754.98	40.51	0.00
hq + ag + s	4	753.59	41.16	0.00
su + hq + ag + s	5	751.73	41.32	0.00
ag + s + ag * s	4	754.81	42.38	0.00
hq + ag + s + ag * s	5	753.48	43.08	0.00
ag + s + su + hq + ag * s	6	751.61	43.25	0.00
hq + ag + s + co + dn	6	751.82	43.46	0.00
hq + ag + s + ag * s + co + dn	7	751.67	45.35	0.00
ag	2	766.01	49.53	0.00
hq + ag	3	765.05	50.58	0.00
bd	2	778.75	62.27	0.00
hq + su + bd	4	777.30	64.86	0.00
hq + bd + ps	4	777.54	65.10	0.00
s	2	782.39	65.91	0.00
su + hq + co + ma + dn	6	779.84	71.47	0.00
hq	2	790.06	73.58	0.00
su	2	790.08	73.60	0.00
su + hq	3	789.41	74.95	0.00
ps + dn	3	790.40	75.94	0.00
dn + co	3	791.06	76.60	0.00
hq + su + co + dn	5	788.51	78.11	0.00

a table entry gives -2*ln(Likelihood of model given the data)

b table entry gives the relative likelihood of model = exp(-0.5*∆i)

c table entry gives the evidence ratio of each model compared to the model with the lowest AICc

Additional variables included in some of the top 13 models were habitat quality and competitors per pair. Population size and density were not in any of the best 13 models. Although models including interactions were among the best-supported models in the *a priori* model set, parameter estimates for interaction terms had low precision. These variables may be important, but limitations of the data available make their estimates unreliable (Anderson 2008). The 6 variables included in the best *a priori* model had the highest relative variable importance with a clear break in importance between these 6 and the remaining 4 variables (Table 12).

Table 12. Relative variable importance and model-average β estimates and their estimated standard errors, for all possible additive models relating the probability of a Florida-Scrub Jay remaining in its natal territory (help) to ten explanatory variables. Calculations based on formulas 4.9 and 6.12 in Burnham and Anderson 2002.

Parameter	Model-average estimated β	Standard error	Relative Variable Importance
Age = adult	-0.94	0.20	1.00
Parent = dad only	1.15	0.37	1.00
Parent = mom only	0.39	0.34	-
Parent = both	1.14	0.28	-
Breeder deaths per pair	-1.93	0.58	0.99
Sex = female	0.56	0.19	0.97
Mates per pair	-0.62	0.27	0.89
Suburb = yes	-0.48	0.31	0.74
Competitors per pair	-0.10	0.20	0.39
Population size	0.00	0.01	0.30
Density (pairs / ha)	0.02	0.26	0.28
Habitat quality = optimal	0.01	0.11	0.27

Of the six variables with high relative variable importance, age, parents, breeder deaths, and sex all had very high importance, meaning that they were included in almost all models with appreciable Akaike model weights. The remaining two variables (mates per pair and suburb) were less important, although still useful predictors of helping behavior. Model-averaged predictions of estimated model coefficients (β's) based on all the possible additive models were given in Table 12.

All of the model-average β estimates for the 6 parameters in the best model (age, sex, parents, breeder deaths per pair, mates per pair, and suburb) had good precision, except suburb. The remaining variables (competitors per pair, population size, density, and habitat quality) had low precision relative to the magnitude of the parameter estimate and contributed little information.

The Global model (i.e., the model with all of the variables included in any of the alternative models) showed no evidence for lack of fit (z = -0.29, p = 0.77; Hosmer and Lemshow 2000). The global model had a Nagelkerke R^2 = 0.20 indicating a structural relationship in the data. This measure is similar to an adjusted R^2 in a multiple regression analysis, but is generally lower than one expects based on regression diagnostics (Nagelkerke 1991). The best supported *a priori* model also showed no evidence for lack of fit (z = 0.003, p = 0.997), and this model had a Nagelkerke R^2 = 0.184. The areas under the ROC curves for the global model and the best supported *a priori* model respectively were 0.74 and 0.73 using the ROCR package in R (Sing et. al. 2005). Pearson product correlations between pairs of continuous dependent variables were small and always less than 0.36, indicating little collinearity.

We examined the scale of all continuous variables in the best model following Hosmer and Lemshow (2000). This addressed our *a priori* selection of linear scale continuous explanatory variables, given we did not hypothesize non-linear relationships between explanatory variables and the probability of helping. Results were consistent with a linear scale for all variables, except 3 that predicted a curvilinear univariate relationship with the probability of helping. The probability of helping was lowest for intermediate levels of mates per pair, population size, and competitors per pair (Figure 13). Based on the results of the model fit diagnostics, we examined new versions of our best 2 models that included quadratic terms for these variables in a *post hoc* analysis (Table 13). Models that substituted the quadratic mates per pair or quadratic competitors per pair effects were superior to the models with the linear predictor variables. For example, the best model with mates per pair^2 had a Nagelkerke R^2 = 0.22 and area under the ROC curve of 0.75.

Nomograms graphically showed the relative effects of each predictor variable to the response variable (Gitzen & Millspaugh 2007). We provide examples of predictions using nomograms below based on the best *a priori* model (Figure 14). Nomogram interpretation relies on the relationship between the “Points Scale” (at the top), “Total Points Scale” (third from the bottom), and “Linear Predictor Scale” and “Predicted Value Scales” (at the bottom). To use the nomogram, one finds the predicted outcome of a combination of variable levels by finding the desired level of each variable and following the position vertically up to the Points Scale. One repeats this for all variables and adds the points and finds that value on the Total Points scale, follows that position directly down, and then examines the predicted levels on both the Linear Predictor (i.e., logit) and the Predicted Value (i.e., the predicted probability of helping).

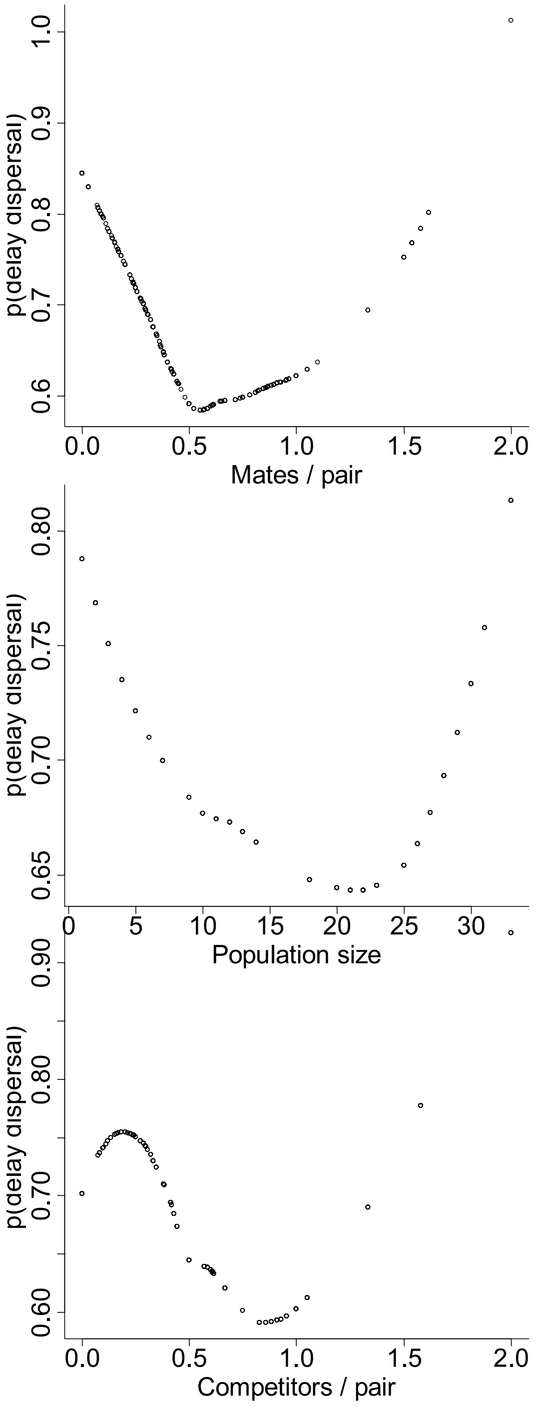

Figure 13. Smoothed plots of univariate models of the probability of a Florida-scrub Jay remaining in its natal territory, p(delayed dispersal), as a function of each of the three continuous explanatory variables which showed evidence of non-linear relationships.

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Table 13. Information-theoretic selection model selection results for post hoc models incorporating nonlinear effects of three continuous variables in the two best supported models relating the probability of a Florida-Scrub Jay remaining in its natal territory (help). ag = age, s = sex, pa = parents, su = suburb, bd = breeder deaths per pair, ma = mates per pair, co = competitors per pair, dn = density (pairs/ha), hq = habitat quality, ps = population size, The first thirteen models have 95% of the weight, and all contain: age, sex, parents, breeder deaths, and mates.

Model with parameters additional to ag + s + pa + su + bd + ma	k	-2loglikelihood[a]	Δ_i	w_i
s * pa + ma^2	13	-341.38	0.00	0.50
ma^2	10	-344.56	0.14	0.47
s * pa + co + co^2	14	-344.32	7.97	0.01
co + co^2	11	-347.45	7.99	0.01
Best *a priori* (ag + s + pa + su + bd + ma)	9	-351.11	11.16	0.00
s * pa	12	-348.17	11.49	0.00
s * pa + ps + ps^2	14	-346.60	12.54	0.00
ps + ps^2	11	-349.75	12.59	0.00
dn + dn^2	11	-349.92	12.92	0.00
s * pa + dn + dn^2	14	-346.89	13.13	0.00
bd^2	10	-351.10	13.22	0.00
ag * s	10	-351.10	13.22	0.00
s * pa + bd^2	13	-348.14	13.53	0.00
ag * s + s * pa	13	-348.16	13.57	0.00
co	9	-353.01	14.96	0.00
hq	9	-353.06	15.06	0.00
hq + s * pa	12	-350.05	15.27	0.00
co + s * pa	12	-350.05	15.27	0.00
co + ag * s	10	-353.01	17.02	0.00

[a] table entry gives -2*ln(Likelihood of $model_i$ given the data)

[b] table entry gives the relative likelihood of $model_i$ = exp(-0.5*Δi)

[c] table entry gives the evidence ratio of each model compared to the model with the lowest AICc

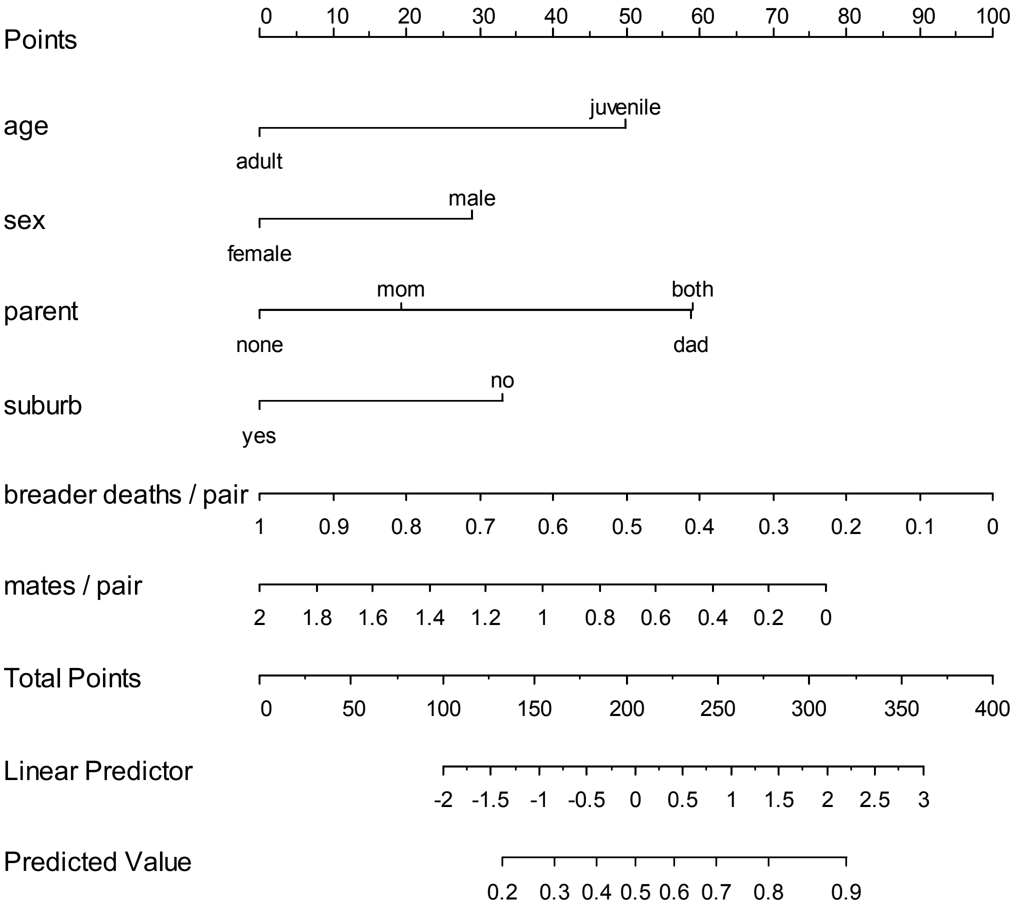

Figure 14. The nomogram for the best *a priori* model describing the effects of variable combinations on the probability of helping. To use the nomogram, one finds the effect of variable combinations by finding the desired level of each variable and following the position vertically up to the Points Scale. Repeat this for all variables and add up the points and find that value on the Total Points scale. Then follow that position directly down, and then examine the predicted levels on both the Linear Predictor (i.e., logit) and the Predicted Value (i.e., the predicted probability of helping).

For example, if one assigned the values age = juvenile, gender = male, parents = both, suburb = yes, breeder deaths = 0.5, and mates = 1, one would then add the corresponding points: 50 + 0 + 58 + 0 + 50 + 38 = 196. By locating 196 on the Total Points scale, and following that value down, one would read the Linear Predictor as -0.14 and the Predicted Values as 0.47 (= probability for remaining a helper).

Nomograms are useful for estimating the effect of changing some variable values while keeping other variables constant. Suppose we were interested in the effect of changing age from juvenile to adult, while holding all other variables constant. We added the points for the new variable levels as: 0 + 0 + 58 + 0 + 50 + 38 = 146. Locating 146 on the Total Points scale, and following that value down we read the Linear Predictor = -1.1 and the Predicted Values = 0.25. Thus the probability of helping decreased by almost half when age changed from juvenile to adult while all other variables were held constant.

The nomogram allows a direct comparison of the effect magnitude for each variable, the direction of effect, and comparisons between categorical variables. For example, age has a greater effect than gender and suburb, but less than parents. Breeder deaths per pair had a slightly greater effect than mates per pair, and both had a greater range of effect than any of the categorical variables. A Florida Scrub-Jay with both parents or just its father was more likely to help than individuals with neither parent or just its mother. Sex and suburb had weak effects on the probability of helping. Males were more likely to help than females, and Florida Scrub-Jays in suburbs (suburb=1) were less likely to help than birds in natural areas (suburb=0). Breeder deaths per pair had a moderate effect; as breeder deaths per pair increased individuals were less likely to help. Most values of mates per pair were between 0.0 and 1.0, but much of the mates per pair influence in the nomogram occurred because the variable ranged from 0-2, even though the data were sparse between 1.0-2.0 (Figures 13, 14).

Predicted probabilities of helping were very similar for the best *a priori* models and post hoc models, except for mates per pair, so we only presented a comparison of linear and quadratic results for mates per pair (Figure 15). The differences between models became great when mates per pair >1.5, which was relatively rare and represented by insufficient data (Figure 13).

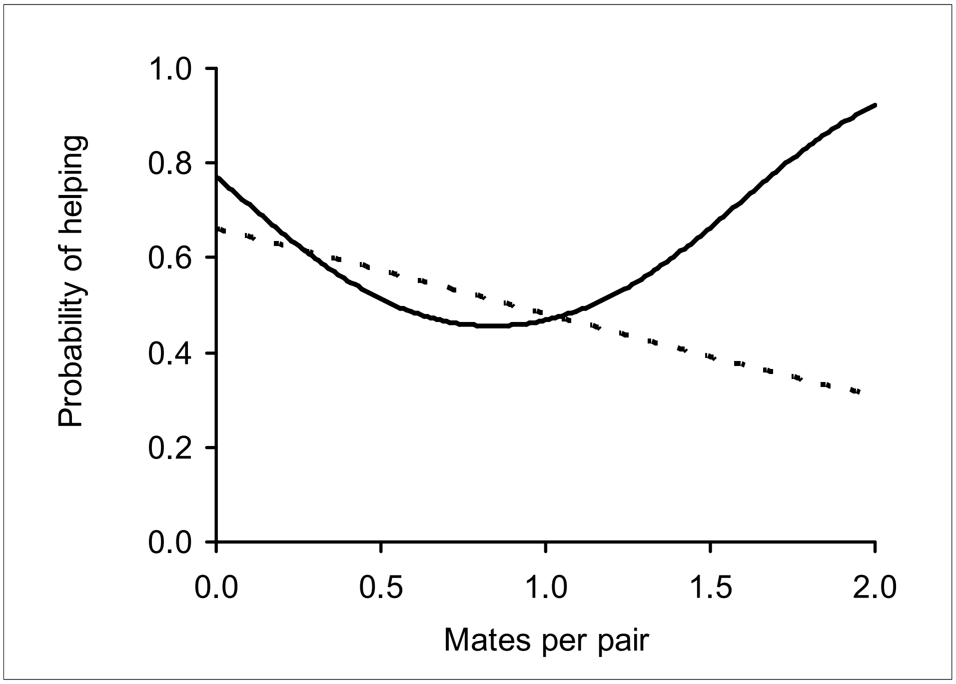

Figure 15. Comparing the influence of linear and quadratic mates per pair models on the probability of breeding. The linear was the best *a priori* model and the quadratic was the best post hoc model. Plots were produced by fitting the predicted probability of helping over the range of observed values of mates per pair while holding all other variables constant.

Discussion

We found many variables were influential in predicting whether Florida Scrub-Jays helped or dispersed to breed and that no single variable was adequate. Koenig et al. (1994) suggested that many variables might be influential in the evolution and maintenance of cooperative breeding in general but that individual variable importance might vary among local populations. Koenig et al.'s predictions were generally supported by the many variables that had support within our best models, including nonlinear parameters that suggest that variable importance would change among populations.

Individual characteristics were useful predictors as predicted, such as males having greater probabilities of remaining helpers than females (Woolfenden and Fitzpatrick 1984). We found that one-year-olds bred much less often then older helpers but more often than in Woolfenden and Fitzpatrick's (1984) study where one-year-olds seldom bred. We most often observed one-year-olds breeding in suburbs, which had declining populations because mortality exceeded recruitment. We first observed this pattern in another suburb Florida Scrub-Jay population on a nearby barrier island (Breininger 1999). We often observed one-year-olds colonizing restored scrub that was formerly unoccupied when these areas were adjacent to their natal territories.

Having both parents remain breeders, or the father, was an important variable that led to a greater probability of helping. Florida Scrub-Jays have very low rates of divorce and most surviving breeders that lose a mate remain in their territory and pair with a replacement breeder (Woolfenden and Fitzpatrick 1984). Replacement breeders sometimes aggressively chase away nonbreeders from the territory.   Males tend to dominate females (Woolfenden and Fitzpatrick 1984), which probably helps explain why keeping the father was more important than keeping the mother. Helping parents also becomes the basis of kinship in that such a bird could be promoting similar genetic information (Woolfenden and Fitzpatrick 1984, Koenig et al. 1994).

An important variable reducing helping probability was breeder deaths, which are habitat-specific with some annual variation associated with disease outbreaks (Breininger et al. in press). Breeder deaths were better predictors of breeding opportunities than population density partially because breeder deaths created immediate breeding opportunities within existing territories for replacement breeders. Florida Scrub-Jay territory sizes along Florida's Atlantic coast vary with population densities (Breininger and Carter 2003) and most suitable habitat in low population density habitat was defended by Florida Scrub-Jay families and not readily available for establishing new breeding territories.

Several variables (mates per pair, competitors per pair, and population size) that were better described by *post hoc* nonlinear models might have better support than linear models because breeding opportunities were greatest at intermediate levels. Small populations often had few potential mates and large populations often had many helpers and greater competition for mates. Small populations usually had only a couple of families that produced young at any one time and therefore nonbreeders were often closely related. Incest is generally avoided (Woolfenden and Fitzpatrick 1984).

We did not find support for our prediction that non-breeders in optimal territories (sources) would have greater probabilities to help than individuals in poor quality territories (sinks). Optimal territories were rare compared to sink territories in most landscapes so that most Florida Scrub-Jays probably needed to disperse from optimal territories to breed (Breininger et al. 2006). Territories can transition between source and sink states between years so that existing habitat quality might not be a critical determinant in choosing to breed or help (Breininger and Carter 2003, Breininger and Oddy 2004). Future studies might also consider whether jays are more likely to help as habitat is restored and most habitat is optimal. Habitat quality remains important for Florida Scrub-Jay conservation because many conservation areas had declining populations that approach extinction because of insufficient optimal habitat (Breininger and Carter 2003, Breininger et al. 2006).

Behavior is often neglected by conservation biologists, except when directly related to maintaining viable populations or population control (Komdeur and Deerenberg 1997, Blumstein and Armitage 1999, Shumway 1999, Grimm et al. 2003, Conner et al. 2008, Croes et al. 2006, Fischer and Linsenmair 2006, Gonzalez-Suarez and Gerber 2008, Maldonado-Chaparro and Blumstein 2008). We agree with Walters et al. (2004) that conservation should seek to manage viable populations of cooperative breeders and maintain their cooperative breeding behavior. It is reasonable to assume that the benefits of philopatry will remain great because the survival of dispersing Florida Scrub-Jays outside conservation areas will remain poor because of urbanization and forestation (Breininger 1999, Stith 1999, Duncan et al. 2004). It is reasonable to assume that management should encourage rapid population recovery and keep Florida Scrub-Jay populations saturated once population recovery is achieved to sustain cooperative breeding by imposing constraints on breeding opportunities. Florida Scrub-

Jays are declining and at great extinction risk because of poor habitat quality that causes poor survival and recruitment and lower probabilities of delayed dispersal (Root 1998; Breininger et al. 1999, 2004; Stith 1999). Maximizing habitat quality in conservation areas would maximize population growth and breeder survival so that the goals of enhancing population persistence and maintaining cooperative breeding behavior are closely related.

FLORIDA GRASSHOPPER SPARROW HABITAT QUALITY MAPPING AND POPULATION MODELING

Introduction

The Florida Grasshopper Sparrow Florida Grasshopper Sparrow is an Endangered species endemic to Florida dry prairie. More than 80% of the native prairie has been destroyed or converted to agriculture and most remaining habitat has been degraded by altered fire regimes (Shriver and Vickery 1999). The Florida Grasshopper Sparrow has declined to <5 known breeding subpopulations and all but 2 are near extinction (Delany et al. 1985, 1999, Delany and Cox 1986, Perkins et al. 2008). Fire frequency and edge effects greatly influence Florida Grasshopper Sparrow habitat use and nest success (Walsh et al. 1995, Shriver 1996, Shriver et al. 1996, Perkins et al. 1998, Perkins 1999).

Population viability analysis (PVA) provides a systematic procedure to quantify how natural and anthropogenic factors influence a population's risk of decline (Burgman et al. 1993). PVA is useful to evaluate alternative management actions under uncertainty, providing that results compare the effects of alternative management actions rather than provide ostensibly exact extinction risk estimates (Beissinger and Westphal 1998, Brook et al. 2000, Breininger et al. 1999, 2002).

One objective was to map habitat for Florida Grasshopper Sparrow at the territory scale to provide input data to a spatially explicit metapopulation model that predicts how habitat potential and management alternatives influence population viability. Mapping was done to represent habitat potential, the hydrological gradient of potential habitat, abundance of tall trees and shrubs, conservation ownership, edge effects, and fire history.

Grid polygon maps, where each grid cell was the size of a average territory, can easily be updated by overlaying them on digital orthophotographs and then classifying each territory based on attributes related to habitat potential, territory quality, and management alternatives (Breininger et al. 2006, Carter et al. 2006). Updating these maps can be efficiently performed and requires minimal geographical information system (GIS) skills because topology does not need to be altered. Thus, managers and biologists can easily refine and update attributes to represent changes and management actions through time. All attributes can be stored in one file, unlike normal grid formats where each attribute represents one file. The grid polygon data base file can be easily loaded into spreadsheets, statistical packages, and the mark-recapture program MARK (White and Burnham 1999) for purposes of quantifying transition probabilities and their variances in relation to covariates such as the number of fires and position along the hydrological gradient.

The first Florida Grasshopper Sparrow population viability model was just published (Perkins et al. 2008). Here, we evaluate additional management opportunities and uncertainties by using the Perkins et al. (2008) PVA and updating it with new habitat information. Our approach will facilitate regular refinement and updating of habitat models and predictions of management action. The uncertainties can be developed into alternative ecological models and management opportunities to support structured decision making and adaptive resource management. Our objectives were to consider some spatially explicit dry prairie restoration scenarios that involve a larger geographical extent than considered by Perkins et al. (2008).

Methods

The study area includes the vicinity of Kissimmee Prairie Preserve State Park (KPPSP), Three Lakes Wildlife Management Area (TLWMA), and Avon Park Air Force Range (APAFR) and all areas between (Figure 16). The KPPSP is located in Okeechobee County (27°34' N 80°58' W) and is managed by the Florida Department of Environmental Protection. Herein, the KPPSP population refers only to areas within the state park, except for several management scenarios that also consider specific adjacent lands. The TLWMA is located in Osceola County (27°47' N 81°06' W) and is managed by the Florida Fish and Wildlife Conservation Commission (FWCC). The APAFR is managed by the U.S. Department of Defense, and is located east of Avon Park in Highlands and Polk Counties (27°37' N 81°19' S). The APAFR has 1 population of Florida Grasshopper Sparrow separated into 3 spatially distinct aggregations: Bravo Range, Delta OQ Range, and Echo Range. Recent analyses suggest that APAFR, KPPSP, and TLWMA appear independent (i.e., annual population estimates fluctuate independent of each other), but trends for the 3 aggregations at APAFR appear to track each other with possible extinction occurring at Bravo Range (J. Tucker and G Schrott personal communication).

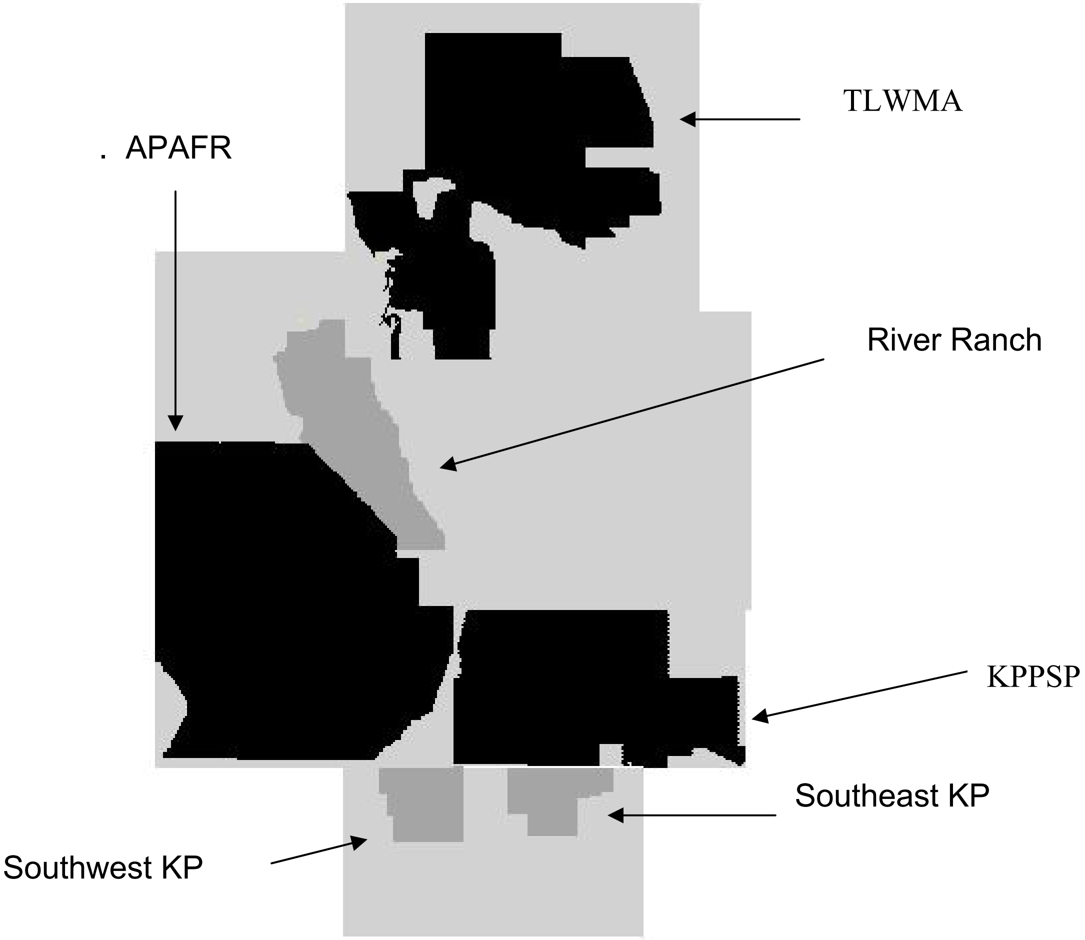

Figure 16. All areas within black and grey shaded areas were mapped. Black areas represent conservation areas important to Florida Grasshopper Sparrows. Dark gray areas represent private lands that include potential habitat used in habitat acquisition scenarios. These areas were not necessarily dominated by dry prairie habitat or even habitat that could be restored to dry prairie.

We included a privately owned landscape termed “River Ranch” that might be potentially significant to Florida Grasshopper Sparrow. River Ranch is located between KPPSP and APAFR and extends north towards TLWMA. This geographic area overlaps River Ranch Acres, which includes thousands of landowners although much of the area appears for sale and is managed by a homeowners association (http://www.mjlands.com/). Conservation activities are not specified although their website claims to work closely with the Florida Division of Forestry and FWCC (http://www.rrpoa.net/). At least some of River Ranch was located within proposed conservation project boundaries (K. Fountain, personal communication).

Habitat was mapped by overlaying a grid polygon layer over 1 m resolution 2004 digital orthophotographs. Grid polygon sizes were 1.8 ha, representing a territory size estimate (Delaney et al. 1995). Vegetation boundaries occurred at a finer scale so that each potential territory could include a mixture of habitat vegetation features. We represented the area around KPPSP by hexagons using PATCH (Program to Assist in Tracking Critical Habitat; Schumaker 1998). We represented all other areas by square polygons using ArcGIS 9.2 and the ARC/INFO Command GENERATE FISHNET (ESRI 2006). The entire geographic area was represented by 6 ESRI shape polygon files to avoid GIS limitations associated with too many features. Shape files can be used in most GIS software packages and each are represented by 3-6 files. One is a database file that contains the attributes and is the only file that regularly needs modification, which can be done using ArcGIS, ARCVIEW, or spreadsheets.

Each grid cell was classified into habitat categories described by Table 14 where the first 8 categories were along a hydrological gradient from dry to wet. Dry prairie.

Table 14. Categories used to map potential habitat. Grid cells were a mixture of vegetation types described by Orzell and Bridges (2006). Driest prairie was a mixture of dry-mesic and mesic prairie. Mesic prairie was comparable to mesic prairie. Mesic and wet prairie mix grid cells were a mixture of wet-mesic prairie, mesic prairie, and wet prairie types.

Code	Habitat	Description
1	Scrub oak	Greater than 50% scrub oak cover
2	Scrub prairie mix	Patches of scrub oak in mesic shrubland
3	Driest prairie	Highest elevation often with sandy patches
4	Mesic prairie	No scrub or wet prairie
5	Mesic and wet prairie mix	Combination of mesic and wet prairie
6	Palmetto wet prairie mix	Wet prairie and saw palmetto
7	Wet prairie	Grassy areas flooded for weeks or less
8	Marsh	Grassy areas flooded for months or less
9	Ruderal	Pasture and cleared areas
10	Forest	Interlocked tree canopy
11	Open water	Lakes
12	Pine flatwoods	Pine flatwoods, pine plantations

vegetation types are described by Orzell and Bridges (2006). These vegetation types of dry prairie often varied at a finer scale than the grid cells, which usually included several vegetation types, making the habitat model a coarser grain than that of Orzell and Bridges but a finer scale grain than the overall dry prairie ecosystem. The habitat maps depicted herein were based primarily on habitat structure and not vegetation composition, which is difficult to distinguish and map across large geographic areas. Other mapped habitat categories were open water, pinelands, forest, and ruderal. Grid cells were also coded into categories along a tall shrub and tree abundance gradient: 1) no trees or no tall shrub clumps, 2) one isolated tree or tall shrub clump, 3) many trees or tall shrub clumps, and 4) small forests (contiguous tree canopies) that did not dominate the grid cells. Trees and tall shrubs refer to features that can be seen on 1 m resolution digital orthophotographs because of textural differences evident once they reach about 2 m tall. Grid cells had an attribute that identified whether they occurred within potential conservation areas, particular populations (e.g. Bravo, Echo, Delta OQ) and private lands that might be significant for Florida Grasshopper Sparrow conservation (e.g., River Ranch). We also identified whether grid cells occurred in presettlement prairies based on Bridges (2006)

We considered the metapopulation initially comprised of 5 subpopulations (KPPSP, TLWMA, Echo, Delta OQ, and Bravo) with the possibility of a sixth population, River Ranch, depending on the management scenario. All but River Ranch occurred on public land. Some scenarios also considered private land south of KPPSP but these scenarios always assumed that conservation of these areas made KPPSP bigger. Many potential territories also occurred on South Florida Water Management District lands that could have importance but were not emphasized herein because we focused on the largest population scenarios. We do not know if these areas have been surveyed for Florida Grasshopper Sparrow.

We first intended to use EPA's PATCH program, where every territory is represented by a hexagon; however, PATCH has been undergoing rapid change and no manual was available. One reason for using PATCH was that it can track movements of individual birds, which became less relevant after we were unable to perform extensive telemetry studies of Florida Grasshopper Sparrow. We developed a stage-structured, spatially explicit metapopulation model using RAMAS/GIS, version 4.0 (Akçakaya 2002). RAMAS has been extensively reviewed (Lindenmayer et al. 1995, Boyce 1997, Brook et al. 2000) and used to model bird populations (LaHaye et al. 1994, Akçakaya and Atwood 1997, Akçakaya et al. 1995, 2003, Perkins et al 2008) and for many management applications using the software (Akçakaya et al. 2004).

We used a juvenile stage and adult stage, 1:1 sex ratio, and a post-reproductive census assuming that no mortality took place between breeding and the census (Perkins et al. 2008). The model is based on male age structure because adult survival rates were based on males (Delany et al. 1993). Survival and fecundity parameters were based on published data specific to Florida Grasshopper Sparrow and were consistent with vital rates used by Perkins et al. (2008) (Table 15).

Table 15. Initial abundances (adult juvenile and adult males) and mean vital rates (with standard deviations in parentheses) of Florida Grasshopper Sparrow based on Perkins et al. (2008). Initial abundances are the number of adult male Florida Grasshopper Sparrow.

Site	Initial abundance	Juvenile fecundity rate F_j	Adult survival rate S_a	Adult fecundity rate F_a	Lambda λ
Echo	22	0.55 (0.19)	0.51 (0.09)	0.80 (0.28)	1.06
Delta OQ	11	0.54 (0.17)	0.48 (0.07)	0.73 (0.26)	1.02
Bravo	0	0.55 (0.19)	0.51 (0.09)	0.80 (0.28)	1.06
Kissimmee Prairie	575	0.62 (0.19)	0.51 (0.09)	0.90 (0.28)	1.13
Three Lakes	328	0.48 (0.20)	0.53 (0.08)	0.73 (0.31)	1.01
River Ranch	58	0.55 (0.19)	0.51 (0.09)	0.80 (0.28)	1.06

Perkins et al. (2008) performed extensive sensitivity analyses on many model assumptions and these were not repeated here. We used published estimates of annual adult male survival from subpopulations at Delta OQ (0.48) and TLWMA (0.53) that were based on capture-recapture analyses of 161 color-banded birds (Perkins and Vickery 2001). The mean of Delta OQ and TLWMA survival rates (0.51) was used for populations where no survival estimates were available. Juvenile survival was the proportion of juveniles that survived to the age of 1 year. A juvenile survival rate (0.35) was used for all subpopulations based on Perkins and Vickery (2001). This estimate is similar for many bird species and the approach is common in the literature because data on juvenile survivorship are rarely available (Pulliam 1988, Pulliam et al. 1992).

We used fecundity rates based on Florida Grasshopper Sparrow nest survival and annual productivity estimates collected at TLWMA, Delta OQ, and KPPSP (Perkins et al. 2003). Perkins et al. (2003) calculated productivity rates by multiplying the number of nesting attempts per year by the number of successful young per successful nest and by the nest success rate. The mean of the 3 sites was used for sites lacking site-specific data. “Fecundity” was the average number of offspring per individual male that survived to breed the following summer.

We used initial abundance values as the number of adult males in each subpopulation based on Perkins et al. (2008). Initial abundances of juvenile males were calculated under a stable age distribution according to the Leslie matrix for each population. The population estimates at each site involved mapping singing locations from 3 5-min point counts. We substituted the Cutrale initial abundance for River Ranch initial abundance because Cutrale had become extinct (T. Dean, personal communications) and we had no population data for River Ranch. The number of optimal grid cells at River Ranch appeared at least as many as the number of optimal grid cells at Cutrale. Cutrale was modeled by Perkins et al. (2008) but we have no detailed spatial information about the population that occurred there.

Perkins et al. (2008) assumed density dependence occurred only at high population levels by applying a ceiling model for survival and fecundity rates (Akçakaya and Atwood 1997). This represented a conservative approach to modeling extinction risk (Ginzburg et al. 1990). The ceiling model assumed that density-dependent factors do not limit populations until they reach a threshold. Perkins et al. calculated carrying capacity on the basis of the highest density observed over 6 years of spot-mapping data (Shriver 1996, Perkins1999). They calculated carrying capacity by multiplying the total dry prairie area for each site by two-thirds because their habitat estimates included depression ponds, roads, and other unsuitable habitat. We instead used the number of grid cells assumed to be optimal as a ceiling, and then varied assumptions about what conditions defined optimal to incorporate uncertainty.

We set local and metapopulation thresholds to account for Allee effects and other threats to small populations, as did Perkins et al. (2008). We used Perkins et al. local extinction threshold of 4 males and a metapopulation threshold of 60 males. Each simulation involved 50 annual time steps with 10,000 trials.

We used adult survival standard deviations of 0.08 measured at Delta OQ, 0.09 measured at TLWMA, and the mean (0.085) for other sites, which was consistent with Perkins and Vickery (2001) and Perkins et al (2008). We used a juvenile survival standard deviation of 0.22 following Perkins and Vickery (2001) and Perkins et al (2008). For productivity, we used the same standard deviations measured by Perkins et al. (2003). We incorporated demographic stochasticity by drawing the number of offspring in each time step from a Poisson distribution.

All known subpopulations of Florida Grasshopper Sparrow were within 30 km of one another; hence, environmental variation may be correlated across sites. We used a spatial correlation coefficient of 0.57 based on Perkins et al (2008). They derived 0.57 from a correlation between densities at Delta OQ and TLWMA for a 6-year period (Shriver 1996, Perkins 1999).

The model assumed that juveniles were responsible for dispersal. Perkins et al (2008) banded 222 adults across the 6 sites from 1995 to 1998 and never observed an adult moving between sites. More recently adult dispersal between populations has been observed, though such movements may be uncommon. There is little genetic differentiation among subpopulations of Florida Grasshopper Sparrows (Delany et al. 2000, Bulgin et al. 2003). Perkins et al. (2008) assumed that dispersing individuals were more likely to find larger sites, making immigration proportional to the size of the site. A coefficient of variation for dispersal stochasticity was assumed to be 0.1.

We modeled alternative management applications that might benefit recovery based on habitat management or acquisition scenarios. Our scenarios had greater geographical extent than those used by Perkins et al. (2008). We depicted uncertainty as directly related to grid cell counts of different combinations of tree density and distance to forest categories that were used to define optimal habitat and the population ceiling. Perkins et al. (2003) inferred that core areas (>400 m) functioned as population sources and territories near edges functioned as population sinks because nest success was only able to offset mortality estimates in core areas. There was poor precision in distance relationships for nest success and uncertainty about what vertical structure comprised an edge.

There are no published data on how low numbers of trees and tall shrubs influence vital rates, though they are believed to make habitat suboptimal. These uncertainties are important because trees and tall shrubs invade Florida grasslands, savannas, and shrublands when frequencies are reduced (Noss and Cooperrider 1994, Leach and Givnish 1996, Noss et al. 1997, Duncan et al. 1999, Duncan and Schmalzer 2004), and possibly as the proportion of dormant season burns increases. Florida Grasshopper Sparrow management options include removing individual trees within prairie landscape and eliminating forest or woodland edges to increase core habitat. Forest and woodland edges also occur because pre-settlement prairies have been replaced by pine plantations in some locations (Perkins et al. 2008).

We identified potential habitat that occurred between or immediately adjacent to populations and used metapopulation modeling to predict how expansion of these areas could contribute to recovery. Potential habitat included driest prairie, mesic prairies, and mixed dry and wet prairie. We considered mixed dry prairie and wet prairie because these were abundantly used by Florida Grasshopper Sparrow during our studies. River Ranch, Southwest Kissimmee Prairie (SWKP), and Southeast Kissimmee Prairie (SEKP) each appeared to have the ability to support many hundreds of Florida Grasshopper Sparrow territories and were considered in several scenarios. The area that appeared most optimal at River Ranch was not directly connected to other populations, so we modeled River Ranch as a separate population. Several scenarios addressed how the 2 relatively large areas SWKP and SEKP could increase the size of the KPPSP population because they are contiguous with KPPSP.

A management scenario varied the percentage of prairie within 2 years post-fire. We estimated the percent of prairie within 2 years post-fire using a fire history GIS file for KPPSP. We classified management units into areas <= 2 years post fire and > 2 years and then overlaid these on potential habitat getting an estimate of 26% of the potential habitat at <= 2 years post fire. We then added scenarios where recently burned areas comprised 52%. Scenarios were developed by multiplying each of these percentages by carrying capacities derived by cross-tabulating distance to forest categories and tree abundance categories. We can update the percent burned estimate if such data become available for TLWMA and APAFR.

Baseline management scenarios assumed that carrying capacity was the number of optimal grid cells and that there were no River Ranch, SWKP, or SEKP populations. Optimal grid cells were >400 m from a forest and had no tall shrubs or trees (Trees/ha = 0) or approximately 1 tall tree or tall shrub clump (Trees/ha = 1). Restored prairie scenarios assumed that tall trees or shrubs were eliminated in all potential prairies (habitat categories 3-5). Restored flatwoods assumed that tall trees or shrubs were eliminated and the understory was restored in all pine flatwoods and pine plantations (habitat category 12) that were once presettlement prairies. Expansions of prairie included restoration of Echo and Delta OQ population areas on public lands and restoration of lands that were now privately owned (River Ranch, SWKP, and SEKP). Expanded Echo and Delta OQ areas are shown in Figure 17. Presettlement prairie maps (Bridges 2006) were used to define the boundaries for expanding existing prairies (Echo and Delta OQ) and private lands (River Ranch, SWKP, and SEKP). No modeling scenarios were identified specifically for potential territories on South Florida Water

Management District Lands because we focused on scenarios that involved the largest geographic areas.

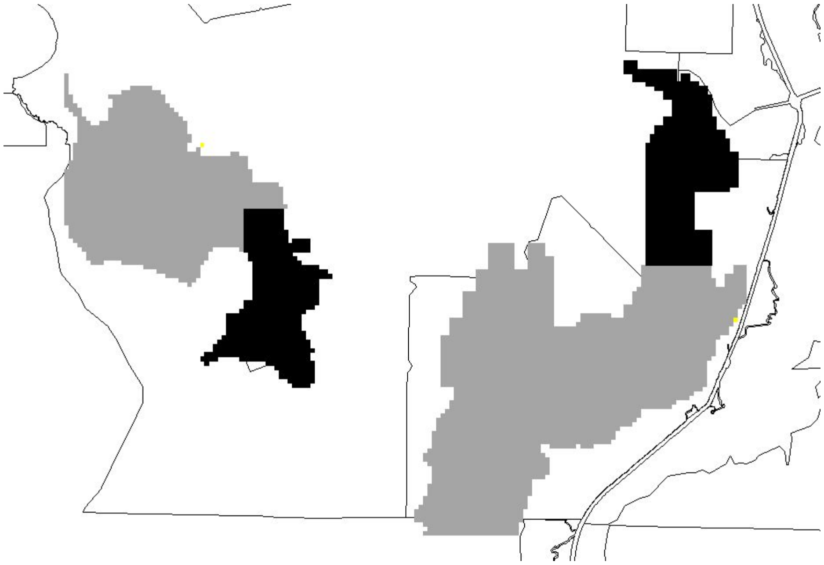

Figure 17. Pine flatwoods and pine plantations at Echo and Delta OQ that were considered in the expansion scenarios (black). Grey areas represent current dry prairie landscapes for Echo (right, east) and Delta OQ (left, west).

The second set of management scenarios incorporated a very broad range of uncertainty regarding how distance to edge and tree/tall shrub abundance influenced habitat quality. In these scenarios we modeled KPPSP, TLWMA, Echo, and Delta OQ populations separately as if they were isolated. These scenarios did not include expansion of dry prairie into pine flatwoods that were formerly dry prairie but focused on increased burning and removal of trees that expanded into existing dry prairies. The purpose of these scenarios was to incorporate a broader range of uncertainty pertaining to distance to forest and tree abundance within individual sites recognizing that uncertainty pertaining to distance to forest versus tree abundance may vary among sites because of landscape composition relative to forest edge and tree abundance within prairies.

Risk in modeling scenarios was expressed as the number adults at the end of 50 years, the probability of declining by 80% anytime during the 50 year interval, the probability of declining below 60 pairs and thus becoming extinct or nearly extinct any time during the 50 year interval, and the mean number of local populations having >4 adult males at the end of the 50 year period. The quasiextinction thresholds of 60 for the entire metapopulation and 4 for local populations were used by Perkins et al. (2008).

Results

We evaluated almost 135,000 1.8-ha grid cells to determine whether they were dominated by prairie habitat. Improved pasture was characterized as ruderal but may have included suitable habitat that was not considered herein because of the uncertainty in population recovery within pastures and the difficulty in mapping suitability for Florida Grasshopper Sparrow in pastures.

Kissimmee Prairie Preserve State Park encompassed the largest and most contiguous remaining tract of potential habitat (Figure 18).

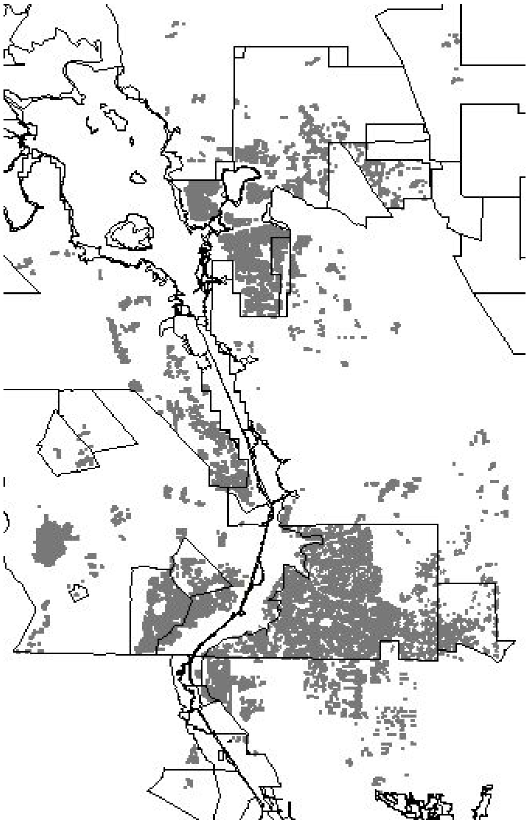

Figure 18. Kissimmee Prairie has the largest and most contiguous area of suitable Florida Grasshopper Sparrow habitat. Potential Florida Grasshopper Sparrow territories are grey; the thin black lines are boundaries of potential conservation areas identified by the Florida Department of Environmental Protection.

Remaining native prairies in the region were relatively isolated. Restoration of pine flatwoods near Echo to prairie and prairie restoration at River Ranch greatly increased connectivity among APAFR, KPPSP, and TLWMA (Figure 19).

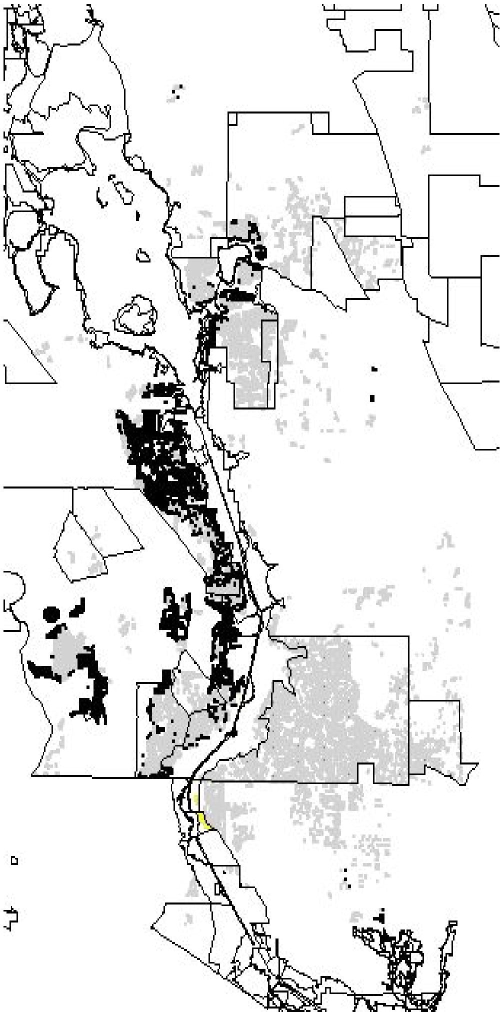

Figure 19. Restoration of areas near Echo and within River Ranch would greatly increase connectivity among APAFR, KPPSP, and TLWMA. Potential Florida Grasshopper Sparrow territories are grey; thin black lines are boundaries of potential conservation areas identified by the Florida Department of Environmental Protection. Pine flatwoods that were pre-settlement prairie are shown in black.

The driest prairie was the least abundant potential territory type (Table 16). There were relatively fewer potential territories at APAFR without trees or tall shrubs compared to KPPSP and TLWMA (Table 17). TLWMA had more potential territories that were near forests (Table 18). Cross-tabulations between tree abundance and distance to forest categories were used to capture uncertainty in defining optimal grid cells and management (Tables 19 -24).

Table 16. Potential Florida Grasshopper Sparrow territories (grid cells). Grid cells were a mixture of vegetation types described by (Orzell and Bridges 2006). Driest prairie was a mixture of dry-mesic and mesic prairie, whereas mesic prairie was dominated by mesic prairie. Mesic and wet prairie mix grid cells were a mixture of mesic prairie, wet-mesic prairie, and wet prairie types.

Site	Driest prairie	Mesic prairie	Mesic and wet prairie mix	Totals	Percent
Kissimmee Prairie Preserve State Park	379	635	3184	4198	39
Three Lakes Wildlife Management Area	91	1056	1399	2546	24
Avon Park Air Force Range	181	1103	839	2123	20
River Ranch	28	434	495	957	9
Southwest Kissimmee prairie	30	215	256	501	5
Southeast Kissimmee prairie	0	168	289	457	4
Totals	709	3611	6462	10782	
Percent	7	33	60		

Table 17. Abundance of trees and tall shrubs within potential Florida Grasshopper Sparrow territories (grid cells). The number of entries represents the number of grid cells in a particular category or the percent of grid cells having particular tree abundance.

	No trees	Isolated trees	Clumps	Forest	Percent with no trees	Percent with no or isolated trees
Kissimmee Prairie Preserve State Park	2023	1088	935	154	48	74
Three Lakes Wildlife Management Area	1073	367	1058	48	42	57
Avon Park Air Force Range	364	906	821	32	17	60
River Ranch	50	194	511	0	7	32
Southwest Kissimmee prairie	35	83	381	2	7	24
Southeast Kissimmee prairie	111	62	273	11	24	38
Total grid cells	3656	2700	3979	247		
Percent	35	26	38	2		

Table 18. Proximity to forest edge for potential Florida Grasshopper Sparrow territories. The entries represent the number of grid cells in a particular distance category. Each grid cell was about 134 m in diameter. Grid cells having a forest edge within them were category 1. Grid cells within category 5 were >536 m from a forest.

	1	2	3	4	5	Total grid cells	Percent >400 m from a forest
Kissimmee Prairie Preserve State Park	154	710	733	620	1983	4200	62
Three Lakes Wildlife Management Area	46	921	635	389	555	2546	37
Avon Park Air Force Range	32	415	472	373	830	2122	57
River Ranch	42	364	281	154	116	957	28
Southwest Kissimmee prairie	2	59	69	62	309	501	74
Southeast Kissimmee prairie	11	138	121	93	94	457	41
Total grid cells	287	2607	2311	1691	3887	10783	
Percent	3	24	21	16	36		

Table 19. Cross-tabulation between tree abundance and distance to forest for potential Florida Grasshopper Sparrow territories near KPPSP. The entries represent the number of grid cells in a particular category or the percent of grid cells having particular tree abundance or in a particular distance category. Each grid cell was about 134 m in diameter. Grid cells containing a forest edge were category 1. Grid cells with category 5 were at least 536 m from a forest.

	Distance to forest					Total grid cells	Percent
Trees	1	2	3	4	5		
None	0	181	299	314	1229	2023	48
One	0	188	221	164	515	1088	26
Clumps	0	341	213	142	239	935	22
Forest	154	0	0	0	0	154	4
Total grid cells	154	710	733	620	1983	4200	
Percent	4	17	17	15	47		

Table 20. Cross-tabulation between tree abundance and distance to forest for potential territories near TLWMA. The entries represent the number of grid cells in a particular category or the percent of grid cells having particular tree abundance or in a particular distance category. Each grid cell was about 134 m in diameter. Grid cells containing a forest edge were category 1. Grid cells with category 5 were at least 536 m from a forest.

	Distance to forest					Total grid cells	Percent
Trees	1	2	3	4	5		
None	0	261	263	214	335	1073	42
One	1	102	96	61	107	367	14
Clumps	0	557	275	113	113	1058	42
Forest	45	1	1	1	0	48	2
Total grid cells	46	921	635	389	555	2546	
Percent	2	36	25	15	22		

Table 21. Cross-tabulation between tree abundance and distance to forest for potential territories near APAFR. The entries represent the number of grid cells in a particular category or the percent of grid cells having particular tree abundance or in a particular distance category. Each grid cell was about 134 m in diameter. Grid cells containing a forest edge were category 1. Grid cells with category 5 were at least 536 m from a forest.

Trees	Distance to forest					Total grid cells	Percent
	1	2	3	4	5		
None	0	16	54	72	227	369	17
One	0	131	215	166	393	905	43
Clumps	0	268	203	136	210	817	38
Forest	33	0	0	0	0	33	2
Total grid cells	33	415	472	374	830	2124	
Percent	2	20	22	18	39		

Table 22. Cross-tabulation between tree abundance and distance to forest for potential territories at River Ranch. The entries represent the number of grid cells in a particular category or the percent of grid cells having particular tree abundance or in a particular distance category. Each grid cell was about 134 m in diameter. Grid cells containing a forest edge were category 1. Grid cells with category 5 were at least 536 m from a forest.

Trees	Distance to forest					Total grid cells	Percent
	1	2	3	4	5		
None	0	8	11	5	26	50	5
One	0	81	70	46	41	238	25
Clumps	0	275	200	103	49	627	66
Forest	42	0	0	0	0	42	4
Total grid cells	42	364	281	154	116	957	
Percent	4	38	29	16	12		

Table 23. Cross-tabulation between tree abundance and distance to forest for potential territories southwest of KPPSP. The entries represent the number of grid cells in a particular category or the percent of grid cells having particular tree abundance or in a particular distance category. Each grid cell was about 134 m in diameter. Grid cells containing a forest edge were category 1. Grid cells with category 5 were at least 536 m from a forest.

Trees	Distance to forest					Total grid cells	Percent
	1	2	3	4	5		
None	0	6	7	8	14	35	7
One	0	3	2	4	74	83	17
Clumps	0	50	60	50	221	381	76
Forest	2	0	0	0	0	2	0
Total grid cells	2	59	69	62	309	501	
Percent	0	12	14	12	62		

Table 24. Cross-tabulation between tree abundance and distance to forest for potential territories southeast of Kissimmee Prairie. The entries represent the number of grid cells in a particular category or the percent of grid cells having particular tree abundance or in a particular distance category. Each grid cell was about 134 m in diameter. Grid cells containing a forest edge were category 1. Grid cells with category 5 were at least 536 m from a forest.

Trees	Distance to forest					Total grid cells	Percent
	1	2	3	4	5		
None	0	32	22	17	40	111	24
One	0	15	18	15	14	62	14
Clumps	0	91	81	61	40	273	60
Forest	11	0	0	0	0	11	2
Total grid cells	11	138	121	93	94	457	
Percent	2	30	26	20	21		

Perkins et al. (2003) noted that Florida Grasshopper Sparrows rarely occupied areas adjacent to forests (distance to forest category 1) and that they had poor nest success at distances <400 m of a forest (distance to forest categories 2 and 3). There were uncertainties in how distance to forest relationships influenced nest survival among study sites and distance categories (Figure 2 in Perkins et al. 2003). Different assumptions about which distance categories described optimal habitat (e.g., distance category 5 only versus distance categories 4 and 5) were used to describe uncertainty in the modeling below. Florida Grasshopper Sparrow often avoid trees and tall shrubs (Paul Miller, personal communication). Therefore, Tables 22 through 27 can also be used to formulate uncertainty in defining optimal habitat by making different assumptions about which tree category defines optimal habitat (e.g., no trees versus 1 or fewer trees per grid cell). Tables 19 through 24 show that tree densities within prairie habitat were greater in grid cells closer to forests.

Results of modeling scenarios with no habitat enhancement predicted a final metapopulation size of 350 adults, assuming that optimal territories have no trees or 545 adults, assuming that optimal habitat could have up to 1 tree or tall shrub in a territory (Table 25). The scenario that involved tree removal within prairies, doubling the area burned within 2 years, and restoring all pre-settlement prairie that degraded to pinelands within Echo, Delta OQ, River Ranch, SWKP, SEKP resulted in a predicted population size of 1639 adults. Many combinations of management improvements increased the mean number of populations occupied at the end of the simulation (Table 25). Many management and restoration scenarios suggested that at least 3-4 populations would remain viable (Kissimmee Prairie, Three Lake Wildlife Management Area, Echo, and Delta OQ).

Uncertainty in final population size at KPPSP was influenced more by tree abundance within prairie than distance to forest (Table 26). Uncertainty in final population size at TLWMA was more influenced by distance to forest than tree abundance (Table 27). Uncertainty in final population size at Echo was more influenced by uncertainty associated with tree abundance than distance to forest (Table 28).

Table 25. Florida Grasshopper Sparrow population modeling results. The first 2 rows represented a baseline without habitat enhancements. Uncertainty is represented by assuming that optimal habitat either has no trees or 1 or no trees/territory. Tree cutting refers to removal of all trees in potential prairie territories. The percent burned scenario assumes 26% of the territories are 2 years since fire (baseline) or 52% representing a doubling in the extent of area 2 years since fire. Restored flatwoods refers to tree cutting and understory restoration in pinelands that were presettlement prairie. Expansion refers to expanding the geographic extent of prairies to presettlement areas as defined in Figure 19. Final size is the final metapopulation size at the end of the 50-year simulation. Interval extinction risk is the probability of the metapopulation falling below 60 adult males. The mean populations occupied is the number of subpopulations with > 4 adults at the end of the simulation.

Management scenario					Result		
Trees /territory	Tree cutting in prairie	Percent burned	Restored flatwoods	Expansion	Final size	Interval extinction risk	Mean populations occupied
0	n	26	n	no	350	0.27	2.4
1	n	26	n	no	545	0.22	3.3
0	n	52	n	no	695	0.20	3.0
1	n	52	n	no	1038	0.19	3.9
0	y	26	n	no	661	0.20	3.5
0	y	52	n	no	1261	0.18	4.1
0	y	26	y	no	701	0.21	4.1
0	y	52	y	no	1303	0.19	4.3
0	y	52	y	Echo	1327	0.19	4.3
0	y	52	y	Delta OQ	1305	0.19	4.3
0	n	26	n	River Ranch	345	0.28	2.4
1	n	26	n	River Ranch	539	0.28	3.7
0	n	52	n	River Ranch	697	0.18	3.3
1	n	52	n	River Ranch	1051	0.17	4.7
0	y	26	n	River Ranch	676	0.20	4.3
0	y	26	y	River Ranch	796	0.19	4.9
0	y	52	n	River	1268	0.17	4.9

0	y	52	y	Ranch River Ranch	1489	0.17	5.1
0	n	26	n	SWKP	357	0.27	2.5
1	n	26	n	SWKP	560	0.22	3.3
0	n	52	n	SWKP	694	0.19	3.0
1	n	52	n	SWKP	1056	0.19	3.9
0	y	26	n	SWKP	736	0.19	3.6
0	y	26	y	SWKP	736	0.19	3.6
0	y	52	n	SWKP	1348	0.13	4.1
0	y	52	y	SWKP	1348	0.13	4.1
0	n	26	n	SEKP	361	26	2.5
1	n	26	n	SEKP	556	0.22	3.3
0	n	52	n	SEKP	720	0.19	3
1	n	52	n	SEKP	1056	0.2	3.9
0	y	26	n	SEKP	678	0.2	3.6
0	y	26	y	SEKP	712	0.2	4.1
0	y	52	n	SEKP	1280	0.19	4.1
0	y	52	y	SEKP	1280	0.19	4.1
0	y	52	y	Echo, Delta OQ, River Ranch, SWKP, SEKP	1639	0.18	5.1

Table 26. Uncertainty in defining optimal territory because of edge distances and trees densities and management scenarios at KPPSP.

Uncertainty		Prescribed fire and restoration options		Modeling results			
Distance to forest	Trees or tall shrubs	Percent Burned	Management action	Carrying capacity	Final size	80% interval risk of decline	Quasiextinction risk
>536	None	26	None	320	232	0.4	0.02
>402	None	26	None	401	288	0.34	0.02
>268	None	26	None	479	342	0.3	0.02
>536	One	26	None	453	324	0.3	0.02
>402	One	26	None	578	408	0.27	0.02
>268	One	26	None	713	501	0.24	0.02
>536	Few	26	None	516	371	0.28	0.02
>402	Few	26	None	677	481	0.25	0.02
>268	Few	26	None	867	606	0.23	0.02
>536	None	0.52	Double area burned	639	456	0.25	0.02
>402	None	0.52	Double area burned	802	562	0.24	0.02
>268	None	0.52	Double area burned	958	662	0.23	0.02
>536	One	0.52	Double area burned	907	634	0.23	0.02
>402	One	0.52	Double area burned	1155	788	0.22	0.02
>268	One	0.52	Double area burned	1426	974	0.21	0.02
>536	Few	0.52	Double area burned	1031	714	0.23	0.02
>402	Few	0.52	Double area burned	1354	911	0.22	0.02
>268	Few	0.52	Double area burned	1735	1144	0.21	0.01
>536	None	26	Prairie restored	545	392	0.27	0.02
>402	None	26	Flatwoods restored	545	392	0.27	0.02
>268	None	26	Prairie restored	707	497	0.24	0.02
>536	None	26	Flatwoods restored	707	497	0.24	0.02
>402	None	26	Prairie restored	904	631	0.23	0.02
>268	None	26	Flatwoods restored	904	631	0.23	0.02
>536	None	0.52	Prairie restored & double area burned	1089	743	0.22	0.01
>402	None	0.52	Flatwoods restored & double area burned	1089	743	0.22	0.01
>268	None	0.52	Prairie restored & double area burned	1414	959	0.22	0.01
>536	None	0.52	Flatwoods restored & double area burned	1414	959	0.22	0.01
>402	None	0.52	Prairie restored & double area burned	1808	1194	0.2	0.01
>268	None	0.52	Flatwoods restored & double area burned	1808	1194	0.2	0.01

Table 27. Uncertainty in defining optimal territory because of edge distances and trees densities and management at TLWMA.

Scenarios				Modeling results			
Distance to forest	Trees or tall shrubs	Percent Burned	Management action	Carrying capacity	Final size	80% interval risk of decline	Quasiextinction risk
>536	None	26	None	87	8	0.98	1.00
>402	None	26	None	143	15	0.94	1.00
>268	None	26	None	211	22	0.92	1.00
>536	One	26	None	115	12	0.97	1.00
>402	One	26	None	186	20	0.92	1.00
>268	One	26	None	280	28	0.89	0.99
>536	Few	26	None	144	15	0.95	1.00
>402	Few	26	None	245	24	0.91	0.99
>268	Few	26	None	410	37	0.87	0.98
>536	None	0.52	Double area burned	174	19	0.93	1.00
>402	None	0.52	Double area burned	285	28	0.89	0.99
>268	None	0.52	Double area burned	422	38	0.87	0.98
>536	One	0.52	Double area burned	230	24	0.91	0.99
>402	One	0.52	Double area burned	373	36	0.87	0.98
>268	One	0.52	Double area burned	560	46	0.86	0.97
>536	Few	0.52	Double area burned	289	29	0.89	0.99
>402	Few	0.52	Double area burned	490	43	0.86	0.97
>268	Few	0.52	Double area burned	820	57	0.85	0.96
>536	None	26	Prairie restored	94	9	0.98	1.00
>402	None	26	Flatwoods restored	90	9	0.98	1.00
>268	None	26	Prairie restored	185	20	0.92	1.00
>536	None	26	Flatwoods restored	192	20	0.92	1.00
>402	None	26	Prairie restored	372	34	0.88	0.99
>268	None	26	Flatwoods restored	383	35	0.88	0.99
>536	None	0.52	Prairie restored & double area burned	188	20	0.93	1.00
>402	None	0.52	Flatwoods restored & double area burned	180	19	0.93	0.99
>268	None	0.52	Prairie restored & double area burned	371	34	0.88	0.98
>536	None	0.52	Flatwoods restored & double area burned	384	35	0.87	0.98
>402	None	0.52	Prairie restored & double area burned	745	52	0.85	0.97
>268	None	0.52	Flatwoods restored & double area burned	765	55	0.85	0.96

Table 28. Uncertainty in defining optimal territory because of edge distances and trees densities and management scenarios at Echo.

Scenarios				Modeling results			
Distance to forest	Trees or tall shrubs	Percent Burned	Management action	Carrying capacity	Final size	80% interval risk of decline	Quasiextinction risk
>536	None	26	None	49	4	0.88	0.88
>402	None	26	None	64	5	0.86	0.86
>268	None	26	None	73	6	0.86	0.86
>536	One	26	None	105	9	0.85	0.86
>402	One	26	None	145	12	0.84	0.84
>268	One	26	None	186	13	0.84	0.84
>536	Few	26	None	138	11	0.84	0.84
>402	Few	26	None	196	13	0.84	0.84
>268	Few	26	None	265	17	0.83	0.84
>536	None	0.52	Double area burned	98	8	0.84	0.85
>402	None	0.52	Double area burned	128	10	0.84	0.84
>268	None	0.52	Double area burned	146	11	0.84	0.84
>536	One	0.52	Double area burned	209	15	0.84	0.84
>402	One	0.52	Double area burned	290	19	0.84	0.84
>268	One	0.52	Double area burned	372	22	0.84	0.84
>536	Few	0.52	Double area burned	277	18	0.84	0.84
>402	Few	0.52	Double area burned	393	22	0.84	0.84
>268	Few	0.52	Double area burned	529	28	0.83	0.83
>536	None	26	Prairie restored	150	12	0.84	0.84
>402	None	26	Flatwoods restored	158	12	0.84	0.84
>268	None	26	Prairie restored	206	14	0.84	0.84
>536	None	26	Flatwoods restored	211	14	0.84	0.84
>402	None	26	Prairie restored	271	17	0.84	0.84
>268	None	26	Flatwoods restored	276	17	0.84	0.84
>536	None	0.52	Prairie restored & double area burned	300	20	0.84	0.84
>402	None	0.52	Flatwoods restored & double area burned	316	20	0.84	0.84
>268	None	0.52	Prairie restored & double area burned	411	22	0.84	0.84
>536	None	0.52	Flatwoods restored & double area burned	422	23	0.84	0.84
>402	None	0.52	Prairie restored & double area burned	543	26	0.84	0.84
>268	None	0.52	Flatwoods restored & double area burned	552	27	0.84	0.84

A table for population responses, management scenarios, and uncertainty was not presented for Delta OQ because all scenarios resulted in extinction when Delta OQ was modeled by itself. The vital rates provided by Perkins et al. (2008) for Delta OQ were relatively poor compared to KPPSP. We substituted KPPSP vital rates for Delta OQ management scenarios, but these still resulted in extinction at Delta OQ. Delta OQ had low initial abundances and so we doubled initial abundances which nearly halved extinction risk estimates. Recovery at Delta OQ might not only require habitat restoration to increase the amount of optimal habitat, but might require also supplementing population size by translocation or greater immigration rates.

Discussion

The proportion of optimal habitat for Florida Grasshopper Sparrow was low compared to the total extent of prairie, if optimal habitat is defined by the area of prairie burned within 2 years, with 1 or no trees, and >400 m from a forest edge. There is a high likelihood of a large decline even for populations for which quasiextinction risk is relatively low, suggesting an urgent need for restoration. The amount of optimal habitat could be greatly increased by cutting trees and keeping a greater amount of the prairie burned at intervals of 2 years or less. Implementing these management actions in our modeling scenarios greatly increased predicted final population size, reduced extinction risk, and increased the number of populations that persisted. Improvement in population viability estimates from these management actions occurred despite considerable uncertainty about how tree densities and distance to forest influence the amount of optimal habitat. Many of the scenarios assumed that prairie could be restored by cutting trees and applying frequent fire, especially in pine flatwoods that were prairie prior to European settlement. The validity of this assumption needs to be tested experimentally; pine flatwoods with a native understory might respond more favorably than pine plantations that have little native ground cover.

Initially, we planned on exploring how the hydrological gradient might influence population dynamics but we lacked sufficient empirical data on demography and habitat relationships. Our field studies occurred during both extreme flooding and drought conditions. The amount of driest prairie was low comparable to mesic prairie suggesting that extreme flooding might occasionally limit the amount of habitat suitable for nesting; hence, it might be wise to perform restoration in the driest parts of the prairie. However, extreme flooding usually only influences a portion of the entire nesting season (e.g., P. Miller pers. comm.). During drought Florida Grasshopper Sparrow were observed nesting at the ecotones between dry-mesic prairie and wet-mesic prairie (M. Korosy pers. obs.). Cells that included this ecotone habitat were relatively common compared to the driest areas.

Extinction risk at Bravo was high regardless of the management scenario. However, no scenarios were performed to convert pine flatwoods or pine plantations to prairie outside the extent of presettlement prairie and Bravo was entirely outside areas mapped as presettlement prairie.

Doubling the amount of prairie burned within 2 years usually resulted in doubling of final population sizes, reductions in extinction risk, and increases in the number of metapopulation sites occupied. Restoration across large areas by removing trees in prairie or restoring pinelands to prairie often resulted in similar demographic outcomes. The relative importance of uncertainties about how the number of trees and distance from forest affect habitat quality varied among populations because forest edge and tree densities varied among populations.

Predicted final population sizes were often far below carrying capacity (modeled as a population ceiling) because stochasticity rates were generally high within the model; lambda calculated from the vital rates never ranged far above 1.0. Perkins et al. (2008) also modeled density dependence with a contest model (Beverton and Holt 1957) assuming average densities represented the equilibrium point in how vital rates were influenced by population size. We could have also used a contest model where the number of optimal territories instead represented the ceiling of source habitat. Poor quality grid cells always exceeded the number of optimal grid cells, so the number of optimal territories could represent an equilibrium point where sparrows could spill into poor quality grid cells when populations exceeded the number of optimal territories. Individuals in suboptimal habitat could then serve as a population buffer that could help keep optimal territories filled and regulate population size by site-dependent population regulation (Rodenhouse et al. 1997). Our empirical studies did indicate that Florida Grasshopper Sparrow moved within prairies at distances greater than previously established, in response to fires and potentially other factors, suggesting that sparrows preferentially select optimal territories when available. The problem in applying contest models in these situations is that these models require an estimate of the maximal population growth rate. Perkins et al (2008) suggested that much suitable habitat was not filled during their studies; therefore, the rates they measured probably did not represent a maximum at low population densities. Perkins et al. (2008) first used 15% to represent maximum growth rates in project reports but later used 30%, noting these estimates might be a conservative approach given that growth rates can increase by as much as 50% annually for passerines at low densities (Ricklefs 1973). The use of 30% greatly influences model output and could greatly underestimate extinction risk (Ginzburg et al. 1990).

We had no information on the status of Florida Grasshopper Sparrow at River Ranch and relied entirely on our interpretation of aerial photographs and interpretations by Bridges (2006) that mapped much of River Ranch as presettlement dry prairie. Final metapopulation sizes, number of populations occupied, and the risk of metapopulation decline and extinction were greatly improved by several management scenarios, such as doubling the area burned, tree removal, and flatwoods restoration. Modeling scenarios assumed that River Ranch had an initial population of 58 adults, and recovery might be greatly influenced by initial population sizes that were low if there was little immigration.

Presettlement maps (Bridges 2006) and habitat mapping results herein suggest that a River Ranch population could be restored to the extent that it would be contiguous with an the Echo population if pine flatwoods north of Echo were restored to prairie based on presettlement prairie maps. The location of River Ranch potential prairie and expansion of Echo would greatly increase connectivity between the Avon Park, Kissimmee Prairie, and Three Lakes populations. Population modeling did not account for increased connectivity among populations if River Ranch population recovery was successful. Changes in connectivity could be modeled by modifying dispersal assumptions, but there were no data on dispersal rates among populations and how these dispersal rates were influenced by distance, matrix habitat, density, and other factors. It is reasonable to assume that River Ranch conservation scenarios might improve metapopulation connectivity, but it is difficult to know whether this influence would significantly influence population abundances. Our modeling results indicated that conservation actions at River Ranch would have value, even without considering the potential influence of this site on metapopulation connectivity.

Southeast and southwest Kissimmee Prairie conservation scenarios increased the carrying capacity of the Kissimmee Prairie population but had relatively minor influences on population viability because the KPPSP population was already large relative to other populations. Conservation of SWKP and SEKP would have greater value to the Florida Grasshopper Sparrow metapopulation if these prairies connected KPPSP and APAFR populations to relatively large populations to the south. However, opportunities to recover large populations south of KPPSP appear to be limited by extensive agriculture. The model assumed that density-dependent dispersal increases as the target population size increases, which can make connectivity among small populations less relevant. The model could assume that exchanges among populations were directly related to distances between populations. These could be considered if the Florida Grasshopper Sparrow Working Group develops some alternative dispersal models. These were not attempted in this draft because the lack of data on population exchanges would make the results speculative.

It will be difficult to determine whether marked Florida Grasshopper Sparrows that disappear have died or emigrated, or whether increases in population size within a particular landscape resulted from recruitment or immigration (Marshal et al. 2004, Franklin et al. 2004, Andres and Marshall 2005). These sources of uncertainty should be investigated by means of extensive color-banding studies. Source-sink dynamics can be assumed but are difficult to verify; alternative population dynamics are possible in open systems (Van Horne 1983, Howe et al. 1991, McPeek and Holt 1992, Hanski 1999, Harrison and Bruna 1999, Watkinson and Sutherland 1995, Diffendorfer 1998, Doncaster et al. 1997, Hixon et al. 2002, Runge et al. 2006). Population viability analyses that use matrix models, as performed herein, rely on parameters that are difficult to estimate for the Florida Grasshopper Sparrow, and it might be wise to replace them or supplement them with mark-recapture reverse-time models or occupancy models that directly incorporate empirical data and detection probabilities (Mackenzie et al. 2006).

Many habitat relationships (e.g., distance to forest, tree abundance, prairie vegetation type, fire intensity and frequency) are interrelated and will be difficult to tease apart using retrospective analyses, especially because of low detection probabilities (Cohen 1986, Nichols 1999, Yoccoz et al. 2001). Many of these habitat relationships can be directly influenced by management actions. An efficient approach to monitoring would not only quantify population trends but also monitor parameters that allow one to discriminate among alternative management decisions and alternative ecological models that cause management uncertainty (Walters 1986, Nichols 2001, Nichols et al. 1995, Possingham 1996, 1997, Nichols and Williams 2006). Combining monitoring of key ecological system attributes with iterative decision making could lead to optimized management and greater learning (Williams et al. 2002).

One ecological hypothesis in this study was that increasing the amount of prairie at less than 2 years since fire should result in doubling population size, except in populations such as Delta OQ that are very small. Increasing the amount of recently burned prairie might require increasing burn frequency and burning larger areas. The model assumption is that all of a unit burned, which may not be true. Many additional uncertainties about fire relate to how seasonality, extent, and intensity of fire influence Florida Grasshopper Sparrow populations albeit existing data point to a strong relationship between population parameters and time-since-fire.

The influence of scattered trees within KPPSP and Echo prairies was a significant source of uncertainty that could form the basis of experimental study by considering how reducing tree canopies influences population occupancy, density, and nest success. The distance to forest relationship appears to be an important influence at TLWMA, where some experimentation might be focused towards restoration of areas that have become forest within or adjacent to prairie. The relatively low lambda associated with TLWMA and Delta OQ was partly responsible for no or limited population expansion in the models because of relatively high environmental stochasticity, which tends to reduce population growth rates (Burgman et al. 1993). It would be useful to know whether the measured vital rates represent real site differences or result from chance or a deterministic habitat factor (e.g., habitat quality). Modeling of the Delta OQ population by itself suggested that the Delta OQ population might not respond to habitat management because of small initial population size. Recovery of the Delta OQ population might require an experimental translocation program coupled with habitat enhancement. Experimental work needs to consider that populations might not respond as expected if they have already declined to levels that diminish the probability of recovery (Schrott et al. 2005a, b).

Some management questions regarding pasture restoration were not investigated because mapping different types of pasture was difficult. Furthermore, uncertainties related to empirical population responses to pasture restoration have received little long-term study. The seasonality of burning (Platt 1999, Beckage et al. 2003, Slocum et al. 2003, 2007) is also a cause of uncertainty, but there is little or no information on responses of Florida Grasshopper Sparrow populations to burn seasonality. Preliminary data from our study, however, show that the sparrows respond to growing season fires more favorably than to winter fires, with birds shifting territories quickly into areas that burned in the growing season (Noss et al. 2008). Mapping fires explicitly requires sophisticated remote sensing procedures because burn boundaries and wet grassy areas are difficult to distinguish (Duncan and Shao unpublished manuscript). A less expensive approach to developing fire history data bases might involve the creation of better GIS data bases of fire extent and season. This information can be directly incorporated into grid cell models.

CONCLUSIONS

Landcover and Florida Scrub-Jay habitat quality dynamics

Traditional landcover mapping techniques, which identified only the largest well-drained oak scrub ridges, greatly underestimated Florida Scrub-Jay habitat (Breininger et al. 2006). Florida Scrub-Jay habitat should be mapped using species-specific criteria. Florida Scrub-Jays not only use large well-drained oak scrub ridges but also use small oak scrub ridges along with mesic flatwoods and ephemeral marshes adjacent to scrub (Breininger and Oddy 2003). Thus, territories often only have a few hectares of oak scrub and many hectares of mesic flatwoods and ephemeral marshes. Overlaying a region with grid polygons, where each polygon approximates the size of a potential territory, provides an efficient tool to map potential habitat, identify habitat quality, and monitor changes in habitat quality directly related to recruitment, survival, and habitat management needs (Breininger 2004).

The potential territory model developed in this dissertation was routinely used to identify and compare the potential conservation value of land by many conservation organizations. The number of primary and secondary territories, which could function as sources (net exporters having recruitment that exceeds mortality), provided a lower estimate of potential population size and the number of primary, secondary, and tertiary territories provided an upper estimate. Tertiary territories normally functioned as population sinks (net importers, mortality that exceeded recruitment) and included only small patches of scrub oaks < 0.4 ha (Breininger and Oddy 2003, Breininger et al.

2006). Primary and secondary territories had scrub oak patches > 0.4 ha in size, but only primary territories occurred on well-drained soils.

Several Florida Scrub-Jay conservation reserve designs have been produced for the mainland population (Swain et al. 1995, Stith 1999). These designs were used and updated by the Brevard County Environmentally Endangered Lands Program to prioritize conservation acquisition and were partially fulfilled. This land acquisition program relied on willing sellers and the ability to get matching funds from state programs, such as Florida Forever. Reserve designs meant to maximize metapopulation viability have not been completed. The study populations include 2 of the 4 largest extant metapopulations, which are genetically distinct and represent important ecosystems for maintaining scrub biodiversity (McDonald and Hamrick 1996, McDonald et al. 1999, Coulon et al. 2009, Koenig and Walters 2009).

Dynamic attributes of habitat quality that could be regularly measured in grid cells include shrub height and tree cover (Breininger et al. 2006). Shrub heights had the greatest influence on recruitment and survival and represented a habitat factor directly related to management needs. Shrub heights were characterized as four habitat states (short, optimal, tall mix, and tall). Short territories had shrubs < 1.0 m tall with many openings among scrub oaks. Optimal territories had many openings but with at least 0.4 ha of medium-height oak patches (1.2-1.7 m tall), identified by uniform texture on 1.0 m resolution aerial imagery. Tall mix included short and/or medium oaks with at least 0.4 ha patches of tall oaks (>1.7 m tall). Tall scrub only had tall oaks, which had a coarse texture on aerial photographs. Only the optimal state was a source; other height states were sinks (Breininger and Carter 2003, Breininger and Oddy 2004, Breininger et al. 2006). These states are being used to identify management needs by many conservation organizations. Repeated monitoring of states can be used to develop adaptive resource management programs that optimize management decisions (Johnson et al. 2003, unpublished manuscript).

Historical photo analyses revealed that most conservation areas were open shrublands and savannas prior to urbanization (Duncan et al. 1999, 2004). Most current potential Florida Scrub-Jay habitat was unoccupied and of poor quality because it hadn't burned for a long time and approached a forested state (Breininger et al. 2006). Most territories in conservation areas either had too much tall scrub or were too short because tall scrub burned poorly and fires repeatedly burned the same areas (Breininger et al. 2006).

Transition probabilities among shrub height states were influenced not only by management activities, but also by edge effects, oak cover, and interactions between oak cover and management activities. Many of these covariate relationships were consistent with chi square comparisons among habitat variables using independent data (Breininger et al. 2006). For example, oak burns less completely than mesic flatwoods and often has taller scrub heights than optimal (Breininger et al. 2006). Projecting shrub height transition probabilities into the future within actively managed areas suggests that most primary and secondary territories will take decades to become optimal. Rates for increasing source habitat are too slow for many fragmented conservation reserves given that most territories are currently sinks and many reserves have fewer than 10 pairs (Breininger 2008). Areas subject to mechanical treatments showed faster improvements in territory quality than can be performed by fire alone. Multi-state capture-recapture models were powerful tools for testing competing hypotheses about state dynamics, which are often described descriptively with rich ideas but limited empirical testing (Warman and Moles 2009).

Florida Scrub-Jay population dynamics

Observed annual rates of 4% Florida Scrub-Jay population decline were many times greater than rates of habitat destruction, corroborating population model predictions that used vital rates specific to the marginal habitat (Breininger et al. 1998, 2006, 2008; Root 2008). Populations in many conservation reserves declined to less than 10 pairs, which was an assumed extinction threshold (Fitzpatrick et al. 1991, Woolfenden and Fitzpatrick 1991, Stith et al. 1996, Stith 1999). These rates of population decline also occurred statewide (U. S. Fish and Wildlife Service 2008).

Dynamic habitat quality factors (i.e., shrub heights and tree densities) were more likely to be optimal within core areas of conservation areas than along edges of conservation areas or within suburbs. Suburbs and edges of conservation areas have mortality that exceeds recruitment for many reasons (Stith et al. 1996, Bowman 1989, Breininger 1999, Mumme et al. 2000). Florida Scrub-Jays are vulnerable to road mortality and some roadsides are population sinks (Dreschel et al. 1990, Mumme et al. 2000). Human handouts can be inferior food and can cause Florida Scrub-Jays to start nesting before natural foods with appropriate protein content are available (Bowman 2008). Florida Scrub-Jay dispersal has often been described as one-way from suburbs to conservation areas or from habitat fragments with few Scrub-Jays to habitat with the last breeding aggregations (Thaxton and Hingtgen 1996, Breininger 1999, Bowman 2001). One reasonable hypothesis is that most of the extant Florida Scrub-Jay range will collapse because few conservation areas have enough population source habitat interior to edges (Bowman 2001).

One reason edges were assumed sinks was that most edges had shrub heights and tree densities that have mortality that exceeds recruitment (Breininger et al. 2006). I found that some edges with optimal shrub heights and tree densities have recruitment that exceeds mortality so that habitat fragments might contribute to total metapopulation size and connectivity if managed carefully (Breininger et al. 2006). Florida Scrub-Jay territories residing along the Habitat Golf Course in Valkaria, for example, have functioned as sources exporting many individuals to core conservation areas that were restored to optimal. Almost all territories along the Viera Scrub Conservation area bordered roads and houses yet many territories produced large numbers of yearlings. Food supplementation can increase reproductive output (Schoech et al. 2008). Therefore, more research is needed to quantify dispersal among different sizes of habitat fragments and interactions between edge characteristics and vital rates to determine a species conservation strategy.

Florida Scrub-Jays avoid areas with high tree densities and forests (>65 % pine cover; Woolfenden and Fitzpatrick 1984, Breininger et al. 1995). Areas with very low pine densities (< 1 pine / 0.4 ha) may be more optimal than areas without pine trees because living and dead pine trees provide hotspots for fire that create and maintain openings (Breininger 1992, Burgman et al. 2001). The exact relationship between pine density and demography is not well-established because territories with moderate pine densities usually have too many tall oaks so that sample sizes for Florida Scrub-Jay families living in areas with more than 1 pine/ha, but otherwise optimal habitat, are small (Breininger et al. 2006). Most long-term researchers, including myself, believe $\geq$ 1 tree / 0.4 ha is suboptimal (G. Woolfenden, J. Fitzpatrick, R. Bowman, G. Carter; personal communication). Sample sizes of territories with tree densities above and below and this threshold, with otherwise optimal conditions, are increasing so that the relationship (e.g.,nonlinear) between pine densities and demographic performance will hopefully be better defined soon. Evidence is increasing that areas within a few hundred meters of a forest have poor demographic success by Florida Scrub-Jays but the exact nature of this relationship based on empirical data is also uncertain (Breininger et al. 1995; Burgman et al. 2001; Carter et al 2007, unpublished manuscript).

Habitat-specific breeder survival rates using multistate mark recapture models were in the same relative order as rates estimated with ad hoc methods that do not directly incorporate detection probabilities (Breininger et al. in press). However, the order of detection probabilities was slightly different from the order of survival rates. This occurred because tall scrub had the lowest detection probabilities and short territories had the lowest survival. Bird territory state transition probabilities were similar to habitat transition probabilities confirming the prediction that bird habitat quality states track the states of the habitats in which they reside. Thus, Florida Scrub-Jay recruitment and survival were greatly influenced by management activities within the territories where jays reside and there was usually little movement into optimal territories if Florida Scrub-Jays resided in poor quality territories. These findings occurred across a broad range of population densities.

Mean dispersal distances for Florida Scrub-Jays on the Brevard county mainland were intermediate between those observed in large conservation areas, such as Archbold Biological Station (Woolfenden and Fitzpatrick 1984) and Kennedy Space Center/Merritt Island National Wildlife Refuge (Breininger et al. 1996) and fragmented suburbs with little or no optimal habitat (Thaxton and Hingtgen, Breininger 1999). This was expected given that most of Brevard County mainland has an intermediate size of suitable habitat patches (Stith 1999, Breininger et al. 2006). The curve showing the number of occupied territories between natal and breeding territories varied little with the degree of habitat fragmentation, indicating that Florida Scrub-Jays generally dispersed into the closest (occupied) territories regardless of the degree of fragmentation (Fitzpatrick et al. 1999, Breininger et al. 2006).

Predicting whether Florida Scrub-Jays chose to breed or help (delay breeding) depended on many factors. Females bred sooner than males and one-year-olds were more likely to breed than help, as expected (Woolfenden and Fitzpatrick 1984, Breininger et al. 1996). Florida Scrub-Jays were more likely to remain helpers if both parents survived, which could be a factor related to kin selection and that breeders are most tolerant of their own offspring. Other important factors distinguishing helping versus breeding probabilities included breeding opportunities and the availability of unrelated mates. Breeder deaths were the most important factor related to breeding opportunities possibly because it was easier to fill a breeding vacancy in an occupied territory than to colonize an unoccupied territory or to carve out a new territory in occupied habitat. Dominant male helpers will help expand their natal territories and then bud off their own new territory (Woolfenden and Fitzpatrick 1984). Territorial budding often leads to slow population growth following restoration. Territory density is related to population density and Florida Scrub-Jays will defend much larger territories than needed (Breininger and Carter 2003, Breininger and Oddy 2004).

Some habitat fragments were small with only 1-3 families of jays, making it difficult for them to find unrelated mates given that incest is avoided (Woolfenden and Fitzpatrick 1984). The nonlinear relationships between the probability of breeding and mates per pair and competing helpers per pair may have occurred because mates were limited in populations with low helper densities and competition for vacancies was great where helper densities were highest. Mates per pair and competitors per pair might have been better predictors of breeding probabilities than breeding pair densities because suburbs often had high bird densities and high breeding opportunities due to poor habitat quality that caused high breeder deaths and poor recruitment leading to little delayed breeding.

I predicted that many Florida Scrub-Jays from the Palm Bay suburb population would colonize reserves because of inferior suburb habitat quality. However, I found that only a few Florida Scrub-Jays emigrated from Palm Bay, perhaps because there was an abundance of local breeding opportunities. In contrast, most yearlings left their natal territories, traveling many kilometers through urban landscapes on the adjacent barrier island where there were almost no scrub patches that could support more than 1-2 families of jays (Breininger 1999). Besides breeding opportunities, conspecific attraction might be important factor in fragmented landscapes (Campomizzi et al. 2007, Fletcher 2008).

For the mainland metapopulation, there was little exchange among conservation areas, which were usually further apart then average dispersal distances. The percent of residents within each local mainland population that came from another population was estimated to between 10 and 20% (Breininger et al. 2006). Many jays that immigrated into reserves came from unknown locations and presumably small habitat fragments. These immigrants probably came from small habitat fragments in suburbs because most were very tame and were quickly banded in contrast to conservation areas under study where jays were either banded or trap shy. Evidence suggests that nonbreeders and surviving breeders that lose their mates in small fragments are attracted to larger aggregations of jays (Breininger 1999). Eventually jays in small habitat fragments should die out, their habitat will be destroyed, or habitat will become unsuitable because small fragments seldom burn (Duncan and Schmalzer 2004).

In future work I plan to use multistate mark-recapture models to quantify exchanges rates and factors that influence them based on metapopulation and gene flow theories. The understanding of movements between conservation areas will increase but there will be changes in the populations as extinction debt is realized (Carroll et al. 2004) and final reserve design and restoration are completed. Because exchange among populations will probably not remain constant and final reserve design will probably be influenced more by human factors and economic markets than by conservation planning, conservations management can not remain static or dependent on exchange rates of the past (Noss and Harris 1986).

Modeling suggests that 1-10 migrants per generation and sufficient to alleviate inbreeding effects and allow local adaptation, regardless of population size (Schwartz and Mills 2005), though slightly higher rates of exchange may be needed to maintain genetic integrity (Vucetich and Waite 2000). Current rates might not be sustained as suburb populations decline and other populations approach extinction. Many existing conservation areas approach sizes where reduced population size and exchange could eventually limit populations without increasing genetic resources (Westemeier et al. 1998), though current bottlenecks probably pertain to habitat quality and habitat specific demography within relatively small subpopulations.

Many reserves are so small that single disturbances (e.g., wildfires) can influence the entire reserve; hence, smaller reserves need to be managed very carefully (Noss 1983, Marzluff and Ewing 2001). If habitat quality within many conservation areas does not rapidly improve, most territories will remain suboptimal and population declines will lead to local extinction. Populations of Florida Scrub-Jays within most conservation areas are precariously close to extinction, underscoring the need to manage for an excess of source territories to provide population growth. Progress towards restoration should not be measured by the amount of area burned each year but by increases in optimal territories because management progress must occur at the territory scale, which is the fundamental population unit. Because most populations are far below carrying capacity, I suggest that potential territories (10 ha grid cells) be used to measure habitat quality.

Improving habitat quality may no longer be enough in many preserves. Resident jays often defend exceptionally large territories in restored areas that experienced population declines. These residents exclude jays that attempt to establish themselves (personal observations). There might not be enough immigrating Florida Scrub-Jays trying to establish new territories to overcome resident families that defend exceptionally large territories. Helpers may have difficulty finding unrelated mates in small local populations. Even if such small populations recover, the individuals may have reduced ability to adapt to stresses (Hale and Briske 2007). Although populations currently show relatively high genetic diversity, compared to many other imperiled taxa, they need to be monitored for signs of future problems and translocation may become a useful tool to increase genetic variation within populations (McDonald et al. 1999, Driscoll 1998).

Translocation of entire families taken from sites where habitat is soon to be destroyed, within the same genetic unit, may be a management technique that replenishes individuals and new genetic information to a reserve (McDonald et al. 1999). Translocation might also be an effective management tool for current demographic bottlenecks because introducing many Florida Scrub-Jays at once may overwhelm the ability of a few residents to defend all habitat. There are 2 dozen Florida Scrub-Jay families written off by incidental take permits that could be used for translocation experiments to immediately increase population sizes in reserves and learn how to move Florida Scrub-Jays for later genetic management. Translocation not only has potential for resource management but tends to generate great public interest, participation, and investment in conservation (Parker 2008). Determining areas that have sufficient habitat for translocation and are of optimal habitat quality is a necessary process (Koehler et al. 2007, Moorhouse et al. 2009) and the grid cell model used herein is well suited for that purpose. Long-term monitoring is critical and translocation should not be restricted to reintroductions but also for supplementation (Fischer and Lindenmayer 2000).

Habitat and Florida Grasshopper Sparrow dynamics

Similar to Florida Scrub-Jay habitat on the Atlantic coast, there were large amounts of unoccupied potential Florida Grasshopper Sparrow habitat on Avon Park Bombing Range (APBR), Riverview Ranch, and Three Lakes Wildlife Management Area. Similar to Florida Scrub-Jay habitat, most potential Florida Grasshopper Sparrow habitat was unsuitable or marginal because of the disruption of fire regimes and proliferation of pines. Much evidence suggests that edges and areas unburned for greater than 2 years are population sinks or are unoccupied by Florida Grasshopper Sparrows (Perkins et al. 2003). An urgent need for restoration for Florida Grasshopper Sparrows is needed given that the endangered bird is down to only two significant populations.

Optimal habitat could be greatly increased by cutting trees and keeping a greater amount of prairie burned at intervals of 2 years or less. Implementing these management actions in modeling scenarios greatly increased final population size and reduced extinction risk. The improvements in population viability occurred despite uncertainty about how tree densities and distance to forest influenced the amount of optimal habitat. Modeling suggested that population recovery of some restored areas might not occur because of small population size, high rates of environmental stochasticity, and poor dispersal abilities, unless translocation was combined with habitat restoration activities. Thus, conservation of Florida Grasshopper Sparrows and Florida Scrub-Jays has several similarities related to the causes of extinction and strategies to reduce extinction.

Mitigating habitat fragmentation effects and disrupting natural fire regimes for Florida Scrub-Jays and Florida Grasshopper Sparrows requires maintaining enough territories that have recruitment rates that match or exceed mortality rates (Breininger et al. 1995, Perkins et al. 2006, Breininger 2004). Philopatric dispersal tendencies, edge effects, and habitat fragmentation suggest a management emphasis on local population dynamics rather than metapopulation dynamics (Drechsler and Wissel 1988). Gloomy projections and knowledge for both species is sufficient to expedite management even though knowledge gaps remain. Both species occur in landscapes with other vegetation types (e.g., marshes) important to other species of conservation concern, yet few are as endangered as these two unique Florida bird species.

Multi-species conservation in Florida Scrub-Jay habitat

The Florida Scrub-Jay has served as the flagship species for conservation of the Florida scrub ecosystem and as a regulatory umbrella for scrub ecosystem protection and restoration (Noss et al. 1997). Nearly all scrub species of conservation concern along central Florida’s Atlantic coast seem to benefit by restoring scrub to optimal conditions for Florida Scrub-Jays; however, this umbrella assumption needs confirmation by long-term monitoring of other species of conservation concern. The umbrella effect of Florida Scrub-Jays on other rare species may not be as strong in other scrub ecosystems across the species’ range (.e.g., the Lake Wales Ridge); hence, the discussion below focuses on the central Atlantic coast. Gopher tortoises and scrub lizards benefit from regular fire, open sandy areas, and lower pine densities (Breininger et al. 1988, 1991, 1994; Branch and Hokit 2000). Indigo snakes may also benefit, but require larger landscapes with lower edge/area ratios between conservation areas and roads, suburbs, etc. (Breininger et al. 2002). Gopher frogs do poorly in marshes invaded by forests (Thurgate and Pechman 2007). Birds that prefer large unburned areas or tall scrub are species common over much of North America (Breininger and Schmalzer 1990, Breininger and Smith 1992). Nesting Bald Eagles require large pine trees suitable for nesting that often occur within open pine stands (Hardesty and Collopy 1991).

A small Red-Cockaded Woodpecker population is being sustained by translocation at Sebastian River Buffer State Park Preserve (SBR). This population is of minor importance in contrast to the importance of SBR to Florida Scrub-Jay (U.S. Fish and Wildlife Service 1983). It is reasonable to assume that a species, such as the Florida Scrub-Jay, that has regional populations critical to species persistence, should take priority over other endangered species, where the region has little or no importance to the species survival (Breininger et al. 1998). The local Red-cockaded Woodpecker population will remain precariously close to extinction regardless of scrub management because of its small potential population size and isolation (Schiegg et al. 2006). Red-cockaded Woodpeckers could be managed within large landscapes of mesic flatwoods without creating conflicts with Florida Scrub-Jay management.

Nearly all plants of conservation concern in central Florida Atlantic coastal scrub benefit from frequent fire and presence of abundant open sandy areas (P. Schmalzer and T. Foster, personal communication). Precise habitat requirements and the amounts and configurations of habitat required to maintain viable populations are often not established for scrub species influenced by fragmentation and the disruption of fire regimes (Menges and Quintana-Ascencio 2003). Many endangered plant species that need different fire return intervals occur within the same landscapes as Florida Scrub-Jays on the Lake Wales Ridge (Satterthwaite et al. 2002, Quintana-Ascencio et al. 2003, Menges and Quintana-Ascencio 2004, Menges et al. 2006). Some of these occur in different locations along the topographic gradient within communities that have different natural fire return intervals.

Many land managers seek “pyrodiversity” (i.e., a diversity of fire return intervals and severities) in order to meet the needs of multiple species, many of which have unknown requirements in terms of fire regime. Pyrodiversity should not be arbitrary burning, however, because most Florida Scrub-Jay populations along Florida’s central Atlantic coast will continue towards extinction under management that focuses on pyrodiversity without regard for habitat structure at the territory scale. There is arguably much pyrodiversity but too few source territories in most mainland conservations areas to sustain Florida Scrub-Jay populations with $\geq$10 pairs (Breininger and Carter 2003, Breininger and Oddy 2004, Breininger et al. 2006). Fire management often needs broader consideration of details at the regional scale emphasizing species at highest risk of extinction (Andersen et al. 2005, Lindenmayer et al. 2008).

I know of no species of conservation concern, besides Red-cockaded Woodpeckers, that would be harmed by managing most conservation areas optimally for Florida Scrub-Jays on central Florida’s Atlantic coast. Nearly 120 million dollars of local money has been allocated for conservation programs supported by 70% of the voters. The Brevard Coastal Scrub Ecosystem program has been one of the three major programs and the Florida Scrub-Jay has been its flagship species. Florida Scrub-Jays are also considered management indicator species for the scrub ecosystem (Noss et al. 1997). Concerns are voiced that managing for optimal Florida Scrub-Jay habitat might harm other species, leading to confusion among mangers and the public, although examples of conflicts or strategies to reduce conflicts among species in this ecosystem have not been described in the scientific literature. Still, the stated goal of the Endangered Species Act is to conserve the ecosystems that support listed species (Noss et al. 1997); therefore, more assurance is needed that Florida Scrub-Jay habitat management indeed benefits and protects all of the biological diversity of the Florida scrub. Scientists who study other taxa need to conduct monitoring and research regarding of the effects of conservations activities for Florida Scrub-Jays on populations of other species, in order to insure their survival.

Mitigating the major fragmentation effect of disrupted fire regimes

The landscape ecology of fire is overlooked in textbooks in ecology, conservation biology, and biogeography, even though many studies identify fire as a major factor shaping ecosystems worldwide (Bond and Keeley 2005). More regional planning is needed to meet objectives (e.g., rare species protection and restoration of ecological structures and processes) that cannot entirely be addressed on a site-by-site basis (Noss et al. 2006). Much greater recognition is needed that fire regimes differ among vegetation types (Dellasalla et al. 2004) and are likely to change as human domination increases its effect (Gill and Allan 2008). One of the biggest problems in scrub management guidelines is that scrub and pine flatwoods management are often thought about independently, despite the fact that they coincide in landscapes and that animal home ranges or average fires almost always intersect both (Breininger et al. 1995, 2002). Different types of scrub and flatwoods vegetation have different fire return intervals (Florida Natural Areas Inventory 1995). Separating scrub and flatwoods with fire lines is a poor practice because oak scrub is not very flammable and proximity to flatwoods may be needed to ignite scrub, yet frequent fires seem necessary for maintaining openings in scrub (Breininger et al. 2002). Many management units only include oak scrub making them difficult to ignite except under the driest circumstances, resulting in complete burns that result in steep population declines in Florida Scrub-Jays. These declines are temporary in large populations but can cause extinction in small populations (Breininger and Oddy 2004).

Worldwide, landscapes rarely respond uniformly to disturbances. Much more research is needed to quantify how fire frequency, intensity, time of day, ignition methods, duration, vegetation, and topography interact to influence nested assemblages of species (e.g., Baker 1994, Parse and Chown 2003, Fischer and Lindenmayer 2005, Hutto 2008). Many species of conservation concern have different optima or contours of habitat suitability, so that sustaining the complex of all species can be challenging when these are unknown. Multispecies conservation usually needs greater monitoring of many species across larger geographical scales and of longer duration using adaptive approaches that maximize the probability of a tolerable outcome (Parr et al. 2004, Burgman et al. 2005). Multispecies conservation requires not only a greater collaboration among managers, but also among scientists at local and regional scales. Funding for conservation acquisition and management is becoming increasingly local, yet funding for research and monitoring is often tied to short-term regulatory requirements, statewide information needs, or national science priorities that do not include adaptive management.

Adaptive management is necessary for many species because their population responses are likely to vary with fire intensity, season, and frequency (Wagner et al. 2003). Most approaches to the integration of management and science include a 2-step approach where scientists produce results to inform scientists. This is inefficient and can lead to displacement behaviors (e.g., the claimed need for more data to make recommendations or change bad management practices; Nichols and Williams 2006). The adaptive management approach is sensible, but only if pursued rigorously with a valid design and monitoring, including the comparative testing of multiple hypotheses (Noss et al. 2006b).

Approaches relatively new to conservation biology are available to integrate monitoring and management in order to quantify the credibility of alternative models of system behavior and alternative management actions in an iterative process known as adaptive resource management (Walters 1986, Williams et al. 2002, McCarthy and Possingham 2007). The importance of using adaptive resource management for endangered birds influenced by fire is being noted worldwide (e.g., Brown et al. 2009). Initial approaches to develop adaptive resource management programs have been outlined for Florida Scrub-Jays on Merritt Island (Johnson et al. 2003, unpublished manuscript). Two workshops have been conducted for mainland Florida Scrub-Jay populations and >30 natural resource managers are interested in collaborating in an adaptive resource management program.

Uncertainties in Florida Scrub-Jay adaptive resource management focus on how to restore open sandy areas amongst medium-height scrub oak, given that open sandy areas often last a couple years after fire and medium height oaks take 3-10 years to develop. Some ecologists and managers believe mosaic fires can be conducted, whereas other managers believe that a fire management unit either burns or doesn't burn. Management is faced with the need to create openings that last longer than a year, while keeping some islands of medium height scrub from burning completely. One promising approach includes scraping narrow undulating lines through the middle of scrub ridges, where the lines are not permanent but temporarily stop fire spread in some places. Such experiments need to carefully consider enhancing the spread of exotics and creating permanent fire shadows.

Other causes of uncertainty include climate change, furthering the need for adaptive management (Heller and Zavaleta 2009). One useful planning measure is to add attributes to the grid cell layer related to topography and vulnerability to climate change and prioritize population recovery of the areas least likely to be inundated by the rising sea. Developing reliable adaptive habitat and population management actions will be needed as sea level rises, given that populations will need to be managed carefully within smaller and more fragmented conservation areas.

The major impact of habitat fragmentation identified in this dissertation that should apply to many organisms in disturbance-prone systems is that fragmentation disrupts natural processes resulting in habitat degradation across large landscapes not threatened by imminent habitat destruction. Literature emphasizes two ways in which habitat fragmentation can exceed the impacts of habitat reduction (e.g., Harrison and Bruna 1999, Fahrig 2003). The first is that patches become too small and isolated to sustain populations, especially for species that disperse poorly between patches. The second is edge effects, which make substantial zones of habitat near patch boundaries different from patch interiors. Much of this dissertation emphasized a third major effect of habitat fragmentation: the disruption of natural fire regimes by the imposition of artificial barriers.

The disruption of fire spread prevents many areas from burning, such that fires no longer maintain optimal habitat structure, leading to high extinction risk for many species (Duncan and Schmalzer 2004, Breininger et al. 2006). The worldwide significance of such effects has been suggested for over a decade (e.g., Leach and Givnish 1996, Noss et al. 1995), but these effects have been given little serious research attention. In contrast, the increase in fire incidence resulting from fragmentation has received much attention in tropical grasslands and forests (e.g., Laurance 2000). Humans managed fire for > 40,000 years, so it should be possible to use prescribed fire to compensate for deleterious effects (e.g., Bowman 1998). This dissertation demonstrates the difficulties inherent in restoring degraded and fragmented systems and provides methods to quantify landscape units into potential source and sink territories. This information, in turn, provides a basis for applying adaptive management to reach populations goals.

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