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EFFECTS OF SUBURBANIZATION AND HABITAT FRAGMENTATION ON FLORIDA SCRUB-JAY DISPERSAL

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Abstract.—Dispersal behavior of Florida Scrub-Jays (*Aphelocoma coerulescens*) was compared for birds with territories in fragmented, suburbanized habitat designated "suburban" and birds with territories in undeveloped habitat designated "preserve." During the 5-year study period, most dispersals from preserve territories occurred in early spring, and from suburban territories in spring and fall. In suburban territories, at least one dispersal occurred during every month of the year. The average dispersal distance for female Florida Scrub-Jays from suburban territories was significantly greater than for females from preserve territories (8.1 km vs. 0.6 km, respectively; $t=10.2$, $p<0.01$). Eight of 29 suburban females of known age dispersed before one year of age. Excluding a daughter that accompanied her mother, none of the 22 female dispersers from preserve territories were less than one year of age. Of 128 dispersals by both sexes, 41 were from suburban to suburban territories, 46 were from preserve to preserve territories, and 41 were from suburban to preserve territories. No birds dispersed from preserve to suburban territories. Longer dispersal distances at an earlier age by suburban females are attributed to habitat fragmentation and the absence of adjacent territories that young birds might monitor for breeding opportunities. The absence of dispersals to suburban territories by preserve birds is attributed to habitat degradation. Higher mortality rates due to dispersal characteristics, and the lack of dispersal from preserve to suburban territories, leave isolated suburban territories more vulnerable to extirpation of their resident birds—a factor that must be considered in conservation plans for this species.

Most Florida Scrub-Jay (*Aphelocoma coerulescens*) habitat in Sarasota County, and in Southwest Florida, has been fragmented and replaced by sprawling suburbs. The scrubby flatwoods preferred by Florida Scrub-Jays is also favored by humans for habitation. It is typically the highest and driest land near the coast, usually consisting of scrub oak-dominated vegetation with scattered patches of bare sand and a few, widely dispersed pine trees. Of an estimated 6,000 ha of scrubby flatwoods originally in Sarasota County, less than 800 ha re-

main (Thaxton, unpubl. data). With the exception of Oscar Scherer State Park near Osprey, Florida, the distribution of scrubby flatwoods occurs as small, scattered "islands" averaging less than 1 ha in size. Suitable habitat maintained at the appropriate successional stage by occasional fires is fundamental to the Florida Scrub-Jay's existence. The future of the species is threatened by habitat fragmentation, degradation, and loss (Cox 1987, Fitzpatrick et al. 1991).

Habitat fragmentation acts in opposition to a central theme for long-term population viability, which is maintenance of genetic variation (Lande and Barrowclough 1987). Isolation of territories to the extent that dispersal mechanisms are thwarted, disrupts genetic exchange. It has been estimated that for an isolated preserve to support a Florida Scrub-Jay population with sufficient genetic heterogeneity to allow at least a 90% chance of persisting more than 100 years, the preserve should be large enough to support 20 to 40 breeding pairs (Woolfenden and Fitzpatrick 1991). Dispersals into the preserve would improve the chances of population viability.

Within a population, dispersals between territories depend on the degree of isolation, which is determined by physical distance and the character of intervening habitat (Gilpin 1987). Specific information on dispersal characteristics is needed to devise management strategies in fragmented habitat. These strategies will depend on the distance birds in fragmented habitat can successfully disperse to find breeding opportunities, on the factors that influence dispersal distance, on the relationship between dispersal characteristics and mortality rate, and on the nature of the dispersal characteristics themselves in fragmented, degraded habitat.

In this paper we compare dispersal characteristics for Florida Scrub-Jay populations in two very different habitat types: suburban areas located on former scrubby flatwoods and undeveloped scrubby flatwoods. We discuss how dispersal characteristics contribute to the decline and potential extirpation of Florida Scrub-Jays in the suburbanized areas of Sarasota County.

Study Area

Sarasota County is on the southwestern coast of Florida, midway between Tampa Bay and Charlotte Harbor (Figure 1). Typical Florida Scrub-Jay habitat in the county consists of scrubby flatwoods (FNAI 1986), that is generally found near the coast and along the original surface drainage features. Predominant vegetative cover consists of a sparse overstory of scattered pines (*Pinus elliottii* var. *densus* and *P. palustris*) and a shrub understory consisting of myrtle oak (*Quercus myrtifolia*), sand live oak (*Q. geminata*), Chapman's oak (*Q. chapmanii*), and saw palmetto (*Serenoa repens*). Bluejack oak (*Q. incana*) also occurs at Oscar Scherer State Park. Other woody shrubs found in the understory include rusty lyonia (*Lyonia fruticosa*), tallowwood (*Ximenia americana*), tarflower (*Befaria racemosa*), and sand holly (*Ilex ambigua*). Portions of the scrubby

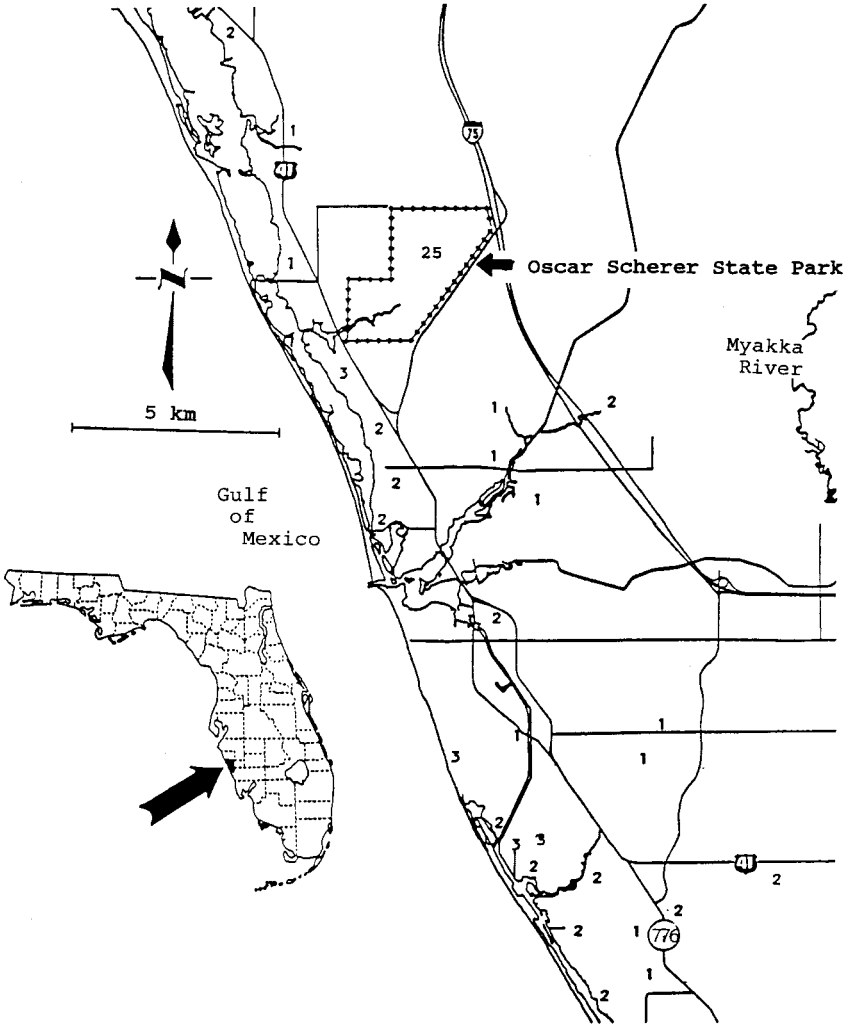

Figure 1. Study area in Sarasota County showing the number and distribution of Florida Scrub-Jay territories. Four outlying territories to the south are not shown.

flatwoods in Oscar Scherer State Park have previously been used as rangeland; introduced pasture grasses still persist.

Oscar Scherer State Park contains the largest undeveloped tract of scrubby flatwoods and the largest Florida Scrub-Jay population remaining in Sarasota County. From 20 to 25 territories ("preserve territories") occur on approximately 250 ha (Figure 1). All Florida Scrub-Jays in Sarasota County outside Oscar Scherer State Park live in suburban habitats. Territories in these areas ("suburban territories") are scattered and often widely separated. Isolated suburban territories in northern Charlotte County were also monitored for dispersing birds.

Some Florida Scrub-Jays persist on suburban territories that are now completely devoid of scrubby flatwoods vegetation. Where such vegetation does remain, it is severely degraded due to partial clearing and fire exclusion. A typical Florida Scrub-Jay territory in a suburban area may include from 0-25% scrubby flatwoods vegetation, with the remainder of the territory developed. Development can include roads, homes, apartment and office buildings, and commercial centers. An abundant food source exists in most suburban territories in the form of handouts (peanuts) from humans.

Data Collection and Definition of Terms

Florida Scrub-Jays are cooperatively breeding birds that reside in territories with well-defined boundaries defended year round by group members. Typically, one monogamous pair of breeding birds occupies each territory (Woolfenden and Fitzpatrick 1984). The members of a Florida Scrub-Jay family can include other adults that are nonbreeding. A "breeder" is a bird that has pair-bonded, built a nest, and laid at least one egg. "Helpers" are mature jays that postpone breeding for one to several years and participate in activities within a breeding pair's territory (Woolfenden and Fitzpatrick 1984). Helpers are often the offspring of the breeding pair.

Nonbreeding adults obtain breeding space in one of several ways (Woolfenden and Fitzpatrick 1984): by (1) "territorial budding" in which a male, paired with an immigrant female, inherits a portion of his natal territory; by (2) direct inheritance of a natal territory following a breeder death; by (3) replacing a breeder on another territory; by (4) establishing a territory *de novo* between existing ones; or by (5) establishing a territory in habitat that was formerly unsuitable but has been restored to an appropriate successional stage (Thaxton and Hingtgen 1994). Typically, females do not acquire territory by territorial budding or direct inheritance. When they pair with a male that has done so, the mechanism of gaining breeding status is designated (6) "mate choice." Occasionally, a female also (7) "shares" a territory with another female.

A "dispersal" is defined as a permanent shift from one territory (usually the natal one) to another. To be considered an "effective" dispersal, the bird must become a breeder in the new territory.

Florida Scrub-Jay dispersals were monitored between April 1989 and April 1994, utilizing unique colored leg bands. A census was conducted monthly, and most nests were located annually allowing offspring to be banded before fledging. Season of dispersal was defined in terms of the Florida Scrub-Jay's breeding cycle. The peak of breeding activity, February through April, was designated "spring." The other seasons followed in sequence.

For statistical analysis, we used the nonparametric chi-square test, uncorrected for continuity, for categorical data (Hayek 1994), and the parametric t-test for distance data. Dispersal distances were calculated by determining the distance from the center of the territory of origin to the center of the new territory. Dispersal distances for territorial budding and direct inheritance, which would have been arbitrarily assigned small values or zero, were excluded from statistical analyses of dispersal distances. In addition, distance data were logarithmically transformed to further correct for non-normality (Steel and Torrie 1980). When variances of samples were unequal, approximations of the t-statistic and degrees of freedom were used (Steel and Torrie 1980). Probabilities of obtaining the observed results under the null hypothesis are given for statistical tests of significance.

Results

Between 1989 and 1994, 816 Florida Scrub-Jays were banded to study population dynamics, including dispersal characteristics. From a

minimum of nine preserve territories and seven suburban territories in 1989, monitoring for dispersals expanded to 25 preserve and 20 suburban territories in 1994 (Figure 1). In addition, 32 suburban territories, located outside the main study area in and around Oscar Scherer State Park, were surveyed for dispersing birds one or more times. During the five years of the study, the dispersal of 128 Florida Scrub-Jays was observed. Forty-six of these were from preserve territories and 32 were from suburban territories (Figure 2).

Eighty percent of dispersals from preserve territories occurred in "spring" (Feb-Apr), with a few observed in other seasons (Figure 3). All preserve dispersers moved to other preserve territories. In comparison, suburban birds dispersed during every month of the year to either preserve or other suburban territories. The destination of suburban dispersers was correlated with season. Most dispersals (51%) from suburban to other suburban territories occurred in "spring", while 71%

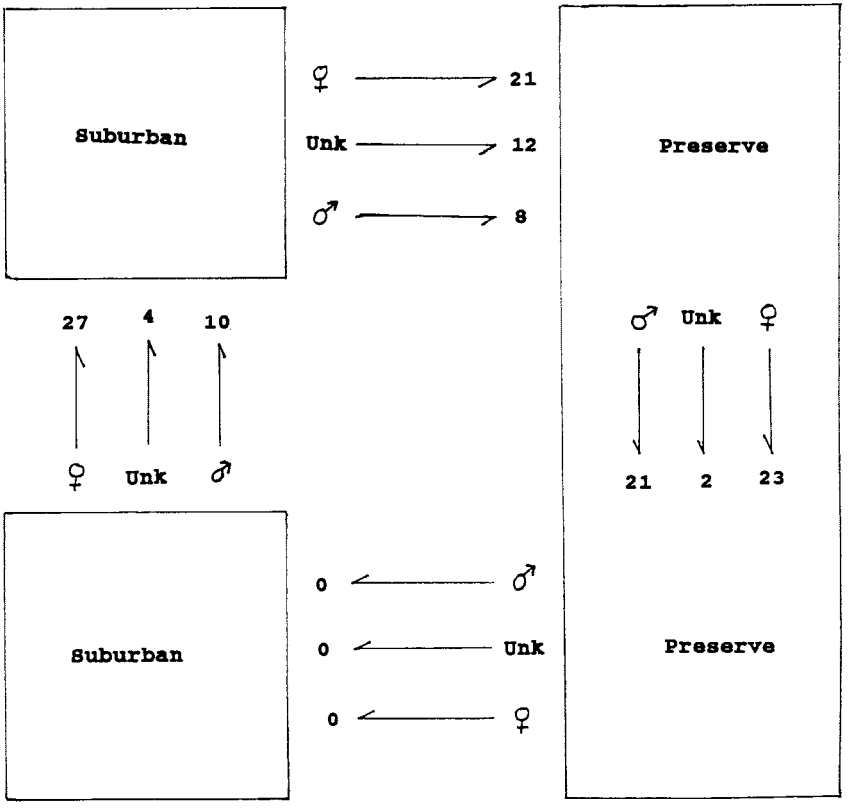

Figure 2. Numbers of dispersals between territory types for Florida Scrub-Jays in Sarasota County.

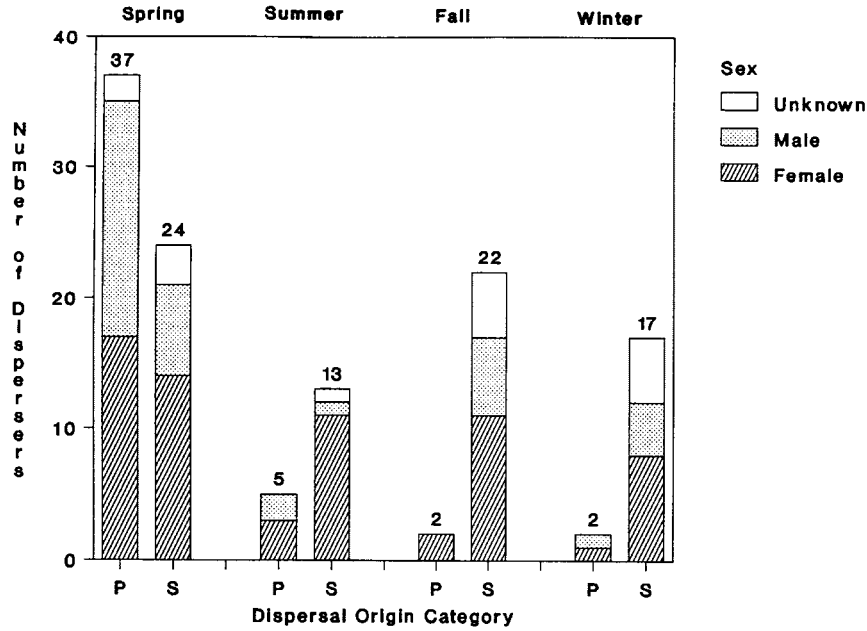

Figure 3. Season of dispersal for Florida Scrub-Jays from preserve (P) and suburban (S) territories, by gender.

of dispersals from suburban to preserve territories occurred in "fall" (Aug-Oct) and "winter" (Nov-Jan) (Figure 4). The seasonal differences were significant for preserve versus suburban dispersers (X^2=29.2, df=3, p<0.001), and for suburban birds dispersing to preserve versus suburban territories (X^2=15.7, df=3, p=0.001). The seasonal patterns of dispersal for preserve and suburban birds were characteristic of both sexes. When only those birds that became breeders ("effective" dispersals) were considered, the pattern was the same, with significantly more suburban than preserve birds dispersing in the "fall" and "winter" (X^2=17.2, df=2, p<0.001), and with late-season, suburban dispersers more likely to move to preserve territories (X^2=10.9, df=2, p=0.004).

Florida Scrub-Jays from suburban territories dispersed significantly farther than did preserve birds of the same sex (Figure 5). Females from suburban territories dispersed an average of 8.1 km, and the dispersal distance was not different for birds moving to preserve versus suburban territories (t=0.4, df=30, p=0.68). This was much greater than the average dispersal distance of 0.6 km for preserve females (t=10.2, df=39.7, p<0.001). The average dispersal distance for suburban males was 1.9 km, compared with only 0.4 km for preserve males (t=3.8, df=17, p=0.002). For suburban but not preserve birds, females dispersed significantly farther than did males (t=3.2, df=37,

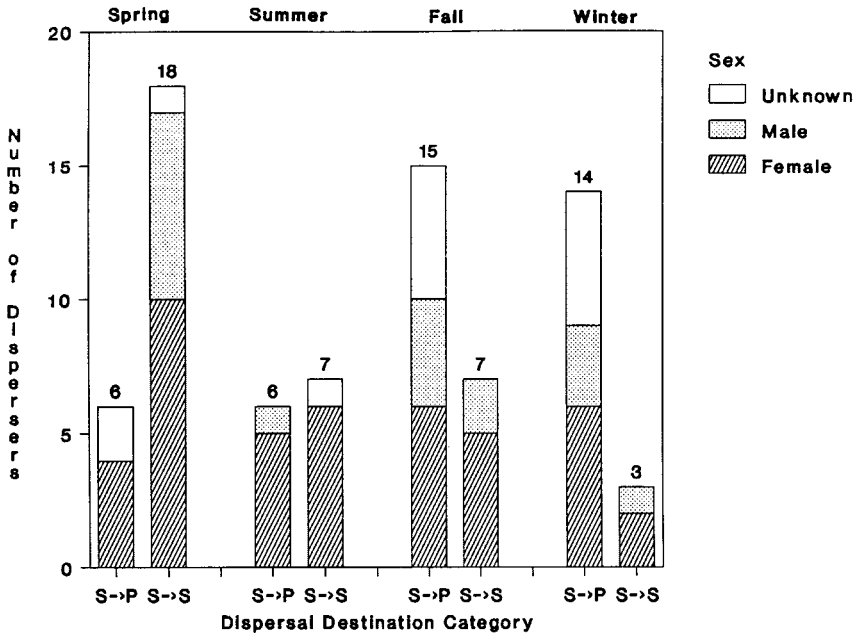

Figure 4. Season of dispersal for Florida Scrub-Jays from suburban territories moving to either preserve (S -> P) or other suburban (S -> S) territories, by gender.

p=0.003; and t=1.1, df=33, p=0.27, respectively). The greatest distances travelled were recorded for four suburban birds of undetermined sex, two which dispersed just over 22.5 km to other suburban territories, and two which dispersed 21.5 km to preserve territories. Another suburban bird, known to be female, dispersed 21.3 km. Suburban females dispersing in the "fall" travelled greater distances than did those dispersing in the "spring" (11.8 km versus 5.8 km; t=3.1, df=12.5, p<0.01).

Some suburban females dispersed at an earlier age than did any other dispersers. Eight of 29 suburban females (28%) of known age dispersed when less than one year old. In contrast, all preserve females, as well as all males in general, participated for a season as helpers in their natal territory before dispersing (with one exception—a young female accompanied her mother in a dispersal from one preserve territory to another).

The fate of female birds after dispersal depended on whether or not they moved to a territory of the same type (Figure 6). Among preserve females, all but one of 22 birds became breeders after dispersing. The single exception did not live long enough to lay eggs. Among suburban females that dispersed to other suburban territories, 21 of 23 birds be-

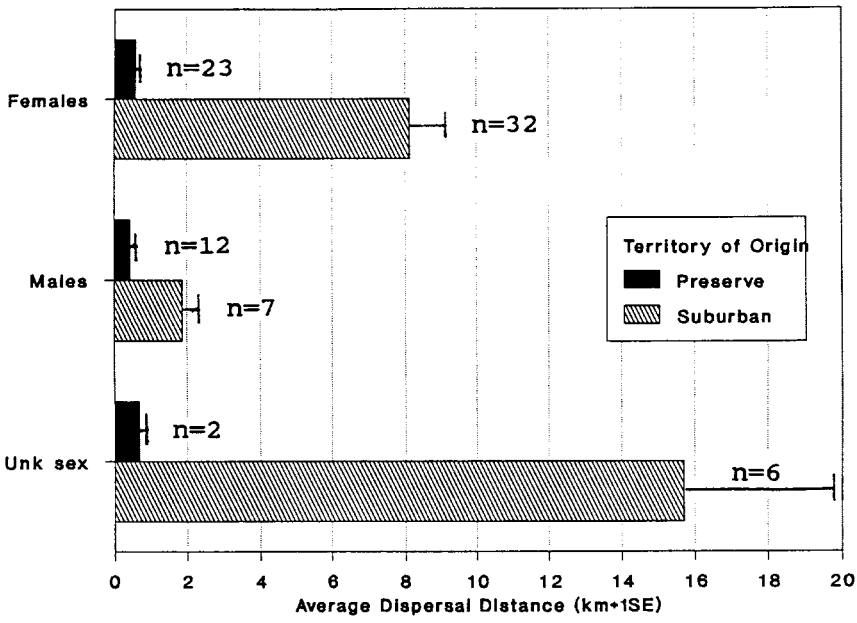

Figure 5. Average dispersal distances from preserve and suburban territories for Florida Scrub-Jays in Sarasota County.

came breeders. One that did not was a juvenile that vanished; the other became a helper. Among suburban females dispersing to preserve territories, only eight of 20 birds became breeders. Six became helpers and six vanished. The latter birds included four of six juveniles (<1 yr) that dispersed to preserve territories. The proportion of suburban females becoming breeders in preserve territories was significantly less than for any other category of dispersers (40% compared with 96% for preserve birds, X^2=15.7, df=1, p<0.001; and compared with 91% for suburban birds moving to other suburban territories, X^2=12.8, df=1, p<0.001). The fate of male birds after dispersal tended to be independent of destination (Figure 7). Approximately 90% of males from all dispersal categories (that is, suburban to suburban, n=10; suburban to preserve, n=8; and preserve to preserve, n=21) became breeders after dispersing.

Dispersing suburban females under one year of age were more likely to disperse to preserve territories than were older females. Among females from suburban territories, six of eight (75%) juveniles moved to preserve territories, compared with 10 of 29 (34%) adults (X^2=4.2, df=1, p=0.04).

The mechanisms of gaining breeding status differed for males and females, and also varied among dispersal categories. Most preserve

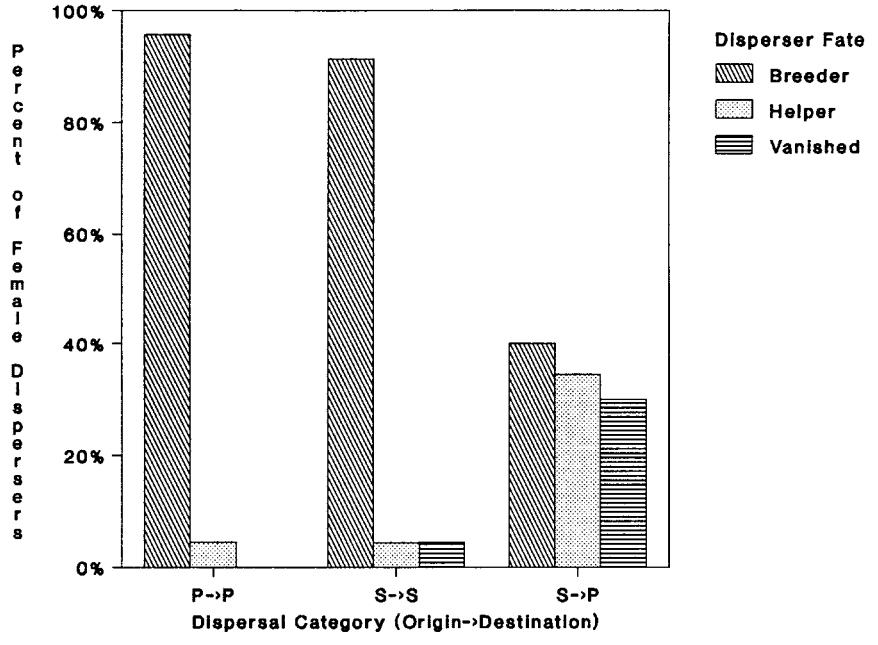

Figure 6. Fate of female Florida Scrub-Jays that dispersed in Sarasota County, grouped by dispersal category ("P" designates preserve and "S" suburban territories).

males gained breeding status by replacing other breeders (37%, n=19) or by territorial budding (32%) (Figure 8). In contrast, only one suburban male (n=14) gained breeding status by territorial budding. Among suburban males effectively dispersing to suburban territories, most (63%, n=8) replaced other breeders. Likewise, most suburban males dispersing to preserve territories (67%, n=6) replaced other breeders. Notably, in the latter category of dispersers, 33% gained breeding status by occupying recently restored scrubby flatwoods.

Preserve females most often gained breeding status by replacing other breeders (77%, n=22) (Figure 9). This was also the mechanism utilized by suburban females dispersing to suburban territories (69%; n=13, excluding eight cases where the mechanism was not determined). Remarkably, among suburban females dispersing to preserve territories, 83% (n=6) gained breeding status by occupying recently restored scrubby flatwoods (Thaxton and Hingtgen 1994). This was the only dispersal category of females to utilize this mechanism.

DISCUSSION

"Dispersal is . . . the most critical issue facing students of most cooperative systems" (Woolfenden and Fitzpatrick 1984). The develop-

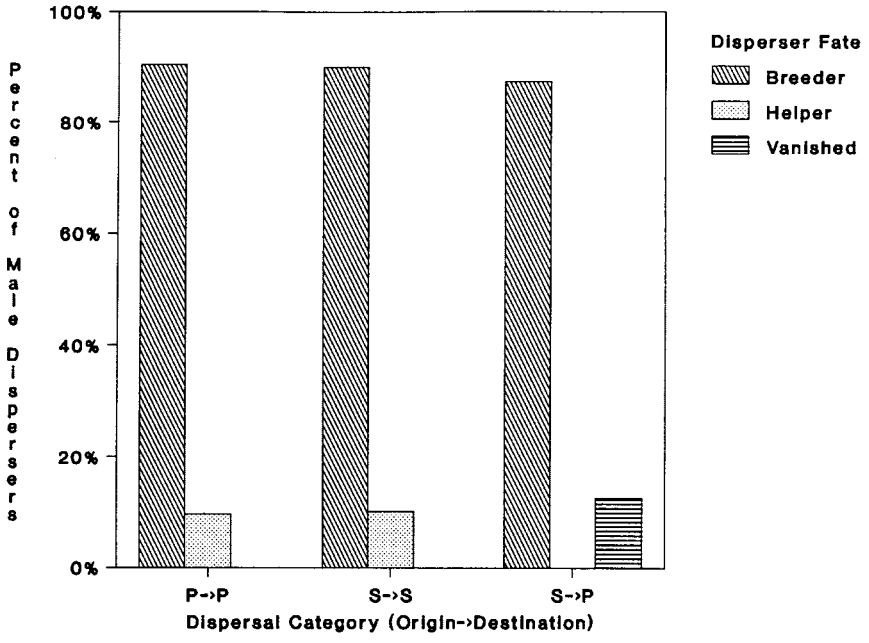

Figure 7. Fate of male Florida Scrub-Jays that dispersed in Sarasota County, grouped by dispersal category ("P" designates preserve and "S" suburban territories).

ment of cooperative breeding seems to be fostered where access is limited to a resource critical for successful breeding, leading some adults to delay dispersal and reproduction (Fitzpatrick and Woolfenden 1986).

Dispersal strategies differ between the sexes (Woolfenden and Fitzpatrick 1984), and data for Florida Scrub-Jays in Sarasota County show significant differences in the dispersal behavior of males and females in suburban and natural environments.

The difference in dispersal strategies for male and female Florida Scrub-Jays is "probably due to the different potential each sex has for inheriting breeding space" (Woolfenden and Fitzpatrick 1984). Males are more likely to spend one to three years helping a breeding pair, whereas females disperse earlier and are less active in defending the territory (Woolfenden and Fitzpatrick 1986). The potential to inherit "quality" habitat is greatly reduced for males remaining as helpers in suburban territories compared with preserve territories. Suburban males were much less likely to maintain any natal territory as breeders. Most replaced deceased breeders on existing territories, that required longer dispersals.

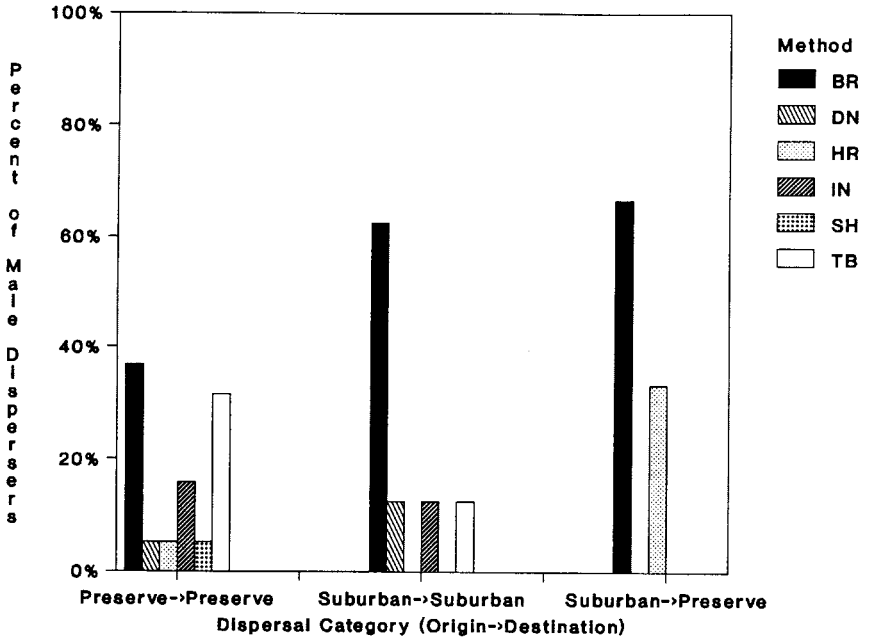

Figure 8. Percent of male Florida Scrub-Jay dispersers that gained breeding status by each of the following methods: BR = breeder replacement, DN = *de novo*, HR = habitat restoration, IN = direct inheritance, SH = sharing, and TB = territorial budding. Grouped by dispersal category.

Female suburban Florida Scrub-Jays exhibited some of the longest dispersals ever reported. One travelled over 20 km to become a breeder in another suburban territory. Suburban females were much more likely to disperse at an earlier age, and dispersals occurred during every month of the year. The tendency to delay breeding and engage in helping behavior, characteristic of birds in natural habitat, is greatly reduced for females that have fledged in isolated, suburbanized territories. The characteristics of suburban territories favor early dispersal and breeding as a superior option for some individuals (See discussion in Koenig et al. 1992). These characteristics include a lack of territories adjoining natal territories that can be monitored by suburban females for breeding space. Females from suburban territories may also have fewer opportunities to pair with single males, because most males that gain breeding space on suburban territories do so by breeder replacement.

The longer dispersals from suburban territories may increase the risk of mortality before a breeding space is found (Woolfenden and Fitzpatrick 1986). In addition, age affects survival rates of dispersers.

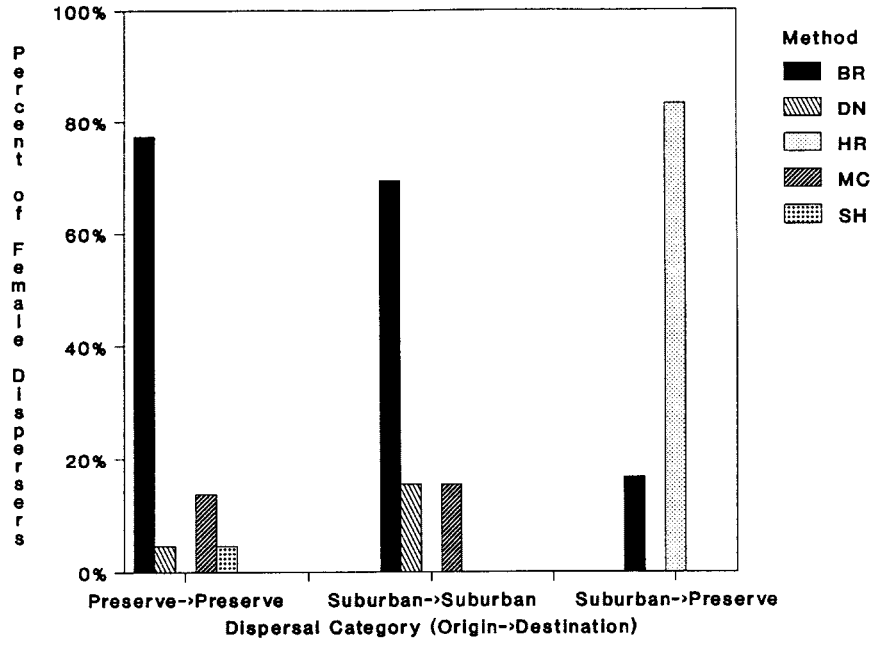

Figure 9. Percent of female Florida Scrub-Jay dispersers that gained breeding status by each of the following methods: BR = breeder replacement, DN = *de novo*, HR = habitat restoration, MC = mate choice, and SH = sharing. Grouped by dispersal category.

Survivorship of females dispersing within their first year is probably much less than 31% (Fitzpatrick and Woolfenden 1986). In our study, if dispersers that vanished are assumed dead, mortality rates for suburban dispersers, especially those moving at a young age, are higher than for dispersers in natural habitat.

When a suburban territory loses its resident birds, it has a higher probability of remaining vacant. Florida Scrub-Jays from preserves are not likely to disperse into suburban areas. Birds from suburban territories will disperse up to 22 km away to obtain breeding space. However, where no scrubby flatwoods habitat remains and where the resident Florida Scrub-Jays are no longer present, suburban territories are probably unattractive to dispersing birds. Consequently, populations in suburban areas are likely to decrease.

Ensuring the survival of Florida Scrub-Jays on territories that have been, or are in danger of becoming, isolated and degraded by suburban encroachment presents a formidable challenge. But, the challenge needs to be addressed to optimize the chances of maintaining a viable Florida Scrub-Jay population on Florida's southwestern coast.

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