

Modelling animal populations in changing landscapes

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Models of Mobile Animal Populations (MAP models) simulate long-term land use changes, population trends and patterns of biological diversity on landscapes of 10^3 – 10^5 ha. MAP models can incorporate information about past land-use patterns and management practices and can project future patterns based on management plans. We illustrate this approach with an example of how implementation of a U.S. Forest Service management plan at the Savannah River Site in South Carolina, U.S.A., might influence population trends of Bachman's Sparrow *Aimophila aestivalis*, a relatively rare and declining species in southeastern pine forests. In this case, a management plan, largely designed to improve conditions for an endangered species, Red-cockaded Woodpecker *Picoides borealis*, may have a negative impact, at least in the short term, on another species of management concern, Bachman's Sparrow.

In a parallel processing version of the MAP models, a single landscape that would ordinarily be too large or detailed to be simulated on a single computer is subdivided into a number of smaller landscapes, and each landscape is simulated in parallel, either on a single multi-tasking machine or on a group of networked machines. With this approach we are attempting to determine just how large a landscape must be before the dynamics of a population within it are more or less independent of factors beyond the landscape boundaries.

A recent trend in population modelling has been to make models spatially explicit, capturing the heterogeneity of real world landscapes (Dunning *et al.* 1995). The need to incorporate habitat heterogeneity into population models has been driven largely by the recognition that the dynamics of small, isolated populations are not independent of what is happening in surrounding patches of habitat. This has led to the development of metapopulation models that explicitly incorporate the dynamics of clusters of habitat linked by immigration and emigration (Fahrig 1988, Stewart & Am- laner 1988, Hanski & Gilpin 1991). The focus of such modelling efforts has been on how the number and size of habitat patches influence the extinction probability of the entire metapopulation. Although metapopulation models include immigration and emigration between habitat patches, they ignore the fact that even clusters of habitat and the metapopulations in them may be embedded in yet larger landscapes and exchange individuals with patches outside the defined metapopulation. This might not be a problem when the metapopulation includes all patches in an isolated archipelago, but in most conservation problems, metapopu-

lations are artificial constructions and it is usually not clear where the boundaries should be drawn.

In this paper we explore a problem related to, but distinct from, the usual question of how do the number and size of patches influence extinction probability. Recognizing that the boundaries around a landscape are usually arbitrary, we ask to what degree the population dynamics of the organisms in a particular landscape are independent of the dynamics of populations in surrounding landscapes. We call this the problem of *spatial autonomy*. We recognize that much of the variability in population size through time is related to the characteristics of the focal landscape and the organisms in it. The concept of spatial autonomy suggests that variability in population size also is related to the characteristics of the adjacent landscapes and the portion of the population which they harbour.

MODELS OF MOBILE ANIMAL POPULATIONS (MAP MODELS)

We have used a class of spatially explicit models called models of Mobile Animal Populations (MAP models) to study landscape effects such as spatial autonomy. MAP models simulate the population dynamics of a mobile animal species on a heterogeneous landscape (Pulliam *et al.* 1992). Land-

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scapes typically are represented in MAP models as large grids of hexagonal cells, each cell being the size of a single territory of the animal species being modelled (Liu 1993, Dunning *et al.* 1995). The landscapes may be totally artificial or may be close approximations to real landscapes, and they may change through time. When a real landscape is approximated, the changes through time may be driven by a proposed management plan for the site.

MAP simulations begin with a complete specification of location, shape and size of all patches of habitat existing at the initial time and a specification of the number and location of all animals on the site. In most cases, MAP models are single-sex models in that only females are counted and located (but see McKelvey *et al.* [1993] for a two-sex model). If the information is known, the animals' locations can be specified based on field surveys of the actual locations of censused individuals. If not, the initial distributions can be determined by randomly assigning individuals to suitable habitat in the landscape.

The reproductive success and probability of survivorship for an individual may depend on the type of habitat occupied. Reproductive success is determined by a random draw of the number of offspring produced from a distribution of possible numbers of offspring produced. In the case of birds, offspring produced is measured as the number of female juveniles fledged, and, in most cases, this distribution is based on actual field measurements of reproductive success. Individuals are assumed to survive the non-breeding season with a fixed probability determined by their age (juvenile or adult) and location. Adults that survive the non-breeding season are assumed to remain on the site they occupied the year before. All juveniles that survive the non-breeding season either inherit their natal territory or leave in the spring in search of a new territory.

Dispersing animals move across the landscape according to specified rules until they either find an unoccupied, suitable site in which to establish a territory or die. Briefly, we assumed that a dispersing bird determines if any of the adjacent cells are suitable and unoccupied. If one or more cells are suitable and unoccupied, the disperser chooses one randomly and moves into it. If no adjacent cells are suitable, the disperser selects an adjacent cell at random, moves into it and then selects another cell from the new set of neighbouring cells. In this way, a disperser moves across the landscape from cell to cell until it finds an unoccupied, suitable patch in which to settle or eventually dies.

The primary dispersal parameter in this type of model is the probability that a disperser dies before reaching a patch in which it can settle. Each time a disperser moves into a new cell, a random value is drawn and compared with a dispersal mortality probability. The dispersal mortality probability is chosen to allow dispersers, on average, to move an expected number of times before dying. For instance we varied the dispersal mortality so as to allow an average of 10, 50 or 100 cells to be examined before dying. We ran a series of simulations varying this dispersal parameter and found that the model was not extremely sensitive to the exact

value of dispersal mortality used in the simulations (see Pulliam *et al.* [1992] and Liu [1993] for a more detailed description of the dispersal protocol and sensitivity analyses).

MAP models typically are run for periods representing 20–50 years. During the simulation, the landscape is updated annually. The initial landscape usually is based on a Geographic Information System (GIS) representation of the initial habitat configuration. Information about the size, shape, age, condition and location of each habitat patch is preserved in the simulations. Patch age and condition are updated each simulation year based on landscape management plans. Patches of habitat may change due simply to succession, or they may change due to management decisions. Habitat suitability for individual species is determined by stand type, age and management history. Habitat-specific demographic parameters, such as reproductive success or survival probability, may be a function of management attributes, such as the number of years since a patch was last burned or the basal area of canopy trees remaining after thinning. Whenever possible, such information should be based on a measured relationship between stand condition and field measurements of demographic conditions.

Habitat use and population status of Bachman's Sparrow *Aimophila aestivalis*

We illustrate the use of MAP models by describing a model that we have developed for Bachman's Sparrow, a permanent resident of pine woodlands in the southeastern United States. The species is of interest because it has been declining for over 50 years and is now rare or absent over much of its former range (Brooks 1938, Dunning 1993). Within its current range, many areas of presumably suitable habitat are not occupied. Bachman's Sparrow is considered a species of management concern by agencies such as the U.S. Forest Service and U.S. Fish and Wildlife Service (Hunter 1990).

Bachman's Sparrow is found in pine-dominated habitats that contain a dense ground cover of grasses and forbs and a relatively open shrub or understory layer (Dunning & Watts 1990). These conditions are found primarily in two age classes of pine forest: open, mature pine forest (>80 years old) and very young successional stages (1–7-year-old clearcuts). Mature forest is generally suitable for breeding by Bachman's Sparrow in every year if the ground vegetation is burned relatively frequently. The number of years that clearcuts are suitable depends on several factors that affect vegetation growth, including soil types and the species of pine planted. When fast-growing pine species are planted in conditions that allow them to quickly form a dense layer of 2–3-m-tall saplings, the time window during which the clearcuts are suitable is shorter than when slow-growing pines are planted.

Intermediate-aged pine forest (8–79 years old) is generally unsuitable because it contains either a dense understory or little ground vegetation, each of which is found in different age classes (Dunning & Watts 1990). Thus, Bachman's Sparrow is restricted to the two extreme age classes of pine forest:

the very youngest stands and the very oldest. In most areas of timber production in the southeastern United States, this means that suitable habitat patches are scattered as isolated islands in a sea of pine forest of unsuitable age classes (Liu *et al.* in press).

Our studies have suggested that isolated patches of habitat, especially the short-lived clearcuts, are less likely to support populations of Bachman's Sparrow (Dunning *et al.* in press). Clearcuts that are more than 0.5 km from other patches of suitable habitat support significantly lower numbers of sparrows (J.B. Dunning, unpubl. data). In addition, regions of pine forest where suitable patches are rare and widely scattered generally support few sparrows. Most patches of suitable habitat are unoccupied in such a landscape (Dunning *et al.* in press). This observation suggests that the landscape distributions of suitable habitat patches may be important in the species' population decline. Thus, we built a MAP model for Bachman's Sparrow to determine how changes in the landscape could affect population dynamics of this species.

A MAP model for Bachman's Sparrow

To build a MAP model for Bachman's Sparrow, we required life history information on this species to design and parameterize the annual cycle simulator of the model. Bachman's Sparrows are permanent residents whose annual cycle is divided into breeding, dispersal and non-breeding phases (Dunning 1993). We compiled information on reproductive success, adult and juvenile mortality and dispersal from our field studies and the literature. Data on reproductive parameters came primarily from the reports of Haggerty (1988, 1992), who has conducted the only thorough study of the breeding biology of this species. Where possible, we compared Haggerty's information with data we collected in our field studies to confirm that Haggerty's data were consistent with patterns we saw in our local study area. There was less information available on mortality or dispersal for this species. We estimated values for these model parameters using a combination of literature estimates for similar species and sensitivity analyses to determine which parameters had the greatest effect on the model performance (Pulliam *et al.* 1992). Subsequent field work has concentrated on those parameters identified as critical in the sensitivity analyses.

As with all models, we have different levels of confidence in the parameter values used in the simulations. The initial distribution of individuals and the patterns of habitat selection are based on our field studies (Dunning & Watts 1990, Dunning *et al.* in press) and are likely to be very accurate. The reproductive parameters are based on a well-designed field study in another portion of the species' range (Haggerty 1988) and are consistent with what we have found in our studies. The survivorship values are not derived from information on Bachman's Sparrow itself but from a variety of other sparrow species. We feel that it is unlikely that Bachman's Sparrow experiences annual survivorships greater than those used in our simulations (60% for adults, 30–40% for

first-year individuals), and we have incorporated lower values in our simulations to determine their impact. Finally, the dispersal parameters are based on the smallest amount of field data, but our sensitivity analyses suggest that our models are not particularly sensitive to the exact values used.

MAP models and land-use change

MAP models can be used to project how populations might respond to proposed management plans. This can be done by incorporating the proposed management changes into the model landscape and running the simulation model on the resulting changes in the landscape. We have done this for a study area at the Savannah River Site, a 770-km² U.S. Department of Energy site in Aiken and Barnwell Counties, South Carolina, U.S.A. Our study area is 5000 ha of managed forest in the southeastern portion of the Savannah River Site and is almost totally forested, consisting of bottomland hardwood species in the riparian bottomlands and managed pine forest in the upland areas. The U.S. Forest Service is responsible for the land management of the region. The study area is divided into several hundred forest "stands". A stand, the basic management unit of the Forest Service, is a patch of forest dominated by trees of a single age class. The Savannah River Site was established in the early 1950s, and the majority (52%) of the pine stands were planted since then. Thus, most of the forest is currently 31–40 years old, an unsuitable age class for Bachman's Sparrow.

In 1992, the Forest Service developed a long-term management plan called the "Savannah River Site Wildlife, Fisheries, and Botany Operation Plan" (U.S. Forest Service, Savannah River Forest Station 1992; hereafter, the "Operation Plan"), which proposes a series of forest manipulations over the next 50 years aimed at both continuing timber production and conserving of rare and endangered species. The manipulations include increasing the amount of mature forest and reducing the current dominance of 31–40-year-old stands. Although the Operation Plan considers the habitat needs of 42 species of plants and animals of management concern, it is clear that a primary biological goal of the plan is to create more mature pine stands of the sort favoured by the endangered Red-cockaded Woodpecker *Picoides borealis*. This will also create habitat for the Bachman's Sparrow, because the sparrow readily uses forest managed for the woodpecker.

We incorporated the major components of the Operation Plan (e.g. harvesting, burning ground and understory vegetation and thinning canopy trees) into the MAP model for the sparrow in order to ask what impact the plan would have on the bird species. The Operation Plan projects the age class distribution of pine stands on the Savannah River Site from 1991 to 2040. Under the plan, the area of new clearcuts produced each year will initially decline because fewer older stands will be harvested than in the past in order to allow more stands to mature to ages suitable for Red-cockaded Woodpeckers.

The short-term result will be less habitat suitable for Bachman's Sparrows because there will be fewer 1–5-year-old stands. Towards the end of the 50-year management period, however, habitat suitable for Bachman's Sparrow will gradually increase as stands that are currently 50–70 years old mature (Fig. 1). Starting around the year 2030, this trend will accelerate as the stands currently 30–50 years old reach the minimum age (80 years) required by Bachman's Sparrow. Therefore, we expect that implementation of the Operation Plan may have a short-term negative effect but a long-term positive effect on the sparrow. Full details of the simulations made to test this expectation can be found in Liu *et al.* (in press).

The Forest Service set a "Minimum Objective" of 1100 pairs of Bachman's Sparrows across the entire Savannah River Site. Since the study area simulated in our model comprised about 10.5% of the entire Savannah River Site, this corresponds to a Minimum Objective of 115 pairs on the region being simulated. We compared the projected population trajectory with a Minimum Objective for Bachman's Sparrow extrapolated for our study region from the Operation Plan. Our simulations suggest that the Minimum Objective will be reached only during the final decade of management under the Operation Plan (Fig. 1). With additional simulations, we were able to test several different changes in the Operation Plan to allow the Forest Service to reach their Minimum Objective goal earlier in the management period (Liu *et al.* in press).

METAMAP AND PARALLEL PROCESSING

The applications of the MAP discussed above were run on a computer representation of our 5000-ha study area. At the time the simulations were performed, 5000 ha was as large an area as we could feasibly simulate, given the computing facilities available to us. How do we know, however, that 5000 ha is an appropriate spatial scale for simulating accurate population dynamics of Bachman's Sparrow? Perhaps if we had simulated the entire Savannah River Site, the dynamics projected for the 5000-ha study area would have been very different because the dynamics on this relatively small area might be dependent on what happens in the larger area around it. On the other hand, perhaps 5000 ha is much larger than is needed. Could we safely predict the dynamics of Bachman's Sparrows on a 500-ha or 1000-ha site without concern for what is happening in adjacent areas? In order to answer questions of this sort, we have now developed an extension of MAP, referred to as METAMAP, that allows much larger landscapes to be simulated using the methods of parallel processing.

Parallel processing was originally developed to perform high-speed matrix manipulation. The special hardware designed to solve large sets of simultaneous equations allowed many small, independent calculations to be made at the same time within one multiprocessor. More recently, these concepts have been applied to groups of cooperating pro-

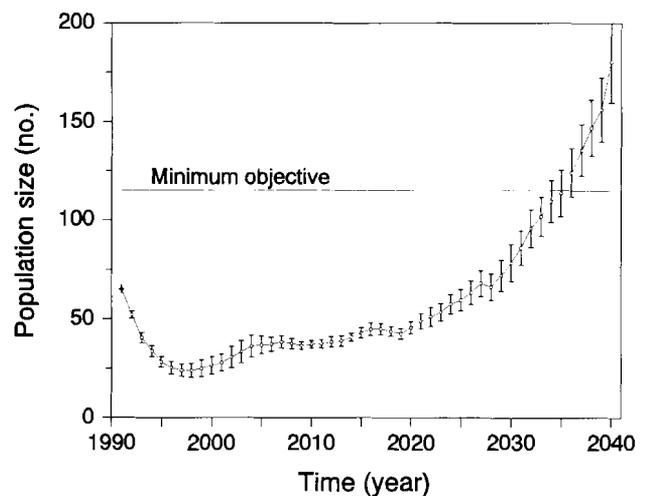


Figure 1. Projections of the number of Bachman's Sparrows on a 5000-ha portion of the Savannah River Site under harvest options based on a proposed U.S. Forest Service management plan for the next 50 years (see text for details).

cessors. Rather than distribute simultaneous algebraic steps throughout a multiprocessor, the goal is to distribute much larger, more complex tasks among a cluster of tightly linked, identical machines. The development of Parallel Virtual Machine (PVM) software takes this process one step further (Geist *et al.* 1993). PVM software permits a loosely networked group of mainframes of any number or mixture of architectures to act as if they were a single multiprocessor (Geist & Sunderam 1992). Any large problem or model that can be divided into a number of smaller, independent components is a good candidate for parallelization with PVM.

We are using PVM to look at the interactions among the populations inhabiting neighbouring landscapes. By dividing a large, heterogeneous landscape into a number of smaller landscapes, we can begin to pose hypotheses about the effect of complex landscapes on population dynamics. Our basic approach using METAMAP has been to simulate nine landscapes in parallel (Fig. 2). The nine landscapes are in a 3×3 array so that we can ask how the dynamics of a population in the central (core) landscape are influenced by the amount of suitable habitat and the sparrow populations in the eight surrounding (matrix) landscapes. If the population size and dynamics in the core landscape are relatively independent of the conditions existing in the surrounding landscapes, we conclude that the core population is "spatially autonomous" from its surroundings.

In this paper, we present some preliminary results using METAMAP to demonstrate the technique and to show that the general approach can yield interesting results. We used METAMAP to compare the spatial autonomy of hypothetical Bachman's Sparrow populations. In particular, we compared the spatial autonomy of sparrow populations on a 1000-ha v a 9000-ha area and asked how sensitive is the population density to changes in the surrounding landscapes?

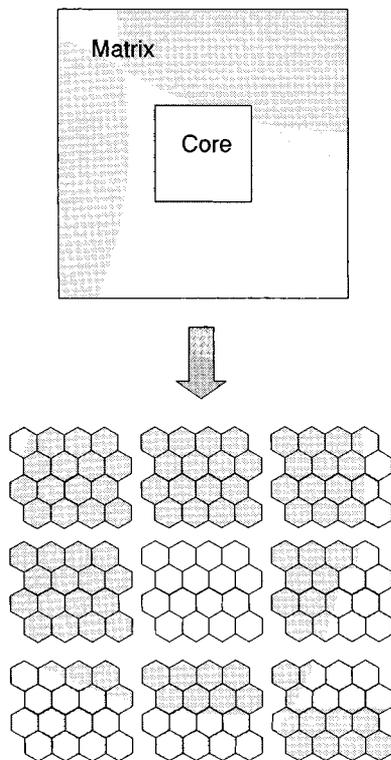


Figure 2. Experimental design for METAMAP studies. (above) Conceptually, a core region is surrounded by a matrix of habitat which might influence population dynamics in the core; (below) Each core landscape (white) in METAMAP is surrounded by eight matrix landscapes (grey).

METAMAP structure

The relative autonomy of a population can be gauged by measuring the degree to which the dynamics of the population are affected by conditions on adjacent landscapes in comparison with conditions on the core landscape. We set up a series of parallel METAMAP simulations to detect the relative influence of changes in the habitat quality in core and surrounding landscapes on the average density of individuals inhabiting the core landscape. In the preliminary trials reported here, we used two levels of habitat quality for the core and two levels for the matrix, and we used two sizes of landscape for each combination.

We simulated Bachman's Sparrow population dynamics on artificial arrays of small and large landscapes. For all landscapes, a stand was taken to be four adjacent territory-sized hexagonal cells. For the arrays of small landscapes, each of the nine landscapes consisted of a 10×10 grid of stands (i.e. a 20×20 grid of territory size hexagons). Thus, each landscape was 1000 ha, and each array of nine such landscapes was 9000 ha in size. For the arrays of large landscapes, each individual landscape in the array consisted of a 30×30 grid of 10-ha stands (i.e. a 60×60 grid of hexagonal cells), making each landscape 9000 ha and an entire array 81,000 ha.

Table 1. Three-factor analysis of variance for population density. For each treatment, Bachman's Sparrow population density in the central (core) landscape was the response variable. For each simulation, all nine landscapes were either small (1000 ha) or large (9000 ha). All four combinations of matrix and core habitat quality were simulated and replicated ten times for each landscape size. Landscapes with poor quality habitat had 2% mature pine stands and those with good quality habitat had 18% mature pine stands

A. Experimental design

Factor	Levels	Values	
Landscape size	2	1000 ha	9000 ha
Matrix quality	2	Poor	Good
Core quality	2	Poor	Good

B. ANOVA

Source	d.f.	Sum of squares	F-value	P
Landscape size	1	464	27	<0.0001
Matrix quality	1	46,079	2693	<0.0001
Core quality	1	3,408,298	99,999	<0.0001
Size \times matrix	1	5111	298	<0.0001
Size \times core	1	4241	247	<0.0001

We varied the habitat quality of landscapes by adjusting the relative proportion of mature, highly suitable patches in the core and surrounding landscapes. In all cases, 80% of each landscape was assumed to be planted with pines which were harvested on a 40-year rotation. Each year, 2% of each landscape was assumed to be clearcut and the remaining 18% of each landscape was either highly suitable mature pine stands or non-pine stands unsuitable for Bachman's Sparrows. Poor and good quality landscapes were defined as having 2% and 18%, respectively, of the landscape in mature pine stands. Thus, a good quality landscape consisted of 80% pines in 40-year rotation, 2% new clearcuts and 18% maintained in mature pines. A poor quality landscape consisted of 80% pine stands in rotation, 2% new clearcuts, 2% mature pine stands and the remainder (16%) non-pine stands.

Eight treatments were simulated with ten replicates for each treatment (Table 1A). For both large (9000 ha) and small (1000 ha) landscapes, all combinations of core and matrix habitat quality (2% mature pine v 18%) were simulated. The final 40 years of each 50-year simulation run were used to calculate the average core population densities.

Landscape size, habitat quality of the core area and habitat quality of the surrounding landscapes all interacted to determine population density in the core (Fig. 3). A three-factor analysis of variance applied to the data showed significant contributions to variation in the core population density by all main effects and interaction terms (Table 1B). As expected, the strongest influence on population density in the core landscape was the density of suitable habitat in the core (Fig. 3). The density of suitable habitat in the matrix (i.e.

surrounding) landscapes and the size of the landscapes also had an influence on population density in the core, though the effects were considerably weaker than the effect of the core habitat quality itself. In particular, we note that the interaction between landscape size and the quality of the matrix landscapes varied in different simulations to the extent of having opposite effects on core population density. For instance, when matrix landscapes were of poor quality (Fig. 3, open and hatched bars), higher population densities were supported in the core landscapes as landscape size increased. The reverse was true when considering poor core landscapes surrounded by good matrix landscapes (Fig. 3, stippled bars).

Sensitivity analyses reinforced our interpretation of the interaction between landscape size and the influence of the quality of the surrounding landscapes. Core population densities were highly sensitive to changes in core habitat quality for small and for large landscapes. In contrast, the sensitivity to changes in matrix quality shows a clear downward trend with increasing landscape size. Sensitivities were moderate for small landscapes and were much less for large ones.

Although we did not perform enough replications to calculate reliable extinction probabilities, we found that populations in small (1000 ha), low quality core landscapes went extinct in several simulation runs when the core landscape was surrounded by equally poor quality landscapes. Core populations, on the other hand, never went extinct when the core was surrounded by high quality landscapes. Apparently the higher population sizes and lower extinction rates in small core landscapes surrounded by high quality landscapes are due to a constant supply of immigrants from the surrounding landscapes. Under these conditions, a small, low quality core landscape may be viewed as a population "sink" and is not autonomous from the surrounding landscapes despite relatively low sensitivity of its average population size to changes in the surrounding landscapes.

CONCLUSIONS

These results demonstrate the utility of spatially explicit population models for answering spatial questions concerning the conservation of avian species. Spatially explicit models linked with landscape maps that capture the heterogeneity of real-world landscapes can be used to suggest the possible response of organisms to proposed management strategies. Large-scale simulations using techniques such as parallel processing may allow us to address a critical question in wildlife management: how large an area must we include in a management plan to ensure that critical population processes are encompassed within the managed area? Each of these innovations in modelling will increase our ability to work with land managers in avian conservation.

The results described in this paper are meant to illustrate the techniques that we have found useful and not to present all details of the studies described. Our work with parallel processing techniques is just beginning, and the above re-

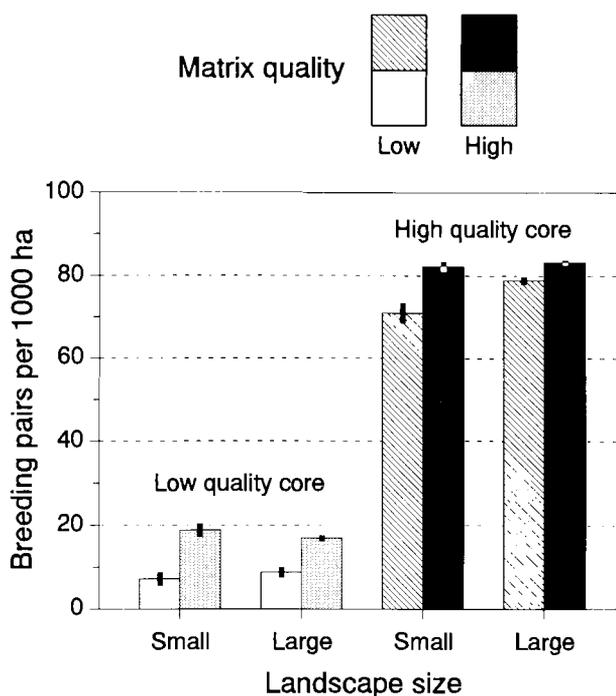


Figure 3. Estimated population density of Bachman's Sparrows in the core landscape as influenced by landscape size and the habitat quality of core and surrounding landscapes. There were a total of eight treatments simulated with ten replicates for each treatment. Vertical lines on top of each histogram bar = 1 s.d.

sults should be considered preliminary. We believe that our work to date has demonstrated the promise of this technology in landscape-level studies.

Some of the results of the METAMAP studies are obvious, such as those demonstrating that population densities in the core landscapes were strongly affected by the habitat quality in the core. As a reviewer pointed out, a complex model is not necessary to predict this result. However, when designing computer programmes, it is always encouraging to generate some results that agree with reality. The more complex interaction between the effects of landscape size and matrix landscape quality illustrate the potential value of this approach in studying more subtle landscape effects.

In most of the METAMAP analyses, the effect of the surrounding landscapes on population density in the core landscape decreases with increasing landscape size, that is, the larger landscapes were more spatially autonomous than the smaller ones. While we conclude that larger landscapes are more autonomous than small ones in the case of Bachman's Sparrow on managed pine plantations, we recognize that even our small landscapes (1000 ha) were large enough to produce some degree of autonomy in most simulations. We are currently expanding these simulation studies to include a wider range of landscape sizes and patch compositions to explore the limits to the spatial autonomy of linked populations.

We believe that spatial autonomy is a fundamentally im-

portant aspect of population dynamics that has been largely ignored in the growing literature on population dynamics in heterogenous landscapes. Spatial autonomy should be of great concern to land managers because they need to know how responsive local populations will be to changes in the management practice on the lands they control. A land manager presumably would not wish to spend much time, effort and money only to learn that habitat improvements on the managed land have relatively little impact on the populations of concern. The same time and money might well have been much better spent purchasing additional land or persuading adjacent landowners to modify their land-use practices.

Spatial autonomy should be of interest to experimental and theoretical ecologists as well as to land managers. Experimental ecologists often may do experiments at too small a spatial scale to obtain the results expected. For example, Pulliam & Dunning (1987) manipulated the sizes and abundance of seeds in six 1-ha tracts of oak woodland in south-eastern Arizona to determine whether or not wintering populations of sparrows (subfamily Emberizinae) were food limited. After getting ambiguous results, they concluded that the spatial scale of their experiments was inappropriate for the question asked (see also Wiens *et al.* 1986). Theoretical ecologists using spatially explicit population models also must be concerned that the land areas simulated in their models may be inappropriate for the questions being asked.

The techniques outlined above should prove useful in helping ecologists know how large an area is necessary before a desired degree of autonomy is achieved. Of course, the degree of autonomy will differ for different species. To date we have only simulated the impact of the proposed management plan on Bachman's Sparrow, but we are currently working to use the same approach on a number of other species of management concern. We are planning to analyse a variety of species with very different life histories and dispersal behaviours in search for general rules about the relationships among species characteristics, landscape characteristics and the spatial autonomy of populations.

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