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Landcover characterizations and Florida scrub-jay (*Aphelocoma coerulescens*) population dynamics

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ABSTRACT

Landcover maps demarcate habitat but might underestimate it where species select features smaller than minimum mapping units used to produce maps. Habitat loss is magnified by fragmentation, which produces edge effects, alters dispersal and natural processes (i.e., fire). We quantified how Florida scrub-jay (*Aphelocoma coerulescens*) habitat varied using traditional landcover maps and methods that considered small focal habitat features (e.g., scrub ridges <2 ha) within an otherwise unsuitable matrix. We collected 7 years of data on color banded Florida scrub-jays to quantify dispersal and investigate how reproductive success and survival varied with habitat potential (scrub ridges), edge effects, and fire history. Landcover maps that identified only large scrub ridges resulted in a potential population of 354 pairs. Including small scrub ridges within an otherwise unsuitable matrix resulted in a potential population >774 pairs. Florida scrub-jays occupied less than half the potential habitat, and their population declined most from disrupted fire regimes. Almost 90% of all breeding dispersers remained within the same cluster of territories that they hatched in emphasizing the need to maximize local habitat quantity and quality. Reduced habitat quality, caused by disrupted fire regimes, was a major fragmentation effect that greatly magnified impacts of habitat loss. The disruption of natural processes is seldom identified as a major fragmentation effect, but studies worldwide have accumulated to demonstrate its significance. We advocated specific mapping approaches for species influenced by small habitat features and species dependent on matrix habitats that advance natural processes, such as fire.

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1. Introduction

Managing landcover 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 distin-

guish 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

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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 landcover 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 did not 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).

2. Methods

2.1. Study areas

We quantify habitat and population dynamics of three Florida scrub-jay metapopulations along central Florida's Atlantic coast (Fig. 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

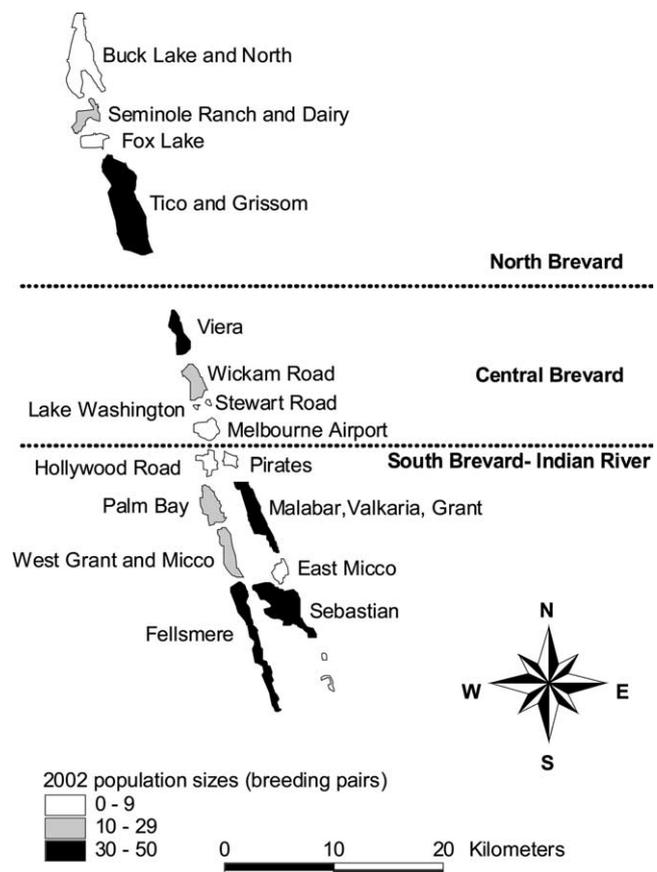


Fig. 1 – Florida scrub-jay territory clusters and 2002 population sizes along the mainland of central Florida's Atlantic Coast. Horizontal lines separate the three Florida scrub-jay metapopulations identified by Stith et al. (1996) and Root (1998).

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*, *Quercus 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. Recently burned scrub and flatwoods have an open tree canopy of longleaf pine (*Pinus palustris*), slash pine (*Pinus elliotii*), or sand pine (*Pinus 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), which can become forests in 20–40 years without fire (Duncan et al., 1999).

2.2. 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 m 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 (>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 m² 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., 2006). 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 and 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).

2.3. 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 to 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.

2.4. Habitat-specific demography and dispersal

Color banding studies began in December 1996 (Fig. 1). 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/h. 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.

2.5. 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 $\geq 85\%$ 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.

2.6. 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.

3. Results

3.1. Habitat and population trends

The amount and contiguity of habitat increased greatly when palmetto-oak was considered (Fig. 2). In 1994, 30% of the oak and palmetto-oak occurred in patches <10 ha within suburbs



Fig. 2 – Potential Florida scrub-jay habitat between Malabar and Fellsmere, which provides the core of the South Brevard-Indian River metapopulation.

and therefore outside PRUs. Five percent 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.

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 0.30.

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 lim-

ited search image. This would have been 16% of the total population for 1992.

Nearly all territory clusters were <50% of carrying capacity (Fig. 3). Palmetto-oak was often occupied when well drained oak was not and much unoccupied scrub became occupied after habitat restoration (Fig. 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 (Fig. 5). Most optimal-height territories were savannas. Road edge and suburb territories almost always had suboptimal tree cover and shrub heights.

3.2. Demography

Height produced the greatest effect on demography among territory quality variables (Fig. 6). Optimal-height territories had the greatest demographic performance and tertiary had the least.

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). The 8 category landcover model showed that optimal-height primary and secondary territories along houses and roads often had recruitment that exceeded mortality (Fig. 7).

3.3. Dispersal

Mean natal dispersal distances were 2.8 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 (Fig. 8). Eighty-seven percent 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 exporters (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).

4. Discussion

4.1. 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 territo-

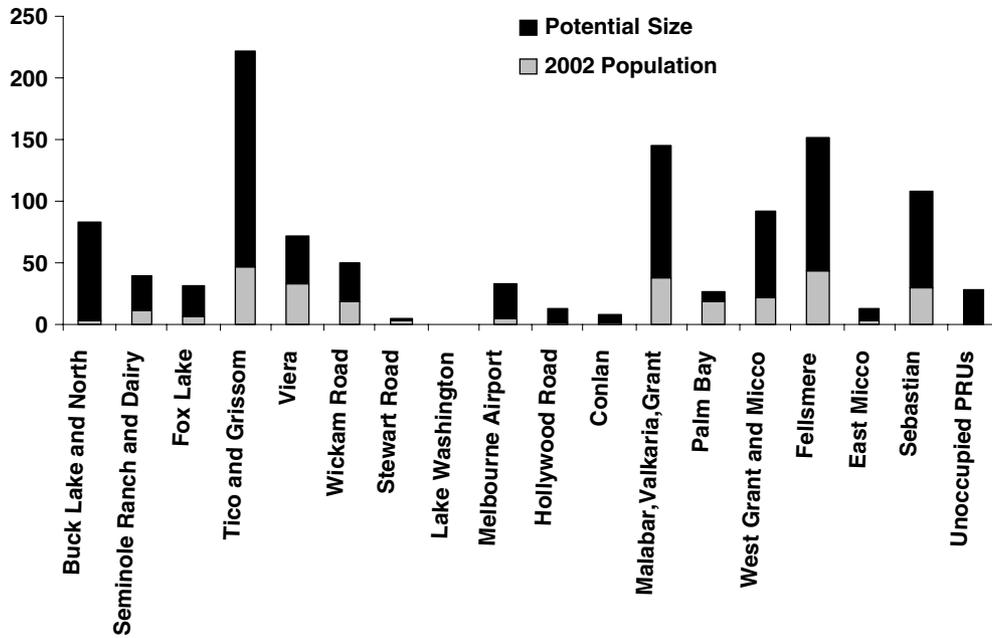


Fig. 3 – Population size (breeding pairs) of territory clusters in 2002 relative to the total potential population size in the cluster. The dark part of the bar represented the number of unoccupied territories in the cluster. The numbers of unoccupied territories within all unoccupied territory clusters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

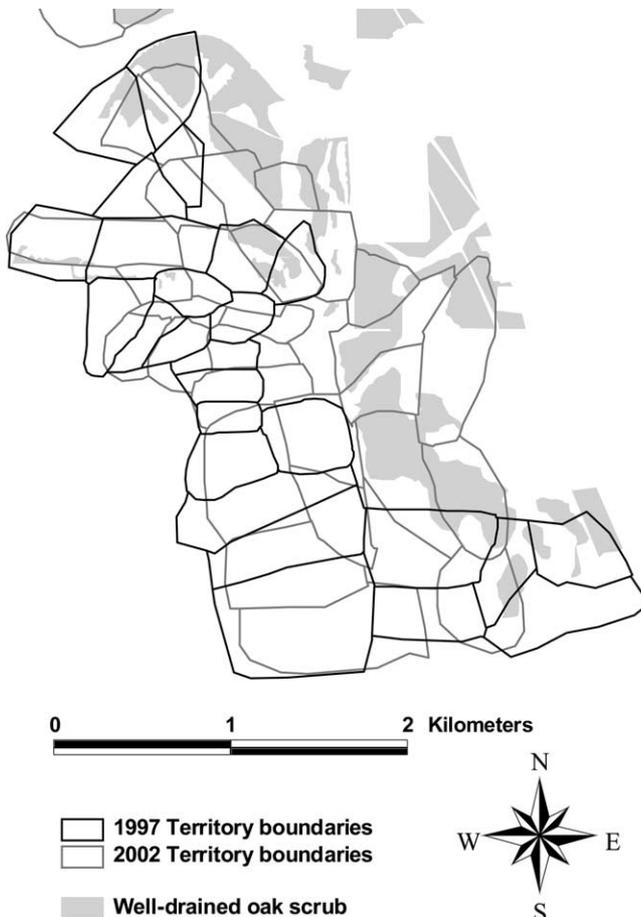


Fig. 4 – Florida scrub-jay territory dynamics in relation to well drained oak scrub (traditional habitat) at Valkaria, Florida.

ries were not contiguous with primary territories. The relative number of underestimated 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

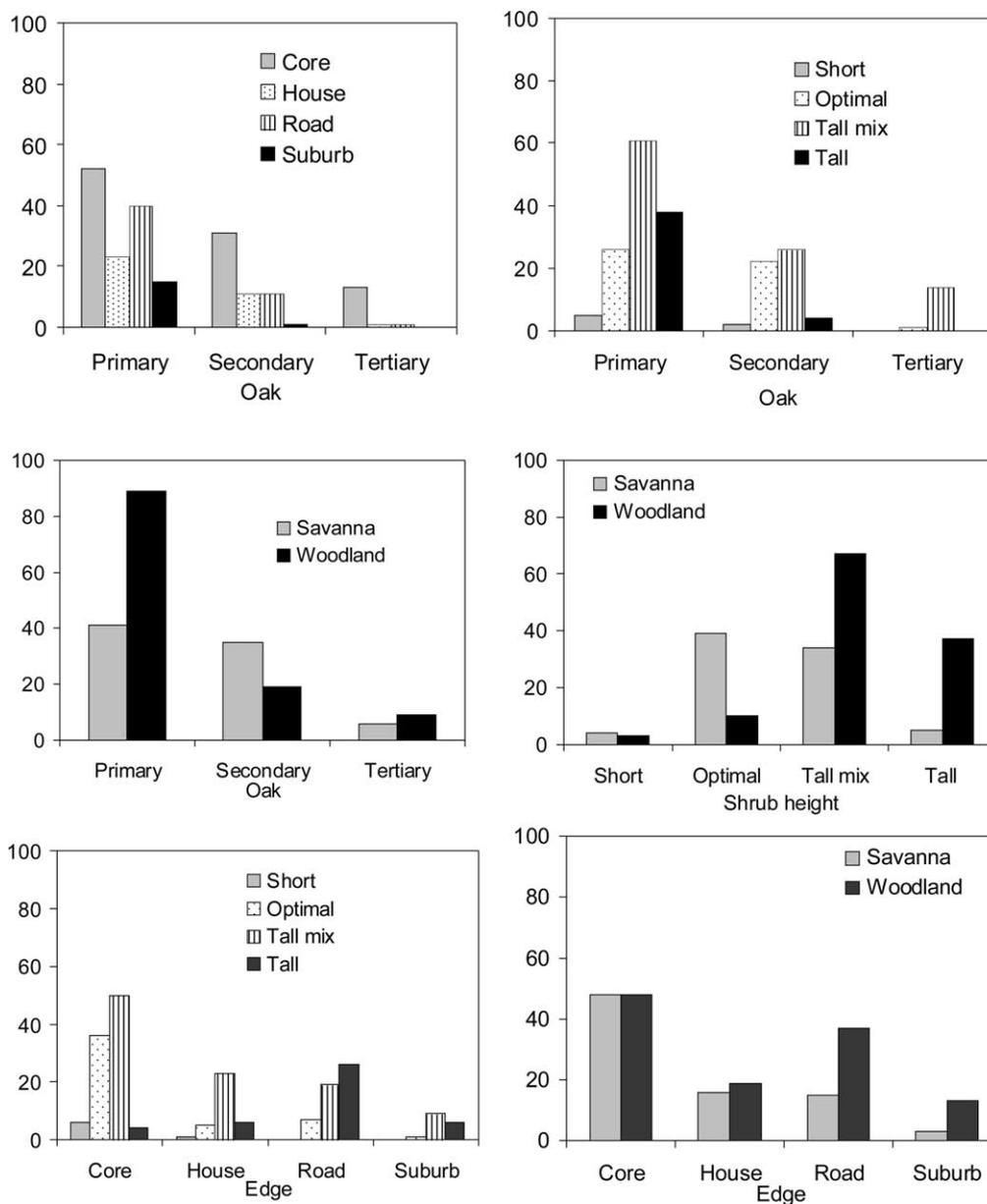


Fig. 5 – Two-way cross-tabulations of all combinations of territory quality categories to study relationships between habitat variables. The y-axis is the count of territories for a particular combination. Territories were pooled for 1997–2002. Likelihood ratio chi-square tests were significant ($p < 0.001$) for all two-way combinations indicating discrepancies between the observed cell counts and the expected if relationships were uniform.

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).

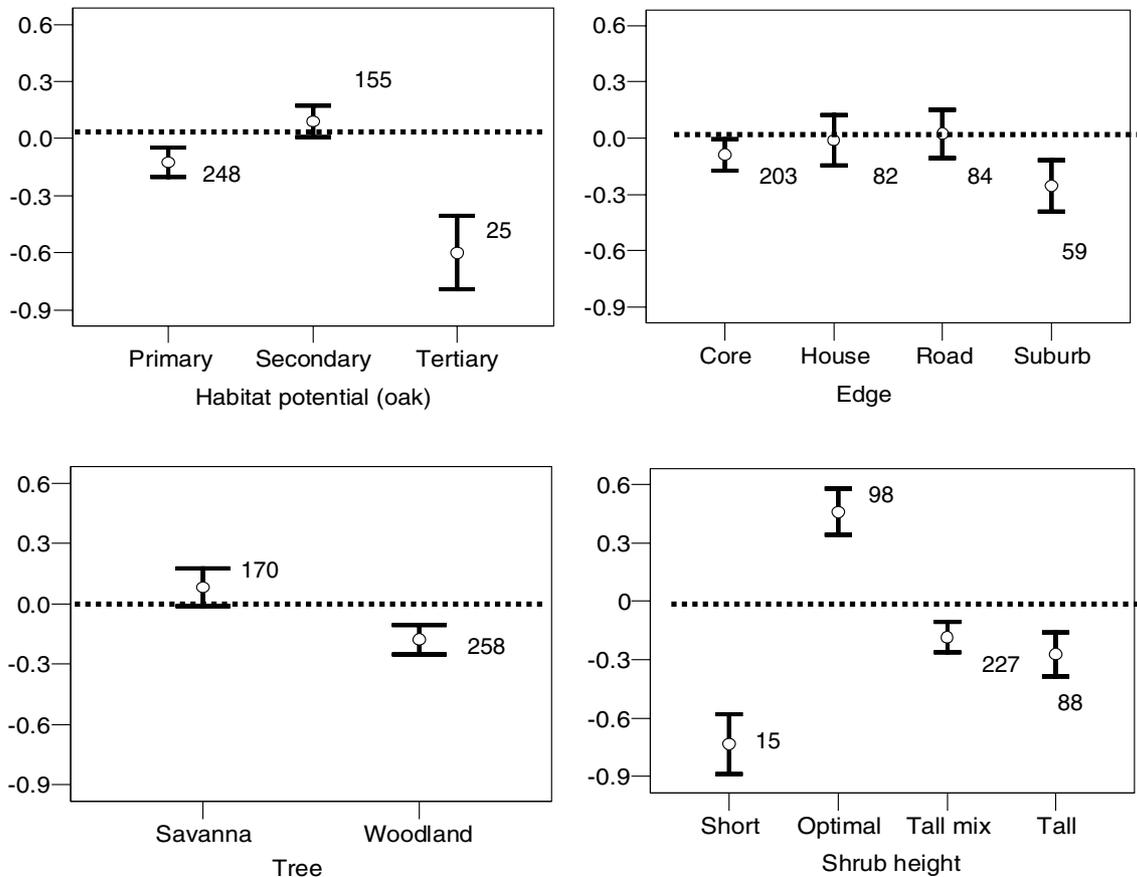


Fig. 6 – Mean \pm 1 SE demographic performance/pair/year (y-axis) for territory quality categories. Mean demographic performance was calculated by subtracting the breeder mortality from yearling production (potential recruitment). Mortality matches recruitment along the dotted lines. Numbers left of error bars represent sample sizes.

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 did not have greatest demographic success. Secondary territories had more optimal shrub heights and tree cover than primary territories because they were

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(L)	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)

	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)
<i>df</i>	797, 3	731, 3	424, 3	6
<i>F</i>	9.893	9.567	14.285	17.401
<i>P</i>	<0.001	<0.001	<0.001	0.008

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.

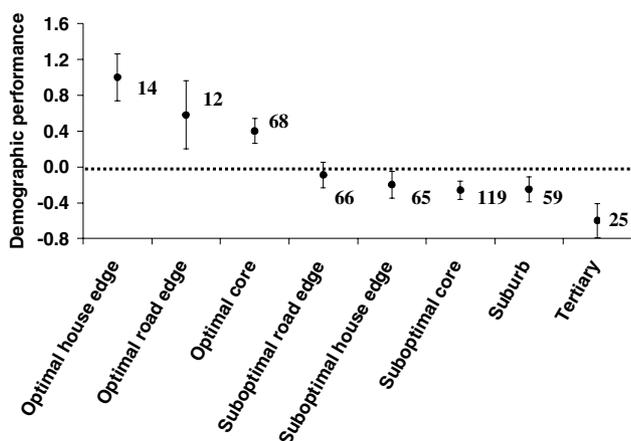


Fig. 7 – Mean ± 1 SE demographic performance/pair/year for the 8 category landcover model where road and house edge effects are separated. Optimal referred to primary and secondary territories with optimal shrub heights and tree canopies within reserves. Mortality matches recruitment along the dotted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

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

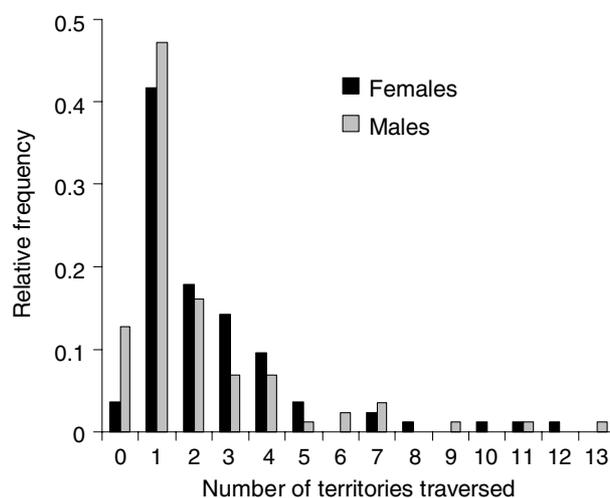


Fig. 8 – Natal dispersal distances of Florida scrub-jays excluding one female that traversed 24 territories. The number of territories traversed was equal to the actual number of territories that occurred between the natal and destination territory.

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 landcover 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

Table 3 – Counts of individuals undergoing natal dispersal among landcover categories along central Florida's Atlantic Coast (1997–2003)

Natal territory	Destination territory category				Total exports
	Optimal primary and secondary	Suboptimal primary and secondary	Tertiary	Suburb	
Optimal primary and secondary	29	27	3	1	31
Suboptimal primary and secondary	17	53	4	3	24
Tertiary	1	3	1	0	4
Suburb	0	0	0	29	0
Total imports	22	30	7	4	

ephemeral marshes are necessary breeding areas for many amphibians, which are important prey that reside in uplands (Moler and Franz, 1987; Herrmann 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).

4.2. 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 a 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.

4.3. 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; Saarienen 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 edges function as sources when in optimal condition.

4.4. Dispersal and population exchanges

Mean dispersal distances were greater than those in unfragmented landscapes (Woolfenden and Fitzpatrick, 1984), as expected (Thaxton and Hinggen, 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).

5. 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 diffi-

cult 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.

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