Landscape Patterns of Florida Scrub Jay Habitat Use and Demographic Success

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Abstract: *Remote sensing and geographical information systems are used to analyze landscapes important to species of conservation concern. The accuracy of the methods depends on how closely habitat mapping classes are linked to population demography. Habitat use by Florida Scrub Jays (*Aphelocoma c. coerulescens*) was quantified using circular plots. Habitat variation was mapped using high-resolution aerial photography on a site where all Florida Scrub Jays were color-banded. Nest site selection, nest success, yearling production, and breeder survival were measured within Florida Scrub Jay territories. Habitat use was lowest in areas without scrub oaks or areas within 136 m from forests. Open oak, dominated by scrub oaks and open sandy areas, had the highest use and nest success among habitats. Open oak occurred as narrow patches (<20 m wide) in landscapes dominated by matrix habitat (palmetto-lyonia and swale marshes). Most wide patches (>50 m) of open oak were potential population sources, where reproduction exceeded mortality. Areas with patches of open oak of less than 1 ha were usually population sinks. Open oak occurred as less flammable patches in a landscape subject to frequent fires. Population sources varied temporally and spatially with fires and site potential to support scrub oaks (soils). Analyses of landscape patterns and dynamics indicated that habitat mapping should not only include patches of currently optimal habitat but should also include landscapes associated with open oak. The influences of landscape patterns on habitat use, reproductive success, survival, and territory size can be quantified at different scales starting with attributes associated with habitat patches, nest sites, and territories. Potential mapping errors occur, however, when habitats are used to quantify the areal extent of sources and sinks and similar population attributes important for species persistence.*

Patrones a nivel paisajístico del uso del hábitat y éxito demográfico del arrendajo del chaparral de Florida

Resumen: *En el presente estudio se utilizan sensores remotos y Sistemas de Información Geográfica para analizar los paisajes importantes para las especies con problemas de conservación. La precisión de los métodos depende de cuán estrechamente estén relacionadas las clases de hábitats utilizadas para el mapeo y la demografía de la población. El uso del hábitat por parte del arrendajo del chaparral de Florida (*Aphelocoma c. coerulescens*) fue cuantificado utilizando parcelas circulares. La variación del hábitat fue mapeada utilizando fotografías aéreas de alta resolución en un sitio donde todos los arendajos del chaparral de Florida fueron marcados. La selección de los sitios para anidar, el éxito en la nidificación, la producción de pichones y la supervivencia de los reproductores fueron medidas dentro de los territorios del arrendajo del chaparral de Florida. El uso del hábitat fue más bajo en áreas sin chaparrales de encinos o áreas que se encontraban a una distancia de los bosques no mayor a 136 m. De todos los hábitats, los bosques abiertos de robles, dominados por chaparrales de encinos y áreas arenosas abiertas, tuvieron el uso y el éxito de nidificación más alto. Los bosques abiertos de robles se dieron en parches angostos (<20 m ancho), en paisajes dominados por una matriz de hábitat (palmetto-lyonia y terrenos de humedeles). La mayoría de los parches anchos (>50m) de bosques abiertos de roble fueron fuentes poblacionales potenciales, dónde la reproducción excedió la morta-*

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lidad. Las áreas con parches menores de 1 hectárea de bosques abiertos de roble fueron usualmente poblaciones sumidero. Los bosques abiertos de robles fueron parches menos inflamables en los paisajes sujetos a fuegos frecuentes. Las fuentes de población variaron temporal y espacialmente debido a los fuegos y a la potencialidad de los sitios para mantener chaparrales de encinos (suelos). El análisis de los patrones y la dinámica del paisaje indicó que el mapeo del hábitat debe incluir no sólo los parches del hábitat real óptimo sino también los paisajes asociados con los bosques abiertos de robles. Las influencias de los patrones del paisaje sobre el uso del hábitat, el éxito reproductivo, la sobre y el tamaño del territorio puede ser cuantificado a diferentes escalas comenzando con los atributos asociados con el hábitat de los parches, los sitios de nidificación y los territorios. Sin embargo, existen errores potenciales de mapeo cuando se utilizan hábitats para cuantificar el areas de las fuentes y sumidero y otoros atributos poblacionales similares que son importantes para la persistencia de las especies.

Introduction

Natural populations are influenced by the complex arrangements of habitats within landscapes, which are dynamic (Howe et al. 1991; Pulliam & Danielson 1991; Pulliam et al. 1992). The influences of dynamic landscape patterns on populations are difficult to study using conventional methods (Pulliam et al. 1992). Remote sensing and geographical information systems are powerful tools for such studies, but the accuracy of their results is usually poorly tested due to insufficient biological data (Breininger et al. 1991). We have shown that particular landscapes provided the most potential habitat for Florida Scrub Jays (*Aphelocoma c. coerulescens*) on Kennedy Space Center based on topography, soils, and vegetation (Breininger et al. 1991). Here, we studied fine-scale variation in habitat quality.

Habitat quality is often inferred from density by assuming that animals prefer higher-quality sites and that density decreases from more suitable to less suitable sites. This is not always true, and better measures of habitat quality also use survival and reproductive success (Van Horne 1983). Most published studies on Florida Scrub Jays are based on data collected in oak-dominated scrub at Archbold Biological Station within central Florida. Suitable habitat at Archbold is excessively drained, with open sandy areas and few or no trees (Woolfenden & Fitzpatrick 1984, 1991). Most habitat occupied by Florida Scrub Jays on Kennedy Space Center lacks openings, has less scrub-oak cover than at Archbold, and occurs on poorly drained soils (Breininger 1981; Breininger et al. 1991; Schmalzer & Hinkle 1992*a*,1992*b*). Although most habitat on the Kennedy Space Center appears marginal, it provides habitat for one of the few large remaining Florida Scrub Jay populations (Cox 1984).

Florida Scrub Jays often occupy marginal habitat conditions on Kennedy Space Center; many areas may be population sinks. Local demographic sources, where reproduction exceeds mortality, may be essential to maintain much larger populations that include sinks, where reproduction is lower than mortality (Pulliam 1988; Howe et al. 1991; Pulliam & Danielson 1991; Pulliam et al. 1992). Failure to maintain sources dooms a population to extinction, but populations may persist for long periods after the loss of a source (Howe et al. 1991). Source and sink populations need not be discrete, isolated units because most species occur within a mixture of habitat types or environmental gradients (Howe et al. 1991).

Few empirical studies have shown that natural populations have a source-and-sink population structure, and even fewer have shown that sources actually sustain sinks (Dunning et al. 1992). But source-and-sink dynamics are frequently cited as important conservation considerations. Florida Scrub Jays are ideal for spatially explicit studies of habitat-specific demography because they are easily censused and because breeders spend their entire lives within a territory (Woolfenden & Fitzpatrick 1984, 1991). All periodically burned scrub is rigorously defended by permanently monogamous breeding pairs; breeders rarely separate, so missing breeders are nearly always attributed to mortality (Woolfenden & Fitzpatrick 1984, 1991). Most dispersal distances are within 300 m for males and 1000 m for females. Young remain with the breeders for at least one year, "helping" to detect and mob predators, defend the territory, and caring for subsequent offspring (Woolfenden & Fitzpatrick 1984; Fitzpatrick & Woolfenden 1988). Thus, measures of habitat-specific breeder survival and yearling production are accurate with few exceptions.

We quantified differences between habitat patches occupied or unoccupied by Florida Scrub Jays and examined correlations among habitat variables and Florida Scrub Jay densities. Nest-site selection among habitat types was tested. Because territories are an important spacing mechanism and must contain the habitat components needed by Florida Scrub Jays, we tested to see whether habitat composition influences territory size and demographic success within territories. We used spatial autocorrelation to test whether territory size and demographic variables vary across a landscape at a scale that includes many territories. Spatial variation in demographic performance is shown as categories in which yearling reproduction exceeds breeder mortality and breeder mortality exceeds yearling production. These respective categories are referred to as potential "sources" and "sinks."

Methods

Study Sites

The Kennedy Space Center is a 57,000-ha barrier-island complex along Florida's Atlantic coast. Florida Scrub Jays reside within scrubby flatwoods and scrub and rarely use other natural communities (Cox 1984; Woolfenden & Fitzpatrick 1984; Breininger 1989, 1990, 1992; Breininger & Smith 1992). Florida Scrub Jay habitat on Kennedy Space Center is dominated by scrub oaks (*Quercus geminata* and *Q. myrtifolia*) on well-drained soils and by saw palmetto (*Serenoa repens*) and mesic shrubs (for example, *Lyonia lucida*, *Ilex glabra*) on poorly drained soils (Schmalzer & Hinkle 1992*b*). Scrub oaks often occur as small patches (<5 ha) within poorly drained areas (Breininger et al. 1991). Scrubby flatwoods are similar to scrub except they have a canopy of sparse slash pine (*Pinus elliottii*). We do not distinguish scrub and scrubby flatwoods hereafter, referring to both as scrub. Scrub on the Kennedy Space Center differs from scrub at Archbold because it has a shallow water table, more saw palmetto, greater nutrient availability, and no *Q. inopina* or *Sabal etonia* (Abrahamson 1984; Schmalzer & Hinkle 1992*b*). Plant composition in scrub is altered little by fires because dominant plants resprout rapidly after fire.

We called the site we used for studies of reproductive success and survival the "demographic site." Recent burns took place in 1981, 1985, 1987, and 1991. The demographic site is mapped as poorly drained except for a 7-ha patch mapped as well-drained (Huckle et al. 1974).

Field and Remote Sensing Data Collection

Comparisons of Florida Scrub Jay densities and habitat variables were made across the range of habitat variation on Kennedy Space Center. Reproductive success and survival were measured in a 295-ha study area.

From February 1985 to February 1986 bird densities and habitat variables were measured at 73 variable-distance circular plots (Reynolds et al. 1980). These plots were used to estimate the Florida Scrub Jay population size (Breininger 1989), to evaluate coarse-scale habitat mapping accuracy (Breininger et al. 1991), and to study the effects of fire on avian communities (Breininger & Smith 1992). These data were reanalyzed here to study the association between Florida Scrub Jay density and fine-scale habitat variables. To estimate the effective detection radius in different habitat types, distances were estimated between the centers of the plots and all birds sighted within seven-minute sampling periods.

Pine cover, percent open space, and scrub-oak cover were measured using a modified point-intercept method (Mueller-Dombois & Ellenberg 1974) because these measures were previously found to be important to Florida Scrub Jays (Breininger 1981). Open space was sparsely vegetated open sand or ruderal grass less than 15 cm tall. Eight lines of four points each, 10 m apart, originated at every 45° angle from the center of each plot. At every point we noted the presence of pine cover, scrub oaks, or open space. We measured the distance from the center of a plot to the nearest forest (>65% canopy closure).

Habitat preference, territory attributes, and demographic success were measured at the demographic site from January 1989 to March 1992. We mapped habitat patches larger than 20 m^2 on a 1:2200-scale color infrared aerial photo. Scrub-mapping classes included open oak (≥51% scrub oak cover), oak-palmetto (31–50% scrub oak cover), and palmetto-lyonia (≤30% scrub oak cover). Open oak was comprised of scrub oaks occurring among open, sandy areas. The other scrub classes had a continuous shrub canopy, except palmetto-lyonia, which had some dense, open patches of wiregrass (*Aristida stricta*).

Color banding, territory mapping, and demographic study methods were adopted from Woolfenden and Fitzpatrick (1984). Florida Scrub Jays were color-banded within a few months of the beginning of the study or upon their immigration into the study area. Once tame (familiar with peanut bits), Florida Scrub Jay family members greeted us upon our arrival into their territories. Nestlings were banded 11 days after hatching. A complete census of the study area was conducted once per month. Territory boundaries were mapped on aerial photographs during April and May of 1989, 1990, and 1991 and were delineated to within a few meters (Woolfenden & Fitzpatrick 1984). Each family was visited at least once per week during the nesting season (March-June) to determine the status of nesting.

Geographical Information Systems Procedures

Habitat, 1985 and 1987 fires, territory maps, and nest sites for 1989, 1990, and 1991 were digitized using ARC/INFO version 6.0 (Environmental Systems Research Institute, Inc. 1991). For each year, family size, the number of breeders that died (disappeared), and the number of one-year-olds produced were assigned as attributes to each territory. Nest locations and territory maps were overlaid (Burrough 1986) on habitat to test nest-habitat associations. We overlaid territories from 1989, 1990, and 1991 to produce a combined territory coverage that included new polygons resulting from the intersection of territory boundaries from the three years. These new polygons included each year's territory attributes of breeder mortality and yearling production. The total number of breeders that died was subtracted from the total number of yearlings within each polygon. The new polygons were classified as potential sources, where yearling production exceeded breeder mortality, and sinks, where breeder mortality exceeded yearling production. Demographic performance was a continuous variable calculated as the sum of breeder survival and yearling production for each new polygon.

Data Analyses

For density estimates the effective detection distance was determined by estimating the inflection point of a graph of the number of birds per area per band counted in 10-m concentric bands (Reynolds et al. 1980). All habitat classes had the same effective detection distance of 70 m (Breininger 1989; Breininger & Smith 1992). For each plot, densities were calculated by totaling the Florida Scrub Jays observed within 70 m, dividing by eight (the number of visits) and dividing by the area within a 70-m radius. For each plot, percentage pine cover and percentage open space were calculated as the percentage of points where pine canopy or open space coincided with the 33 sampling points within each plot (Breininger & Smith 1992). Percentage scrub-oak cover equaled the number of points occupied by a scrub oak divided by the number of points where shrubs of any species were present. To avoid a strong negative correlation between open space and scrub-oak cover, scrub-oak cover represented the percentage of shrub cover (not total ground cover) occupied by scrub oaks (Breininger 1981).

Differences between mean habitat variables for occupied and unoccupied plots were tested using Mann Whitney *U* tests (SPSS, Inc. 1990). Linear and quadratic regression analyses were used to compare densities and habitat variables (Cohen & Cohen 1975; Meents et al. 1983; SPSS, Inc. 1990). Regressions with many unoccupied plots violate assumptions concerning variance (Rice et al. 1986), but the range of habitat conditions should be sampled (Best & Stauffer 1986). We excluded plots that had marginal habitat conditions for variables other than the independent variable under immediate regression analysis. Marginal habitat conditions were defined by habitat variables with values equal to or less than the means of unoccupied habitat. Marginal habitat conditions included only variables that had significantly different means ($p < 0.05$) between occupied or unoccupied plots (from the Mann Whitney *U* tests).

For each of the three years we tested for spatial autocorrelation, using Moran's I (Cliff & Ord 1973), on the territory attributes: territory size, family size, yearling production, breeder mortality, and demographic performance (breeder survival + yearling production). The Kolmogorov-Smirnoff test was used to test nest-site selection among habitat types (Taylor 1977). Pearson product correlation analyses were used to examine associations among family size, territory size, demographic performance, and habitat composition after we determined that these variables did not differ significantly from a normal distribution (SPSS, Inc. 1990).

Results

Habitat Use

Scrub-oak cover was positively correlated with distance from forests ($r = 0.71, p < 0.001$ $n = 73$) and negatively correlated with pine cover ($r = 0.35$ $p = 0.002$, $n = 73$). Openings were associated with shrub vegetation dominated by scrub oaks, resulting in a positive correlation between scrub-oak cover (percentage of shrub cover comprised of scrub oaks) and open space ($r = 0.46$, $p < 0.001$, $n = 73$). Means of scrub oak cover, open space, and distance to forest were lower for unoccupied plots than occupied plots (Table 1). Although densities within circular plots varied, Florida Scrub Jays occurred in nearly all plots with more than 29% scrub oak cover and more than 4% open space when the plots were more than 136 m from a forest (Fig. 1). Plots within 136 m from a forest or with more than 20% pine cover were used infrequently by Florida Scrub Jays even where scrub-oak cover exceeded 29% and open space exceeded 4% (Fig. 2).

In the demographic site, where all Florida Scrub Jays were color-banded, habitat patches were represented by polygons. The northern and eastern boundaries were bordered by pine forests that developed on human-disturbed scrub and marsh soils. Pine cover was sparse (<20%) in other areas. Ruderal-maintained (mowed) grass bordered the site along northern, western, and southern boundaries. Open oak occurred on the highest ridges throughout the demographic site but occurred as large patches (>5 ha) in few areas (Fig. 3). Nearly all open oak occurred further than 136 m from a forest. Marshes occupied the lowest elevations between patches

Table 1. Mean habitat characteristics (± 1 SE) of sites occupied[a] and unoccupied by Florida Scrub Jays across Kennedy Space Center.

Habitat variable	*Unoccupied (n = 32)*	*Occupied (n = 41)*	*Significance[b] (p)*
Scrub oak cover (%)	29 ± 4.1	47 ± 4.1	0.002
Open space (%)	4 ± 1.2	10 ± 1.8	0.008
Pine canopy cover (%)	24 ± 4.3	13 ± 2.8	0.504
Distance to forest (m)	136 ± 31	230 ± 21	0.004

[a] *Based on one or more Florida Scrub Jays sighted during at least one of the eight visits to a circular plot of 70-m radius.*
[b] *Mann Whitney U test was used to test for significant differences in habitat characteristics.*

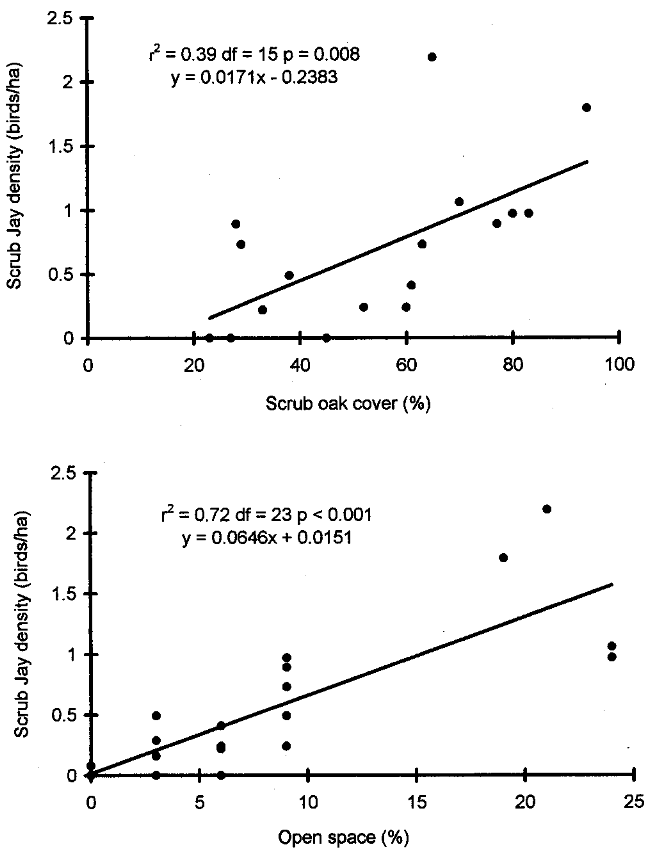

Figure 1. Regression analyses between Florida Scrub Jay density and shrub habitat variables collected from plots scattered throughout Kennedy Space Center. Scrub-oak cover represented the percentage of the shrub layer comprised of scrub oaks. Open space was represented by sparsely vegetated, sandy areas among shrubs.

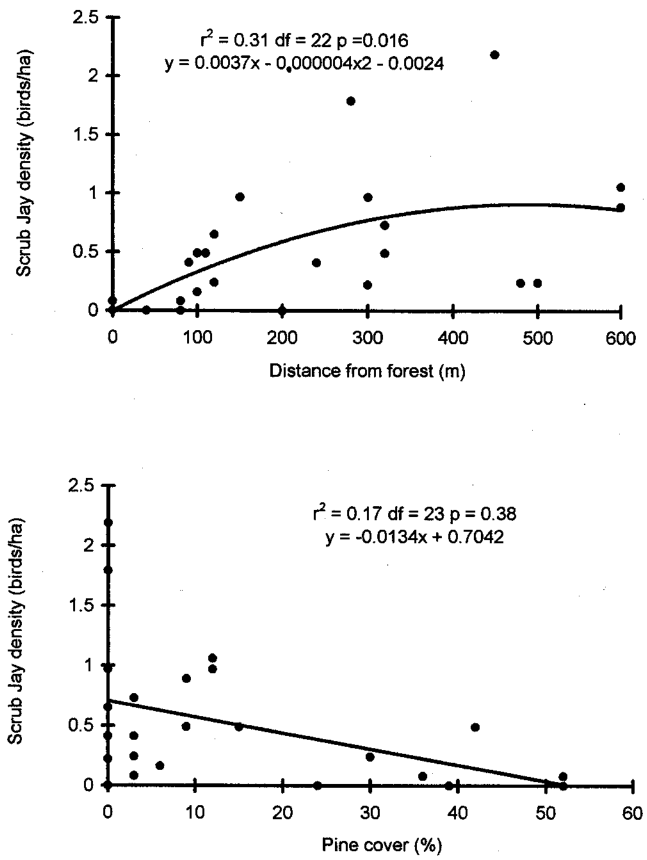

Figure 2. Regression analyses between Florida Scrub Jay density and tree habitat variables collected from plots located throughout Kennedy Space Center.

of open oak. Palmetto-lyonia occurred between open oak and marshes. Oak-palmetto occurred between open oak and palmetto-lyonia, especially in areas that did not burn in 1985 or 1987. Fires in 1985 and 1987 burned nearly all of the study area except wide areas of open oak. The late December 1991 fire did not burn areas with wide patches of open oak but burned many narrow patches of open oak and most large tracts dominated by palmetto-lyonia.

The observed proportions of nests among habitats differed significantly (Kolmorov-Smirnoff test statistic: dmax = 0.30, $n = 49$, $p < 0.01$) from those expected based on the proportions of each habitat in the study area (Table 2). Florida Scrub Jays preferred to nest in open oak, which had the highest nest success.

Territory and Demographic Characteristics

All but three territories (CENT/CEN2, SPOO/SPOB, TRAI/TRA2) were intact between successive years (Fig. 4). Only one territory (ROWD) produced yearlings each year. All territories remaining intact for all three years were successful at producing yearlings for at least one year. Suitable habitat within territories averaged 9.3–9.7 ha, but open oak and oak-palmetto within territories averaged only 2.4–2.9 ha (Table 3). All small territories were clustered at the south end of the demographic site during 1989, resulting in significant spatial autocorrelation ($r = 0.56, p = 0.02, n = 12$) for 1989 territory sizes. Spatial autocorrelations for territory sizes were not significant for 1990 or 1991, although territory sizes were consistently small near the south end. Territorial budding (Woolfenden & Fitzpatrick 1984) occurred from RIDG to MIDR and from BLUE to JAYG, resulting in small territory sizes. Budding occurred when a male helper attracted a female from outside his family and established a new territory from a portion of the territory in which he helped. Territory size was positively correlated with the amount of oak-palmetto and palmetto-lyonia within territories for all three years (Table 4). Correlations between territory size and demographic performance were inconsistent and were significant only in 1989.

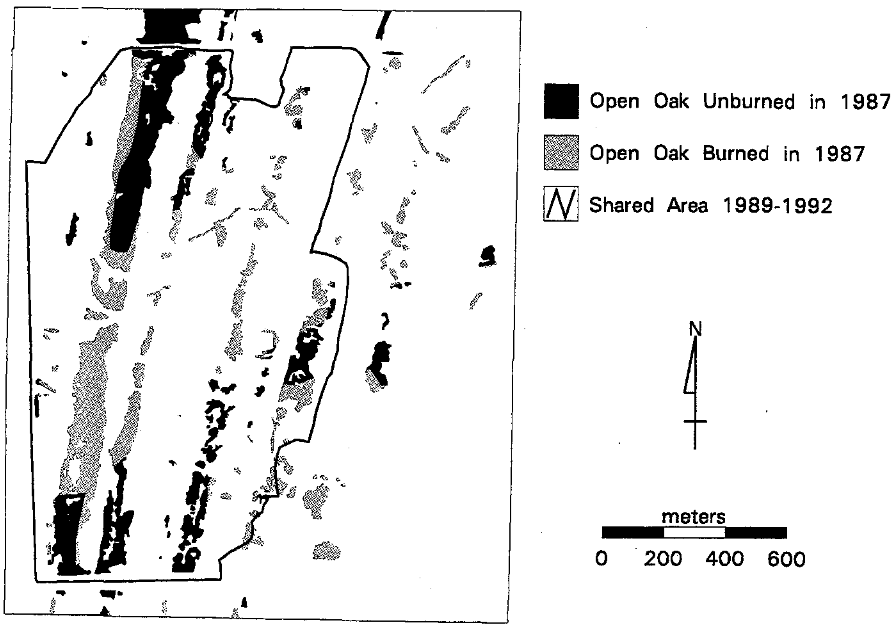

Figure 3. Map of open oak burned and unburned in the 1987 fire. The shared area includes territories studied during all three years and excludes the territory (TRA1/TRA2) because we did not measure its demographic performance in 1989.

Mean family sizes were similar to those at Archbold (Woolfenden & Fitzpatrick 1984). Only one separation of pairs was observed. All other broken pair bonds involved breeder mortality. All young that survived to the next breeding season remained as helpers throughout that first breeding season after hatching, except one female that paired during its first nesting season after hatching.

Family size, yearling production, breeder mortality, and demographic performance were not spatially autocorrelated ($p > 0.05$) for any year. Low statistical power resulted from small sample sizes (number of territories) for all correlations, so that only conspicuous correlations could be expected to be significant. Demographic performance was not correlated with the acreage of matrix (palmetto-lyonia + marsh) habitat during any year (Table 5). Family size was positively correlated with the amount of open oak within the territory for each year. Areas with wide (>50 m) patches of open oak were potential sources, except for a few areas where scrub was less than 1.0 m tall due to fires in 1987 (Figs. 4 & 5). Areas with only narrow (<20 m) patches of open oak were population sinks, except where they were near wide patches of open oak. Patches 20–50 m wide were usually sources where they remained unburned in 1987 but were sinks in areas burned in 1987.

Discussion

Habitat Preferences and Territory Size

Scrub-oak cover influenced Florida Scrub Jay habitat use at regional (Cox 1984; Woolfenden & Fitzpatrick 1984; Breininger et al. 1991) and local scales. Florida Scrub Jay densities were highest where scrub-oak cover exceeded 60%, open space exceeded 10%, pine cover was less than 20%, and forests were more than 136 m away. Habitats were often unoccupied or had low use when any one of several habitat variables was marginal. Florida

Table 2. Florida Scrub Jay nest-site selection and nest success within scrub types on Kennedy Space Center.

	Number of nests observed/ Number of nests expected[a]					
Habitat type	*1989*	*1990*	*1991*	*Total*	*Successful nests*[b] *(%)*	*Study areas comprised of each scrub type (%)*
Open oak	7/3	12/4	6/3	25/10	56	20.5
Oak-palmetto	3/1	4/2	1/1	8/4	38	8.4
Palmetto-lyonia	4/10	4/14	8/11	16/25	38	71.1
Total	14	20	15	49	47	100.0

[a]*The number of nests expected was calculated by multiplying the proportion of the habitat type by the total number of nests observed during that year.*
[b]*Percentage of nests that were observed to have fledged young.*

Table 3. Yearly habitat and demographic characteristics (means ± 1 SE) of territories.

Characteristic	Year 1989 n = 12	1990 n = 14	1991 n = 15	Archbold[a]
Mean habitat (ha)				
Territory size[b]	9.7 ± 0.9	9.7 ± 0.9	9.3 ± 1.6	9.0
Open oak	2.2 ± 0.3	1.7 ± 0.4	1.8 ± 0.4	—
Oak-palmetto	0.7 ± 0.1	0.7 ± 0.1	0.8 ± 0.2	—
Palmetto-lyonia	6.5 ± 0.8	6.8 ± 0.8	6.5 ± 1.3	—
Ruderal-maintained	0.5 ± 0.1	0.5 ± 0.1	0.3 ± 0.1	—
Marsh	2.1 ± 0.3	2.0 ± 0.3	1.9 ± 0.4	—
Demographic[c]				
Family size	2.42	2.93	3.21	3.00
Independent young per pair	1.08	1.00	0.64	1.23
Yearlings per pair	0.69	0.77	0.57	0.68
Breeder mortality	0.17	0.26	0.21	0.18
Emigrants	3	2	0	—
Immigrants	10	3	4	—

[a]*Long-term average based on studies by Woolfenden and Fitzpatrick (1984) at Archbold Biological Station, Lake Placid, Florida.*
[b]*Excluded marsh habitat (Woolfenden & Fitzpatrick 1984).*
[c]*Family size represented the number of birds per family during April; independent young represented juveniles present in late July; breeder mortality was calculated as the number of breeders that disappeared per number of breeders; emigrants represented the number of helpers that became breeders outside the study area; immigrants represented the number of birds dispersing into the study area.*

Scrub Jays prefer to nest and hunt for prey within scrub oaks, which provide acorns that are needed during the winter (Woolfenden & Fitzpatrick 1984). Areas with low (<30%) scrub-oak cover were seldom occupied except near (<300 m) well-drained soils (Breininger et al. 1991). The dense grass layer associated with areas of low scrub-oak cover (Breininger et al. 1994*a*) may impede jays from spotting prey or ground predators.

Areas with more than 30% open space occurred only in areas subjected to mechanical clearing of the shrub layer. Acorn caching occurs in openings, and nests are often adjacent to openings (Woolfenden & Fitzpatrick 1984). Increased habitat use between 0% and 30% open space was consistent with earlier studies that showed that Florida Scrub Jay use increased between 0% and 50% open space but declined as open space increased past 50% (Breininger 1981). The nonlinear relationship occurs because openings are needed, but Florida Scrub Jays require openings in association with scrub oaks.

Table 4. Correlations (Pearson product) between territory size, habitat, and demographic variables.

Variables	Territory size 1989 n = 12	1990 n = 15	1991 n = 14
Open oak	0.59[a]	0.22	0.36
Oak-palmetto	0.62[a]	0.71[b]	0.77[b]
Palmetto-lyonia	0.89[b]	0.90[b]	0.95[b]
Family size	0.40	0.13	0.15
Demographic performance[c]	0.52[a]	−0.26	0.40

[a]$p < 0.05$.
[b]$p < 0.01$.
[c]*Number of breeders surviving plus the number of 1-year-olds produced within a territory.*

Habitat use was low in pine woodlands (>20% tree cover) or within 136 m of a forest (>65% tree cover). Florida Scrub Jays may avoid areas near forests because they reduce their ability to spot woodland hawks (accipiters) and reach escape cover in time to evade capture. Florida Scrub Jays do not use pine forests (Cox 1984), and they avoid Blue Jays (*Cyanocitta cristata*), which are competitors and nest predators (Woolfenden & Fitzpatrick 1984, 1991). Blue Jays are common in woodlands and near forests but are rare in recently burned scrub (Breininger 1990; Breininger & Schmalzer 1990; Breininger & Smith 1992). Pine woodlands and forests often occur within habitat fragments that have not burned for more than 20 years or where the soils have been mechanically disturbed by humans.

Open oak, dominated by optimal amounts of scrub oaks and open space, was the preferred habitat for nesting and had the highest nest success. All oak-dominated scrub in the demographic site had numerous openings due to frequent fires. But much oak-dominated scrub on Kennedy Space Center lacks openings among scrub oaks due to human alterations of natural fire regimes (Breininger & Schmalzer 1990; Schmalzer & Hinkle 1992*a*, 1992*b*; Schmalzer et al. 1994). Palmetto-lyonia was seldom used for nesting and had scrub-oak cover and open space characteristic of unoccupied habitat. Palmetto-lyonia was the most abundant habitat within most territories. All scrub within the demographic site was occupied by Florida Scrub Jays except for small (<1 ha) patches surrounded by forests, similar to findings by Woolfenden and Fitzpatrick (1984).

Table 5. Correlations (Pearson product) between demographic variables and habitat composition within territories.

Demographic variable	Open oak[a]			Oak-palmetto[a]			Palmetto-lyonia and marsh[a]		
	1989	1990	1991	1989	1990	1991	1989	1990	1991
Family size	0.72[b]	0.44[c]	0.63[b]	0.22	0.00	−0.04	0.14	−0.08	−0.18
Performance[d]	0.53[c]	0.17	−0.16	0.56[c]	−0.37	0.45	0.33	−0.42	0.39

[a] 1989, $n = 12$; 1990, $n = 15$; 1991, $n = 14$.
[b] $p < 0.01$.
[c] $p < 0.05$.
[d] Number of breeders surviving plus the number of one-year-olds produced within a territory.

Florida Scrub Jay families occupied areas that lacked wide ridges of open oak by defending many small patches of open oak. In some species territory size is negatively correlated with the amount of optimal habitat (Zack & Ligon 1985; Conner et al. 1986; Smith & Shugart 1987; Renken & Wiggers 1989; Catchpole & Phillips 1992). Perhaps Florida Scrub Jay territory size was positively correlated with the amount of open oak because

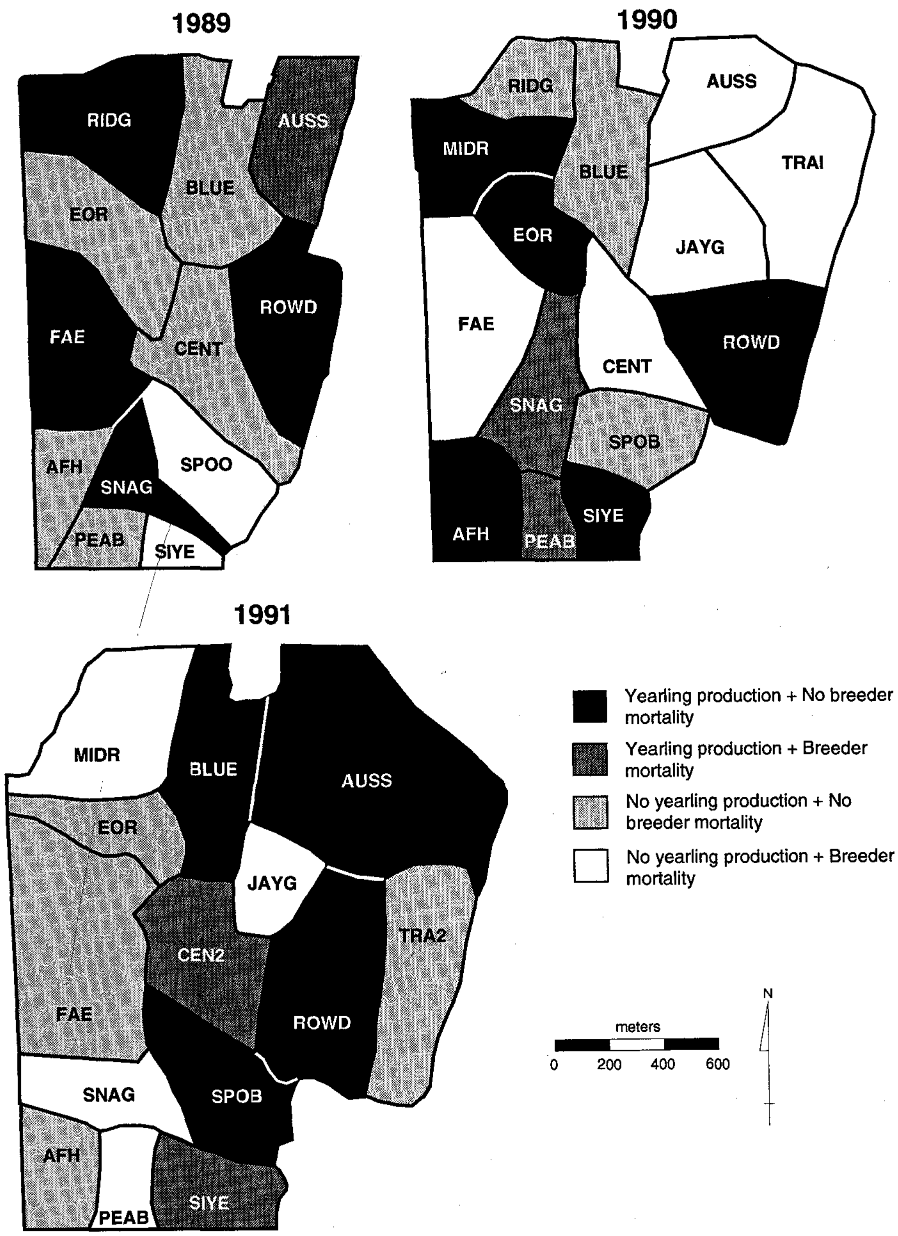

Figure 4. Florida Scrub Jay territories mapped during the nesting season. The presence or absence of yearling production and breeder mortality is provided for individual territories represented by codes. Territory codes including a "2" represent replacement territories where breeders disappeared during the previous year.

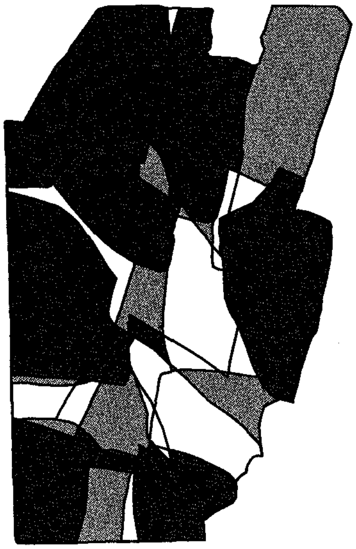

Figure 5. Demographic performance for the area occupied by territories studied during 1989-1991. One territory, TRA1/TRA2, was excluded because we did not measure its demographic performance in 1989. Territory boundaries were overlaid for all 3 years, and the difference between yearling production and breeder mortality was attributed to each polygon. Potential sources represented areas where reproductive success exceeded breeder mortality and sinks where breeder mortality exceeded reproductive success.

larger families, with experienced breeders, could defend more optimal habitat (Woolfenden & Fitzpatrick 1984).

Landscape Patterns

Territory size was spatially autocorrelated during only one year, although territories along the southern study site edge were consistently small. We also observed small territories in our other study areas where scrub oaks were adjacent to sandy areas among ruderal grass. Territories were not small along ruderal edges in areas that had few scrub oaks or that bordered forest. Spatial autocorrelation tests for territory size were not significant during 1990 and 1991, probably because territorial budding resulted in small territories in areas adjacent to the southern edge. No demographic attributes were spatially autocorrelated during any year. Spatial variation of yearly demographic performance values might have been influenced by factors operating at scales smaller than the territories.

Demographic performance was related to landscape features, when data were combined for three years, thereby reducing temporal stochastic events. All young that became breeders were raised in potential source areas that included wide patches of open oak. Fires burn into wide patches of scrub oaks, where the fires often stop due to low flammability (Webber 1935). Saw palmetto, gallberry holly, and grasses, which dominate palmetto-lyonia and marshes, are more flammable and accumulate fuel more rapidly than scrub oaks do (Abrahamson 1984; Abrahamson & Hartnett 1990; Myers 1990; Schmalzer et al. 1991; Schmalzer & Hinkle 1992*a*). Wide patches of open oak were potential sources except where burned by fires in 1981, 1985, and 1987. It takes almost 10 years for scrub oaks to grow to optimal height of 1.5 m (Schmalzer & Hinkle 1992*b*). Most areas that burned in the 1987 fires were sinks or had unusually large territory sizes. Earlier, we found no relationship between time-since-fire and Florida Scrub Jay density, perhaps because plots were surrounded by patches of varying fire history (Breininger & Smith 1992). Reproductive success and survival, but not always density, are crucial measures of habitat quality because Florida Scrub Jays occupy nearly all oak-dominated scrub across a broad range of fire history (Breininger et al. 1991).

Territory boundaries shifted slightly through time and seldom followed habitat boundaries, making it difficult to establish boundaries between sources and sinks. Measuring habitat-specific dispersal from sources to sinks was compromised by several years of delayed breeding and changing habitat conditions due to frequent fires and the recovery of vegetation after fire (Schmalzer & Hinkle 1992*a*). Our accurate measurements of reproductive success and survival were most important because Florida Scrub Jay dispersal was rarely impeded within large tracts of contiguous habitat on the Kennedy Space Center. Models suggest that population size and persistence are often more influenced by reproduction and survival than by dispersal in local landscapes (Pulliam et al. 1992).

We chose to identify all potential sources, recognizing that not all yearlings would become breeders, thereby overestimating the areal extent of sources. Sources could be estimated more stringently by multiplying yearling production by the mean probability of yearlings becoming breeders before subtracting breeder mortality from yearling production. Theory treats sources and sinks as probabilistic expectations of demographic performance (Pulliam & Danielson 1991; Howe et al. 1991; Pulliam et al. 1992). Our data support this view: sites classified as sinks were sometimes successful at producing yearlings, and sites classified as potential sources were not successful each year.

Sources and sinks do not need to be stable features of a landscape (Pulliam et al. 1992). Wide areas of open oak that are often sources for Florida Scrub Jays can temporarily (1–8 years) become sinks after extensive fires, until the vegetation recovers. Florida Scrub Jays have poor demographic success and attempt to gain better habitat away from declining habitat conditions when open oak remains unburned for more than 20 years (Woolfenden & Fitzpatrick 1984). Dispersal of Florida Scrub Jays from suburban tracts into large, high-quality scrub tracts occurs where the large tracts do not act as sources to suburban populations, which have poor demographic success (R. Bowman, personal communication). Many of the immigrants in our study were unusually tame, appearing to be from scrub fragments among nearby housing developments. Thus, movements are not always from sources to sinks.

Conclusions

Comparisons of habitat types with measures of density and demographic performance showed that open oak was the optimal habitat type for Florida Scrub Jays, consistent with results at Archbold Biological Station (Woolfenden & Fitzpatrick 1984). But suitable habitat at the Kennedy Space Center included landscapes not excessively drained or dominated by preferred habitat. We showed that open oak occurred as patches dominated by matrix habitats that received little use by Florida Scrub Jays. Native matrix habitats are important because they provide prey species for Florida Scrub Jays and habitat for other species of conservation concern (Moler & Franz 1987; Breininger et al. 1994*a*, 1994*b*). The flammability of native matrix habitats is important for spreading fires into oak-dominated areas, which often burn poorly. Replacement of native matrix habitats with urban habitats adds predators of Florida Scrub Jays, such as Blue Jays Fish Crows (*Corvus ossifragus*), and house cats (*Felis catus*) that are rare in most regularly burned (every 3–15 years), native matrix habitats (Woolfenden & Fitzpatrick 1991; Breininger & Smith 1992). Florida Scrub Jay reserves should include most native habitat types associated with open oak in scrub landscapes; the preservation of only patches of open oak in a suburban matrix is not sufficient.

The fragmentation of scrub landscapes commonly results in an increase in woodlands and forests because of human landscaping practices, fire suppression, and other disruptions of natural fire patterns. Forests not only replace scrub in habitat fragments but negatively influence the suitability of nearby habitat. Reserve design and habitat management activities should minimize fragmentation and the interspersion of woodlands and forests within landscapes important to Florida Scrub Jays. Florida Scrub Jays have a keenly developed sentinel system for detecting predators such as hawks (McGowan & Woolfenden 1989). Florida Scrub Jay families surrounded by other families, not forests, receive early warnings when woodland hawks are nearby. Thus, the composition of matrix habitats is relevant to reserve design even though matrix habitats may receive little use by species of concern.

Environmental assessments of proposed construction projects usually underestimate the amount of suitable habitat for Florida Scrub Jays because they identify only large patches of open oak. Stable populations may sometimes be dominated by sink habitat that is crucial to population persistence (Pulliam 1988; Howe et al. 1992). Matrix habitats may be essential to population persistence if open oak patches are too small. Florida Scrub Jay territories associated with large patches of open oak may be too few to persist without suitable surrounding habitat. Fine-grain habitat components are important. Mapping applications that operate only at the regional scale are often unable to identify individual patches important to species of conservation concern. All regional-scale mapping applications should consider including important fine-grain habitat components as attributes to vegetation polygons. Attribute data can be used to classify habitat within landscapes without mapping each small patch independently. For example, the presence of scrub-oak patches that are smaller than the minimum mapping unit can be attributed to polygons that are dominated by shrubs other than scrub oaks. Landscapes not dominated by scrub oaks could then be identified as potential Florida Scrub Jay habitat. Heterogeneity within polygons and the difficulty of establishing discrete boundaries between habitats that influence demography are not mapping problems unique to scrub or Florida Scrub Jays. Maps of environmental features commonly represent polygons that include variable data, and attribute data can provide mechanisms for describing the uncertainties of applications (Goodchild 1992, 1993).

Similar quantitative studies are needed for longer periods and across wider landscape conditions to identify the range of habitat composition and arrangements suitable for sustaining Florida Scrub Jay populations. Models suggest that population persistence probabilities can be estimated from the proportions of populations within sources and sinks, using the demographic rates associated with sources and sinks (Pulliam 1988; Howe et al. 1991). Mapping habitat types is often more feasible than determining the proportions of populations comprising sources and sinks. Sources and sinks were convenient categories for graphically portraying spatial differences in demographic performance. Sources and sinks were not homogeneous, however, because demographic performance was a continuous variable, and source and sink boundaries did not coincide exactly with habitat boundaries. Despite problems associated with the exact delineation between boundaries of sources and sinks, locating sources remains critical for conservation (Pulliam 1988; Howe et al. 1991). Our results suggest that habitat maps could allow location of potential sources and sinks but that many errors could occur when the proportions of each are quantified.

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