

POPULATION DYNAMICS IN COMPLEX LANDSCAPES: A CASE STUDY¹

H. RONALD PULLIAM, JOHN B. DUNNING, JR., AND JIANGUO LIU
Institute of Ecology, University of Georgia, Athens, Georgia 30602 USA

Abstract. The abundance and distribution of natural populations can be strongly influenced by the types and arrangement of habitat patches within a landscape. The impact of landscape change on population dynamics is difficult to study using conventional population models and field techniques. Spatially explicit simulation models provide a powerful method for modelling landscape and population changes at large spatial scales and may prove useful as a management tool for mobile animal populations. As an example of this approach, we present a model designed to elucidate the effects of landscape-level variation in habitat dispersion on the size and extinction probability of avian populations in a region managed for timber production. In the model, habitat suitability and availability within the landscape change annually as a function of timber harvest and management strategies. The model incorporates life history characteristics of Bachman's Sparrow (*Aimophila aestivalis*), a species of management concern in the southeastern United States, and the landscape characteristics of the Savannah River Site, South Carolina, an area managed for timber production where the sparrow is relatively common. Life history characteristics used in the model include dispersal, survivorship, and reproductive success information reported for Bachman's Sparrow at this site or elsewhere in its range. Results of the simulations suggest that variation in demographic variables affects population size more than variation in dispersal ability. Changes in adult and juvenile survivorship have especially large impacts on the probability of population extinction. The presence of habitat types that serve as permanent sources of dispersers increases the total population size in the landscape, and lowers the probability of extinction. Results of models such as BACHMAP can suggest modifications to current management plans that would increase the probability of population persistence for species of special concern in managed landscapes.

Key words: *Bachman's Sparrow; dispersal; extinction probability; forest management; habitat dispersion; habitat-specific demography; landscape; population dynamics; Savannah River Site; spatially explicit simulation model.*

INTRODUCTION

Most mobile animal populations inhabit a variety of different habitats even within a relatively small geographic region. Individuals of the same species may have quite different reproductive success and chances of survival, depending on which habitat type they inhabit. Furthermore, the array of available habitats in the landscape may vary through time due to land use changes associated with human activities or succession. Accordingly, any model capable of predicting landscape-level population dynamics of such populations must explicitly consider what habitats are available in the local landscape, how these habitat availabilities change through time, how the animals are distributed among these habitats, and the demographic success that each organism obtains in each habitat.

In order to predict the effects of landscape change, population models must be spatially explicit. Both the spatial arrangements of patches (i.e., the landscape physiognomy; J. B. Dunning, B. J. Danielson, and H. R. Pulliam, *unpublished manuscript*), as well as the

relative amounts of different habitat types (landscape composition) within the landscape must be specified. When both landscape physiognomy and composition are incorporated into a population model, the dispersal of organisms across the landscape can be followed, and the impact of changes in habitat arrangement within the landscape can be assessed (Fahrig 1988).

We have developed a class of spatially explicit population models that we call MAP, an acronym for Mobile Animal Population. The models are single-sex "grid" models (Fahrig 1988), in which the exact location of individuals on a gridwork of habitat patches is followed through time. In this paper, we illustrate the utility of these models by focusing on BACHMAP, the version of the model parameterized for the Bachman's Sparrow (*Aimophila aestivalis*), a potentially threatened bird found in the pine woods of the southeastern United States. Bachman's Sparrow has declined over much of its range since the 1930s (Brooks 1938, Haggerty 1986), and is currently a species of management concern. The United States Fish and Wildlife Service classifies the sparrow as a Category 2 species, indicating that the species is possibly threatened or endangered, but that too little information ex-

¹ Manuscript received 19 June 1991; accepted 12 August 1991.

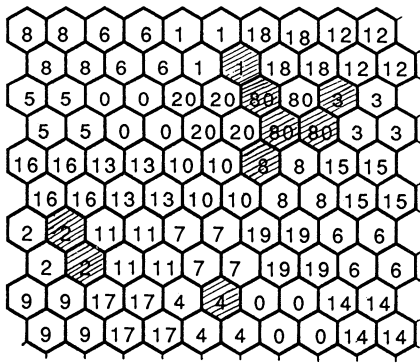


FIG. 1. Landscape structure at end of a sample simulation run. Numbers inside each hexagonal cell indicate age of pines: 1–20 = age (in years) of stand in harvest rotation; 80 = mature stand. Shaded cells are occupied by Bachman's Sparrow. Total landscape size = 800 cells.

ists regarding its status and management. The United States Forest Service considers Bachman's Sparrow to be a sensitive species and a management priority for the Southeast.

Bachman's Sparrows breed in a variety of different habitats, including managed pine plantations in the southeastern United States. Pine forests in the Southeast consist mostly of mosaics of even-aged stands of different management histories. One factor thought to be a primary contributor to the sparrow's decline has been regional and local changes in the availability of suitable habitats (Dunning and Watts 1990). We developed **BACHMAP** as a way of considering both the demographic and dispersal characteristics of Bachman's Sparrows as well as the changes in the availability of suitable habitat as factors affecting population size in managed landscapes. In this way, we hoped to relate the sparrow's population dynamics to land use characteristics of the regions it inhabits.

METHODS

Any model of the population dynamics of a mobile species inhabiting a complex landscape must incorporate three categories of variables: (1) landscape variables that describe habitat abundance and the spatial arrangement of habitats, (2) habitat-specific demographic variables (reproductive success and survivorship), and (3) behavioral variables that describe the dispersal characteristics of the species. In the case of Bachman's Sparrow, some information exists concerning landscape, demographic, and dispersal variables, but in each case some degree of uncertainty exists regarding estimates of these variables used in the models. In this section we discuss what is known about each category of variable and what assumptions we have made regarding the model's parameter values. In general, our approach has been to evaluate the amount of uncertainty associated with each variable and then, with the model, to vary the appropriate parameters

within a range of feasible values in order to determine the sensitivity of the model output regarding population size and distribution to these variations.

We hope **BACHMAP** will eventually prove useful as a management tool for Bachman's Sparrows in pine habitats at the Savannah River Site (hereafter, SRS) near Aiken, South Carolina. Although we have studied the species for 3 yr at SRS (Dunning and Watts 1990), we still have few data on most of the critical demographic and dispersal variables from this site. Accordingly, we will, as necessary, use information gathered from other studies of the species in other areas to make initial estimates of the parameter values needed for **BACHMAP**. Using the best information available from other studies is an efficient way to parameterize our current models; however, we recognize that for management purposes we will eventually need accurate life history data from the geographic location where the model will be applied.

The model landscape

Our simulations were performed on a hypothetical 2000-ha landscape consisting of a 20×40 array of 800 2.5-ha hexagonal cells (Fig. 1). Bachman's Sparrow breeding territories are typically 2–3 ha (Haggerty 1986; J. B. Dunning and B. D. Watts, *personal observations*) making each 2.5-ha cell approximately the size of a territory. Hexagonal cells were used for two reasons. First, densely packed bird territories in continuous habitat are thought to approximate hexagons in shape (Grant 1968, Verner 1977). Secondly, hexagons share extensive borders with six other cells and allowed dispersal, as we modeled it, in six directions. This is somewhat more realistic than the four directions allowed in a grid of squares.

For our initial model explorations, we chose to use hypothetical landscapes that embody several characteristics of the SRS where our field studies are in progress. At the SRS most pine plantings are on stands of 5–50 ha. In our model landscapes, we assumed that all stands (called "tracts" in our model) are 10 ha, each consisting of four (2×2) cells. Since there are a total of 800 cells, the landscape consists of 200 10-ha tracts. For our simulations, we assumed that the entire landscape is dominated by pines. Old-growth pine was restricted to relatively few tracts, and the rest of the landscape consisted of pine plantations on a 21-yr harvest rotation. Counting (1) old-growth pine, (2) the 20 age classes of pine plantations, and (3) the clearcuts present in the year following harvest, there were 22 vegetation age classes in the simulation model. At the beginning of each simulation, we randomly assigned one of these age classes to each tract. A variable number of tracts (ranging from 0 to 8) were assigned the status of old-growth sites, which were never harvested. The remaining tracts were divided (with equal probability) among the 20 age classes plus clearcuts. Model simulations were run for 105 yr (five harvest rotations). Each

plantation tract was harvested when it reached 20 yr of age, and remained idle for 1 yr after harvest.

Reproductive success

Haggerty (1986, 1988) followed the fate of 66 Bachman's Sparrow nests from more than 30 territories during the breeding seasons of 1983 through 1985 in Arkansas. Based on these data, he used the Mayfield method (Mayfield 1975) to calculate seasonal breeding success, defined as the number of fledglings produced per pair per season. He calculated that the sparrows laid an average of 11.9 eggs per pair and that 25% of these survived to the fledgling stage, giving a reproductive success of 2.97 young fledged per territory.

Based on the above calculations and the assumption of an equal sex ratio for fledglings, we have assumed that territorial pairs produce an average of 1.5 female offspring per season. However, not all territories are equally productive. Based on Haggerty (1986), we calculated that $\approx 18\%$ of all territories produced no female offspring. In our simulations, we assumed that each territorial pair could produce 0, 1, or 2 female offspring. Starting with 0.18 as the fraction of pairs that failed to produce any female offspring, we used 0.14 and 0.68 as the fraction of territories producing either 1 or 2 female offspring, respectively, in order to give an expected number of 1.5 female offspring per territorial pair.

Bachman's Sparrows breed in a variety of habitats ranging from mature pine woods to early successional areas. These habitats all have certain features in common: they are characterized by high light penetration, relatively open, grassy ground cover, and a few scattered understory trees or shrubs (Dunning and Watts 1990). In many pine-dominated landscapes, Bachman's Sparrows breed in both old-growth pine stands and in newly planted pine fields. Haggerty found no difference in reproductive success of Bachman's Sparrows in mature pine stands and in young pine plantations; however, some uncertainty exists concerning exactly what age classes of pine stands are used for breeding.

At the SRS, we find that Bachman's Sparrows occur primarily in very young pine stands (<10 yr after planting) and in mature pine stands (>50 yr old). Based on our observations at SRS, we believe the sparrows rarely breed in young pine stands >5 yr old, but adults exhibit high site fidelity and sometimes remain in older stands that may no longer be suitable for breeding.

The very youngest stands (1–2 yr) appear to be the most suitable for breeding, though birds commonly breed in 3–5 yr stands (J. B. Dunning and B. D. Watts, *personal observations*). In our simulations, we assumed that mature pine stands and 1–2 yr old stands were equally suitable for breeding (producing an average of 1.5 female offspring per pair per year). However, due to the uncertainty about 3–5 yr old stands, we varied the reproductive success achieved in these stands. Most

likely, reproductive success declines gradually from 3 yr onward, but, lacking any specific data, we looked at two extremes. First, we assumed that reproductive success is high (1.5 female offspring per territory per year) in 1–2 yr stands but much lower (0.50 female offspring per year) in 3–5 yr stands. We contrasted this to the assumption that reproductive success remains high (1.5 female offspring per year) in all stands of 1–5 yr.

Survival rates

Haggerty (1988) relocated only 18% of territorial adults on the territories where they had bred the previous year. For several reasons, we view this as an inadequate estimate of adult annual survival rates for Bachman's Sparrow. First, Haggerty's sample size was very small and he made no major effort to estimate adult survival rates. (Haggerty's study was focused on reproductive success and his estimates of reproductive success are based on much larger sample sizes than the very small sample for adult survival rate.) Secondly, published estimates of survival rates of sparrows of similar body size suggest adult survival rates mostly in the range of 40–60% (Ricklefs and Bloom 1977). Finally, a survival rate of 18% is nowhere near sufficient to maintain a stable population given an annual rate of 3.0 offspring (1.5 females) per territory per year.

Juvenile survival rates are notoriously difficult to measure in birds because juveniles disperse from their natal sites, and birds that disappear from a study area may survive elsewhere. Adults, on the other hand, typically return year after year to the same breeding site, making estimating adult survival relatively easier. Published estimates of survival rates for juvenile sparrows range from 5 to 20% (Nice 1937, Knapton 1978, Ross and McLaren 1981, Sullivan 1989), though methods vary considerably and most investigators agree these are underestimates due to the problem of relocating surviving juveniles. Survival rates of juveniles are almost certainly less than survival rates of adults because juveniles face additional mortality hazards, especially during the post-fledgling period and during dispersal (Sullivan 1989).

Our approach was first to estimate a feasible range of adult and juvenile survival rates based on demographic considerations and then to perform simulations with survival estimates spanning this range. Using this approach, we can determine the sensitivity of sparrow population size and extinction rate to variation in survival rates vs. the sensitivity to other parameters. To determine the feasible range of survival rates, we used the reproductive estimate of 1.5 female offspring per territory and then calculated the combinations of adult and juvenile survival rates required to achieve a stable population size. (Although Bachman's Sparrows are declining in many parts of the species' range, we have no evidence that the local population is declining at our study site.)

To achieve positive population growth, the finite rate

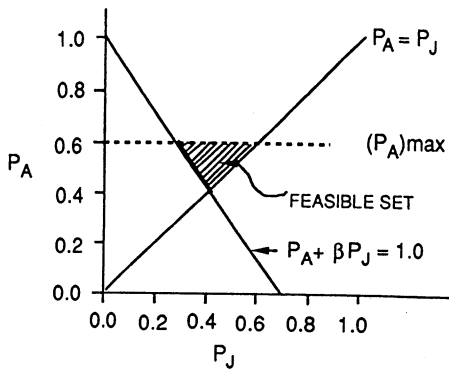


FIG. 2. Set of feasible adult and juvenile survival rates used in computer simulations. Feasible set (shaded region) consists of values of adult survival (P_A) and juvenile survival (P_J) rates that satisfy the equation $P_A + \beta P_J \geq 1.0$, where β = per capita reproductive success. Feasible set is limited by the constraints that (1) maximum $P_A = 0.6$, and (2) $P_A \geq P_J$. When $\beta = 1.5$ female offspring/season, the extremes of the feasible set are ($P_A = 0.6, P_J = 0.27$), ($P_A = 0.4, P_J = 0.4$), and ($P_A = 0.6, P_J = 0.6$).

of increase (λ) must equal or exceed 1.0, which is to say that every individual must, on average, be replaced by at least one other individual. Setting the value of per capita reproductive success (β) at 1.5 female offspring per breeding female, a positive population growth requires that

$$\lambda = P_A + \beta P_J \geq 1.0 \quad (1a)$$

or

$$P_A \geq 1.0 - 1.5 P_J, \quad (1b)$$

where P_A and P_J are the adult and juvenile survivorship rates, respectively. Fig. 2 shows the feasible set of survival rates for Bachman's Sparrow based on constraint 1b above and the additional assumptions that adult survival is not greater than 60% and juvenile survival is less than adult survival. Furthermore, a stable population requires that $\lambda = 1.0$ and this additional constraint requires that the survival values fall on a line between the extremes ($P_A = 0.6, P_J = 0.27$) and ($P_A = 0.4, P_J = 0.4$).

Dispersal

We designed **BACHMAP** to fit the annual cycle of an avian population in a seasonal environment (see Pulliam 1988). The population was censused in the spring at the initiation of the breeding season. Adult pairs alive at the start of the breeding season produced an average of β female juveniles. Adults and juveniles survived the nonbreeding (winter) season with probabilities P_A and P_J , respectively. At the end of the nonbreeding season, excess individuals in each territory dispersed to find an unoccupied, suitable cell and the cycle was repeated.

Dispersal by juveniles.—Simulation studies of population dynamics in patchy environments have mod-

eled dispersal in several ways, many of which incorporate a dispersal distance as one of the primary dispersal variables (Urban and Shugart 1986, Fahrig 1988, Fahrig and Paloheimo 1988a). Dispersal distance is the average distance moved by a dispersing individual, included as either a success probability function that decreases with increasing distance (Urban and Shugart 1986), or as a constant distance that each disperser moves before searching for a suitable patch (Fahrig 1988). While accurate for organisms that display a relatively simple search strategy (Fahrig and Paloheimo 1988b), dispersal distance techniques are probably not realistic for models of relatively complex search strategies such as avian dispersers might display. Thus, we chose to model dispersal as a series of discrete steps, where a disperser entered and searched patches sequentially, experiencing a probability of dispersal mortality with each step (Lande 1988). Dispersal ended when an individual reached an unoccupied, suitable patch and settled there, or when the disperser died.

To search for an unoccupied habitable patch, a juvenile left its natal patch by entering one of the neighboring cells (Fig. 3). We assumed individuals could identify whether neighboring cells were habitable or uninhabitable, but could not determine if neighboring habitable cells were occupied without visiting them. If several neighboring cells were habitable, the dispersing individual randomly moved to any one of the neighboring habitable cells. If the selected cell was occupied, the juvenile left that cell and moved to a new, adjacent cell. This procedure was repeated until the dispersing juvenile found an unoccupied, suitable cell, or died.

If none of the cells adjacent to a dispersing juvenile's current patch was habitable, we assumed the dispersing juvenile had an equal probability of moving into any one of the neighboring cells. As long as the cell into which the juvenile moved was not habitable, and had no adjacent habitable cells, the dispersing individual continued to move from cell to cell in a straight line. Dispersers encountering an edge of the entire 800-cell grid changed directions to avoid leaving the grid. Thus, individuals never disappeared off the simulation landscape. Likewise, individuals never entered the grid from outside, so, in effect, we modeled the population as a closed population inhabiting a 2000-ha area. Our decision to treat the grid edges as "reflecting boundaries" is roughly equivalent to assuming that the 2000-ha grid was embedded in similar habitat on all sides and that for each individual that left the grid, one came in from outside (Fahrig 1991).

Memory.—In different simulations, we varied an individual's ability to remember its search path. In some trials, individuals were "with memory" and never re-entered the patches that had been previously searched. In other trials, individuals were "without memory" and did not turn back immediately to the patch that had just been searched, but other previously searched patches could be re-entered. Memory allowed dispers-

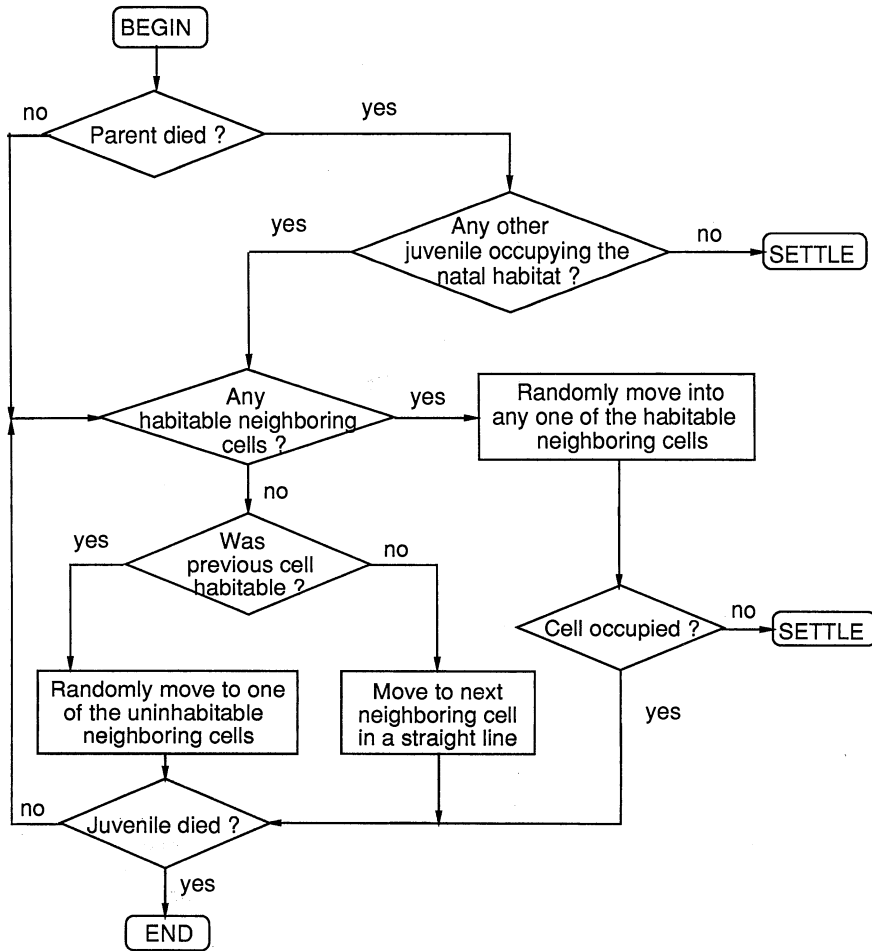


FIG. 3. Flow diagram outlining juvenile dispersal without memory.

ers to search a larger portion of the landscape since no dispersal time was consumed revisiting previously visited patches. Simulations that incorporated memory are labeled "MEM" in the tables and figures.

Selectivity.—As discussed in the *Reproductive success* subsection, above, in some simulations we assumed that reproductive success in the 3–5 yr age classes was lower than that attainable in either the 1–2 yr age classes or in the mature pine habitat. To determine how the ability to discriminate such differences in habitat quality affected population dynamics, we varied the ability of the dispersing individuals to select between 1–2 yr cells and 3–5 yr cells. Individuals that had high selectivity (HS) settled only in patches that yielded high reproductive success, i.e., mature or 1–2 yr age class cells. Individuals with low selectivity (LS) settled into 1–5 yr cells and mature pine cells indiscriminately. Selectivity did not apply in simulations where the same reproductive success was attainable in all suitable stands.

Dispersal mortality.—We assumed that dispersing juveniles experienced a stochastic mortality hazard

while searching for a habitable territory. In our model, a disperser had a fixed probability of death each time it moved from one cell to another. We used dispersal mortality probabilities (DM) of 0.10, 0.02, and 0.01 per move, in an attempt to span the range of values that we felt were feasible for Bachman's Sparrow. DM values <0.01 were not used because they would require an excessive amount of computer time for each simulation. Also, since simulations with DM = 0.01 had neither larger populations nor lower extinction probabilities than simulations with DM = 0.02, we assumed that population size had already plateaued in response to decreases in dispersal mortality.

The dispersal mortality probabilities can be compared by considering the average expected number of territories that could be searched by a disperser with a given DM value before the disperser dies (Lande 1988, Thomas et al. 1990). For DM = 0.10, 0.02, and 0.01, the expected number of territories that could be searched was 10, 50, and 100, respectively. Because each cell was 2.5 ha in size, dispersers could therefore search on average between 25 and 250 ha before dying,

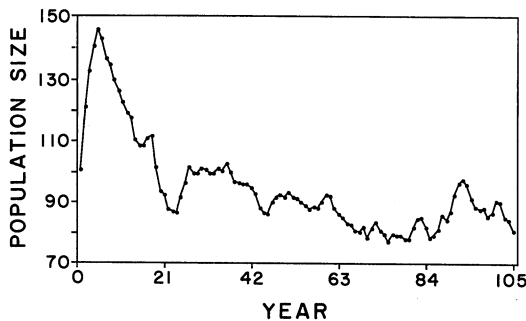


FIG. 4. Annual total population size throughout one simulation run of five harvest rotations (105 yr). Note high variation during first rotation (years 1–21).

depending on the exact dispersal mortality used in a given simulation. A disperser with $DM = 0.01$ would travel ≈ 9 km before dying if it stayed on a straight-line path through uninhabitable cells.

Adult dispersal.—Adults usually remained to breed in the cell where they bred the previous summer; that is, they showed strong site fidelity. In **BACHMAP**, adults dispersed only when their patches were older than 5 yr. At that point, an adult dispersed to an adjacent suitable cell, if one was present and unoccupied. If no neighboring cell was suitable and unoccupied, the adult stayed in its original site, even though reproductive success in cells older than 5 yr was zero.

Validity of dispersal assumptions.—As with other parts of the model, the assumptions built into the dispersal process were based on our field experience with Bachman's Sparrows and similar sparrow species. For instance, habitat types on the SRS are relatively discrete, consisting of pine forests, clearcuts, and unsuitable habitats such as wetlands and deciduous woodland. Different-aged stands in pine forests are significantly different in a number of vegetative characteristics (Dunning and Watts 1990), so that they are recognizable from a distance to human observers. We therefore believe it is reasonable to assume that the sparrows can distinguish clearcuts from forest, and recognize suitable (mature) and unsuitable pine forest areas without having to enter the stands physically. On the other hand, female Bachman's Sparrows are extremely cryptic in behavior, unlike the males who advertise their presence through singing. Thus, we believe it is most realistic to assume that the dispersing females must physically enter and search habitable cells to determine if they are already occupied by another female.

We assumed that dispersing birds move in straight lines through unsuitable habitat. While there is some evidence that is true for other bird species (Belthoff and Ritchison 1989), we have no direct evidence for this type of dispersal behavior in Bachman's Sparrows. In our simulation landscapes, however, dispersing birds rarely traveled for great distances through unsuitable habitat; thus, straight-line dispersal was probably a mi-

nor portion of the total movements of most individuals.

We have observed that sparrow occupancy appears to decline rapidly in older clearcuts (> 5 yr after pine planting, Dunning and Watts 1990). With our assumptions concerning adult dispersal, the model mimics this rapid reduction in cell occupancy after year 5. The assumptions are based on the general tendency for breeding resident passerines to be site philopatric. Whether adult birds actually shift to neighboring patches as their original sites get less suitable can only be determined through future field studies involving marked individuals.

Simulation methods

We designed our simulations to mimic a timber-management plan that included a harvest rotation of 21 yr. Each tract was planted in the year after harvest, and the pines were allowed to grow for 20 yr, at which time the tract was harvested again. At the beginning of each simulation, adult females were randomly assigned into old-growth pine habitats and 1–5 yr old cells with probability 0.50. Therefore, initial population size for each simulation was equal to approximately one-half the number of habitable cells. Each year during the simulation, the avian population went through the annual cycle discussed previously. The population went extinct if all individuals died prior to year 105. We calculated an extinction probability for each type of simulation as the number of replicates in which extinction occurred divided by the total number of replicates. Each type of simulation was replicated from 10–50 times, depending on the variability found in the simulation results. All simulations were programmed using Quickbasic (4.5) (Microsoft Corporation 1988) on a Zenith 386 computer.

Calculation of population size.—In most simulations, population size fluctuated more widely during the first 21 yr (first rotation) than during the final four rotations from year 22 through year 105 (Fig. 4). Accordingly, we calculated the average population size as the mean population size during the final four rotations. Simulations that resulted in population extinction were not included in calculation of average population size.

Sensitivity analysis.—To evaluate the sensitivity of the simulation results to variation in specific parameters, we recorded the change in total population size that resulted from small changes in the values of the parameters of interest. We calculated the sensitivity (S_x) of population size as:

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

where $\Delta x/x$ is the observed change in the total population size resulting from a change ($\Delta P/P$) in the parameter P (Jørgensen 1986). Large values of this index indicate that the model shows increased sensitivity to change in a particular parameter. We examined the

TABLE 1. Effect of selectivity among habitat types by dispersing juvenile Bachman's Sparrows on probability of population extinction, and on population size found in different habitat types. Values of parameters that were fixed in these simulations are: $P_A = 0.6$, $P_J = 0.4$, $DM = 0.1$, $\beta_{1-2} = 1.5$, $\beta_{3-5} = 0.5$, $MH = 8$, and MEM. Abbreviations of the fixed parameters are detailed in the Methods section.

Population location	Population size		P
	High selectivity	Low selectivity	
Total landscape	10.61 \pm 0.38	12.02 \pm 0.23	.0066
In mature habitats	6.84 \pm 0.04	6.55 \pm 0.11	.0588
In 1-2 yr habitats	1.17 \pm 0.25	0.77 \pm 0.05	.0125
In 3-5 yr habitats	2.12 \pm 0.28	3.23 \pm 0.13	.0002
In 6-20 yr habitats	0.48 \pm 0.04	1.47 \pm 0.08	.0001
Extinction probability*	0.00 (0/10)	0.17 (2/12)	.0885

* In parentheses are the number of simulations that went extinct/total sample size.

model's sensitivity to variations in the following variables: dispersal mortality (DM), adult and juvenile survivorship (P_A and P_J), reproductive success in 3-5 yr stands (β_{3-5}), and the amount of mature habitats (MH).

In addition to testing for sensitivity in single factors, we sought to determine how simultaneous variation in several factors would influence population size. We used a 2^3 factorial design to look at interactions among three variables (MH, DM, and β_{3-5}) each at two levels. These variables were chosen because MH is the primary factor under control by forest managers, while DM and β_{3-5} are the factors we know the least about in our field studies.

We used two-tailed t tests to test for significant differences in population sizes. We tested for differences in extinction probabilities by using a test for comparing binominal proportions (Ott 1988). Means of population sizes are presented with one unit of standard error.

RESULTS

As previously mentioned, our model incorporates three categories of variables that influence population dynamics. Dispersal variables represent factors influencing the ability of individuals to find suitable, unoccupied patches; demographic variables describe habitat-specific survivorship and reproductive success; and landscape variables describe the types and arrangement of habitat patches available to dispersing individuals. We will discuss the effects of variables in each of these categories on population size and extinction probability.

Dispersal variables

Selectivity.—When reproductive success in the 3-5 yr age classes was lower than that attainable in 1-2 yr or mature age classes, simulations incorporating high selectivity (the ability to select only highly productive habitat) resulted in slightly lower total population sizes than found in simulations using low selectivity (Table 1). Approximately equal numbers of breeding birds were found in the mature tracts in both types of simulations; however, more individuals were able to locate and settle in the 1-2 yr age class in the high selectivity

simulation. No juveniles with high selectivity settled in cells of the 3-5 yr age class; thus the relatively small populations in the 3+ yr age classes resulted from site fidelity of breeders from previous seasons. With low selectivity, dispersers could settle in both the highly productive age classes and the less productive 3-5 yr cells. Although mean total population size was increased in the low selectivity simulations, some populations with low selectivity went extinct (Table 1). Extinction probabilities were not significantly different ($P = .088$), however, between the high and low selectivity simulations.

Memory.—Dispersers that remember previously searched patches can avoid using their limited amount of dispersal time to revisit areas that have already been rejected. We expected that memory of previously searched patches should allow more efficient searches, and therefore an increase in the number of dispersers that find suitable patches. As expected, total population size in simulations that incorporated memory was higher than in simulations in which dispersers searched with no memory (Table 2).

Population size in the mature tracts did not differ significantly between the memory and nonmemory simulations. Dispersers with memory were able to find more 1-5 yr cells, resulting in higher populations in these age classes, as well as higher residual populations in the nonproductive 6-20 yr age class, compared to nonmemory simulations. No populations went extinct in these simulations.

Dispersal mortality.—Higher dispersal mortality results in fewer patches being searched, on average, before a suitable unoccupied patch is found or the disperser dies. In our simulations, dispersal mortality had a significant effect on the disperser's ability to locate productive patches, and therefore on the total population size. Simulations with $DM = 0.01$ had higher total population sizes, with significantly more individuals in all age classes of pines, compared to simulations with $DM = 0.10$ (Table 3). Similarly, dispersers with $DM = 0.02$ were able to find and settle in more 1-5 yr cells, resulting in a higher population size compared to simulations with $DM = 0.10$. There were no sig-

TABLE 2. Effect of memory of habitat quality in dispersing juvenile Bachman's Sparrows on probability of population extinction, and on population size found in different habitat types. Values of parameters that were fixed in these simulations are: $P_A = 0.6$, $P_J = 0.4$, $DM = 0.02$, $\beta_{1-2} = 1.5$, $\beta_{3-5} = 0.5$, $MH = 8$, and HS . Abbreviations of the fixed parameters are detailed in the Methods section.

Population location	Population size		
	Memory	No memory	<i>P</i>
Total landscape	14.83 ± 0.79	9.74 ± 0.28	.0001
In mature habitats	6.94 ± 0.04	6.94 ± 0.04	.9827
In 1–5 yr habitats	6.90 ± 0.66	2.49 ± 0.20	.0001
In 6–20 yr habitats	0.99 ± 0.12	0.31 ± 0.04	.0001
Extinction probability*	0.00 (0/10)	0.00 (0/10)	

* In parentheses are the number of simulations that went extinct/total sample size.

nificant differences, however, in population sizes between simulations with $DM = 0.01$ and $DM = 0.02$. No populations went extinct in these simulations with different dispersal mortalities.

Demographic variables

Survivorship.—Decreases in adult or juvenile overwinter survival resulted in smaller total population sizes and higher extinction probabilities (Table 4). When juvenile survivorship was decreased from 0.40 to 0.30, total population size decreased $\approx 30\%$. Similarly, a 25% decrease in adult survivorship resulted in a population size reduction of 36% and a fourfold increase in extinction probability (from 17 to 70%). These results indicate that, in general, changes in adult survivorship had larger effects on population size and extinction than did changes in juvenile survivorship.

Reproductive success.—Reproductive success in the 3–5 yr age classes had strong effects on total population sizes (Table 5). In simulations with high values of β_{3-5} , population sizes were twice as large as those found in simulations with low reproductive success in the 3–5 yr age classes. Populations were significantly increased in all age classes. In addition, no extinctions were recorded in simulations where reproductive success in the 3–5 yr tracts was high (Table 5). An extinction probability of 17% was recorded in the simulations where 3–5 yr cells yielded low success; however, this

was not significantly different from the 0% extinction probability recorded when reproduction was uniformly high ($P = .088$).

Landscape variables

Availability of mature pine habitats.—Pulliam (1988) suggests that the presence of stable sources of dispersers in a landscape can have a pronounced effect on population size. We examined the importance of mature pine habitat as a stable (i.e., permanent) source of dispersers by varying the number of tracts of mature pines within the landscape. Reproductive success in mature pines did not exceed that achieved in very young pine tracts; however, mature pine tracts were permanently available as suitable breeding habitat (since they were never harvested), whereas tracts of young pines became unsuitable after 5 yr.

Total population size increased linearly with the number of cells of mature pine habitat (Fig. 5), even though the amount of mature habitat was always a small fraction of the total landscape size. Regression coefficients (r^2) from linear regressions were equal to or close to 1.0 for all habitat age categories.

Habitat occupancy and pine age class.—We define habitat occupancy as the percentage of cells of a particular age class occupied by the sparrows. Occupancy increased from age class 0 (clearcuts) through age class 5, and then sharply decreased in older age classes (Fig.

TABLE 3. Effect of dispersal mortality (DM) in juvenile Bachman's Sparrows on probability of population extinction, and on population sizes found in different habitat types. Values of parameters that were fixed in these simulations are: $P_A = 0.60$, $P_J = 0.40$, $\beta_{1-2} = 1.5$, $\beta_{3-5} = 0.5$, $MH = 8$, HS , and MEM . Abbreviations of the fixed parameters are detailed in the Methods section.

Population location	Population size			Probability of difference		
				DM = 0.01 vs. DM = 0.02	DM = 0.01 vs. DM = 0.10	DM = 0.02 vs. DM = 0.10
	DM = 0.01	DM = 0.02	DM = 0.10	DM = 0.02	DM = 0.10	DM = 0.10
Total landscape	16.68 ± 0.50	14.83 ± 0.79	10.61 ± 0.38	0.0851	0.0001	0.0001
In mature habitats	7.00 ± 0.05	6.94 ± 0.04	6.84 ± 0.04	0.6089	0.0329	0.3043
In 1–5 yr habitats	8.49 ± 0.44	6.90 ± 0.66	3.29 ± 0.32	0.0831	0.0001	0.0002
In 6–20 yr habitats	1.19 ± 0.06	0.99 ± 0.12	0.48 ± 0.04	0.0636	0.0001	0.0035
Extinction probability*	0.00 (0/10)	0.00 (0/10)	0.00 (0/10)			

* In parentheses are the number of simulations that went extinct/total sample size.

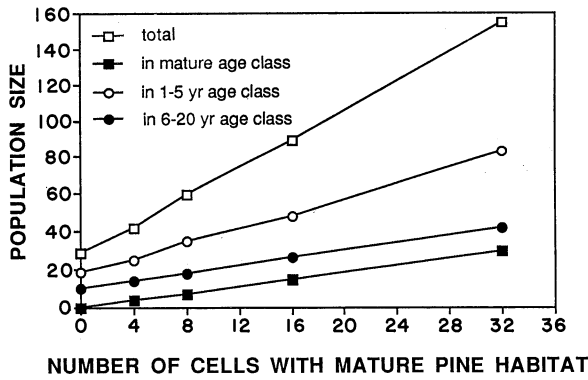


FIG. 5. Population sizes attained in landscapes with different amounts of mature pine habitat. Parameter values used in these simulations: $P_A = 0.6$, $P_J = 0.4$, DM (probability of dispersal mortality) = 0.02, MEM, $\beta = 1.5$. No selectivity level was selected because all suitable sites yielded the same reproductive success.

6). Increasing the amount of mature pine habitat within the landscape increased the population size and hence the occupancy in each age class, but did not affect the shape of the population distribution among age classes.

Number of occupied neighbors.—If the cells neighboring a focal territory were habitable, they might be occupied by breeding individuals, whose offspring could disperse into the focal tract in subsequent seasons. This suggests that the cells in a tract are more likely to be occupied if some of the cells in the immediate neighborhood are occupied. Therefore, we investigated how population size in a given tract was affected by the number of occupied cells in the surrounding landscape.

Each cell in our simulation landscape was part of a four-cell tract of similar habitat (see *Methods*). Around each four-cell tract, there were up to 10 adjacent cells that shared at least one border (hereafter, “neighboring cells”) with the focal tract. (A tract along the edges of the landscape had fewer neighboring cells and tracts in the four corners of the grid had only five neighboring cells.) About 90% of the tracts had no adjacent occupied cells, while only a few tracts had >4. We therefore examined the number of occupied cells in tracts that were surrounded by between 0 and 4 occupied neighboring cells.

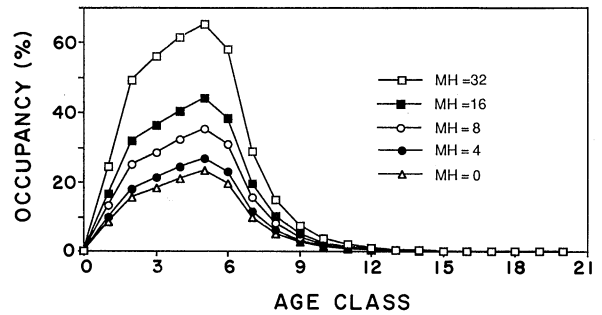


FIG. 6. Proportion of cells in age classes 1–20 that were occupied by Bachman’s Sparrow. Parameter values as in Fig. 5. Amount of mature habitat varied from 0–32 cells. Each data point is the average of 10 simulations.

Tracts with at least one occupied neighboring cell were much more likely to be occupied than tracts that had no occupied neighboring cells (Fig. 7). Each tract consisted of four cells or potential territories so that the potential maximum abundance in any tract was 4.0. Abundance within the focal tract increased to as high as 3.25 breeding females in tracts of 5-yr-old pines with four occupied neighboring cells. Tracts with suitable breeding habitat were rarely occupied if they had no occupied neighboring cells.

Sensitivity analysis

We examined the sensitivity of total population size to variation in several variables, including three demographic (adult survivorship, juvenile survivorship, and reproductive success in cells of the 3–5 yr age classes); one dispersal (dispersal mortality); and one landscape (the amount of mature pine habitat) variable. Total population size was more sensitive to the three demographic variables examined than to dispersal mortality (Table 6). Sensitivity was greatest to adult and juvenile survivorship and showed intermediate levels of sensitivity to reproductive success and the amount of mature pine available.

Sensitivity analysis compares the relative change in population size to the relative change in a parameter of interest. It is therefore a useful way to compare the sensitivity of population size to quantitative parameters such as survival probability and reproductive

TABLE 4. Effect of survivorship on probability of population extinction, and on total population size. Values of parameters that were fixed in these simulations are: DM = 0.10, $\beta_{1-2} = 1.5$, $\beta_{3-5} = 0.5$, MH = 8, LS, and MEM. Abbreviations of the fixed parameters are detailed in the *Methods* section.

Population parameter	Survivorship			Probability of difference		
	A	B	C	A vs. B	A vs. C	B vs. C
	$P_A = 0.60$ $P_J = 0.40$	$P_A = 0.60$ $P_J = 0.30$	$P_A = 0.45$ $P_J = 0.40$			
Total population size	12.02 ± 0.23	8.36 ± 0.23	7.81 ± 0.25	0.0001	0.0001	0.0984
Extinction probability*	0.17 (2/12)	0.35 (6/17)	0.70 (35/50)	0.1251	0.0055	0.0002

* In parentheses are the number of simulations that went extinct/total sample size.

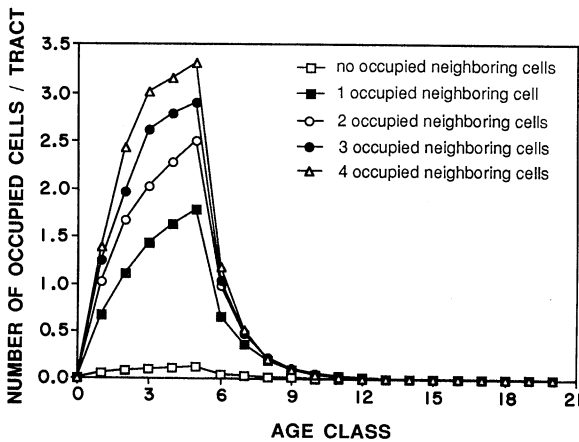


FIG. 7. Effect of occupation of neighboring cells on the number of cells occupied within a tract. Maximum occupancy within a tract = 4.0. Parameter values as in Fig. 5. Note that occupancy within tracts increased dramatically if at least one neighboring cell outside the tract was occupied.

success. It is not useful, however, for evaluating the sensitivity to changes in qualitative factors such as the presence or absence of a behavior. Two of the dispersal variables considered were of this qualitative nature. The presence or absence of memory about the previous search route had a moderate impact on population size (Table 2). In simulations where dispersing individuals could remember and avoid cells they had previously visited, population size was $\approx 35\%$ greater than when dispersing individuals had no memory of their previous search route. Another qualitative dispersal variable considered was high vs. low selectivity (Table 1). When dispersing individuals accepted only cells in the 1–2 yr age class (where expected reproductive success was higher), population size averaged $\approx 15\%$ lower than in simulations where dispersing individuals would accept any unoccupied 1–5 yr cell (low selectivity).

Interactions between variables

In our simulations we varied each parameter independently to determine its effect on total population size. Significant effects on population size could also be caused by interactions between several parameters

TABLE 6. Sensitivity analysis. Values of parameters that were references for the sensitivity analysis are: $P_A = 0.60$, $P_J = 0.40$, $DM = 0.10$, $\beta_{1-2} = 1.5$, $\beta_{3-5} = 0.5$, $MH = 8$, MEM , and LS . Abbreviations of the fixed parameters are detailed in the Methods section. Please note that Tables 1–5 use different values for some parameters.

Parameter	$\Delta x/x$	$\Delta P/P$	S_x
P_A	4.21/12.02	0.15/0.60	1.40
P_J	3.66/12.02	0.10/0.40	1.22
MH	4/8	5.59/12.02	0.92
β_{3-5}	-1.00/0.50	-12.08/12.02	0.51
DM	-40/10	-1.70/12.02	0.04

varying simultaneously. A full discussion of such interactions is beyond the scope of this paper; however, we will present one example of such interaction effects. In a 2^3 factorial design, we set two levels of variation for each of three variables: the amount of mature pine habitat present in the landscape (MH), dispersal mortality (DM), and reproductive success in 3–5 yr cells (β_{3-5}). As in previous simulations, increasing each of these variables alone significantly increased the total population size (Table 7). The interactions of β_{3-5} with MH or DM were also significant ($P = .0001$ for both). However, no significant interaction effect existed between MH and DM , and there was no second-order interaction effect among the three variables.

We interpret the significant interaction terms in the following way. Increasing the reproductive success in the 3–5 yr cells to the level of reproductive success found in the best habitats (1–2 yr and mature cells) greatly increased the total number of suitable cells within the landscape that yielded high reproductive success. With the larger number of suitable cells, good dispersers ($DM = 0.01$) were able to attain particularly high populations, while poor dispersers were not. This resulted in a significant interaction between DM and β_{3-5} . Similarly, the large number of suitable sites in the simulations where both β_{3-5} and the amount of mature habitat were at high levels supported a substantially increased population, leading to the significant $MH \times \beta_{3-5}$ interaction. Interestingly, increasing the amount of mature habitat was not enough to make good dispersers

TABLE 5. Effect of reproductive success in Bachman's Sparrows in 3–5 yr old pine plantation habitats (β_{3-5}) on probability of population extinction, and on population size found in different habitat types. Values of parameters that were fixed in these simulations are: $P_A = 0.6$, $P_J = 0.4$, $DM = 0.10$, $\beta_{1-2} = 1.5$, $MH = 8$, LS , and MEM . Abbreviations of the fixed parameters are detailed in the Methods section.

Population location	Population size		
	$\beta_{3-5} = 1.5$	$\beta_{3-5} = 0.5$	P
Total landscape	24.31 \pm 1.59	12.02 \pm 0.23	.0001
In mature habitats	6.90 \pm 0.06	6.55 \pm 0.11	.0433
In 1–5 yr habitats	11.32 \pm 0.46	4.00 \pm 0.17	.0001
In 6–20 yr habitats	6.09 \pm 0.22	1.47 \pm 0.08	.0001
Extinction probability*	0.00 (0/10)	0.17 (2/12)	.0885

* In parentheses are the number of simulations that went extinct/total sample size.

TABLE 7. Interaction effects among three variables on population size. Values of parameters that were fixed in these simulations are: $P_A = 0.6$, $P_J = 0.4$, and HS. Abbreviations of the fixed parameters are detailed in the Methods section.

a) Population size				
MH	DM = 0.10		DM = 0.01	
	$\beta_{3-5} = 0.5$	$\beta_{3-5} = 1.5$	$\beta_{3-5} = 0.5$	$\beta_{3-5} = 1.5$
8	10.62 \pm 0.31	32.74 \pm 2.58	16.62 \pm 0.51	89.02 \pm 5.3
32	39.52 \pm 1.40	91.39 \pm 3.51	42.05 \pm 0.93	175.51 \pm 5.26

b) Analysis of variance					
Source	df	Mean square	F	P	
MH	1	217.70	752.80	.0001	
β_{3-5}	1	397.65	1375.07	.0001	
DM	1	87.29	87.29	.0001	
MH \times DM	1	0.40	1.40	.2407	
$\beta_{3-5} \times$ DM	1	51.97	179.71	.0001	
MH \times β_{3-5}	1	6.07	20.98	.0001	
MH \times $\beta_{3-5} \times$ DM	1	0.35	1.20	.2776	

more effective; thus, the MH \times DM interaction term was not significant, suggesting that the ability to find good sites did not limit population size, at least in the simulation populations.

DISCUSSION

Few previous models of population dynamics in patchy landscapes have incorporated temporal landscape variation as well as spatial variation (e.g., Urban and Shugart 1986, Fahrig and Paloheimo 1988b, Pulliam 1988). Fahrig (1991) determined that temporal variation in habitat patch life-span had a much greater effect on local population size than did the spatial characteristic of patch isolation in a landscape. Lande (1988) and Thomas et al. (1990) have shown that population persistence of the Spotted Owl (*Strix occidentalis*) decreases as habitat availability decreases with time through timber harvest. These studies emphasize that models such as ours must incorporate changes in habitat distributions through time in order realistically to model landscape impacts on populations.

In our analyses, we calculated population size as the average population size over the last 84 yr (four rotations) of a 105-yr simulation. Over the entire 105-yr period, we assumed that the forest management scheme was invariant such that each year the birds faced a landscape with approximately the same proportions of each habitat type. We excluded the first 21 yr of the simulation from our calculations of average population size because population sizes fluctuated widely during this initial period. We have thus presented results appropriate for estimating the effects of a stable long-term management regime on the long-term (average) population size of a mobile animal species.

Most natural landscapes are very dynamic and only rarely would the same management scheme be in effect for such a long period of time. The patterns of abundance and distribution of a natural population may

reflect not only the current landscape characteristics but also the characteristics of the past landscape as well. Therefore, to apply BACHMAP or related models to the management of a real population, the simulation landscape would need to reflect characteristics of the real land use history. In the case of Bachman's Sparrows at the SRS, we are developing a Geographic Information System-based model incorporating current land use and management practices as well as a land use history from approximately 1950 to the present.

In general, variation in demographic variables had a greater influence on population size than did variation in dispersal variables. Within the range of the variables explored, increasing the reproductive success in 3-5 yr old pines from 0.5 to 1.5 female offspring resulted in 100% increase in population size (Table 5), while decreasing either adult or juvenile survival by only 25% decreased population size by \approx 25-30% (Table 4). These figures for percent change in population size are based on the average long-term population size in those simulations where the population did not go extinct. Changes in both adult and juvenile survival had a dramatic effect on the likelihood of population extinction. A 25% decrease in juvenile survivorship resulted in a 100% increase in extinction probability, and a 25% decrease in adult survivorship resulted in a 400% increase in extinction probability. These results clearly indicate the need for accurate habitat-specific demographic information, particularly, in our case, regarding reproductive success in 3-5 yr pine stands.

Variation in the dispersal variables generally had less influence on population size. Changing from high selectivity to low selectivity increased population size by \approx 15%, while an increase in the dispersal mortality from 0.01 to 0.02 decreased population size by <20%. A further increase in DM from 0.02 to 0.10 decreased population size slightly more; however, we feel that a dispersal mortality of 0.10 per move, corresponding to an expected number of only 10 territories searched, is

unrealistically high. Memory of the previous search path during dispersal increased population size by $\approx 35\%$ as compared to simulations with no memory. While changes of this magnitude were significant in the computer simulations, they would be relatively difficult to detect in natural populations.

Previous models of populations in fragmented habitats have also stressed the sensitivity of model results to variation in demographic characteristics. For instance, in current population models based on Spotted Owl demography, λ is most sensitive to changes in adult survival (Lande 1988, Noon and Biles 1990). In a general model of avian population dynamics in fragmented habitats, limits on fecundity have greater effects on population persistence than do limits on dispersal ability (Urban and Shugart 1986). Similarly, changes in fecundity have a large effect on population dynamics of breeding forest-interior birds (Temple and Cary 1988).

Despite the fact that our sensitivity analyses showed demographic factors to have a stronger impact on population size than dispersal characteristics, population sizes attained in many of our simulations were small, compared to the total number of suitable cells present in the landscape (Tables 1–4). In some cases, the bulk of the population was restricted to the mature habitat, while few suitable 1–5 yr cells were occupied (Tables 1 and 2). This suggests that dispersal may have played a role in limiting population size in these simulations that was not identified by our sensitivity analyses. This was also suggested by the strong effect that occupied neighboring cells had on the population size within tracts (Fig. 7). Better field data on dispersal may be necessary to examine this possibility further.

Simulations where reproductive success in some habitat types was lower than that attainable elsewhere in the landscape measured the importance of marginal habitat types within the landscape. When dispersers could settle in these marginal habitats, total population sizes were greater than in simulations where dispersers settled only in the higher quality habitat (Table 1). In this case, the presence of marginal habitats within a landscape increased the total population supported, even if these habitats were not especially productive (Holt 1985, Pulliam 1988, Pulliam and Danielson 1991).

Our simulations were designed as a single-sex model; that is, we calculated reproductive success as the average number of female offspring that a breeding female sparrow will produce. This perspective is traditional for many models of population dynamics, since females are the reproductive unit (e.g., Noon and Biles 1990); however, some of the data used to guide our simulations were more accurate for breeding males, especially the data on habitat use and territory size. To be more accurate, models such as this one should incorporate dispersal strategies for both males and fe-

males; however, this information is rarely available (but see Thomas et al. 1990).

Several results of the simulations have proven useful in guiding our field research on Bachman's Sparrows at the SRS. The strong effect that occupied neighboring cells had on occupancy within tracts suggests that the colonization of newly created habitat patches may depend critically on the relative isolation of these patches from previously colonized areas. Accordingly, the pattern of timber harvest on the SRS may have a strong effect on the sparrow's local distribution, since clearcuts with newly planted pines are the primary source of new habitat for Bachman's Sparrows in our study area. We are testing the idea that neighboring habitat patches have a strong influence on colonization by monitoring the sparrow's colonization of a series of clearcuts created in 1990 in an area of the SRS hit by a tornado in the fall of 1989. The United States Forest Service, which manages timber production on the SRS, cleared the area damaged by the tornado, creating a series of replicate plots extending across the southern portion of the SRS. By chance, these plots extend from an area of high sparrow density (including some plots immediately next to existing sparrow territories) to an area where Bachman's Sparrows are almost completely absent, even from suitable habitat. Thus, we have an opportunity to monitor colonization of a series of sites that differ in the number of breeding sparrow populations found in the immediate landscape.

If the field study in the tornado region confirms that colonization is strongly affected by the existing distribution of sparrow populations, we may be able to suggest to managers an improved pattern of timber harvest that allows the sparrow to colonize newly created patches of prime habitat more readily. **BACHMAP** could be used to design a network of contiguous, suitable habitat patches scattered throughout the region devoted to pine production. Our results to date suggest that such a network would greatly increase the total population size supported in the managed area. This is an example of how simulation models such as **BACHMAP** can be used to design management strategies.

A second result of management interest is the importance of stable source habitat in maintaining population size of poorly dispersing species. Pulliam (1988) suggested that a small amount of source habitat may be responsible for maintaining a much larger population in marginal or sink habitat. Our results confirm this suggestion for a species such as Bachman's Sparrow in highly managed landscapes (Fig. 5). Current methods of identifying critical habitat for species of management concern emphasize habitat-specific densities. In these methods, the habitat holding the largest population is usually identified as the most critical habitat. Using density data alone to define critical habitats is unlikely to identify source habitats when such habitats

are rare in the landscape, as is currently true of mature pine stands at the SRS. Our simulation results suggest that these rare habitats can be crucial to the maintenance of populations with particular life history characteristics. Habitat-specific demography and dispersal characteristics must be evaluated along with density information to determine critical habitat for a particular species (Van Horne 1983).

We emphasize that our simulations were designed with the landscape characteristics of the SRS in mind, and the results may not be applicable to areas with different landscape dispersions of habitats. For example, we have found that sparrow use of clearcut habitat is different in regions where mature pine habitat is much more common than at SRS (Dunning and Watts 1990). For the greatest accuracy in suggesting management strategy, models such as BACHMAP must be tailored to meet specific local conditions of landscape characteristics, and must use locally accurate information of habitat-specific demography and dispersal behavior.

ACKNOWLEDGMENTS

We thank Lenore Fahrig, Barry Noon, Scott Pearson, Bryan Watts, David Duffy, Thomas Haggerty, Joan Walsh, Thelma Richardson, Ronen Kadmon, Brent Danielson, and two reviewers for comments and discussion. Development of BACHMAP was supported primarily by Department of Energy grant DE-FG09-89ER60881 to H. R. Pulliam and Odum Research Award to J. Liu; field studies of Bachman's Sparrow were supported by National Science Foundation grant BSR-8817950 to H. R. Pulliam and J. B. Dunning, Jr.

LITERATURE CITED

- Belthoff, J. W., and G. Ritchison. 1989. Natal dispersal of Eastern Screech-Owls. *Condor* **91**:254-265.
- Brooks, M. 1938. Bachman's Sparrow in the north-central portion of its range. *Wilson Bulletin* **50**:86-109.
- Dunning, J. B., and B. D. Watts. 1990. Regional differences in habitat occupancy by Bachman's Sparrow. *Auk* **107**:463-472.
- Fahrig, L. 1988. A general model of populations in patchy habitats. *Applied Mathematics and Computation* **27**:53-66.
- . 1991. Relative importance of spatial and temporal scales in a patchy environment. *Theoretical Population Biology*, *in press*.
- Fahrig, L., and J. Paloheimo. 1988a. Determinants of local population size in patchy habitats. *Theoretical Population Biology* **34**:194-213.
- Fahrig, L., and J. Paloheimo. 1988b. Effect of spatial arrangement of habitat patches on local population size. *Ecology* **69**:468-475.
- Grant, P. R. 1968. Polyhedral territories of animals. *American Naturalist* **102**:75-80.
- Haggerty, T. M. 1986. Reproductive ecology of Bachman's Sparrow (*Aimophila aestivalis*) in central Arkansas. Dissertation. University of Arkansas, Fayetteville, Arkansas, USA.
- . 1988. Aspects of the breeding biology and productivity of Bachman's Sparrow in central Arkansas. *Wilson Bulletin* **100**:247-255.
- Holt, R. D. 1985. Population dynamics in two-patch environments: some anomalous consequences of an optimal habitat distribution. *Theoretical Population Biology* **28**:181-208.
- Jørgensen, S. E. 1986. Fundamentals of ecological modeling. Elsevier, Amsterdam, The Netherlands.
- Knapton, R. W. 1978. Breeding ecology of the Clay-colored Sparrow. *Living Bird* **17**:137-158.
- Lande, R. 1988. Demographic models of the northern spotted owl (*Strix occidentalis caurina*). *Oecologia* (Berlin) **75**:601-607.
- Mayfield, H. F. 1975. Suggestions for calculating avian breeding productivity. *Wilson Bulletin* **87**:456-466.
- Microsoft Corporation. 1988. Microsoft QuickBASIC, version 4.5. Microsoft, Redmond, Washington, USA.
- Nice, M. M. 1937. Studies in the life history of the Song Sparrow. Volume IV. Transactions of the Linnaean Society of New York, New York, New York, USA.
- Noon, B. R., and C. M. Biles. 1990. Mathematical demography of spotted owls in the Pacific Northwest. *Journal of Wildlife Management* **54**:18-27.
- Ott, L. 1988. An introduction to statistical methods and data analysis. Third edition. PWS-Kent, Boston, Massachusetts, USA.
- Pulliam, H. R. 1988. Sources, sinks, and population regulation. *American Naturalist* **132**:652-661.
- Pulliam, H. R., and B. J. Danielson. 1991. Sources, sinks, and habitat selection: a landscape perspective on population dynamics. *American Naturalist* **137**:S50-S66.
- Ricklefs, R. E., and G. Bloom. 1977. Components of avian breeding productivity. *Auk* **94**:86-96.
- Ross, H. A., and I. A. McLaren. 1981. Lack of differential survival among young Ipswich Sparrows. *Auk* **98**:495-502.
- Sullivan, K. A. 1989. Predation and starvation: age-specific mortality in juvenile juncos (*Junco phaeonotus*). *Journal of Animal Ecology* **58**:275-286.
- Temple, S. A., and J. R. Cary. 1988. Modeling dynamics of habitat-interior bird populations in fragmented landscapes. *Conservation Biology* **2**:340-347.
- Thomas, J. W., E. D. Forsman, J. B. Lint, E. C. Meslow, B. R. Noon, and J. Verner. 1990. A conservation strategy for the northern spotted owl. Report of the Interagency Scientific Committee to Address the Conservation of the Northern Spotted Owl. United States Government Printing Office 1990-791-171/20026.
- Urban, D. L., and H. H. Shugart, Jr. 1986. Avian demography in mosaic landscapes: modeling paradigm and preliminary results. Pages 273-279 in J. Verner, M. L. Morrison, and C. J. Ralph, editors. *Wildlife 2000: modeling habitat relationships of terrestrial vertebrates*. University of Wisconsin Press, Madison, Wisconsin, USA.
- Van Horne, B. 1983. Density as a misleading indicator of habitat quality. *Journal of Wildlife Management* **47**:893-901.
- Verner, J. 1977. On the adaptive significance of territoriality. *American Naturalist* **111**:769-775.