FLORIDA SCRUB-JAY DEMOGRAPHY AND DISPERSAL IN A FRAGMENTED LANDSCAPE

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ABSTRACT.—I measured population dynamics and cooperative breeding in an isolated population of Florida Scrub-Jays (Aphelocoma coerulescens) on an urban barrier island in southern Brevard County, Florida. In 1992, the scrub-jay population consisted of 29 breeding pairs within six population clusters that comprised two subpopulations. By 1998, the population declined to 10 pairs in four clusters because of poor reproductive success. The frequency of breeding by one-year-olds was related to the availability of breeding vacancies that increased as the population declined. Nearly half of the breeding vacancies were filled by jays that had bred previously but lost their mates. Sex differences in dispersal tendencies led to frequent exchanges of females (but not males) among clusters. The largest clusters did not sustain the smallest ones. Mortality of scrub-jays that resided in the smallest subpopulation exceeded reproductive success, but this subpopulation served as a net source of replacement breeders for the largest subpopulation as the population declined. Received 7 July 1997, accepted 30 October 1998.

THE EFFECTS OF LANDSCAPE FRAGMENTATION on the biology of many species are often described using metapopulation theory (Harrison 1991, Stith et al. 1996). Despite the importance of this theory, modeling of metapopulations has proceeded well ahead of field biology (Doak and Mills 1994, McCullough 1996). Empiricists should test for plausible metapopulation structures and collect data on dispersal and demography that can be used for parameterizing models to enhance our understanding of fragmentation effects (Doak and Mills 1994, McCullough 1996, Harrison and Taylor 1997).

Most studies of Florida Scrub-Jays (Aphelocoma coerulescens) have occurred within large tracts of scrub at the Archbold Biological Station (Archbold; e.g. Woolfenden and Fitzpatrick 1984) and the Kennedy Space Center (KSC; e.g. Breininger et al. 1996a). Florida Scrub-Jays at Archbold and KSC occupy all-purpose territories that are defended year-round by permanently monogamous breeding pairs. Suitable habitat is saturated by breeders, and young scrub-jays remain as nonbreeders for more than one breeding season after hatching, during which time they participate in predator detection, territory defense, and care of offspring (Woolfenden and Fitzpatrick 1984, 1991; Breininger et al. 1995, 1996a).

Most Florida Scrub-Jay habitat no longer occurs as large tracts of scrub and instead is in a matrix of agricultural, suburban, and urban habitats (Woolfenden and Fitzpatrick 1991, Stith et al. 1996, Thaxton and Hingtgen 1996). The study population considered here occupies fragments of scrub surrounded by urban areas from Satellite Beach to Melbourne Beach, Florida. These jays must transverse urban areas for any exchange of individuals to occur among isolated fragments of suitable habitat. In other landscapes, it is difficult to quantify dispersal by Florida Scrub-Jays across urban areas because the exact path taken by jays that disperse is unknown.

Stith et al. (1996) described the spatial structure of Florida Scrub-Jay populations using data on geographic distribution and natal dispersal distances. Based on their terminology, "subpopulations" are separated by gaps of 3.5 km, which represents the maximum dispersal distance for 80% of all dispersals at Archbold. "Metapopulations" are separated by 12 km, representing the maximum dispersal distance for more than 99% of all dispersals at Archbold. Subpopulations that contain fewer than 10 breeding pairs are "islands" that probably will become extinct without immigration (Woolfenden and Fitzpatrick 1981). Subpopulations that contain between 10 and 99 breeding pairs are "midlands" that might not be large enough to

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avoid extinction when subject to catastrophic events. The study population that I consider here is a "midland-island" system that differs from classic metapopulation structure in which all patches are assumed to be equal (Stith et al. 1996).

Theoretical treatments of population dynamics also focus on the concept of source and sink populations (Pulliam 1996). Many Florida Scrub-Jays reside in sources, which are associated with optimal habitat, that sustain sinks within marginal habitat (Breininger et al. 1995, 1998). In this paper, my objectives are to assess whether biological attributes of Florida Scrub-Jays that live in a fragmented urban landscape differ from those that live in natural landscapes. The attributes measured include stability of population size, dispersal distance, reproductive success, annual survival, influence of nonbreeders on demographic success, and age of first breeding. These data are needed for conservation planning to evaluate the probability of population persistence in urban areas and the ability of Florida Scrub-Jays to traverse urban areas. Objectives also include quantifying emigration, immigration, and possible source-sink relationships of a midland-island system to evaluate metapopulation structure and provide information for population modeling.

STUDY AREA AND METHODS

Study site.—The study area is the barrier island in southern Brevard County, Florida. Based on historical photographs, the barrier island was dominated by coastal scrub before extensive fragmentation began in the 1960s. Coastal-scrub plant species include oaks (Quercus virginiana, Q. geminata, Q. myrtifolia), saw palmetto (Serenoa repens), rapanea (Rapanea punctata), nakedwood (Myrcianthes fragrans), tough buckthorn (Bumelia tenax), Hercules-club (Zanthoxylum clava-herculis), and red bay (Persea borbonia). Scrub plants and animals are adapted to periodic fires, and burning has little effect on species composition (Woolfenden and Fitzpatrick 1984, Schmalzer and Hinkle 1992, Breininger et al. 1995). Most scrub habitat in the study site has remained unburned for at least 20 years because of fire suppression.

Field procedures.—A complete census of scrub-jays was conducted in April 1992, and most jays were banded in 1993 (most of the juveniles were banded in July of each year). All scrub was censused quarterly, and all known territories were censused bi-monthly from August to February. Territories were censused monthly from March through May to verify breeding and more frequently throughout June and July to count juveniles. I did not conduct detailed nesting studies because initial studies revealed that nest predators (Blue Jays [Cyanocitta cristata], Fish Crows [Corvus ossifragus], Boat-tailed Grackles [Quiscalus major], Common Grackles [Q. quiscalus]) were abundant, and scrub-jay fledgling production was unusually low (Hogan 1994).

The scrub-jay population was divided into clusters based on territory contiguity, not on the distribution of contiguous scrub. Areas between the clusters were not occupied by scrub-jays. Many elements of human-altered landscapes were used by the jays and defended within their territories if they occurred near scrub habitat.

Data analyses.—Study years from 1993 to 1998 were defined to be from 1 April to 31 March. During 1997, an epizootic agent was believed to be responsible for a catastrophic loss of Florida Scrub-Jays along the Atlantic coast (D. Breininger, D. Oddy, V. Larson, and R. Smith unpubl. data) and in central Florida (R. Bowman, G. Woolfenden, and J. Fitzpatrick pers. comm.). Epidemic years are best treated as rare stochastic events that have their own unique values for some demographic parameters (Woolfenden and Fitzpatrick 1984, 1991). A hurricane that hit the study area in 1995 represented a second potential catastrophe (Hooper et al. 1990), but because this event resulted in no mortality of Florida Scrub-Jays, 1995 was not treated separately in my analyses.

Natal dispersal distance was calculated as the distance from the center of the natal area to the center of the territory on which an individual first became a breeder (Woolfenden and Fitzpatrick 1984). Sex differences in mean dispersal distances were tested using Mann-Whitney exact tests (SPSS 1996).

For each cluster and subpopulation, demographic performance, emigration, and immigration rates were tallied to determine whether clusters or subpopulations functioned independently or as sources and sinks. Demographic performance was calculated by subtracting the number of breeders lost to mortality from the number of novice breeders produced for every pair during every year before 1997. Potential population sources referred to clusters (or subpopulations) where the production of new breeders exceeded the mortality of breeders, and potential sinks referred to clusters (or subpopulations) where the mortality of breeders exceeded the production of new breeders. Mann-Whitney exact tests were used to determine whether demographic performance from 1993 to 1996 differed between the north and south subpopulations.

Movement data for emigration and immigration tallies included jays with and without breeding experience and required that movements involved a change in residency and were not just dispersal forays. Forays referred to observations of Florida Scrub-
Jays moving among clusters without residing in a cluster for several months. Data on the continuity of pair bonds between successive breeding seasons were compiled for all years to quantify reasons for movements. Four categories were used to describe changes in pair bonds between breeding seasons: (1) pairing with another jay after the death of a spouse, (2) mortality of both breeders, (3) becoming a non-breeder after loss of a territory following the death of a spouse, and (4) divorce. The influence of sex and breeding experience on movements that led to new pair bonds was tested using likelihood-ratio exact tests (SPSS 1996). Movements were summarized by the frequencies that jays remained in the same cluster, emigrated to new clusters within the same subpopulation, or emigrated to the other subpopulation.

Juveniles were defined as young jays that were present in July, when most of them approached nutritional independence (Woolfenden and Fitzpatrick 1984). For each year, I calculated the number of juveniles and yearlings produced per breeding pair. Annual survival was calculated as the number of jays that survived during a study year divided by the number alive at the beginning of the study year. Survival was not limited by the observer's ability to find jays because of the small size and number of scrub patches. Annual means and standard deviations were calculated for survival based on Zar (1996: equation 23.21).

Arithmetic means of annual means from 1993 to 1996 were calculated for reproductive success, survival, and mean family size. Mann-Whitney tests were used to test whether annual means of juvenile production, yearling production, breeder survival, and mean family size from 1993 to 1996 in urban areas were different from annual means for large tracts of scrub not subject to epidemics. Annual means were pooled for data from a periodically burned site at Archbold from 1970 to 1978 (Woolfenden and Fitzpatrick 1984) and from two periodically burned sites (T4 and HC) at KSC from 1988 to 1993 (Breininger et al. 1996a).

Data from all years were combined to assess the influence of nonbreeders on production of juveniles and breeder survival because of low sample sizes for pairs with nonbreeders. The above approach maximized sample sizes but was vulnerable to biases associated with pseudoreplication when sample sizes were low. A second test for helper effects was used to reduce potential biases associated with pseudoreplication and breeder experience because experienced breeders have higher demographic success than novice breeders (Woolfenden and Fitzpatrick 1984, Breininger et al. 1996a). Only experienced pairs that had nonbreeding helpers during some years were selected for analyses. Differences in juvenile production were tested using Mann-Whitney exact tests, and differences in breeder survival were tested using likelihood-ratio exact tests.

All Florida Scrub-Jays having a known history since hatching were combined to quantify how jays delayed breeding during the first two nesting seasons after hatching. Likelihood-ratio exact tests were used to assess whether sex influenced the frequency that one-year-olds delayed breeding and whether the frequency that one-year-olds delayed breeding during the first three years of the study differed from the frequency during the last three years of study. I compared data from Woolfenden and Fitzpatrick (1984) and Breininger et al. (1996a) to assess whether one-year-olds delayed breeding at different frequencies in populations occupying urban fragments and large, periodically burned tracts of scrub.

**RESULTS**

The fragmented population that I studied comprised three northern and three southern clusters (see Fig. 1). Northern and southern subpopulations were separated by 4.2 km of continuous urban landscape. The longest natal dispersal distance was 15.0 km for females and 1.6 km for males. The mean natal dispersal distance was farther for females ($\bar{x} = 7.3 \pm SD$ of 5.7 km, $n = 15$) than for males ($\bar{x} = 1.0 \pm 1.1$ km, $n = 6$; Mann-Whitney test, $U = 10.5, P < 0.01$). Mean dispersal distances were 8.1 km for females and 1.9 km for males originating from territories in suburban areas (Thaxton and Hingtgen 1996), and 1.0 km for females and 0.3 km for males in unfragmented scrub at Archbold (Woolfenden and Fitzpatrick 1984).

Mean demographic performance (i.e. the number of novice breeders produced minus the number of breeders lost to mortality) per breeding pair per year did not differ for north ($\bar{x} = -0.23 \pm 0.80, n = 62$) and south ($\bar{x} = -0.42 \pm 0.72, n = 24$) subpopulations ($U = 634, P = 0.24$). Demographic performance values were $-0.13, -0.26, -0.40, -0.44, -0.30, and -0.60$ for clusters N1, N2, N3, S1, S2, and S3, respectively. Nine scrub-jays emigrated into the north subpopulation from the south subpopulation, but only two emigrated from the north subpopulation into the south subpopulation (Table 1). Twelve scrub-jays emigrated from smaller clusters to larger clusters, and seven emigrated from larger clusters to smaller clusters.

The frequency that scrub-jays filled vacancies within the same cluster, among clusters in the same subpopulation, and among subpopulations differed significantly by sex (likelihood ratio $= 7.2, P = 0.03$) but not by experience (likelihood ratio $= 3.8, P = 0.19$). For females,
11 filled vacancies within the cluster they resided in before the vacancy, 6 filled a vacancy in another cluster within the same subpopulation, and 11 filled a vacancy within the other subpopulation. For males, 10 filled vacancies within the cluster they resided in before the vacancy, 1 filled a vacancy in another cluster within the same subpopulation, and 1 filled a vacancy within the other subpopulation. Of the jays that had never bred previously, 8 filled vacancies within the cluster they resided in before the vacancy, 5 filled vacancies in another cluster within the same subpopulation, and 8 filled vacancies within the other subpopulation. For jays that lost their mates and then moved to become breeders elsewhere, 13 filled vacancies within the cluster they resided in before the vacancy, 2 filled vacancies in another cluster within the same subpopulation, and 4 filled vacancies within the other subpopulation. In natural landscapes, surviving spouses do not usually abandon their territories because immigrants without prior breeding experience usually replace lost breeders (Woolfenden and Fitzpatrick 1984, Breininger et al. 1996a).

**TABLE 1.** Movements by Florida Scrub-Jays to fill breeding vacancies within or among clusters in the urban population. Values refer to the number of replacement breeders.

<table>
<thead>
<tr>
<th>Moved from cluster</th>
<th>Moved to cluster</th>
<th>Moved to cluster</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>N1</td>
<td>N2</td>
</tr>
<tr>
<td>N1</td>
<td>5</td>
<td>2</td>
</tr>
<tr>
<td>N2</td>
<td>1</td>
<td>12</td>
</tr>
<tr>
<td>N3</td>
<td></td>
<td>1</td>
</tr>
<tr>
<td>S1</td>
<td>1</td>
<td></td>
</tr>
<tr>
<td>S2</td>
<td>1</td>
<td>3</td>
</tr>
<tr>
<td>S3</td>
<td></td>
<td>3</td>
</tr>
<tr>
<td>No. of immigrants</td>
<td>3</td>
<td>9</td>
</tr>
<tr>
<td>No. of emigrants</td>
<td>3</td>
<td>3</td>
</tr>
</tbody>
</table>

FIG. 1. Location of Florida Scrub-Jay clusters in north (N) and south (S) subpopulations on the barrier island of southern Brevard County, Florida. Each subpopulation had three clusters (N1, N2, etc.). Numbers of breeding pairs in each cluster from 1992 to 1998 are shown in parentheses. All scrub-jays on the barrier island resided within the areas designated in black. These areas are not entirely scrub and include roads, buildings, yards, and other human facilities. White areas represent water, and gray areas represent land that was predominately urban on the barrier island.
Sixty of 100 pairs remained together between successive nesting seasons from 1993 to 1997. Pair bonds were disrupted by mortality of a breeder in 37 of 100 pairs. In 24 of the 37 cases where one breeder died, the surviving breeder found a new mate by the next breeding season. In the remaining 13 cases, 9 surviving breeders died by the next breeding season, and 4 surviving breeders remained unpaired for a breeding season. Four of the pair bonds were disrupted by divorce. Similar to the situation in the urban landscape, most Florida Scrub-Jays in natural landscapes remain paired between successive breeding seasons and have low divorce rates (Woolfenden and Fitzpatrick 1984, 1991; Breininger et al. 1996a).

Reproductive success, but not breeder survival, was low in the urban population (Table 2). Mean production of juveniles from the urban population was lower than the pooled annual means from unfragmented scrub at Archbold and KSC (U = 13.5, P = 0.038; Table 2). Annual yearling production means from the urban population were lower than those for unfragmented scrub (U = 10.5, P = 0.02). Annual breeder survival means from the urban population did not differ from those for unfragmented scrub (U = 39.5, P = 0.98). Annual mean family sizes from the urban population were lower than those for unfragmented scrub (U = 0.0, P < 0.01).

Mean juvenile production did not differ between pairs with nonbreeders (\( \bar{x} = 0.36 \pm 0.74 \) juveniles per pair, \( n = 14 \)) and pairs without nonbreeders (\( \bar{x} = 0.44 \pm 0.76 \) juveniles per pair, \( n = 86 \)); \( U = 558.0, P = 0.66 \)). Annual breeder survival did not differ (likelihood ratio = 0.7, \( P = 0.48 \)) between breeders with nonbreeders (\( \bar{x} = 0.69 \pm 0.09, n = 29 \)) and breeders without nonbreeders (\( \bar{x} = 0.76 \pm 0.03, n = 174 \)). No territory or breeding pair had the same nonbreeders for more than one year, resulting in no pseudoreplication for pairs with nonbreeders. Pseudoreplication occurred among pairs without nonbreeders because most territories consisted of the same breeders for successive years, but sample sizes were large for pairs without nonbreeders. Mean juvenile production did not differ for experienced pairs when they had nonbreeders (\( \bar{x} = 0.17 \pm 0.41 \) juveniles per pair, \( n = 6 \)) versus when they did not have nonbreeders (\( \bar{x} = 0.36 \pm 0.67 \) juveniles per pair, \( n = 11 \)); \( U = 25.0, P = 0.41 \)). Breeder survival

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**Table 2. Demography of urban Florida Scrub-Jays compared with other published studies. Values are \( \bar{x} \pm SD \), with \( n \) in parentheses.**

<table>
<thead>
<tr>
<th>Year(s) to 1996 (x)</th>
<th>Breeder survival</th>
<th>Nonbreeder survival</th>
<th>Yearlings/pair</th>
<th>Mean family size</th>
</tr>
</thead>
<tbody>
<tr>
<td>1993</td>
<td>0.35 ( \pm 0.63 ) (26)</td>
<td>0.33 ( \pm 0.52 ) (26)</td>
<td>0.31 ( \pm 0.62 ) (26)</td>
<td>1.26 ( \pm 0.36 ) (269)</td>
</tr>
<tr>
<td>1994</td>
<td>0.27 ( \pm 0.63 ) (19)</td>
<td>0.47 ( \pm 0.47 ) (19)</td>
<td>0.14 ( \pm 0.63 ) (22)</td>
<td>0.80 ( \pm 0.63 ) (152)</td>
</tr>
<tr>
<td>1995</td>
<td>0.42 ( \pm 0.63 ) (14)</td>
<td>0.57 ( \pm 0.76 ) (14)</td>
<td>0.22 ( \pm 0.63 ) (14)</td>
<td>0.90 ( \pm 0.63 ) (143)</td>
</tr>
<tr>
<td>1996</td>
<td>0.57 ( \pm 0.76 ) (86)</td>
<td>0.63 ( \pm 0.94 ) (86)</td>
<td>0.47 ( \pm 0.94 ) (86)</td>
<td>0.72 ( \pm 0.36 ) (269)</td>
</tr>
<tr>
<td>1997</td>
<td>0.72 ( \pm 1.10 ) (71)</td>
<td>0.76 ( \pm 0.87 ) (71)</td>
<td>0.96 ( \pm 0.63 ) (71)</td>
<td>0.72 ( \pm 0.36 ) (269)</td>
</tr>
<tr>
<td>Kennedy Space Center</td>
<td>0.80 ( \pm 0.87 ) (152)</td>
<td>0.80 ( \pm 0.87 ) (152)</td>
<td>0.80 ( \pm 0.87 ) (152)</td>
<td>0.72 ( \pm 0.36 ) (269)</td>
</tr>
<tr>
<td>Archbold Biological Station</td>
<td>0.72 ( \pm 0.36 ) (269)</td>
<td>0.72 ( \pm 0.36 ) (269)</td>
<td>0.72 ( \pm 0.36 ) (269)</td>
<td>0.72 ( \pm 0.36 ) (269)</td>
</tr>
</tbody>
</table>

*This study overall mean does not include 1997 data (see Methods).*
TABLE 3. Breeding status of one-year-old Florida Scrub-Jays on the barrier island of southern Brevard County, Florida. Values are numbers of jays.

<table>
<thead>
<tr>
<th>Year</th>
<th>Males Breeders</th>
<th>Males Non-Breeders</th>
<th>Females Breeders</th>
<th>Females Non-Breeders</th>
</tr>
</thead>
<tbody>
<tr>
<td>1993</td>
<td>1</td>
<td>1</td>
<td>2</td>
<td>3</td>
</tr>
<tr>
<td>1994</td>
<td>1</td>
<td>3</td>
<td>0</td>
<td>4</td>
</tr>
<tr>
<td>1995</td>
<td>2</td>
<td>0</td>
<td>0</td>
<td>1</td>
</tr>
<tr>
<td>1996</td>
<td>3</td>
<td>0</td>
<td>2</td>
<td>0</td>
</tr>
<tr>
<td>1997</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td>1998</td>
<td>0</td>
<td>0</td>
<td>3</td>
<td>0</td>
</tr>
</tbody>
</table>

did not differ (likelihood ratio = 0.2, \( P = 1.00 \)) for experienced breeders when they had nonbreeders (\( \bar{x} = 0.83 \pm 0.09, n = 12 \)) versus when they had no nonbreeders (\( \bar{x} = 0.77 \pm 0.11, n = 22 \)). In contrast, pairs with nonbreeders have higher demographic success than pairs without nonbreeders in periodically burned scrub at Archbold and KSC (Woolfenden and Fitzpatrick 1984, Mumme 1993).

The frequency of breeding by one-year-olds was independent of sex (likelihood ratio = 0.62, \( P = 0.34 \); Table 3). One-year-olds bred less frequently during the first half of the study than during the second half (likelihood ratio = 12.6, \( P < 0.01 \)). In addition, one-year-olds were more likely (likelihood ratio = 42.3, \( P < 0.001 \)) to breed in the urban area (16 of 29 jays) than in natural landscapes (10 of 197 jays; Woolfenden and Fitzpatrick 1984, Breininger et al. 1996a). In the urban area, all of the two-year-olds bred by their second nesting season after hatching (\( n = 15 \)), whereas only 50% bred in the unfragmented landscapes (Woolfenden and Fitzpatrick 1984, Breininger et al. 1996a).

DISCUSSION

Dispersal distances were longer for urban Florida Scrub-Jays than for those in natural landscapes where nonbreeders have opportunities to monitor many adjacent territories for breeding vacancies. Dispersal patterns and population dynamics did not neatly fit previously described metapopulation structures, partially because of sex differences in dispersal strategies. Frequent dispersals by females within and among the two subpopulations revealed that clusters were not independent. More females dispersed between the subpopulations than dispersed among clusters within the same subpopulation. However, many clusters were sufficiently isolated that males often represented the limiting sex in a cluster even when the total population had fewer females. Most exchanges among clusters were attributed to females that never bred or females that lost their mates and needed to move to the largest clusters to find new mates. Females that lost their mates were much more likely to move to other clusters or another subpopulation to find mates. Male breeders that lost their mates often joined nearby families as nonbreeders until a breeding vacancy became available in the cluster of their residence.

The larger north subpopulation was not a net source of new breeders to the south subpopulation. Most of the smaller clusters were temporarily a net source of replacement breeders to the largest cluster (N1) even though their mortality rates exceeded reproductive success rates. Jays from larger clusters had more chances to fill breeding vacancies without leaving their cluster compared with jays from smaller clusters. Thaxton and Hingtgen (1996) also found that many Florida Scrub-Jays dispersed from scrub fragments into larger tracts of scrub but that Florida Scrub-Jays did not disperse from the large tracts into fragments. There are several advantages to residing within larger population clusters besides the need to find mates. For example, because Florida Scrub-Jays have a well-developed sentinel system for detection of avian predators (McGowan and Woolfenden 1989), jays that live in territories that are partially surrounded by other territories are safer than those that live in isolation.

Local extinctions are not always as stochastic as metapopulation theory assumes, particularly where populations are influenced by disturbance or long-term habitat change (Harrison and Taylor 1997). Poor habitat quality of all habitat fragments was one explanation for population decline. Periodic fires are needed to maintain optimal habitat (Woolfenden and Fitzpatrick 1984, 1991; Schaub et al. 1992; Breininger et al. 1995, 1998; Duncan et al. 1995). Models predict population declines of 25% every five years in large unburned tracts of scrub (Breininger et al. 1996b). The urban population had a higher rate of decline than expected for unburned scrub even before the epidemic. Fragmentation also reduced demographic success because Florida Scrub-Jays were vulnera-
ble to road mortality, and because many predators (Blue Jays, Fish Crows, Boat-tailed Grackles, Common Grackles, house cats [Felis felis]) were abundant in the matrix (Dreschel et al. 1990, Fitzpatrick et al. 1991, Breininger et al. 1995).

Consistently poor reproductive success caused the gradual population decline prior to 1997. Poor habitat quality of urban areas and longer dispersal distances explained the higher mortality rates of nonbreeding Florida Scrub-Jays (Thaxton and Hingtgen 1996). Low breeder survival in 1997 perpetuated the population decline. During 1997, breeder survival in the urban population was nearly identical to that during a previous epidemic in central Florida (Woollenden and Fitzpatrick 1991). No young jays survived to become yearlings during the previous epidemic (Woollenden and Fitzpatrick 1984), but several yearlings were produced in several Atlantic coast populations during 1997 (D. Breininger and D. Oddy unpubl. data). The low abundance of nonbreeders did not explain the urban population decline, because pairs with and without nonbreeders had poor demographic success, and pairs with nonbreeders did not have higher demographic success than pairs without nonbreeders.

This study differed from many other studies of cooperative breeders that reported a stable density of breeders and rare breeding by one-year-olds (e.g. Woollenden and Fitzpatrick 1984, Brown 1987). Although Curry and Grant (1989) observed a stable breeding density of Galapagos Mockingbirds (Nesomimus parvulus), they also found that one-year-olds often bred when harsh years led to low numbers of mockingbirds. One-year-old Florida Scrub-Jays frequently bred in the declining urban population because delayed breeding was influenced by demographic success and the resulting availability of breeding vacancies (Breininger et al. 1996a). The social structure in the highly fragmented landscape changed from a saturated society with many nonbreeders to a more traditional avian society in which only a breeding pair resided within each territory.

Conservation efforts must emphasize acquisition and management of the remaining large tracts of scrub and reserve tracts with minimal fragmentation. Urban fragments probably will contribute little to long-term population size of Florida Scrub-Jays in metapopulations because of poor demographic success. Most fragments would probably seldom be colonized by jays from large tracts of scrub once extinction occurs in small fragments (Thaxton and Hingtgen 1996). Although temporary, Florida Scrub-Jays in fragments can be an important source of individuals to colonize unoccupied areas following restoration in reserves that have remained unburned for too long.

Reserves should be close together because of the low dispersal tendencies of males. Female dispersal might occur at least temporarily across urban landscapes for 15 km providing that scrub fragments are not more than 4.2 km apart. In this study, the frequent propensity to disperse across urban landscapes could have been influenced by the low quality of habitat in all of the fragments. Frequent dispersal by either sex might not occur across similar landscapes once extinction occurs in intervening fragments, because dispersing Florida Scrub-Jays might cue on the presence of other resident jays and not necessarily on scrub habitat alone (Stith et al. 1996).

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**LITERATURE CITED**


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