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EVALUATING THE EFFECTS OF HABITAT QUALITY, CONNECTIVITY, AND CATASTROPHES ON A THREATENED SPECIES

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Abstract. Conserving threatened and endangered species requires an understanding of the effects that variability in habitat, environment, demographics, and genetics have on the long-term viability of the species. The Florida Scrub Jay (*Aphelocoma coerulescens*), which has been the focus of intensive, long-term study and recent conservation efforts, makes an excellent candidate to illustrate how population modeling can be used to examine these effects on a threatened species. A stage-based population model, including density dependence and stochasticity, was used to explore the effects of habitat quality, connectivity, and catastrophes on long-term survival for four populations of Scrub Jays in Brevard County, Florida, United States. Restoring high-quality habitat was critical for long-term viability of these Scrub Jay populations. The quality of the scrub habitat, based on field surveys, is too overgrown to support the populations for the next 60 yr, and extinction is likely in <30 yr. These populations are unlikely to survive an epidemic or catastrophe without dispersal among the habitat patches and populations. The present research effectively illustrates how population modeling can be used to explore links between demographic processes and the environment, and to evaluate management strategies for habitat specialist species.

Key words: Aphelocoma coerulescens; *connectivity; conservation; epidemics; Florida Scrub Jay; habitat quality; habitat specialist; population modeling; population viability analysis; quasiextinction; spatially explicit metapopulation model.*

INTRODUCTION

Populations of rare species are influenced by a variety of deterministic and stochastic factors such as hurricanes or fires, random changes in birth or death rates, changes in habitat quality or amount, and inbreeding or genetic drift (Gilpin and Soulé 1986, Soulé 1987, Burgman et al. 1993). To conserve such rare species, there is a critical need to assess the impacts of these factors on the long-term survival of an individual population. This requires detailed information about the biology of the species concerned, the habitat it prefers, and the factors that might affect both of these (Shaffer 1990, Boyce 1992, Burgman et al. 1993).

In contrast to species such as the Northern Spotted Owl *Strix occidentalis* (Thomas et al. 1990, Lamberson et al. 1992) and Florida panther *Felis concolor coryi* (Maehr 1990), the Florida Scrub Jay *Aphelocoma coerulescens* is an excellent candidate for such analysis, because much is already known about the biology of this rare species from long-term field studies (Woolfenden and Fitzpatrick 1984, 1991). Also, extensive spatial data, including habitat quality (Swain et al. 1995), have been collected for both Scrub Jays and scrub habitat in Brevard County, Florida, United States. These data provide a suitable case study for demonstrating the effective use of population modeling to examine the impacts of habitat quality, connectivity, and catastrophes on small populations.

Habitat loss or modification is regarded as the major threat for most of the world's threatened and endangered species (Burgman et al. 1993, Kerr and Currie 1995), affecting 76% of these species (World Conservation Monitoring Centre 1992). It is thought to be the single most important cause of extinctions past (Gould and Eldredge 1977) and present (May 1988, 1990, Boyce 1992). The loss of stochastic elements such as periodic fires also drastically reduces the quality and suitability of habitat for many rare species adapted to disturbance-prone environments (Hawkes and Menges 1996). The Florida Scrub Jay is no exception. The rapidly expanding human population of Florida has caused a dramatic reduction in the amount of suitable habitat for Scrub Jays, through development and changes in agricultural practices (Cox 1987, Bergen 1994, Pranty 1996). The quality of the remaining habitat has declined because of suppression of the natural fire cycle that historically maintained such scrub habitat (Myers 1990).

Throughout the state of Florida, little of the original scrub habitat remains (Cox 1987, Fernald 1989; J. W. Fitzpatrick, R. Bowman, D. Breininger, M. A. O'Connell, B. Stith, J. Thaxton, B. Toland, and G. E. Woolfenden, *unpublished manuscript*). Concomitantly, the Scrub Jay has been effectively extirpated in 10 out of 39 counties of Florida and is present, as fewer than 10 families, in five out of the 39 counties. Today's

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TABLE 1. A comparison of the number of Florida Scrub Jay families, the total habitat occupied by Scrub Jays, and the area of scrub habitat in four habitat quality classes and in four populations in Brevard County, Florida, USA.

				Scrub habitat quality class (ha):			
Population	Jay families (no.)	Area occupied by jays (ha)	Total scrub (ha)	Optimal	Slightly overgrown	Moderately overgrown	Very overgrown
South Brevard	175	4925.6	1726.0	50.3	481.0	719.8	475.0
Central Brevard	50	1133.1	740.4	0.0	185.4	269.2	285.8
North Brevard	101	3355.8	2553.2	45.2	439.0	1492.2	576.8
South Beaches	29	519.0	363.5	0.0	59.6	266.5	37.4
Total	355	8895.5	5383.1	95.4	1164.9	2747.7	1375.0

Note: Data are based on extensive field surveys (Swain et al. 1995, Root 1996).

statewide population is probably <10% of its original number (Pranty 1996; J. W. Fitzpatrick et al., *unpublished manuscript*). In Brevard County, where 38% of the remaining Scrub Jays in Florida reside, 68% of the scrub habitat in the north and central parts of the county has been lost since 1943 (Bergen 1994). Therefore, the Scrub Jay in Brevard County represents a clear example of a rare habitat specialist threatened by habitat loss and modification and by suppression of natural stochastic processes. The Florida Scrub Jay's threatened status demands careful population modeling to assess long-term viability.

Effective population modeling, however, requires detailed information about the demographics, density dependence, dispersal characteristics, habitat requirements, exposure to catastrophes, population sizes, and distribution of required habitat of the species. The Florida Scrub Jay is one of the few species for which we have such information, based on 30-yr ecological studies in central Florida.

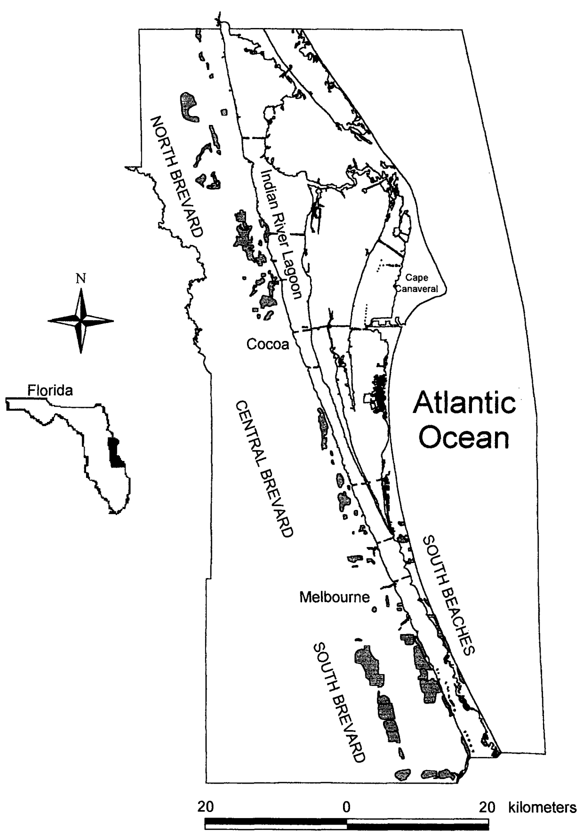

FIG. 1. The distribution of Florida Scrub Jay areas of occupancy on nonfederal land in four satellite populations in Brevard County, Florida, USA, based on field surveys from February to September 1993 (Swain et al. 1995). The four populations are South Brevard, Central Brevard, North Brevard, and South Beaches.

These long-term studies have shown that the Florida Scrub Jay is a long-lived, slowly reproducing, monogamous, territorial, scrub habitat specialist, as well as a cooperative breeder and a poor disperser (Woolfenden and Fitzpatrick 1984, 1991). On average, a Scrub Jay family, i.e., a mated pair with 1–5 juveniles and up to six helpers, vigorously defends 9 ha of scrub habitat for foraging and nesting (Woolfenden and Fitzpatrick 1984). Nonbreeding adults may remain at the natal territory as helpers for up to 5 yr before dispersing, on average <1 km, in search of a mate or territory (Woolfenden and Fitzpatrick 1986, 1991). Also, Florida Scrub Jays require infrequently burned (5–40 yr, on average; Myers 1985, 1990) oak scrub habitat found on well-drained soils. Suitable Scrub Jay habitat has little or no canopy, consists of small oaks (*Quercus* spp.) and shrubs (<2 m in height), and has bare open patches of sand scattered throughout.

In Brevard County, a regional conservation effort, the Scrub Conservation and Development Plan, included extensive field surveys (Swain et al. 1995, Root 1996) of the 374 families or breeding pairs of Scrub Jays and the available 5383 ha of scrub habitat on nonfederal lands (Table 1). Scrub Jays are found in six discrete populations, which are separated from each other by barriers to normal dispersal, i.e., urban areas of the cities of Melbourne and Cocoa, or open water of the Indian River Lagoon. This research focused on four populations (South Brevard, Central Brevard, North Brevard, and South Beaches) on the nonfederal lands of Brevard County (Fig. 1). These four populations were considered a metapopulation, generally functioning as independent populations that were connected by rare long-distance dispersal events.

The question of interest is the long-term viability of

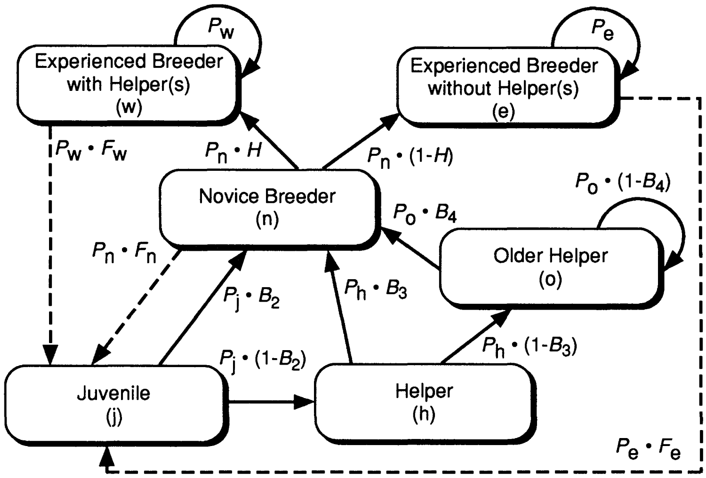

FIG. 2. Schematic representation of the relationship among the six Florida Scrub Jay life history stages in the population model constructed. Solid lines represent the movement of individuals from one stage to another; dashed lines represent production of new individuals. P_x is the annual probability of survival of stage x, B_y is the probability of breeding in year y, H is the probability of having helper(s), and F_x is the fecundity of stage x.

a rare species threatened by habitat loss and modification. With the four Scrub Jay populations in Brevard County as a case study, I used population modeling to address the following questions, applicable for conservation efforts of rare species. (1) What effect does habitat quality have on the probability of extinction? (2) What is the likelihood of persistence, given field-surveyed habitat conditions? (3) How does the introduction of a natural catastrophe or epidemic affect long-term survival? (4) How does the spatial distribution of suitable habitat patches affect extinction rates? (5) Is dispersal among patches within a population critical for long-term viability?

METHODS

I constructed a female-only, stochastic, six-stage population model in RAMAS STAGE (Ferson 1991), and a slightly modified version in RAMAS GIS (Akçakaya 1994). Using these models, I examined the effects of the habitat conditions as measured at the time of the field surveys, gradually deteriorating habitat quality, and full, rapid restoration of habitat quality, in turn, for each of four populations of Florida Scrub Jays in Brevard County (Fig. 1) in RAMAS STAGE. I also examined the effects of dispersal among the populations and of local and regional epidemics in RAMAS GIS for each population.

Basic stage-based model

The six-stage population model (Fig. 2; Root 1996) retains distinct helper stages, separates experienced breeders with helpers from those without helpers, and achieves a finite growth rate close to 1.0 (as measured in field studies; Woolfenden and Fitzpatrick 1984). This model successfully predicts the population size of a 10 yr subsample of the Archbold field data (Woolfenden and Fitzpatrick 1984).

Juveniles in the model were individuals from age 0 to 11 mo. Helpers and older helpers were nonbreeding adults 1 yr and >2 yr old, respectively. All breeding adults were either first-time (i.e., novice) breeders (>2 yr old), or experienced breeders (>3 yr old) without (EBO), or with (EBH) one or more helpers. Implicit in the model were the following assumptions: the four Scrub Jay populations were independent, the Scrub Jays were monogamous, and there was a 1:1 sex ratio.

The standard deviation around the mean trajectory produced by any stage-based model in RAMAS STAGE increased enormously beyond 60 yr of simulation; therefore, I ran the model for 60 yr for a minimum of 1000 simulations (Root 1996). Additionally, in RAMAS STAGE (Ferson 1991), I performed sensitivity and elasticity analyses on the deterministic version of the basic model.

Model parameters

Demographic parameters.—Woolfenden and Fitzpatrick (1984, 1991) have collected detailed demographic data from long-term studies of Florida Scrub Jays in optimal habitat at Archbold Biological Station in Central Florida. From these data, I estimated the probability of survival for juveniles, helpers, older helpers, and novice breeders, based on a life table of 20 yr of field data for 725 banded individuals (Table 2; Woolfenden and Fitzpatrick 1984). It is important to note that these data included a single epidemic event in which all of the juveniles and half of the adults perished between September 1979 and February 1980 (Woolfenden and Fitzpatrick 1984). For experienced breeders with and without helpers, I determined the probability of survival separately, using a data set based on 523 breeder years (Table 2; Woolfenden and Fitzpatrick 1984).

The annual probability of breeding at each stage, B_i, was determined using the life table and the following equation:

$$B_i = \frac{\mathrm{Nov}(x)}{1 - \mathrm{Exp}(x)}$$

where Nov(x) was the proportion of novice breeders at

TABLE 2. (A) Annual probabilities (mean ± 1 SD) of survival, breeding, and having a helper, and (B) annual fecundity. EBO denotes an experienced breeder without helpers, and EBH denotes an experienced breeder with helpers.

A)

Event	Annual probability, by habitat condition			
	Optimal†	Slightly overgrown‡	Moderately overgrown§	Very overgrown‖
Survival				
Juvenile	0.34 ± 0.09	0.32 ± 0.08	0.31 ± 0.08	0.31 ± 0.08
Helper	0.64 ± 0.16	0.61 ± 0.16	0.58 ± 0.15	0.58 ± 0.15
Older helper	0.74 ± 0.19	0.70 ± 0.18	0.67 ± 0.17	0.67 ± 0.17
Novice	0.74 ± 0.08	0.70 ± 0.08	0.67 ± 0.07	0.67 ± 0.07
EBO	0.77 ± 0.09¶	0.73 ± 0.08	0.69 ± 0.08	0.69 ± 0.08
EBH	0.85 ± 0.09¶	0.81 ± 0.09	0.76 ± 0.09	0.76 ± 0.09
Breeding				
At age 2	0.52	0.52	0.52	0.52
At age 3	0.31	0.31	0.31	0.31
At age ≥ 4	0.23	0.23	0.23	0.23
Helper(s)	0.52	0.52	0.52	0.52

B)

Life history stage	Fecundity††			
	Optimal	Slightly overgrown	Moderately overgrown	Very overgrown
Novice	0.88 ± 1.11‡‡	0.84 ± 1.06	0.80 ± 1.00	0.00
EBO	0.90 ± 1.07‡‡	0.85 ± 1.02	0.81 ± 0.96	0.00
EBH	1.29 ± 1.23‡‡	1.23 ± 1.17	1.16 ± 1.11	0.00

† From Woolfenden and Fitzpatrick 1984: Table 9.10, based on $N = 725$.
‡ A 5% reduction in optimal parameter means.
§ A 10% reduction in optimal parameter means.
‖ Same as § but with no reproduction.
¶ G. Woolfenden and J. Fitzpatrick, *personal communication* ($N = 523$ breeder years).
†† Fecundity represents the number of 1-yr-olds produced per female per year.
‡‡ From raw data for Marzluff et al. (1996), supplied by G. Woolfenden ($N = 477$).

age x and Exp(x) was the proportion of experienced breeders at age x (Table 2; Woolfenden and Fitzpatrick 1984).

From a larger data set ($N = 477$ pairs), I calculated the fecundity of each breeder stage and the probability of having helpers (G. Woolfenden, *personal communication*). To simplify the model, I assumed that the life history stage of novice breeders represented only pairings of novice with novice. Novice breeders paired with experienced breeders were placed in one of the two experienced-helper life history stages, based on whether or not they had helpers. I assigned coefficients of variation for the probability of survival as 25.7% for nonbreeders and 11.1% for breeders; coefficients of variation for fecundity were 126%, 119%, and 95.2% for novice, EBO, and EBH, respectively (Table 2).

Scrub Jays.—In Brevard County, Swain et al. (1995) documented and incorporated into a GIS (Geographic Information System) coverage in PC ARC/INFO (version 3.4.2, Environmental Systems Research Institute, Redlands, California, USA) four populations on nonfederal lands (Table 1, Fig. 1). South Brevard had 175 families, Central Brevard had 50 families, North Brevard had 101 families, and South Beaches had 29 families of Florida Scrub Jays. Swain et al. (1995) estimated the sizes of the populations based on field surveys. These surveys used high-quality audio recordings of territorial calls to attract Scrub Jays along parallel line transects (Fitzpatrick et al. 1991) of nearly all patches of scrub with xeric oak on well-drained soils (Breininger in Swain et al. 1995). For all patches, i.e., polygons, the number of breeders present was noted. Swain et al. (1995) defined an occupied-area polygon as the area occupied by a group (one or more families) of Scrub Jays up to some discrete boundary, e.g., unsuitable habitat, major roads, or large bodies of water. These occupied-area polygons were not strictly territories, because they included areas occupied by more than one family, as well as human-made structures and small wetlands that may be unimportant to Scrub Jays.

Scrub habitat.—Swain et al. (1995) surveyed all xeric oak, scrubby flatwoods, coastal-strand scrub, and sand-pine habitats in the four Brevard Country populations and compiled these into in a GIS coverage in PC ARC/INFO. In addition, ~86% of the total area was rapidly field-characterized as to area, location, type of habitat, quality, and restoration requirements (Table 1; Swain et al. 1995). The unsurveyed polygons were isolated, usually very small (8 ha), of generally poor habitat quality, and sometimes inaccessible.

Breininger (1992) developed a model of Scrub Jay preferences and corresponding reproductive success for Kennedy Space Center in Brevard County, which was recently field verified (Breininger et al. 1995). His model suggested that the best sites for jays were: >50% scrub oak; <16% pine canopy; a mean height of 1–2 m; 20–50% open space; >100 m from a forest or closed canopy edge; and ≥300 m from a road with a speed limit >35 miles per hour (56.3 km/h). Loosely based on this model, I classified habitat quality for each scrub polygon, based on Scrub Jay requirements (Table 1; Root 1996). Using these classifications, ~one-half of the scrub habitat that is available for these four Scrub Jay populations in Brevard County on nonfederal land is currently unoccupied, and only 24% of the scrub habitat is in excellent condition, in terms of Scrub Jay requirements (Table 1; Root 1996).

Density dependence.—To incorporate density dependence into the population model, I used a ceiling on the number of experienced breeders allowed in RAMAS STAGE and a Beverton-Holt function, which mimics contest competition or territoriality in RAMAS GIS. Based on territory sizes measured in the field (Woolfenden and Fitzpatrick 1984, 1991), I allowed only one experienced female breeder per 9 ha of scrub habitat at saturation. At saturation, 47.6% of the breeders had no helpers and 52.4% had one or more helpers (Root 1996).

For the spatially explicit variants of the model, I utilized the Beverton-Holt function (Akçakaya 1994) to simulate density dependence:

$$R(t) = \frac{R_{max}K}{(R_{max}N(t)) - (N(t) + K)},$$

where R_{max} was the maximum growth rate, $N(t)$ was the number of Scrub Jays at time (t), and K was the carrying capacity. The Beverton-Holt function was chosen in place of the ceiling on only the breeder stages, which was not an option in RAMAS GIS. Based on field studies and the constraints of the program, I assumed that the maximum growth rate (R_{max}) was 1.01 and the carrying capacity (K) for each population was one female breeder per 9 ha of scrub habitat.

Habitat quality

In the model, varying habitat quality was simulated by modifying the demographic rates, based on the field surveys of scrub habitat quality (Root 1996). I classified scrub habitat as optimal (OP), slightly overgrown (SO), moderately overgrown (MO), or very overgrown (VO), based on Scrub Jay requirements (Table 1). Unsurveyed scrub habitat was assumed to be moderately overgrown. Suggestive field data (Woolfenden and Fitzpatrick 1984, 1991; D. Breininger, *unpublished data*; R. Bowman, *unpublished data*) provided guidelines for the following reductions. Scrub Jays in slightly overgrown scrub habitat were assigned a 5% reduction in the optimal mean probability of survival and fecundity values for each stage (Table 2). Birds in moderately overgrown scrub habitat were assigned a 10% reduction in the optimal survival and fecundity values for each stage. Birds in very overgrown scrub habitat were assigned a 10% reduction in optimal survival plus a zero fecundity value. Scrub Jays in optimal scrub habitat were assigned the optimal survival and fecundity values (Table 2).

I constructed a variant of the model in which the scrub habitat and the Scrub Jays occupying it were assigned to OP, SO, MO, or VO, based on the field surveys (Table 1; Root 1996). First, I examined the effects of habitat quality as measured in the field surveys, assuming no changes in habitat quality for each of the populations. In the absence of fire, however, it is likely that the scrub habitat would deteriorate, not remain static, as it became more overgrown. Second, I simulated deteriorating habitat quality with a 0.25% decline per year in demographic rates for each independent category. Within 40 yr, Scrub Jays in all habitat categories experienced demographic rates equivalent to those in very overgrown habitat and, these conditions prevailed for the remainder of the simulation (Table 2). Because the reintroduction of fire or a similar disturbance management regime could restore the quality of these scrub habitats, I simulated rapid restoration of scrub habitat with a 1% increase per year in demographic rates, until Scrub Jays in all habitats experienced demographic rates equivalent to those in optimal habitat for the remainder of the simulation (Table 2).

Dispersal

I assessed the effects of connectivity using a spatially explicit variant of the model, in RAMAS GIS, with each population represented by the occupied-area polygons from the GIS coverage (Fig. 1; Root 1996). In this model, dispersal among all occupied-area polygons was a function of the nearest neighbor distance, measured using PC ArcView (version 2.0, Environmental Systems Research Institute, Redlands, California, USA), and the frequency distribution of Scrub Jay dispersal based on long-term studies (Woolfenden and Fitzpatrick 1984). Because the probability of dispersal across large bodies of water is low for Scrub Jays (J. W. Fitzpatrick et al., *unpublished manuscript*), I assigned an annual probability of 0.001 to dispersal across the open water of the Indian River Lagoon to or from South Beaches, regardless of the distance.

Catastrophes

Woolfenden and Fitzpatrick (1984, 1991) documented a single epidemic event at Archbold in which half of the adult Florida Scrub Jays and all of the juveniles perished due to a virus (Marzluff et al. 1996). I incorporated such a catastrophic element into the model with an annual probability of 5%. In the model, local epidemics affected only an individual population and regional epidemics affected areas in more than one population. I made no assumptions in the model about the causative agent of the catastrophes included.

RESULTS

The basic stage-based model, which included density dependence and assumed static optimal habitat conditions, produced a slight initial increase and then stable mean population trajectories for the four Florida

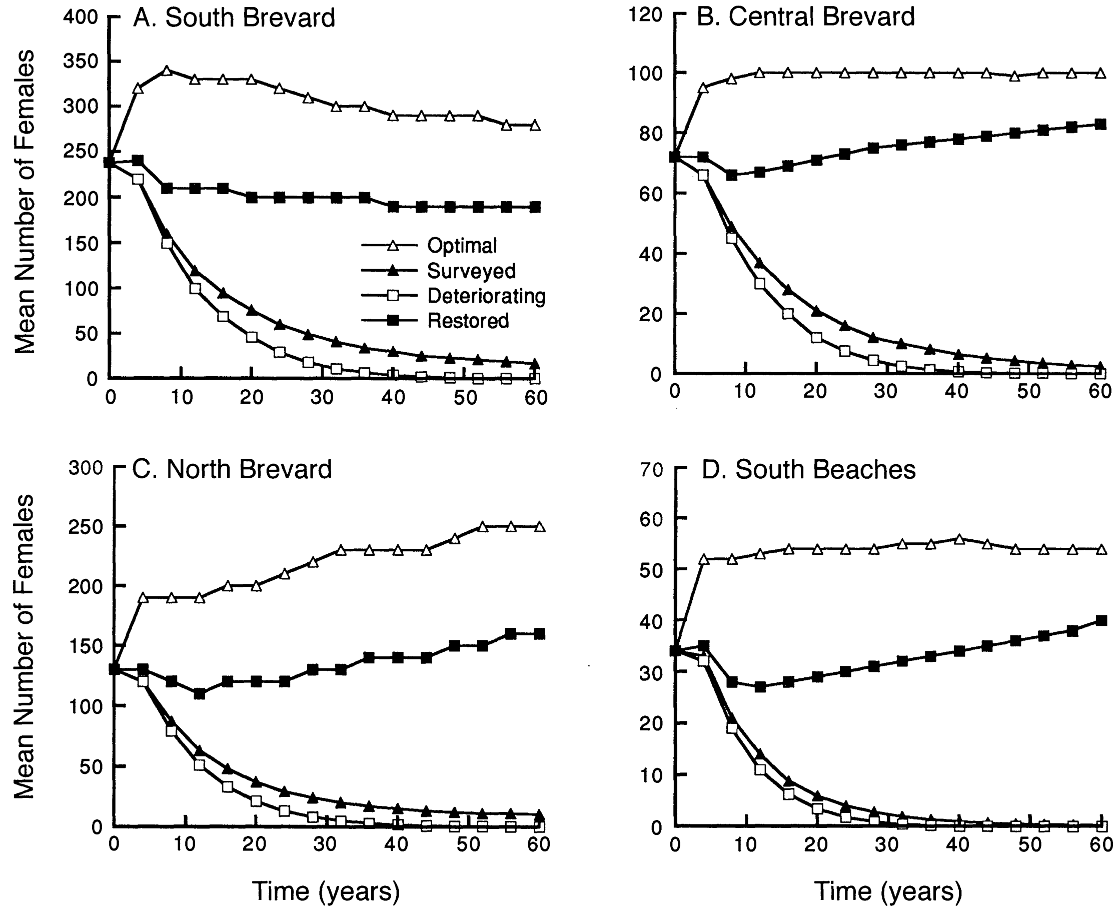

FIG. 3. Mean population trajectories over 60 yr for female Florida Scrub Jays under the stage-based population model for (A) South Brevard, (B) Central Brevard, (C) North Brevard, and (D) South Beaches, with assumed optimal, field-surveyed (surveyed), deteriorating, or fully restored scrub habitat quality conditions.

Scrub Jay populations, with a finite growth rate of 1.009. North Brevard and South Beaches showed the largest increase in final mean female abundance, 159%, and South Brevard the smallest, 117%. The mean trajectories reflected the relative initial densities of the four populations. South Brevard, which has the highest bird density, reached the breeder ceiling early in the simulation period and leveled off at a slightly lower female abundance. North Brevard, on the other hand, which has the lowest initial density, continued to increase in mean abundance over the entire simulation, never reaching the imposed breeder ceiling. The mean number of females for Central Brevard and South Beaches rapidly increased to the breeder ceiling and stabilized there. The probability of any of the populations dropping below 10 females (quasiextinction) was slight; the chance of quasiextinction at 60 yr ranged from 27.5% to 0.1% under optimal habitat conditions.

An elasticity analysis, which assessed the impact of changes in model parameters on the growth of the population, suggested that changes in experienced-breeder survival, as well as survival and breeding in the second year of life, had the largest impact on the population growth trends. Overall, breeder survival had a greater impact on the population trajectories than did reproductive output.

Effects of habitat quality

The imposition of field-surveyed conditions of habitat quality resulted in a marked decline for all four populations (Fig. 3). By 21 yr, each of the four populations had, on average, <40 females (an 83–100% reduction). South Brevard and North Brevard, which had >100 birds initially, declined more slowly than Central Brevard and South Beaches. The probability of quasiextinction (P(qe)) for each of the populations under these static, field-surveyed conditions was much greater than under optimal habitat conditions. P(qe) reached 100% for Central Brevard, North Brevard, and South Beaches, and increased from 0.1% to 84% for South Brevard, the largest population (Fig. 3).

Progressively deteriorating habitat conditions resulted in an even faster decline for each population;

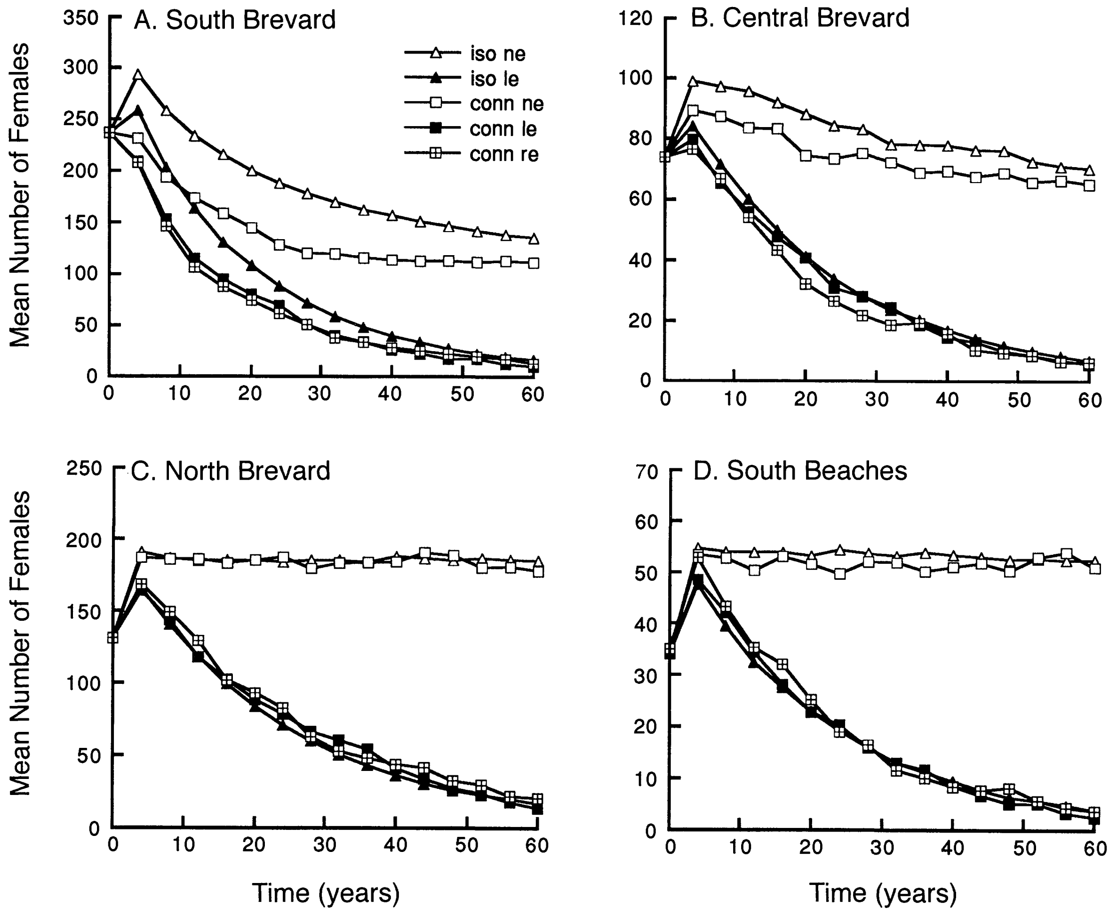

FIG. 4. Mean population trajectories for Florida Scrub Jays, assuming optimal habitat, under the stage-based population model for (A) South Brevard, (B) Central Brevard, (C) North Brevard, and (D) South Beaches, over 60 yr. Shown are the results for isolated populations without epidemics (iso ne) and with local epidemics (iso le); and for populations connected by dispersal with no epidemics (conn ne), with local epidemics (conn le), and with regional epidemics (conn re).

within 19 yr of simulation, all four populations had dropped below 40 females, on average (an 83–100% reduction; Fig. 3). The larger populations of South Brevard and North Brevard persisted longer, but all went extinct by the end of 60 yr. The probability of quasiextinction under progressive habitat deterioration was 100% within 5–50 yr. Within a given population, only Scrub Jays occupying scrub of optimal habitat quality were able to maintain their complement of breeders for any period. Those occupying the overgrown and severely overgrown habitat showed dramatic and immediate declines (Root 1996).

Following an initial immediate decline in female abundance, rapid restoration of habitat quality produced a recovery, with increases of 115–123% of initial population levels, for Central Brevard, North Brevard, and South Beaches (Fig. 3). In South Brevard, though, it was not clear at 60 yr whether the population was recovering or continuing a slow decline (190 females compared to an initial 230). In contrast to the high quasiextinction risk under static field-surveyed or declining habitat quality conditions, the probability of quasiextinction under restoration of habitat conditions was 0% for the entire simulation period of 60 yr for all four Scrub Jay populations (Fig. 3).

Effects of connectivity

The basic stage-based model constructed in RAMAS GIS, with density dependence modeled as contest competition, produced slightly different trajectories under assumed optimal habitat conditions than those produced in RAMAS STAGE, with breeder ceilings. The probability of quasiextinction averaged 68% under contest competition, compared to an average of 9% under breeder ceilings (Root 1996). The spatially explicit variants of this model, using the Beverton-Holt function, are, therefore, more conservative in estimating the probability of quasiextinction than are the variants using breeder ceilings.

This spatially explicit population model resulted in a higher mean final abundance for Central Brevard, North Brevard, and South Beaches than did the nonspatially explicit model (Fig. 4). The spatially explicit model for South Brevard, however, produced results similar to those of the nonspatially explicit model for that population. For all of the populations, the probability of quasiextinction with dispersal was dramatically reduced from 52–87% to zero for the entire 60-yr of simulation.

The incorporation of dispersal both within and among the four populations clearly benefited South Beaches and North Brevard, with 149.9% and 135.9% increases over the initial abundance, respectively. Central and South Brevard, however, ended the simulation period at 88% and 47% of the initial abundance, respectively (Fig. 4). On average, 0–25% of a given occupancy polygon's population dispersed annually to its neighboring polygons. The probability of quasiextinction for all four populations, with dispersal among and within populations, remained zero over the entire simulation period.

Effects of catastrophes

Catastrophic events reduced the mean number of females for all four populations whenever such events were included in the model, even under optimal habitat conditions. If dispersal occurred only within a population, local epidemics dramatically reduced the mean final abundance of each of the four populations to 7.0–13.0% of the initial abundance. Catastrophes in these independent populations increased the probability of quasiextinction at 60 yr from zero to 64.8–99.2%.

The inclusion of dispersal among, as well as within, the four Scrub Jay populations did not lessen the negative impact of local catastrophes. It resulted in slightly greater reductions in the mean final abundance (to 4.2–10.4% of initial abundance) compared to the model that only included dispersal within a population (Fig. 4). The probability of quasiextinction under local epidemics, with dispersal among and within the populations, was also slightly larger (72.0–100%) than without connections among the four populations. Regional epidemics, like local epidemics, reduced the mean final abundance and increased the probability of quasiextinction (Fig. 5).

Nevertheless, a critical difference between regional and local epidemics was evident at a regional scale for the total metapopulation including all four Scrub Jay (meta)populations (Fig. 5). The total metapopulation showed the same dramatic declines in mean final abundance under both local and regional epidemics. The probability of quasiextinction was 14% with the inclusion of local epidemics, but 74% when regional epidemics were included, despite a similar mean final abundance under both types of epidemics (Fig. 5).

In general, incorporating the spatial complexity of the areas occupied by Scrub Jays, rather than assuming a single, contiguous habitat patch within a population, had little effect on the final mean number of females. This spatial complexity, however, consistently reduced the probability of quasiextinction, especially under catastrophes, for all populations except South Beaches.

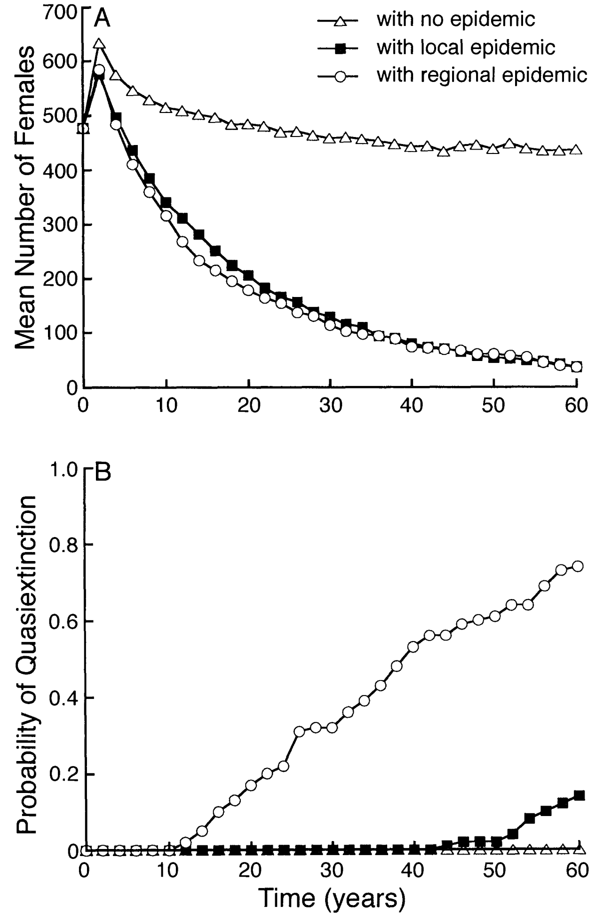

FIG. 5. The mean population trajectories (A) and probability of quasiextinction (B) for the total metapopulation, including South Brevard, Central Brevard, North Brevard, and South Beaches, under assumed optimal habitat conditions with no epidemics, with local epidemics, and with regional epidemics.

South Beaches, isolated on the barrier island from the mainland populations, was largely unaffected by the inclusion of dispersal. On a regional scale, the addition of dispersal among all occupied areas dramatically decreased the probability that the metapopulation would go extinct under large-scale regional catastrophes.

DISCUSSION

Although this model was conservative, due to a number of assumptions and limitations of the data, several conclusions are quite clear and the results are similar, regardless of the population modeling software. Habitat quality is critical to the long-term viability of the Scrub Jay populations in Brevard County. Present habitat quality, based on field surveys, will not support the Florida Scrub Jay populations for the next 60 yr. Without dispersal among the populations, these populations are not likely to survive an epidemic (or natural catastrophe) that eliminates all of the adults and half of the juveniles. These models provide clear, consistent predictions and a time frame for the probability of extinction of these populations, e.g., the four populations are likely to go extinct under deteriorating habitat conditions in <30 yr.

Influences on population growth

These results were based on models that are conservative for a number of reasons. Both the Scrub Jay and scrub habitat surveys in Brevard were rapid assessments of conditions in the field at that time. Swain et al. (1995) estimate that these numbers probably lie within 10% of the actual number of families present. Only a substantial addition to the initial abundance, though, would increase the probability of survival under field-surveyed conditions.

The 30 years of demographic data used in these models (Woolfenden and Fitzpatrick 1984, 1991) encompass the normal range of variability in a stable population. These data, however, were not measured in habitats as overgrown as the scrub in Brevard County. Short-term studies from 1989 to 1991 on Kennedy Space Center (in Brevard County) indicate that demographic parameters in Brevard County are likely to be similar to those in Archbold, but with some differences. For example, Breininger et al. (1995) found 2.88 birds per family compared to 3.0 found at Archbold. In suburban areas, Bowman et al. (1996) found larger clutch sizes and more frequent second broods than in Scrub Jay populations at Archbold. Within the context of these models, however, only large changes in adult survival and fecundity are likely to make a significant difference in the results based on the elasticity and sensitivity analysis.

Simulated catastrophes with an annual probability of 5% were too severe for the populations in Brevard County to survive. The catastrophes included in the model acted as acute events, with all of the negative effects felt in a single year of the simulation. The demographic parameters in the model, however, implicitly included the effects of a single documented epidemic (Woolfenden and Fitzpatrick 1984). The model with catastrophes may simulate the effects of both chronic and acute episodes of catastrophes. These predictions, therefore, are pessimistic and should be viewed with some caution.

In this model, the scrub habitat quality classes were assumed to be independent. Therefore, no Scrub Jays were simulated as moving among the habitat quality classes; the habitat in each quality class was assumed to be deteriorating or recovering independently. These models predicted that restoration of the moderately overgrown and severely overgrown habitat was unlikely to conserve the Scrub Jays in these habitats. However, Scrub Jays are likely to move into subpopulations in optimal or slightly overgrown habitat and to be successfully retained in their natural setting. Concentration only on restoring the optimal and slightly overgrown habitat would significantly reduce costs involved in management of the scrub habitat and would probably be more successful than these models predict. Because other Scrub Jays may move into the retained population, such a "rescue effect" (Brown and Kodric-Brown 1977), i.e., rescue from extinction by immigration from other independent populations, is likely to have a large impact on the long-term viability of the Scrub Jay metapopulation in Brevard County.

The density dependence limitations imposed in the model caused the permanent loss of extra Scrub Jays in occupied areas where density exceeded the limits. These extra birds probably would, more realistically, serve as an important source for the nearby patches of scrub habitat within dispersal range that are currently unoccupied or are being restored. Pulliam (1988) suggests that such source patches of habitat could maintain a population, even with large amounts of unsuitable or "sink" habitat included in the population; that is, 10% of the population could act as source habitat and maintain 90% of the population in poor or sink habitat. The importance of source–sink dynamics has been shown for a number of species including the Northern Spotted Owl (McKelvey et al. 1993), the bay checkerspot butterfly (Murphy et al. 1990), the Peregrine Falcon (Wootton and Bell 1992), and the Ovenbird, Red-eyed Vireo, and Wood Thrush (Donovan et al. 1995).

Essentially ignored in this model were any context effects of the surrounding landscape on the Scrub Jay dispersal rates, because a uniform permeability of the landscape to movement by the Scrub Jays was assumed. More than half of the surrounding landscape was either forested, rangeland, or medium suburban developments, habitat types that are likely to reduce normal Scrub Jay dispersal (Swain et al. 1995). The predictions made by the model including dispersal were likely to be slightly optimistic. A better approach would include the matrix surrounding each habitat patch (or population) and a differential dispersal rate based on this context. Alternatively, a cell-based approach, such as that used for Bachman's Sparrow (Dunning and Watts 1990, Liu 1992, Pulliam et al. 1992), would be useful for evaluating the effects of differential dispersal.

Implications

What are the implications of this research? Scrub habitat quality is an important factor in the long-term viability of Florida Scrub Jays within the next 60 yr; simulated populations in Brevard County went extinct without restoration of the habitat quality. The importance of high-quality scrub habitat is supported by empirical work on Scrub Jays (D. R. Breininger, M. A. Burgman, and B. Stith, *unpublished manuscript*; J. Thaxton, *unpublished data*), and is similar to findings for other threatened and endangered species. An important factor in the recent decline of the Northern Spotted Owl was loss of old-growth habitat (Thomas et al. 1990, Bart and Forsman 1992). For the Spotted Owl, habitat quality was determined predominantly by forest age; reproduction in second-growth (younger) forests was quite poor (Lande 1988). Menges (1990) demonstrated that long-term survival of Furbish's lousewort depended on recently disturbed river embankments. Stage-structured modeling revealed that growth of giant kelp (*Macrocystis pyrifera*) was determined largely by habitat quality, i.e., properties of the ocean floor substrate (Burgman and Gerard 1990). Therefore, a plan for conservation of a species must address the need for specific type(s) and quality of habitat for that species.

Any species that is restricted in range is more prone to extinction from local forces (Soulé 1987). The Scrub Jay in Brevard County is quite restricted in the availability of suitable habitat. The small size of the Scrub Jay populations also lessens their chance of surviving an epidemic. This research suggests two ways of improving the chances that these populations will survive an epidemic: (1) acquire and/or restore more habitat to optimal condition, and (2) maintain dispersal by connections among patches within a population and among populations. This supports long-standing recommendations to protect suitable habitat (Noss 1983, Freemark and Merriam 1986, Meffe and Carroll 1994) and arguments for increased connectivity among habitat patches (Brown and Kodric-Brown 1977, Fahrig and Merriam 1985, Pulliam 1988, Burkey 1989, Saunders and Hobbs 1991, Stacey and Taper 1992, Beier 1993).

In general, the larger simulated populations fared better, i.e., had a smaller quasiextinction probability, than the smaller populations. However, the situation is complicated by a crowding effect (Leck 1979, Noss 1981) seen in the largest population, South Brevard, which often showed a declining mean abundance over 60 yr. North Brevard, which has fewer birds per hectare of available scrub, usually showed a stable or increasing mean abundance under the same conditions. These results suggest that long-term viability cannot be predicted simply from initial population size.

Catastrophes simulated in this model had dramatic negative effects on the Scrub Jay populations. An annual rate of epidemics as low as one in 1000 yr produced high quasiextinction probabilities, even under optimal habitat conditions. These four Brevard County Scrub Jay populations appear to have little capacity to independently absorb the impacts of an acute natural catastrophe. Their vulnerability to catastrophes is not surprising, given the current level of habitat fragmentation and degradation, historically unprecedented, together with a naturally low fecundity. It is likely that most small, isolated populations of species with low reproductive capacity will be very vulnerable to catastrophic events (Meffe and Carroll 1994).

Spatial structure in a model allows one to account for the different living conditions that individuals within a population experience (Burgman et al. 1993, Liu et al. 1995). This research suggests that the scale of connectivity may also be an important consideration when evaluating long-term viability. Without the influx of new individuals from other areas, a slowly reproducing species such as the Scrub Jay is likely to experience local extinction, especially under epidemic conditions (Brown and Kodric-Brown 1977, Hanski 1989, Gilpin and Hanski 1991). The importance of this connectivity for long-term viability has been demonstrated for such species as the cougar *Felis concolor* (Beier 1993), the white-footed mouse *Peromyscus leucopus* (Fahrig and Merriam 1985), and the Acorn Woodpecker *Melanerpes formicivorus* (Stacey and Taper 1992).

The results of this research suggest that the situation for the Scrub Jays in Brevard County is dire, but not without hope. The prognosis for their long-term survival in Brevard County is good if there is: continued acquisition of as much scrub habitat as possible for conservation; careful management of existing scrub, with emphasis on restoration; maintenance of the connectivity of the habitat to allow dispersal throughout the system; and continued exploration, using simulation models, of the factors that affect long-term success of the Scrub Jay. Swain et al. (1995) detail some of the slow progress of ongoing acquisition and management efforts for scrub habitat conservation in Brevard County.

For threatened species, it is important to evaluate the factors that influence long-term viability. Population modeling is a valuable tool for evaluating potential threats that face rare species and for suggesting future research avenues. Habitat specialists like the Florida Scrub Jay are likely to be influenced by habitat loss and fragmentation as well as degradation. Such species also may be vulnerable to catastrophic events, which is not evident simply from a census. Spatial modeling provides the means to examine these issues and evaluate the potential impacts of future threats. Therefore, it is important to collect spatial, as well as demographic, data for conservation planning.

Management recommendations

Based on these simulation models, the following recommendations for management of Scrub Jays and other long-lived, slowly reproducing habitat specialists are proposed: restore, maintain, and connect.

1) Focus on maintaining adult breeders. Sensitivity analysis suggested that the changes in the number of experienced breeders, especially those with helpers, had a large impact on population growth (Root 1996). Any strategies that increase survival of breeders, such as maintenance of habitat quality in occupied territories, will enhance growth of the Scrub Jay population.

2) Restore and maintain habitat with the species' requirements in mind. Breininger's (1992) habitat suitability model was used a guideline for the scrub field assessment (Swain et al. 1995) and classification of habitat; this serves as a good starting point. The scrub habitat must be burned periodically at a 10–20 yr in-

terval (every 40 yr at least) to maintain the open sandy patches and low shrubs and to minimize canopy cover. My simulation model in this paper suggests that only habitat in optimal or slightly overgrown condition is likely to sustain Scrub Jay populations; it should be restored first. To restore more severely overgrown habitats with many mature trees, mechanical means, in addition to fire, may be needed.

3) Maintain or make connections between patches of suitable habitat. Dispersal is likely to be important to mitigate epidemic effects, especially at a regional scale. Dispersal is also likely to be important in the restoration process. Presumably, if suitable scrub patches are close enough, Scrub Jays will move into a restored patch that was previously unoccupied (Stith et al. 1996). The caveat is that these connections may increase dispersal of predators or disease agents (Simberloff and Cox 1987, Simberloff et al. 1992, Hess 1994), factors that must be weighed against the benefits of such connections.

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