STUDYING WILDLIFE AT LOCAL AND LANDSCAPE SCALES: BACHMAN'S SPARROWS AT THE SAVANNAH RIVER SITE

JOHN B. DUNNING, JR., BRENT J. DANIELSON, BRYAN D. WATTS, JIANGUO LIU, AND DAVID G. KREMENTZ

Abstract. In the late 1980s and early 1990s, mutual research interests between land managers at the Savannah River Site and biologists at the University of Georgia resulted in a landscape-ecology study of the Bachman's Sparrow (Aimophila aestivalis). This species had been declining throughout its range for several decades and was considered a species of management concern by the U.S. Forest Service. The reasons for its decline were obscure, but the distribution of suitable habitat across complex landscapes was a possible factor. Thus the species seemed well suited for a pioneer study on landscape influences on avian population dynamics. A cooperative research program developed from these mutual interests, including quantifying the landscape and local habitat patterns shown by the sparrow, spatially explicit modeling of population response to landscape change, and demographic field studies of reproductive success, survivorship and dispersal. These studies are summarized, and the value of the research to both management and research interests is discussed.

Key Words: Aimophila aestivalis, Bachman's Sparrow, BACHMAP, demography, habitat distribution, landscape ecology, management impacts, spatially explicit modeling.

Ecologists, wildlife biologists, and land managers have seen the importance of expanding the spatial scale of research and land-use planning from the traditional focus on local, site-specific phenomena to those that operate over landscape scales (Haas 1995, Turner et al. 1995, Villard et al. 1995). Active land management is one anthropogenic force that changes the distribution and quality of habitat patches across large, complex areas (i.e., "landscapes"). Land managers are interested in how organisms and populations respond to landscape change, because such responses are critical to understand if managers are to consider how wildlife will be affected by regional land management. Ecologists, on the other hand, have expanded the spatial and temporal scales of population biology and community ecology to create the relatively new field of landscape ecology. The study of impacts of experimental changes in the distribution or quality of habitats across a landscape is often a desired goal of landscape studies. However, landscapes are difficult to manipulate experimentally for all but the smallest organisms (Forman and Godron 1986, Wiens and Milne 1989, Johnson et al. 1992). In managed landscapes, such changes occur regularly, are predictable (in fact, are planned well in advance), and are roughly replicated in space at scales that are normally hard to manipulate experimentally. Thus, the needs and interests of managers and basic ecologists coincide to make managed lands an excellent opportunity for studies in landscape ecology.

In 1988, when students and associates of Dr. H. Ronald Pulliam at the University of Georgia began studies of Bachman's Sparrows (Aimophila aestivalis) at the Savannah River Site

(SRS), it quickly appeared that the species might be a good candidate for landscape-level studies. The sparrow was found in pine stands managed by the U.S. Forest Service for threatened and endangered species, native communities, and timber production. Timber management changed the within-stand characteristics of individual stands on a semi-annual basis, and therefore the locations of suitable habitat for a given species were temporally dynamic. Thus, the management strategy at SRS could potentially have a strong impact on species that occupy pine woodlands. Little was known locally about Bachman's Sparrow at the time our studies began; published reports even seemed to disagree about what habitat the species occupied and whether it was migratory or a permanent resident (Hardin and Probisco 1983). Most importantly, throughout its range Bachman's Sparrow was often described as being absent from seemingly suitable habitat (Nicholson 1976, Hall 1983). Our initial surveys (described below) indicated that the bird was often absent from stands that were isolated from other occupied habitat patches. This suggested to us that landscape effects could be important—"suitable" patches might be unoccupied if they were located in disjunct or unsuitable landscapes.

The Savannah River Natural Resources Management and Research Institute (SRI) was also interested in gaining more information about the sparrow because the species had declined throughout its range since the 1930s, and was absent from large portions of its former range (Brooks 1938, Haggerty 1988, Dunning 1993, Sauer et al. 1997). In the southeastern United States, Bachman's Sparrow was one of the high-

est ranking "species of management concern" for the U.S. Forest Service (a classification that includes species not on the official list of threatened and endangered species). The sparrow was classified as a "Category 2" species by the U.S. Fish and Wildlife Service (USFWS) in the 1980s. This ranking suggested that the species might warrant listing under the U.S. Endangered Species Act, but too little information existed to make such a determination. (The list of Category 2 species was eliminated by the USFWS in 1996, but the species formerly on the Category 2 list are still of management concern to the USFWS [Crystal 1997].)

Thus, our interest in Bachman's Sparrow as a study organism for landscape studies coincided with the SRI's need for better local information on how this species might be affected by timber management. We began a study of the sparrow's habitat use, both on a local and landscape scale, with funding from the Savannah River Ecology Laboratory (University of Georgia) and the SRI (U.S. Forest Service), with additional support in later years from the National Science Foundation and the U.S. Environmental Protection Agency. Studies ran from 1988–1997, with some continuing studies planned for the future.

Our work has included (1) local-scale habitat analysis; (2) landscape-scale analyses; (3) theoretical analyses linking spatially explicit population models to dynamic landscapes created by a geographic information system (GIS); and (4) demographic field studies in different habitats, emphasizing demographic variables found to be important in model simulations. In this paper, we briefly summarize these integrated studies, emphasizing the benefits we have seen from working in these rapidly changing landscapes.

LOCAL SCALE STUDIES

Bachman's Sparrow is associated with various age classes of pine forest throughout the southern portion of its range (Dunning 1993). In fact the subspecies found in South Carolina was long called the "Pine Woods Sparrow." But at the start of our study, it was not clear what kinds of pine woods were used. Some published sources described sparrow habitat as old-growth pine forest (Allaire and Fisher 1975, Meanley 1988), while other sources emphasized open habitat such as the edges of fields, old pastures and clearcuts (Burleigh 1958, Hardin et al. 1982, Hardin and Probisco 1983). Our initial study in 1988 therefore focused on the local-habitat characteristics that have been emphasized in traditional avian ecology: we surveyed sparrows across a spectrum of age classes and pine species to determine which habitats were occupied (Dunning and Watts 1990). We found that Bachman's Sparrows occupied the youngest (1–5 year old clearcuts) and oldest (open mature pine at least 80 years old) age classes, but not pine stands of intermediate age. The occupied age classes shared a suite of vegetation characteristics, including a relatively dense layer of grasses and forbs in the ground layer and few tall shrubs or understory trees (Dunning and Watts 1990).

We confirmed these local-habitat patterns by examining habitat occupancy in other South Carolina regions where management practices differed from those on the SRS. For the most part, the sparrows occupied stands whose ground vegetation had the same characteristics as occupied sites on the SRS. For instance, at the Francis Marion National Forest, near Charleston, South Carolina, sparrows were present in middle-aged (30–80 year old) pine forest, an age class that was not occupied at the SRS (Dunning and Watts 1990, 1991). At Francis Marion National Forest, middle-aged and mature pine stands are managed similarly and have the same vegetation characteristics.

In some regions, the density of suitable habitat patches was much lower than at either the SRS or the Francis Marion National Forest. In these regions, our ability to identify occupied sites by their vegetation characteristics was much poorer. For instance, at the Sumter National Forest in the Piedmont of South Carolina, most patches of clearcut habitat were scattered in small portions of National Forest land, which were themselves distributed over a matrix of privately owned farmland and forest. In spite of what appeared to be suitable vegetation in many of these clearcuts, few sparrows were found. For example, only 8 of 38 clearcuts surveyed in 1990 were occupied (Dunning et al. 1995a). This further suggested that sparrows might not occupy isolated clearcuts even if the local site characteristics were suitable.

LANDSCAPE-LEVEL STUDIES

During our initial 1988 surveys, sparrows were not present in all patches that appeared to contain suitable vegetation characteristics. A wider set of surveys in 1989 confirmed that many clearcut patches of suitable age and condition were not occupied in the western half of the SRS. We surveyed 50 stands from 1989-1991 to determine if landscape characteristics helped explain this pattern of sparrow occupancy (Fig. 1). The 50 sites were stratified by clearcut age (1-2 yr old versus 3-5 yr old) and landscape quality (study site close to [<0.6 km] or far from [>0.6 km] other suitable habitat). A complex pattern emerged suggesting landscape variables were important. Young clearcuts close to other suitable habitat supported significantly

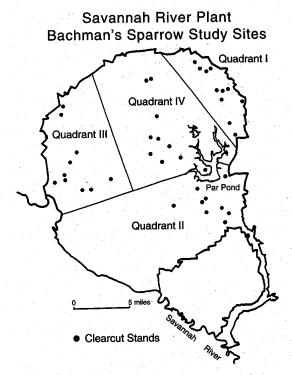


FIGURE 1. Locations of 1989 study sites on Savannah River Site. Grouping of study sites into four quadrants reflected differences in landscape characteristics among regions of the SRS.

more sparrows than isolated clearcuts, and regions of the SRS dominated by older or more isolated clearcuts supported very few sparrows (Fig. 2). In particular, the western portion of the SRS had few sparrows in suitable habitat patches, which were mostly isolated, older clearcuts.

One factor that could account for decreased occupancy in isolated stands is poor dispersal ability by the sparrow. If sparrows did not disperse freely across unsuitable habitat, then the Forest Service policy of scattering clearcuts throughout the forest could create many landscapes where individual patches of suitable habitat are too distant from existing sparrow populations to be occupied readily. This problem would be exacerbated by the narrow time window during which most clearcuts were suitable. Due to rapid regrowth of planted pines on the SRS, many clearcuts had the open field characteristics that seemed most attractive to the sparrows for only 3-4 years post-planting. Thus, the sparrows may be dispersing across a landscape where suitable habitat exists only briefly and in unpredictable locations. This should put a premium on dispersal ability (Dunning and Watts 1990).

Unfortunately, Bachman's Sparrows proved

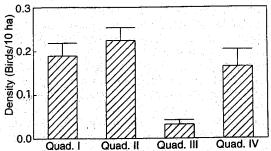


FIGURE 2. Effect of regional (quadrant) grouping of study sites on Bachman's Sparrow density in 1989. Density = number of singing male sparrows per 10 ha. Quadrants refer to regions numbered in Fig. 1. Error bars = 1 se.

difficult at first to catch, band, and follow in large numbers. Thus, documenting their dispersal ability directly was problematic, and we measured dispersal ability indirectly by monitoring the sparrow's colonization of patches of different isolation within small regions of the SRS (Dunning et al. 1995a). In these regions, we selected study sites that were different from one another in their degree of isolation. We hypothesized that if sparrows had poor dispersal ability, then newly available sites close to known sparrow populations should be occupied earlier and support larger populations than sites that were more isolated, but of the same age. We monitored sparrow occupancy in two regions that allowed this comparison from 1991-1993, and found strong support for the poor-dispersal hypothesis (Dunning et al. 1995a). Sparrows colonized the clearcuts closest to existing populations first. Most interestingly, the most isolated patches in one study region were never colonized during the 3-4 years in which their local (within-patch) characteristics appeared to be suitable. Thus, the hypothesis that patch isolation strongly affects sparrow distribution was supported (albeit indirectly). It should be noted that other bird species occupied all of the study sites in these regions, suggesting that the landscape was not as limiting to other species.

GIS/POPULATION MODELING

Although Bachman's Sparrows occupy both clearcuts and mature (>80 yr old) pine forest, the vast majority of the sparrow population on the SRS is found in clearcuts, primarily because mature forest is locally rare. Less than 200 ha (0.5%) of mature forest exists on the 770 km² SRS. For the most part, therefore, timber harvest by the U.S. Forest Service determines the land-scapes in which the sparrows exist by creating clearcuts. Because an individual clearcut is suit-

able for only 3-8 years (most commonly 3-4 years during our study), regional landscapes change quickly. A portion of the SRS may lose most of its suitable habitat within 5 years if new clearcuts are not generated. This rapidly changing landscape is tailor-made for landscape ecology, since researchers can expect a population response to a specific landscape design within a short time period (e.g., Dunning et al. 1995a).

On a more practical level, the SRI was interested in how their management strategies affected the status of the sparrow within the SRS. The SRI adopted a new management plan for plant and animal populations in 1992 (SRFS 1992). This plan proposed many changes in forest management over a 50-year period, with the probable result of substantially changing forest structure during that period (Liu 1992, 1993). The SRI was interested in assessing how species of management interest such as the sparrow might respond to changes in landscape structure proposed in the management plan. Because the management plan covers a 50-year period, field experiments were not a practical way to answer this question. Instead, we developed a spatially explicit population model to simulate landscape change and sparrow population dynamics at the required spatial and temporal scales (Pulliam et al. 1992, Liu et al. 1995).

Spatially explicit models incorporate the exact spatial locations of objects of interest in the landscape (Dunning et al. 1995b). These objects can include individual organisms, populations, habitat patches, barriers to dispersal, and other relevant factors. In our spatially explicit population model, individual organisms were placed on a grid representing a specific landscape (Pulliam et al. 1992). The individuals gained habitatspecific demographic traits (reproductive success, survivorship, estimated from published literature sources) associated with the habitat patch in which they were located. Individuals moved across the landscape according to specific dispersal algorithms. The model we developed (called BACHMAP) followed individuals through an annual cycle of reproduction, mortality and dispersal, and then derived population characteristics such as population size or time to extinction by summing over all individuals. Population characteristics can be estimated annually during a simulation period, projected over an entire simulation, or averaged among replicate simulations (Liu 1993, Liu et al. 1995). Spatially explicit models are extremely data-intensive and subject to error if initialized or structured poorly (Conroy et al. 1995), but when used carefully, the models provide a means of examining possible population responses to long-term manage-

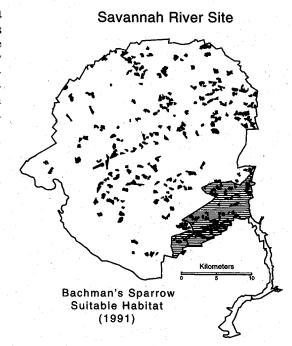


FIGURE 3. Locations of suitable patches of clearcut habitat (as defined by stand age) in 1991. Hatched area in lower right corner represents the SE corner region used in BACHMAP modeling.

ment over large spatial scales (Dunning et al. 1995b, Turner et al. 1995).

We built a spatially explicit model by linking a sparrow population model to a landscape map of the southeast corner of the SRS (Fig. 3). The landscape map included about 6000 ha, and was created from the stand-and-compartment timber database maintained by the SRI (CISC database; see Hamel and Dunning this volume). The map of stands was digitized into ARC/INFO, and a grid of hexagons was overlaid onto the original map. Each hexagon cell represented 2.5 ha, which is the size of a Bachman's Sparrow territory (Haggerty 1988, Stober 1996), and, thus, could be occupied by a single reproductive female. Characteristics of the original stands were assigned to the associated hexagonal cells in the grid data layer. The result was a hexagon grid of cells whose habitat characteristics and spatial distributions were similar to the original landscape (Liu et al. 1995).

BACHMAP placed individuals on this landscape grid to match known patterns of habitat occupancy in 1989, and followed individuals and their progeny for 50 simulated years. At the start of each simulation year, the ages of habitat in all cells were increased by 1 yr, and management options were applied. For instance, under a 30-yr forest rotation, all 30-yr-old stands

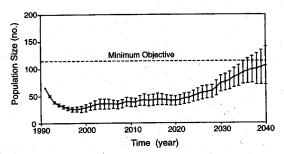


FIGURE 4. Typical BACHMAP population trajectory using forest management options outlined in SRFS (1992). Error bars = 1 se. Adapted from Liu et al. (1995), reprinted by permission of Blackwell Science, Inc.

would be harvested, creating new clearcuts. Stands were selected for harvest based on the broad guidelines of the management plan (SRFS 1992). Dispersing sparrows settled in 1–5 yr old clearcuts and mature stands, and gained a habitat-specific reproductive success depending on the age of the stand in which they settled. For more details on the model structure and parameterization see Liu (1993).

Our simulations suggested that the population of Bachman's Sparrows in the southeastern region would decline sharply during the first decade of the 50-yr management plan, then eventually increase slowly (Fig. 4). The simulations suggested that the sparrow population would meet or exceed the Forest Service management goals for this species, but only during the final decade of the management plan. Liu et al. (1995) simulated several modifications of the plan to see how the management goals could be met more quickly. One such modification was to change management in the middle-aged stands (especially 40–80 yr stands) to provide the same ground-cover characteristics found in mature pine forest.

This suggestion from the simulations is being field tested by a pilot program adopted by the SRI in the early 1990s. To provide more habitat for the endangered Red-cockaded Woodpecker (Picoides borealis), which also uses older forest with the same vegetation structure associated with the sparrows, the SRI is thinning and burning middle-aged forest stands. These modified sites (referred to as "woodpecker recruitment stands") have the potential for providing more suitable habitat for the sparrow in middle-aged stands, as suggested by the sparrow model simulations and field studies (Gobris 1992, Liu et al. 1995, Wilson et al. 1995). In April 1997, a male Bachman's Sparrow was heard singing on territory in a woodpecker recruitment stand, two years after treatment (J. B. Dunning, pers. obs.); this particular stand had not been occupied by sparrows prior to modification. Demographic studies (see below) have also established that sparrows will occupy the woodpecker recruitment stands (Stober 1996, Christie 1997). If implemented throughout the SRS, our simulations suggest that the woodpecker recruitment program will provide enough habitat to stabilize the sparrow population and meet or exceed management goals through most of the 50-yr extent of the current plan (Liu et al. 1995).

DEMOGRAPHIC FIELD STUDIES

One of the important uses of spatially explicit population models is to identify the demographic variables that may have the greatest impact on populations in a given landscape (Dunning et al. 1995b). Once identified, field researchers can concentrate their field studies on the most important demographic and life history traits. Since there is never enough time, personnel, or money to study all possible aspects of a species of interest, field research will be most effective if focused on a limited number of critical variables likely to be affecting a population. Modeling can help identify these most critical variables through sensitivity analyses (Jørgensen 1986, Pulliam et al. 1992).

In sensitivity analyses, a series of simulations are run where input values for a single parameter in the model are varied within a predetermined range (i.e., a percentage of nominal values) while other model parameters are held constant. Output from the model is monitored to determine how sensitive model performance is to the nominal value used for the parameter under study. If the model output does not vary substantially despite large changes in input value, the model is said to be relatively insensitive to the nominal value used for that parameter. If small changes in the initial parameterization yield large changes in model output, then the model is relatively sensitive to that parameter. Care must be taken that accurate initial values be used for sensitive parameters, because parameterization errors may be magnified during model performance (Conroy et al. 1995). In the most complex sensitivity analyses, values for combinations of parameters can be varied in a factorial experimental design, to test for sensitivity to interaction effects between model parameters (see Pulliam et al. 1992).

Pulliam et al. (1992) and Liu et al. (1995) examined model sensitivity to reproductive success, survivorship, dispersal, and landscape characteristics. The BACHMAP model proved to be most sensitive to demographic traits, especially survivorship and reproductive success. In response to these results, we initiated field demographic studies in 1994 (Stober 1996, Christie 1997). While we had collected data on

reproductive success and other demographic traits since the beginning of this project, this kind of data was extremely hard to gather in sufficient samples, because the sparrows are difficult to follow in the field, and nests are hard to find. Survivorship data are even scarcer, because the species is relatively difficult to capture, mark, and relocate (Dunning 1993). In the absence of local field data for these traits, we depended on published information (especially Haggerty 1986, 1988) for model parameterization.

Starting in 1994, David G. Krementz and colleagues initiated a series of studies on survival rates, reproductive rates, habitat use, and homerange size. Using an intensive mark-recapture study, they were able to capture many sparrows (~150 individuals). A subsample of these were marked with radio transmitters during the 1994-1997 breeding seasons. Sex-, habitat- (clearcut versus mature forest), and year-specific patterns in breeding-season survival rates were estimated. Comparisons of survival rates between sexes, habitats, or among years failed to reveal any significant differences. However, statistical power of these tests were low, ranging from 20-60%. Point estimates suggested habitat-specific differences for all factors.

Reproductive rates were comparable to those determined by Haggerty (1988, 1998) for Arkansas populations. Differences in daily nest-survival rates were determined for early- versus late-initiated nests, egg versus nestling periods, and between years (1995–1996; Stober 1996). All monitored females made multiple nesting attempts, and one female attempted to triple brood. Sparrows proved to be persistent nesters through a long breeding season (April–August).

Home ranges were estimated using radiotelemetry locations. Again, these estimates were comparable to those by Haggerty (1986, 1998) estimated from Arkansas. Home-range size was significantly larger in mature than in younger stands. We hypothesize that differences in food availability and abundance between forest age classes might cause these differences. Typical daily sparrow movements were restricted to a core area of ~ 1 ha within the home range. In most cases, all activities were confined to the home range, although we documented dispersal movements most often associated with failed nesting attempts. In addition, we documented large scale (>1 km) movements in response to prescribed summer burns. To the best of our knowledge, these dispersing individuals did not obtain mates during the remainder of the breeding season.

WHAT HAS BEEN GAINED?

The research has proven beneficial in a number of ways, spanning the information needs of both basic researchers and land managers. First, we have a better ecological understanding of a species that has undergone a dramatic population decline in the last 50 years, and which is of management concern in the southeastern United States. More fundamentally, the research program has explored how a species of apparently limited dispersal ability (compared to most passerines found in the same study sites) is affected by rapid landscape change. This knowledge has given us a better understanding of the importance of monitoring habitat change at different spatial scales, and a working system for studying landscape ecology with birds. Parts of the research program have profitably explored new techniques for studying small passerines, including miniaturized radio transmitters for the study of dispersal and demography, and spatially explicit models for population and landscape studies. Comparison of our demographic studies and published values from other parts of the species' range is an important part of validation of the BACHMAP model.

The research also yielded results that support the mission of the Savannah River Institute on the SRS. We believe our results give managers a better appreciation of how timber management affects target species, especially by modifying the landscape through which these birds disperse and breed. By linking our population model to the stand-and-compartment database that the SRI compiled for timber management purposes, we increased the value of SRI data and thus increased the value of their research and data collection programs. Finally, our research created new databases that can be used by other researchers within the SRI for other purposes. For example, the distributional and density data collected during field work has been used to parameterize a new set of bird/habitat models by U.S. Forest Service researchers (J. C. Kilgo, pers. comm.). Thus, this collaboration between researchers and the SRI has increased the value of the research done by both parties.

ACKNOWLEDGMENTS

This research has been funded by grants from the National Science Foundation, U.S. Environmental Protection Agency, U.S. Forest Service, and the Savannah River Ecology Laboratory of the University of Georgia. The Savannah River Institute of the U.S. Forest Service provide logistical support in addition to funding. We thank the small army of field research technicians that have contributed to the project. In particular, J. Stober and A. Beheler worked for several years in the field and helped to coordinate field crews. We thank J. Blake of SRI for consistent support and encouragement.