Potential Effects of a Forest Management Plan on Bachman's Sparrows (*Aimophila aestivalis*): Linking a Spatially Explicit Model with GIS

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Abstract: *By combining a spatially explicit, individual-based population simulation model with a geographic information system, we have simulated the potential effects of a U.S. Forest Service management plan on the population dynamics of Bachman's Sparrow (*Aimophila aestivalis*) at the Savannah River Site, a U.S. Department of Energy facility in South Carolina. Although the Forest Service's management plan explicitly sets management goals for many species, most of the prescribed management strategy deals with the endangered Red-cockaded Woodpecker (*Picoides borealis*) because of legal requirements. We explored how a species (the sparrow) that is not the target of specific management strategies but that shares some habitat requirements with the woodpecker, would fare under the management plan. We found that the major components of the proposed management plan may allow the sparrow population to reach and exceed the minimum management goal set for this species, but only after a substantial initial decline in sparrow numbers and a prolonged transition period. In the model, the sparrow population dynamics were most sensitive to demographic variables such as adult and juvenile survivorship and to landscape variables such as the suitability of young clearcuts and mature pine stands. Using various assumptions about habitat suitability, we estimated that the 50-year probability of population extinction is at least 5% or may be much higher if juvenile survivorship is low. We believe, however, that modest changes in the management plan might greatly increase the sparrow population and presumably decrease the probability of extinction. Our results suggest that management plans focusing on one or a few endangered species may potentially threaten other species of management concern. Spatially explicit population models are a useful tool in designing modifications of management plans that can reduce the impact on nontarget species of management concern.*

Impactos potenciales de un plan de manejo del bosque sobre los gorriones de Bachman (*Aimophila aestivalis*): vinculando un modelo espacialmente explícito con SIG

Resumen: *Hemos simulado los impactos potenciales de un plan de manejo del Servicio Forestal de los Estados Unidos, sobre la dinámica poblacional del gorrión de Bachman (*Aimophila aestivalis*) en un sitio de Savannah River, que es propiedad del Departamento de Energía de los Estados Unidos, en Carolina del Sur. La estrategia utilizada combinó un modelo de simulación espacialmento explícito de las individuos miembros de la población, con un Sistema de Información Geográfico. Si bien el plan de manejo del Servicio Forestal, explícitamente establece medidas de manejo para varias especies, debido a requerimientos legales la mayoría de las estrategias de manejo prescriptas, consideran al pájaro carpintero de cucarda coloradá (*Picoides borealis*) en peligro de extinción. Exploramos como se desenvolvería dentro del plan de manejo, una especie (el gorrión), que no está en la mira de ninguna estrategia específica de manejo, pero que comparte algunos de los requerimientos de hábitat con el pájaro carpintero. Encontramos que los componentes más importantes del plan de manejo le permiten a la población de gorriones llegar y exceder la metal mínima trazada para esta especie, pero sólamente después de una disminacion sustancial en el número de gorriones y de un prolongado período de transición. En el modelo, la dinámica de población*

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del gorrión fue más sensible a variables demográficas, tales como supervivencia de adultos y juveniles, y variables del paisaje, tales como la aptitud de los clareos recientes del bosque y los rodales de pinos maduros. Utilizando varias suposiciones sobre la aptitud del hábitat, estimamos que la probabilidad de extinción al cabo de 50 años es de por lo menos un 5% pudiendo ser más alta si la supervivencia de juveniles baja. Una expansión de un programa del Servicio Forestal podría incrementar ampliamente la población de gorriones y presumiblemente disminuir la probabilidad de extinción. Nuestros resultados sugieren que los planes de manejo que se centran en una o en unas pocas especies en peligro de extinción, pueden potencialmente poner en riesgo otras especies cuyo manejo es de importancia. Los modelos poblacionales espacialmente explícitos, constituyen una herramienta útil en el diseño de modificaciones de planes de manejo, pudiendo reducir el impacto en especies cuyo manejo es de importancia, pero que no constituyen el objetivo principal del plan.

Introduction

Land mangers face a major challenge in understanding the long-term effects of management strategies on the population dynamics of animal and plant species. Many aspects of management strategies will have consequences that are difficult to predict prior to the implementation of a management plan. This is especially true of management options that affect habitat distribution and quality over large spatial scales or that cause changes that unfold over long periods of time. For example, increases in timber-harvest rotations (the age at which trees are harvested) in a forest district managed for timber production will change the age distribution of the forest and the amount and distribution of clearcuts produced through timber harvest. These changes will affect both the organisms found in forest patches of different ages as well as early successional species found in the clearcuts, but the impact on the species may not be identifiable for years. It is difficult prior to the implementation of management changes to predict what the effects will be and how to mitigate severe effects before they occur. This is especially true when field experiments are hard to design and implement at the proper spatial and temporal scales.

Spatially explicit population models provide a tool for exploring the possible effects of management plans on selected species prior to implementation (Dunning et al. 1995). Population models can be designed to simulate the life history of a species on a specific landscape and to measure population change resulting from specific changes to the landscape. Models can be used to study landscape changes that cover large spatial areas and occur over long periods. Although the predictive ability of such models is limited by their assumptions and the researchers' ability to validate and verify the model (Conroy et al. 1995), spatially explicit models can be used to suggest possible population responses to landscape change and therefore may be especially useful in examining whether management strategies designed to meet particular goals have detrimental effects on non-target wildlife species.

As an example of this approach, we have developed a class of spatially explicit, individual-based simulation models to explore the possible effects of land-use changes and forest management practices on animal populations that inhabit changing landscapes (Pulliam et al. 1992; Liu 1992; 1993*a*, 1993*b*; Liu et al. 1994). In this paper we link the latest version of this model with a geographic information system (GIS) database of the Savannah River Site, a Department of Energy facility in Aiken and Barnwell counties, South Carolina. The U.S. Forest Service manages the majority of the 770-km^2 site for timber production and biodiversity conservation. The Forest Service's Savannah River Forest Station (SRFS) recently developed a long-term management plan called the "Savannah River Site Wildlife, Fisheries, and Botany Operation Plan" (SRFS 1992), hereafter called the "operation plan". The operation plan gives general and specific management goals in quantifiable terms, such as the number of animals desired of each endangered, threatened, or key species. The operation plan also proposes a series of manipulations, such as changing the composition of forest stands over a 50-year period, that are designed to achieve specific management goals. We incorporated the basic components of the forest management plan in a series of simulations designed to test their effects on the population dynamics of Bachman's Sparrow (*Aimophila aestivalis*), a potentially threatened species found in pine woodlands. We were able to simulate the primary components (such as harvesting, burning, and thinning) of the operation plan but not some secondary components (such as retention of standing snags or cavity trees and application of herbicides). Thus, our simulations should be considered suggestive of the effects of the overall management strategy but not precise predictions of how the actual sparrow populations will change. We also discuss the implications of our results for management of biodiversity and address the potential danger of using knowledge of habitat requirements of the Red-cockaded Woodpecker to infer the needs of other species such as Bachman's Sparrows.

Methods

The Simulation Model and Geographic Information System

ECOLECON is an ecological-economic model that is capable of simulating animal population dynamics and economic revenues in response to different forest landscape structures and various timber management scenarios (Liu 1992, 1993*b*). ECOLECON is spatially explicit and object-oriented. It was programmed in Borland C++2.0 (Borland International 1991) and can be implemented on IBM-compatible computers.

ECOLECON's economic information includes subroutines for forest growth and yield, income from timber harvest, cost, and net income. Its ecological components integrate information about animal habitat use, demography, and dispersal. All of these subroutines are hierarchically structured (Liu 1992, 1993*b*). The model predicts animal population dynamics, spatial distributions, and extinction probabilities, as well as forest growth and yield and economic income from timber harvest. The outputs of the model provide valuable information for balancing the conflicts between the generation of economic revenues and the conservation of endangered species.

ECOLECON is a "second generation" model that is built on BACHMAP, a spatially explicit model of the population dynamics of Bachman's Sparrows. BACHMAP is one of a class of new models, referred to as MAP models, an acronym for Mobile Animal Population (Pulliam et al. 1992). ECOLECON adds more features (such as dispersal rules) and flexibility to the ecological components of BACHMAP.. This paper reports simulation studies done with ECOLECON but does not include the economic results because the Savannah River Site is not managed solely for timber revenues and the economic parameters in ECOLECON do not apply directly to the Savannah River Site. For additional information about the economic aspects of ECOLECON, see Liu (1992, 1993*b*) and Liu et al. (1994).

All MAP models, including ECOLECON and BACHMAP, are individual-based grid models (Fahrig 1988). Each individual in the population is followed through its annual cycle of birth, dispersal, reproduction, and death (Pulliam 1988). Dispersal strategies and habitat-specific fecundity are incorporated into MAP models. Forest succession and management schemes are also mimicked by annually increasing the age of the habitat in each grid cell and harvesting forest stands when they reach an appropriate age as specified by the timber management regime.

Forest compartment maps supplied by the Savannah River Forest Station were used to create several databases, including the age, size, and spatial distribution of forest stands. This information was represented in ARC/INFO, a GIS operated on a Sun Sparc workstation (Sun Microsystem 1991). The data generated from the GIS was transferred to IBM-compatible computers as simulation inputs. The operation plan (Savannah River Forest Station 1992) was used to project land use patterns up to 50 years into the future.

Study Area

The Savannah River Site is located in western South Carolina along the Savannah River. It is a 77,000-ha facility of the U.S. Department of Energy and an "experimental forest" managed by the U.S. Forest Service (see Dunning & Watts 1990). Past silvicultural practices have produced many even-aged forest stands ranging from 5 to 100 ha in size. A stand is a patch of forest in which the trees are of the same age and that has been subjected to uniform management. The largely forested landscape consists of uplands dominated by loblolly pine (*Pinus taeda*) and longleaf pine (*P. palustris*), bottomland wetlands dominated by sweetgum (*Liquidambar styraciflua*) and yellow poplar (*Liriodendron tulipifera*), and swamps dominated by bald cypress (*Taxodium distichum*) and water tupelo (*Nyssa aquatica*) (Dukes 1984). The region was largely agricultural when the Federal government assumed control of it in the early 1950s. The Forest Service planted the former agriculture fields with pines that are now mostly 30–50 years old and that were being harvested under the previous management plan. Because of the historical use of the land, relatively few mature pine stands (older than 80 years) are currently found on the Savannah River Site. Mature longleaf pine stands cover only 0.2% of the total forested area on the site, while intermediate-aged (30–80 years old) stands of loblolly and longleaf pines cover 47.7% of the entire site. About 14% of the Savannah River Site is in early successional habitats (Savannah River Forest Station 1992).

Our study area was a 5924-ha region in the southeastern corner of the Savannah River Site. In 1989, this area included 4725 ha of pines and 1199 ha of hardwoods (Fig. 1). ECOLECON represents a landscape as a grid of hexagons in which each hexagon approximates the size of a typical breeding territory of the species being modeled. Bachman's Sparrow territories average 2.5 ha (Haggerty 1986), so we overlaid the landscape map (Fig. 1*a*) with a grid of approximately 2370 2.5-ha hexagonal cells (Fig. 1*b*). If a hexagonal cell was completely within a forest stand, we assigned the cell the same characteristics (such as forest type and age) as found in that stand. When a hexagonal cell contained portions of two or more stands, we assigned the cell to the stand type that covered the greatest portion of the cell. Thus, there existed some discrepancies between the real stand and its hexagonal representation. The average discrepancies were less than 10% (compare Fig. 1*c* with Fig. 1*a*); that is, the average accuracy of hexagonal representation was greater than 90%. The resulting hexagon-based map (Fig. 1*b*) was used for simulations.

Savannah River Site Wildlife, Fisheries, and Botany Operation Plan

The operation plan was prepared to provide both short-term (10 years) and long-term (50 years) objectives for managing endangered, threatened, and key wildlife species and communities. Specific management strategies were proposed in the operation plan to reach these ob-

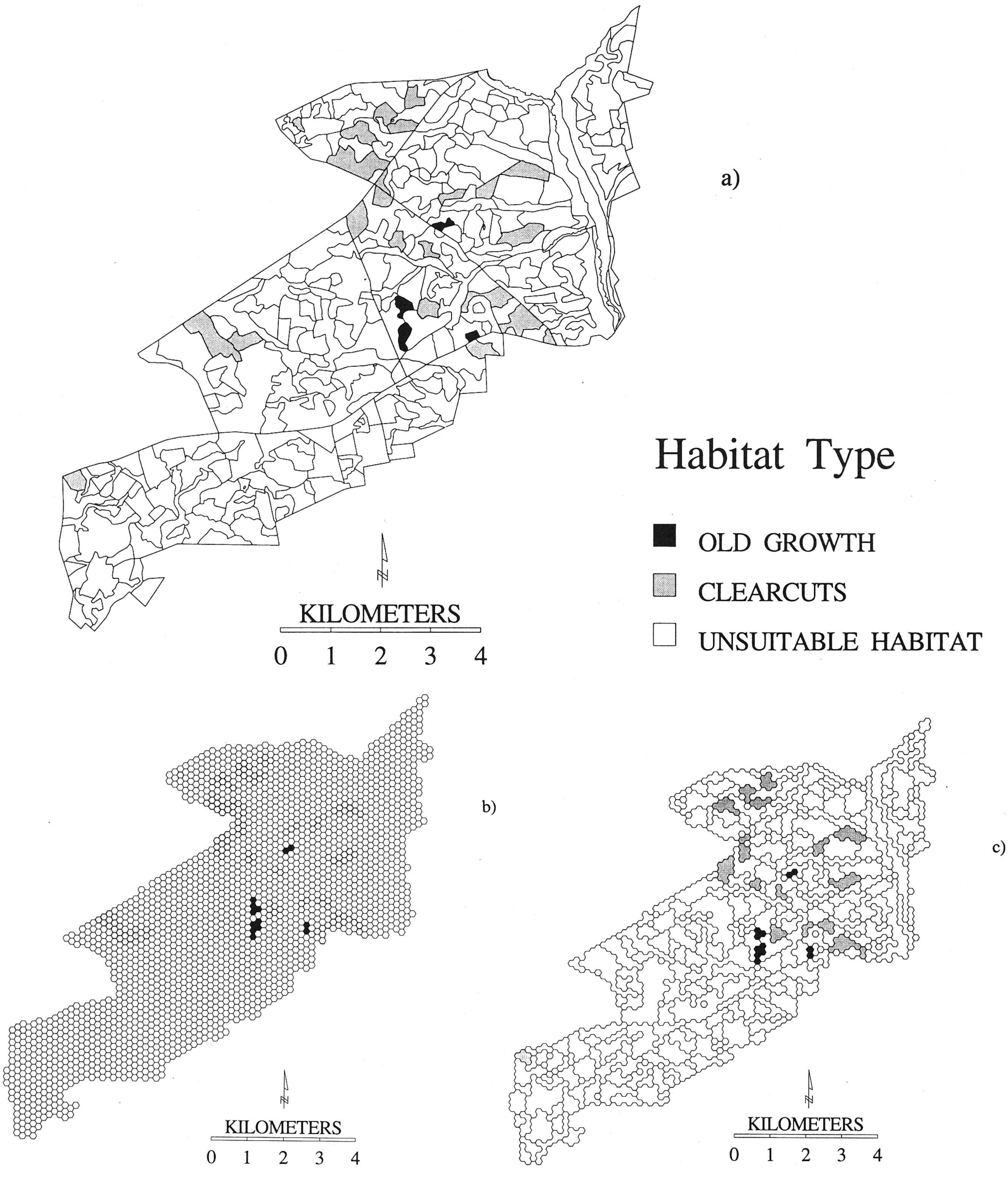

Figure 1. (a) A GIS map of forest stands in our study area at the Savannah River Site. The black lines are stand boundaries. Shaded stands are suitable habitat patches for Bachman's Sparrows (1- to 5-year and mature pine stands); unshaded stands are unsuitable habitat (hardwoods, intermediate-aged pine stands (6- to 79-year) and stands that have just been harvested (0 year age class). (b) Study area as represented by ECOLECON showing the map overlaid with a grid of hexagonal cells. (c) A map of forest stands with each cell assigned to one habitat type. This map was used to run ECOLECON for simulating the sparrow population dynamics.

jectives. For instance, an increase in harvest rotation length was proposed to create more mature pine stands of the sort favored by the Red-cockaded Woodpecker (*Picoides borealis*), an endangered species whose habitat needs are a management priority of the Forest Service as mandated by the listing of woodpecker under the Endangered Species Act.

The forest composition of our study area was fairly representative of the entire Savannah River Site (Liu, unpublished data), so we used the operation plan to project the future composition of the pine stands in our study area. In 1991 the pine regions of the Savannah River Site were dominated by a few age classes of pines. Over 50% of the pines were 31 to 40 years old and more than 20% were 0 to 10 years old (Fig. 2). There were no pine stands older than 90 years. The operation plan calls for harvest of the most common pine age classes to produce a forest with a more even composition (Fig. 2). The Operation Plan establishes minimum objectives for maintaining 42 species of management interest, including the Red-cockaded Woodpecker and Bachman's Sparrow. For Bachman's Sparrow, the minimum objective is to maintain 1100 breeding pairs on the entire Savannah River Site and to attain a sparrow density of five breeding pairs per 640 acres (about 259 ha) in the region where our study area is located. Extrapolation from the operation plan to our 5924-ha study site yields a goal of about 115 breeding pairs of Bachman's Sparrow for the study area.

Biology of Bachman's Sparrow

Bachman's Sparrow is a potentially threatened species of the southeastern United States (Dunning & Watts 1990; Pulliam et al. 1992). Its range has declined significantly in the past several decades (Haggerty 1986; Dunning 1993). The species breeds in pine woodlands and feeds on insects and seeds on the ground (Dunning & Watts 1990). Dunning and Watts (1990) reported that the sparrows' favored habitats are those with substantial amounts of herbaceous vegetation (grasses and forbs) within the first meter above the ground and with an open understory (the second through fourth meters above ground) with few tall shrubs. The sparrows usually shun sites with dense understory vegetation. On the Savannah River Site, they are found breeding in 1-to-5-year-old pine stands (clearcuts) and powerline rights-of-way as well as in mature pine stands (older than 80

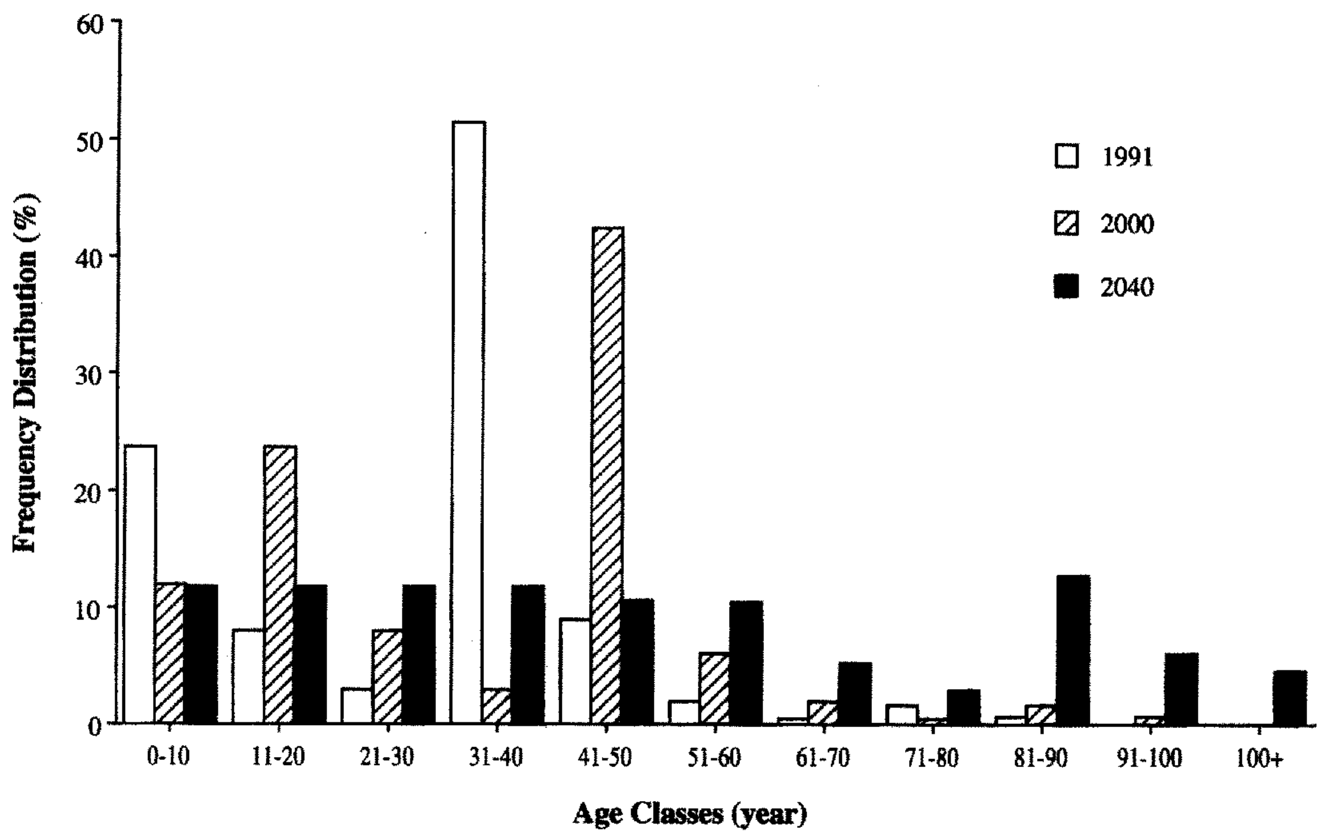

Figure 2. Frequency distribution of forest stands in the field study area. The data for 1991 were derived from a GIS database of 1989, and the distributions of age classes for 2000 and 2040 were projected according to the proposed operation plan.

years). The mature stands are suitable habitat for the sparrows because mature stands also have dense ground vegetation and open understories when burned on a frequent basis (Dunning & Watts 1990; Gobris 1992).

The survivorship, reproduction, and dispersal of Bachman's Sparrow are currently under intensive investigation at the Savannah River Site, but there remains uncertainty concerning some parameters needed for the model. Accordingly, we have made some assumptions for the simulations based on the current field investigations and a literature survey. The assumptions are discussed in detail by Liu (1992) and Pulliam et al. (1992). For most simulations, reproductive success was assumed to be 3.0 offspring per pair per year in 1-to-2-year clearcuts and in mature pine stands (≥80 years) and 1.0 offspring in 3-to-5-year pine stands (Haggerty 1988; Liu 1992). Adult survivorship of Bachman's Sparrow was set at 60% and juvenile survivorship at 40%. Survivorship was annual and it was assumed constant in every year. For each individual, however, survival or death in a particular year was stochastic and was randomly assigned. This paper presents the results of varying the values of selected demographic and behavioral parameters. For a more detailed sensitivity analysis, see Liu (1992) and Pulliam et al. (1992).

Juveniles are assumed to disperse from their natal sites in the spring, just prior to territory acquisition. The model assumes an even sex ratio but traces the dispersal movements of females only. A juvenile female is assumed to inherit her natal territory only if the female parent on that territory has died. Juvenile females not inheriting a natal territory must disperse in search of an unoccupied, suitable breeding site. In the model, this means finding an unoccupied cell (hexagon) of the correct vegetation type and age (1–5-year or ≥80-year pine stands). Dispersing juveniles can move to any adjacent cell, but we assumed that they move preferentially to adjacent cells of suitable vegetation type and age. Thus, in the model a dispersing female moves with equal probability into any adjacent suitable cells. If none of the adjacent cells are suitable for breeding, the female moves at random to an adjacent unsuitable cell. The search continues until an unoccupied, suitable cell is found or the disperser dies. Dispersal involves extra mortality risks, and we assume that with each move to a new cell a dispersing female has a 2% chance of dying. Further details about the dispersal rules can be found in Pulliam et al. (1992) and Liu (1992, 1993*a*, 1993*b*).

The field data presented on the population abundance and distribution of Bachman's Sparrow in the study region was collected in the summer of 1989 (J. B. Dunning, Jr., B. J. Danielson, and B. D. Watts, unpublished data). There were 64 pairs of Bachman's Sparrow on the study area, of which 12 pairs were in mature stands, 40 pairs in 1-to-2-year stands, and 12 pairs in 3-to-5-year stands.

Simulated Management Options

HARVEST OPTIONS

The operation plan describes how much forest should be harvested over the 50-year period but does not specify which forest stands should be harvested or how much forest should be cut each year. We assumed that an equal area of forest stands would be harvested each year until the desired forest structure is reached. We considered three options for selecting the eligible forest stands for harvest each year: (1) harvesting the forest stands randomly, (2) harvesting the oldest stands first, and (3) harvesting clusters of adjacent stands. Under the random harvest option, we selected stands without regard to their proximity to other selected stands. The option of harvesting the oldest eligible stands first recognizes that older timber often produces greater economic return. Under this option, the stands to be cut were grouped according to age, and the oldest eligible stands were selected until the required acreage for that year was attained. We assumed that this option would approximate a management strategy of maximizing income within the constraints of the operation plan. The final option, harvesting by clusters, recognized that the Forest Service classifies stands into compartments of 30–100 stands for administrative purposes. Timber sales are organized on a compartment level, with the result that the stands harvested each year are often clumped spatially. The option of harvesting in clusters was therefore designed to be similar to the actual harvest strategy used at the Savannah River Site. The algorithm to cluster the cuts was that the stands in one compartment were cut first, then stands in a neighboring compartment were harvested until the required acreage for a specific year was obtained. A stand in our model was defined as a group of cells that were uniform in species composition and age. For example, if a single hexagonal cell was surrounded by cells of different ages, then the single cell was a stand. If adjacent cells were of the same age and species composition, then all similar adjacent cells belonged to the same stand.

Our GIS database included the age, size, and boundaries of forest stands in the study region as of 1989. Since the operation plan had a 1992 starting date, we wished to begin our simulations with the 1991 landscape. To generate this landscape, we increased the age of each stand in the 1989 database by two years. We therefore assumed that there was no harvest in 1989 or 1990. In fact, some harvest did occur during these years, especially in an area damaged by a tornado in the fall of 1989 (Dunning et al., in press). The increased harvest due to salvage logging made the region affected by the tornado less typical of the Savannah River Site as a whole, so we preferred to use the original distribution of habitat patches to explore the operation plan. Thus, our landscape maps do not portray the exact stand distributions present in 1991. Because we are attempting to explore possible responses of the sparrow population to landscape change and not to predict precise population change, the projected 1991 maps are adequate for this study.

OPTIONS ON THINNING AND BURNING MIDDLE-AGED PINE STANDS

Thomas et al. (1990) suggested that to create more suitable habitat for the Northern Spotted Owl (*Strix occidentalis caurina*), younger stands may be modified to include structural characteristics of old-growth forests (Murphy & Noon 1992). This option may also be a viable management strategy for the Bachman's Sparrow because some individuals have been found to breed in pine stands between 50 and 80 years old where the structure of these stands appeared similar to that of mature forest (Haggerty 1986; Dunning & Watts 1990; Gobris 1992). Dunning and Watts (1990) stated that forest management practices, particularly burning and thinning, can reduce the density of understory vegetation and thus improve habitat suitability for the sparrows. Also, Gobris (1992) found that middle-aged pine stands on the Piedmont National Wildlife Refuge in central Georgia regularly support Bachman's Sparrows when maintained with the same burning regimes as used there in mature pine forest. This suggests that thinning and burning 50-to-80-year stands on the Savannah River Site to generate ground-layer and understory conditions similar to older forest may render these stands more suitable for Bachman's Sparrow, increasing the total amount of suitable habitat.

A program of thinning and burning middle-aged pine stands has been initiated by the Forest Service on the Savannah River Site. The purpose of this program is to generate suitable conditions for the Red-cockaded Woodpecker and other species found in open, mature pine forest. The operation plan did not contain enough details on this program to include these management options in our main simulations. To explore the possible effects of such management, we assumed in a series of simulations that stands of 50+, 60+, or 70+ years old were thinned and then burned at rotations of 3–5 years each, and that sparrows in the modified stands had the same reproductive success as those in mature stands of 80 years or older. We assumed that the eligible forest stands in these simulations were harvested in clusters.

OPTIONS ON PLANTING DIFFERENT PINE SPECIES

In the study area, there were three primary species of pine trees: loblolly, longleaf, and slash pines (*Pinus elliotii*). These three species accounted for 41%, 48%, and 11%, respectively, of the area covered with pine forests on the Savannah River Site. Because the growth functions of longleaf and slash pines were not as complete as those of loblolly pines, we used the models of loblolly pine growth for the entire pine area. This simplification certainly caused some discrepancies, especially for longleaf pines. While the growth rate of slash pines is about the same as that of loblolly pines, longleaf pines grow much slower than loblolly pines, at least in their early years (Clutter et al. 1983). This suggests that the period during which clearcuts planted in longleaf pine are suitable for Bachman's Sparrows might be longer than that of young loblolly pine stands (Hunter 1990). In fact, field surveys on the Savannah River Site show that the sparrows occupy longleaf pine stands 1–8 years after planting, while the birds occupy loblolly stands only from 1–5 years after planting (Dunning, unpublished data).

We simulated the effects of planting different pine species by varying the maximum age at which young stands are suitable. We ran a series of simulations in which the maximum suitable age of young stands varied from 2 to 10 years. Reproductive success (1.5 female offspring per season) was assumed to be equal in all clearcuts of suitable age. We assumed that a smaller maximum suitable age reflects the effects of planting loblolly and slash pine, while a larger maximum suitable age mimics the effects of planting longleaf pines.

Sensitivity Analysis

Pulliam et al. (1992) performed extensive sensitivity analyses on the BACHMAP model and found that the model results were, in general, much more sensitive to demographic parameters, particularly survivorship, than to model parameters associated with dispersal behavior.

For the current study, we examined the sensitivity of estimated total population size to variation in five variables. These variables were dispersal mortality, adult survivorship, juvenile survivorship, and two landscape variables—the number of years that clearcuts were suitable (young stands) and the minimum age at which older stands became suitable (older stands).

The sensitivity index (S_x) was calculated as

$$S_x = (\Delta x/x)/(\Delta P/P),$$

where $\Delta x/x$ is the observed change in the total population size due to a change ($\Delta P/P$) in the parameter P (Jørgensen 1986; Pulliam et al. 1992). A larger S_x indicates a higher sensitivity of population size to change in a particular parameter.

To see how the sparrow population size changed as several factors varied simultaneously, we used a 2^3 factorial design to determine the interaction effects among three variables each at two levels. The three variables included adult and juvenile survivorship and reproductive success of 3-to-5-year stands because these variables were among the most important factors that influenced the sparrow's population size and dynamics in previous analyses (Pulliam et al. 1992).

Simulation and Statistical Methods

All simulations were run for 50 years, the length of the long-term objectives set by the operation plan (Savannah River Forest Station 1992). Each simulation run had 100 replicates. Extinction probability was calculated as the number of simulations in which population extinction took place divided by the total number of replicates. Population sizes were averaged over the entire simulation period for runs in which populations did not go extinct. To test for significance of differences in population sizes, we used two-tailed *t*-tests and *F* tests. Differences in extinction probabilities were tested with a test for binominal proportions (Ott 1988).

Results

Effects of Management Options

HARVEST OPTIONS

The general pattern of sparrow population dynamics was very similar under the three harvesting options considered. In all three cases the population first decreased to a "valley" and then increased gradually (Fig. 3). There were, however, three major differences between the harvest options regarding management goals. First, harvesting the eligible stands randomly (Fig. 3*a*) never allowed the sparrow population to reach the minimum objective set by the operation plan. Population sizes reached and exceeded the minimum objective (115 breeding pair) before the year 2040, when the stands were cut in clusters (Fig. 3*b*) or the oldest stands were harvested first (Fig. 3*c*). Second, clustered harvesting had the highest average population size over the 50 years of simulations (Table 1), while random harvesting had the lowest. Finally, the average yearly standard error under random harvesting (11.14) was about twice as large as that under harvesting in clusters (5.60) or harvesting the oldest stands first (5.28).

EFFECT OF THINNING AND BURNING MIDDLE-AGED STANDS

When we varied the minimum age at which stands became suitable for Bachman's Sparrow, the sparrow population became much larger as the minimum age was reduced (Fig. 4*a*). The average population size over the 50 years of simulations (*POP*) decreased linearly as the minimum suitable age of 50–80-year stands (*OS*) increased according to the relationship $POP = 648.51 - 7.534\ OS$ ($R^2 = 0.969$).

The simulation results (Fig. 4*b*) also indicated that the younger the suitable age of forest stands the earlier the population size reached and exceeded the minimum objective set by the operation plan. When 50-year-old pine stands were maintained in a condition suitable for the sparrow, the minimum population objective of the operation plan was reached in 2007, 17 years into the simulation period. The relationship between the minimum suitable age of 50–80-year stands (*OS*) and the first year by which the minimum objective was reached

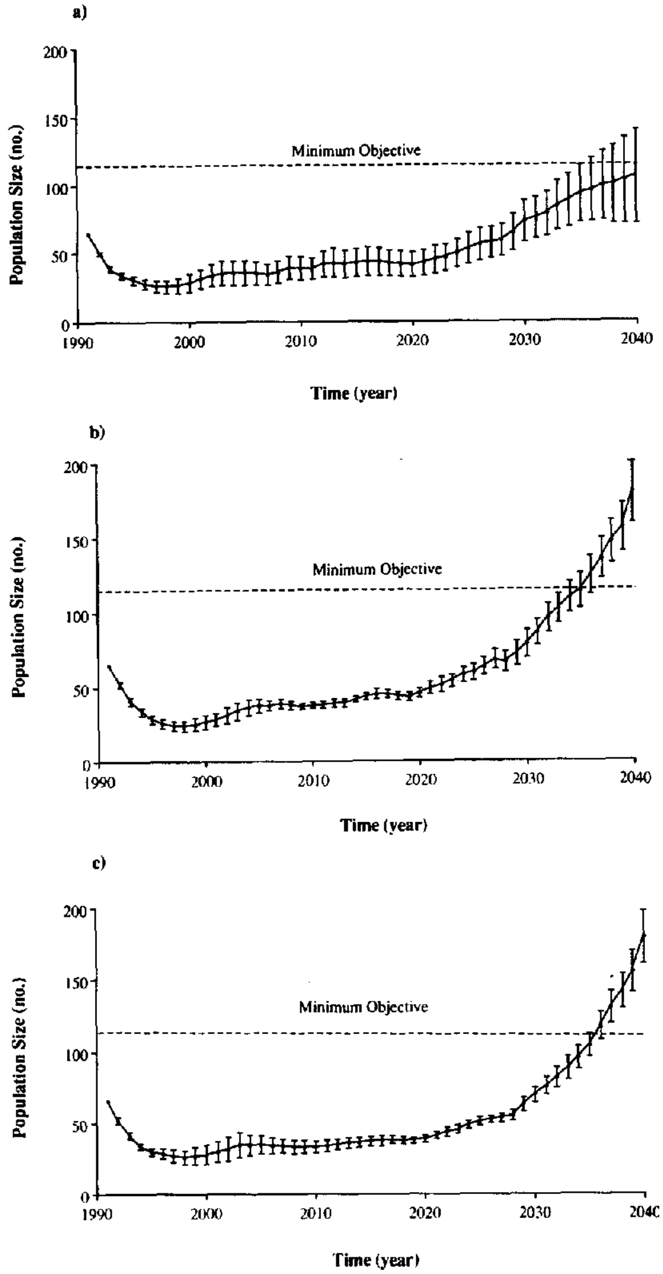

Figure 3. The sparrow population dynamics resulting from harvesting the stands randomly (a)*, harvesting the stands in clusters* (b)*, and harvesting the oldest stands first* (c)*. Minimum objective refers to the minimum management goal proposed by the operation plan, extrapolated to our study area. Vertical bars indicate 1 s.e.*

Table 1. Effects of three harvesting methods on the average population size (±SE).

Harvesting option	*Population Size (no.)*[*]
Harvest oldest stands first	54.81 ± 0.79[a]
Harvest stands randomly	50.08 ± 2.74[b]
Harvest stands in clusters	59.69 ± 0.80[c]

[*] *Letters* a, b, *and* c *indicate whether two numbers are significantly different at the 5% level. If two numbers have different letters, they are significantly different.*

(Y) is described by the linear function $Y = 1957.6 + 0.96\ OS$ ($R^2 = 0.977$).

EFFECTS OF PLANTING DIFFERENT PINE SPECIES

As the maximum suitable age of young stands (YS) increased, the average population size (POP) increased linearly (Fig. 5*a*, $POP = 25.42 + 10.83\ YS$, $R^2 = 0.942$). Also, a larger YS enabled the sparrow population to reach the minimum objective sooner (Fig. 5*b*); this relationship was a negative linear function ($Y = 2042.8 - 2.2941\ YS$, $R^2 = 0.913$).

The time window during which clearcuts were suitable also changed the population dynamics (Fig. 5*c*). When the maximum suitable age of young stands was 2, the population size decreased to a valley before eventually increasing to exceed the management goal of population size. This is the pattern we observed with our first set of simulations (Fig. 3). When the time window of suitability increased to at least 5 years after planting, population size first increased for a few years and then decreased before increasing again. Finally, when the time window of suitability was at least 7 years after planting, the peak population that occurred prior to population decline reached or exceeded the minimum objective goal before declining (Fig. 5*c*).

Sensitivity Analysis

Similar to the findings by Pulliam et al. (1992), the model was much more sensitive to survivorship than to dispersal mortality (Table 2). The minimum suitable age of older stands was the most sensitive parameter determining the average population size. The sensitivity of population size to adult and juvenile survivorship was intermediate, with similar S_x indices for these two parameters. Although the time window for clearcut suitability (YS) had a lower sensitivity than the two survivorship parameters, and the other landscape parameters. YS had a sensitivity value that was three times as high as the S_x value for dispersal mortality.

The effects of the minimum suitable age of older stands (OS) were dramatically offset when juvenile survivorship was low. We ran a set of simulations with juvenile survivorship at 0.3 instead of 0.4. As in previous simulations with the higher value of juvenile survivorship, the population size (POP) when juvenile survivorship was low decreased with an increase in minimum suitable age of older stands (OS) ($POP = 61.97 - 0.50\ OS$, $R^2 = 0.943$, Fig. 6). The population sizes recorded in the simulations with juvenile survivorship at 0.3, however, were an order of magnitude lower than population sizes in previous simulations (Fig. 4*a*) and never reached the minimum objective.

The sparrow population frequently went extinct in the simulations with low juvenile survivorship (Table 3). Under the most restrictive conditions, the frequency of extinction was extremely high. When both adult and juvenile survivorships were low and the suitable age of older stands set at the maximum of 80 years, the extinction probability was 0.85 or higher. With adult survivorship at 0.6, extinction probability was less than 0.1. Even with the minimum suitable age of older stands reduced to 70 years, there was still a 5% chance for the population to go extinct before the year 2040. The level of reproductive success in young stands also influenced the total population size. For example, when reproductive success was low in 3- to 5-year clearcuts (0.5 female offspring/year), average population size was significantly higher than when reproductive success was zero in these stands (0.0 offspring/year, Fig. 7).

There were very strong interactions among adult survivorship, juvenile survivorship, and the reproductive success in 3- to 5-year stands (Table 4). Even the second-order interaction among the three variables was significant at the 5% level (Table 5).

Discussion and Conclusions

Our simulations suggest that management strategies that combine harvesting, thinning, and burning of selected forest stands could achieve the minimum objectives set by the operation plan of 115 breeding pairs of the sparrows in the study area. This assumes that the parameter estimates used in the majority of our simulations are correct. When juvenile survivorship was low in our simulations, however, the sparrow population size was always lower than the initial population size and never reached the minimum objective. Although we have little direct data on juvenile survivorship from the field studies at the Savannah River Site, a comparison of mortality estimates for other sparrow species suggests that 30% survivorship would not be unusually low (see Pulliam et al. 1992). This result underscores the need for caution when applying results of the model and for the need for further field investigations to reduce parameter uncertainty.

Management Simulations

HARVEST OPTIONS

The reason clustered harvesting resulted in the highest population size in the simulations is probably that clus-

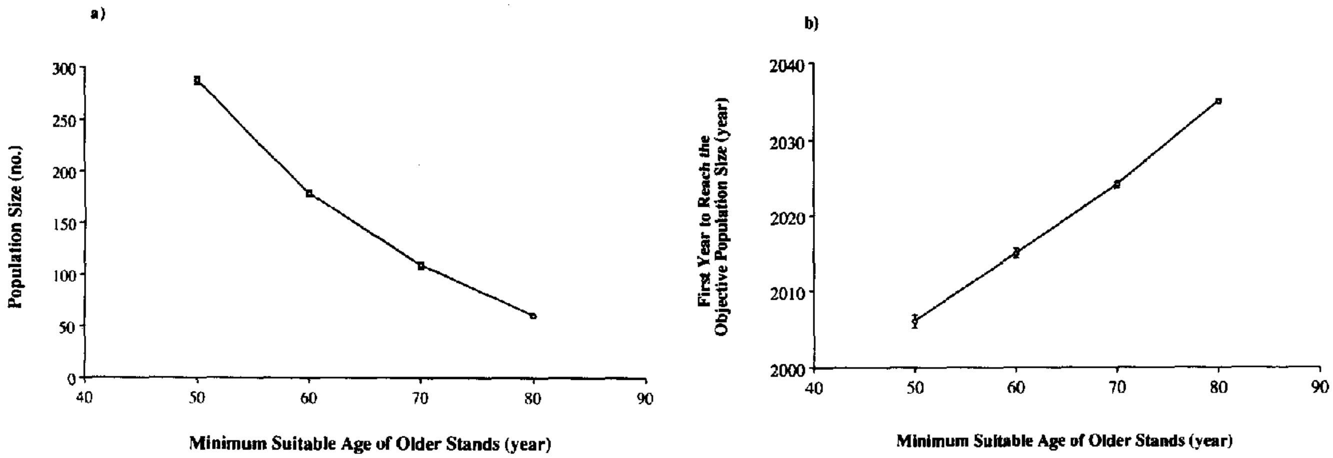

Figure 4. Changes in total population size caused by manipulating the age at which 50- to 80-year stands become suitable for breeding (a), and effects of manipulating the age at which 50- to 80-year stands become suitable for breeding on the year when the sparrows first reach the objective population size (115 breeding pairs) (b).

tered harvesting produced clustered patches of newly suitable habitat, making it easier for a dispersing juvenile to locate a suitable patch. Random harvesting created a landscape that was probably presented the most difficulties for a dispersing juvenile seeking a suitable patch, and the population size was the lowest under this option.

The projected sparrow population sizes under all three harvesting options were closely related to the amount of suitable habitat. For example, under clustered harvesting the mature stands increased over time, while clearcut habitat decreased during the first few years and then later increased to a stable level (Fig. 8*a*). The relationship between the population size (*POP*) and the amount of suitable habitat, including young and mature habitat (X), under clustered harvesting is shown in Fig. 8*b* and can be represented as $POP = -20.625 + 0.1241\,X$ ($R^2 = 0.934$).

THINNING AND BURNING MANAGEMENT

Two harvest options—harvesting the oldest stands first and harvesting the stands in clusters—allowed the simulated sparrow population sizes to achieve the minimum objective proposed by the operation plan (Savannah River Forest Station 1992), but the sparrow populations went through a long transition period with a very low abundance (Fig. 3*b* & *c*). One silvicultural practice incorporated in the operation plan that would make stands suitable at earlier ages is to thin and then periodically burn 50- to 80-year stands so that the understory becomes less dense and ground vegetation is encouraged (Dunning & Watts 1990). This practice would make forested stands suitable for the sparrow at an age earlier than the mature stands currently found on the Savannah River Site. Making 50- to 80-year stands suitable for the sparrows increased the total amount of suitable stands in the landscape. As shown in Fig. 4*a*, the sparrow population increased with a decrease in the age at which stands were first suitable as breeding habitat.

EFFECT OF PLANTING DIFFERENT PINE SPECIES

According to the operation plan, while the total area of pines at the Savannah River Site will remain the same, slash pine stands will be converted into longleaf pine stands. By the year 2040, the proportion of pine species on the Savannah River Site will be about 61% longleaf and 39% loblolly pines. Because longleaf pines grow slower than loblolly pines, the young longleaf stands are suitable for sparrows for longer periods of time. In our main set of simulations, we assumed that no difference existed for longleaf and loblolly pines in terms of maximum suitable ages. In our later simulations we varied the time window during which stands were suitable for the sparrow and found that the sparrow population increased with an increase in the suitability window. The model results will be more accurate when the maximum suitable ages of both longleaf and loblolly pine stands are treated differently, but this will require additional local growth information on longleaf pines.

Implications for Land Management of Biodiversity

Land managers are focusing more attention on conserving and managing for biodiversity. In many cases, this new emphasis results in management for particular species of management concern, especially endangered species. Single-species management is often emphasized for two reasons. First, the selected species are often habitat specialists, and it is assumed that habitat patches that can support specialists will also be of sufficient quality to support a wide range of other species. For example, the forest stands on the Savannah River Site

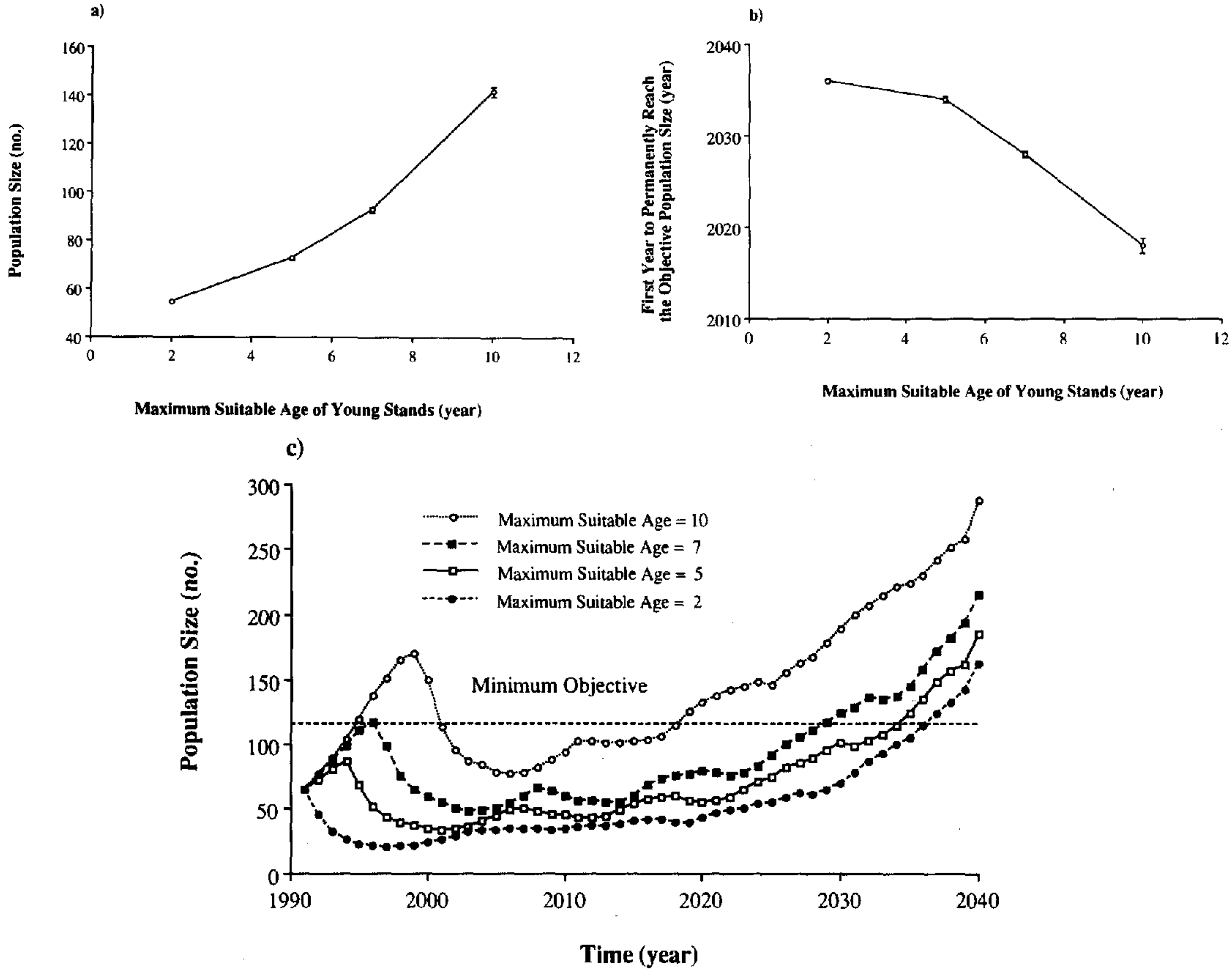

Figure 5. Effects of maximum suitable age of young stands on average population size (a), the first year to permanently reach the minimum objective set by the operation plan (b), and population dynamics (c).

Table 2. Sensitivity of estimated total population to five variables (Sx = (Δ x/x)/(Δ P/P)).

*Parameter**	Δ x/x	Δ P/P	Sx
Adult Survivorship (0.60)	33.88/72.71	0.10/0.60	2.79
Juvenile Survivorship (0.40)	49.40/72.71	0.10/0.40	2.72
Dispersal Mortality (0.01)	10.38/72.71	0.01/0.01	0.14
Young Stands** (5)	18.08/72.71	3/5	0.41
Older Stands*** (80)	−37.31/72.71	10/80	−4.10

**Default values for each variable given in parentheses. Analyses varied one parameter at a time in a simulation while using default values as constants for all other parameters.*
*** Number of years clearcuts were suitable.*
**** Minimum age at which older stands became suitable.*

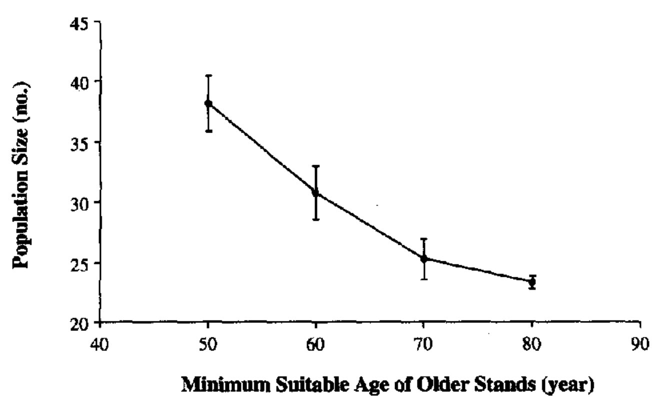

Figure 6. Effects of manipulating the age at which 50- to 80-year stands become suitable for breeding on average population size when juvenile survivorship = 0.3. (Compare with Fig. 4a in which juvenile survivorship was 0.4.)

Table 3. Extinction probability under low juvenile survivorship (0.3).

Adult Survivorship	*Young Stands**	*Older Stands***	*Extinction Probability****
0.6	2	80	0.08[a]
0.6	2	70	0.05[a]
0.6	5	80	0.06[a]
0.5	2	80	0.89[b]
0.5	5	80	0.85[b]

* *Number of years clearcuts were suitable.*
** *Minimum age at which older stands became suitable.*
*** *Letters* a *and* b *indicate whether two numbers are significantly different at the 5% level. If two numbers have different letters, they are significantly different.*

that contain suitable habitat for the endangered Red-cockaded Woodpecker also supply habitat for Bachman's Sparrows and 16 of the 42 other vertebrates on the Forest Service's list of management indicators for this region (Savannah River Forest Station 1992).

The second reason management plans often emphasize single species is that the habitat requirements for endangered species or other "charismatic megafauna" are relatively well known or at least under intensive study (see Ligon et al. 1986; Thomas et al. 1990; Murphy & Noon 1992). Research can therefore give managers a specific set of guidelines for how to manage for these species. It is less clear how to manage for a variety of species simultaneously or for "biodiversity," with all its connotations.

Our study provides an example of the problems faced by managers concerned with multiple species management. The operation plan proposed by the Forest Service at the Savannah River Site is a model plan of multiple species management, in that it sets specific management goals for many plants, fish, terrestrial animals, and even whole communities. Most of the management strategies outlined in the Operation Plan for the area in which our study site is located, however, concern habitat improvement for the Red-cockaded

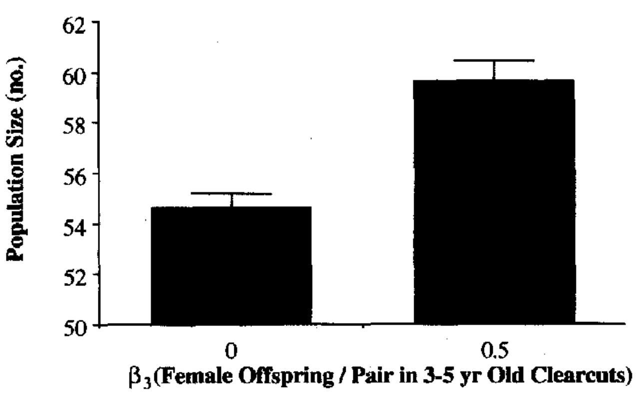

Figure 7. Influence of reproductive success in older clearcuts (3- to 5-year stands) on average total population size.

Table 4. Interaction effects among three variables (P_A, P_J, and β_{3-5})* on population size (mean ± standard error).

	$\beta_{3-5} = 0.0$		$\beta_{3-5} = 1.5$	
	P_J		P_J	
P_A	*0.3*	*0.4*	*0.3*	*0.4*
0.5	8.90 ± 0.25	33.10 ± 0.74	10.26 ± 0.37	38.83 ± 0.76
0.6	16.76 ± 0.66	54.63 ± 0.56	23.31 ± 0.62	72.71 ± 0.67

* P_A *is the adult survivorship,* P_J *is the juvenile survivorship, and* β_{3-5} *is the reproductive success (female offspring per pair) in pine stands of 3–5 year old.*

Woodpecker. Eighteen of the 26 specific standards and guidelines for Management Area II, where our study area is located, on the Savannah River Site contain a reference to the Red-cockaded Woodpecker, while an additional three guidelines refer indirectly to habitat improvement for this species (Savannah River Forest Station 1992). The dominance of woodpecker-related standards and guidelines leaves the impression of single-species management, even though the operation plan explicitly states that "The need to use [Red-cockaded Woodpecker] terminology to describe habitat parameter objectives should in no way detract from the comprehensive wildlife and botanical objectives that have been developed for this area" (Savannah River Forest Station 1992:15).

These standards and guidelines might be thought to provide adequate protection for Bachman's Sparrow because sparrow and the woodpecker share a critical habitat—mature pine forest. But our study indicates that because the sparrow also inhabits clearcuts and other early successional habitats, it does not necessarily benefit from woodpecker-based management, at least in the short term. In effect, the two species occupy different portions of the landscape, although they share one landscape component. Thus, implementation of the operation plan may increase the population of the Red-cockaded Woodpecker, but at the cost of possibly threatening Bachman's Sparrow locally. Over the long term (50 years), the strategy outlined in the operation

Table 5. Variance analysis of the interaction effects among three variables (P_A, P_J, and β_{3-5})* on population size (mean ± standard error).

Source	*df*	*Mean square*	*F***
P_A	1	13388.30	590.28
P_J	1	52876.20	2331.29
β_{3-5}	1	2973.21	131.09
$P_A \times P_J$	1	2710.63	119.51
$P_A \times \beta_{3-5}$	1	549.53	24.22
$P_J \times \beta_{3-5}$	1	680.46	30.01
$P_A \times P_J \times \beta_{3-5}$	1	106.99	4.72

* P_A *is the adult survivorship,* P_J *is the juvenile survivorship, and* β_{3-5} *is the reproductive success (female offspring per pair) in pine stands of 3–5 year old.*
** $p < 0.01$ *for all but* $P_A \times P_J \times \beta_{3-5}$ *which is* $p < 0.05$.

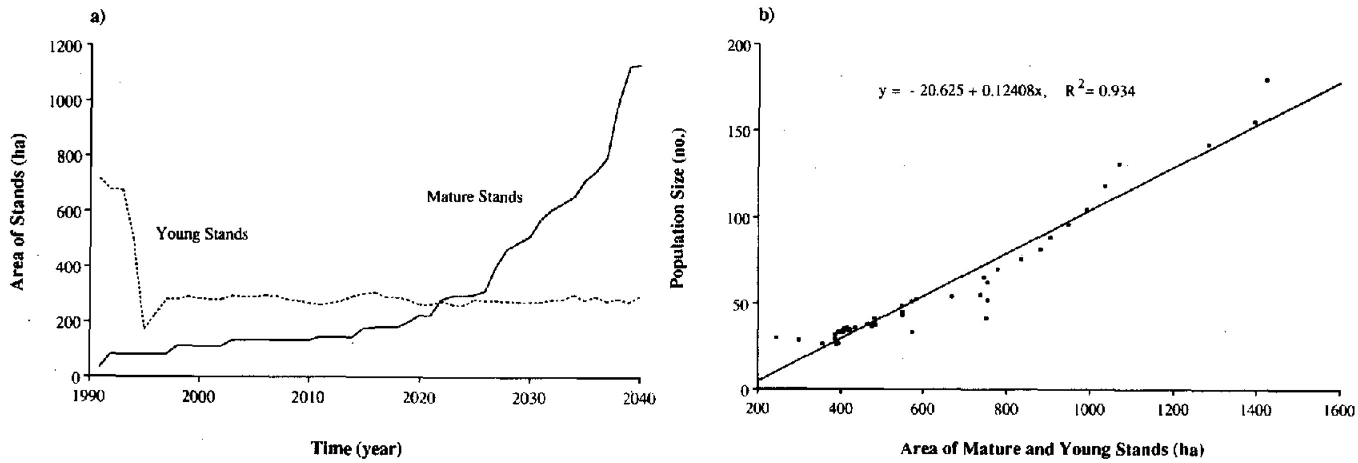

Figure 8. Annual change of area of young (1- to 5-year) and mature stands (80+ years) under clustered harvesting (a), *and the linear relationship between the sparrow population size and the total area of mature (80+ years) and young stands (1- to 5-years)* (b).

plan should support sparrow populations that eventually meet management goals. Over the short term, however, the management strategy may cause the sparrow population to decrease substantially. Our simulation results show that the short-term objectives (10 years in the operation plan) can rarely be achieved. During the first several decades of the operation plan, our results suggests that the sparrow population may remain very low or become extinct, especially if juvenile survivorship is low. If a stochastic event caused the sparrow population to drop even further in the valley—the transitional period—the chances of local extinction would be greatly increased because low population size increases the chance of extinction (Shaffer & Samson 1985). The loss of mature pine stands due to insect outbreak, tornado, or hurricane (Dunning & Watts 1991) is an example of such a stochastic event. Under some simulated scenarios, this potential threat is large: populations in over 80% of simulation replicates went extinct. If a population becomes extinct in the transitional period, the mature pine stands available later are meaningless for the sparrow unless some individuals from other locations immigrate into the new habitats.

Our simulations suggest that management of the middle-aged (50-to-80-year) pine stands to generate vegetation conditions similar to those in mature forest is critical for quickly reaching the Forest Service's management goal for Bachman's Sparrows. The Forest Service has initiated a pilot program of converting middle-aged stands to conditions suitable for Red-cockaded Woodpeckers. This program includes mechanically clearing all shrubs, burning the debris, and regular burning of the understory and ground vegetation. Stands selected for this program are thinned to basal areas considered optimal for the woodpeckers. These stands are intended to produce areas of local range expansion for the woodpecker and the re-establishment of the longleaf pine community. Our simulations suggest that expansion of this program would be the most direct method of mitigating the possible negative effects on the sparrow caused by the reduction in clearcut habitat under the operation plan.

By linking models such as ECOLECON with GIS landscapes of a particular region, managers could test the effect of a particular management strategy on a variety of species. Each species-specific version of the model would have to include a flexible life-history subroutine that could be parameterized for the species in question and a landscape scaled to the species' movements and dispersal abilities. In addition, because animals in the real world interact with one another, there is a need for models that consider the interactions and population dynamics of multiple species on a specific landscape. Such a flexible combination of GIS analysis and population modeling could provide managers with the ability to examine management effects on a variety of species and to search for ways of mitigating the effects on species of management concern caused by implementation of plans designed to improve habitat for single species at the top of the priority list.

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