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# Theoretical Models of the Impact of Climate Change on Natural Populations, Communities and Ecosystems

Final Report

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# Final Report of DOE Grant No. DE-FG09-89ER60881

This Final Report is separated into four parts; an introductory section, followed by three sections describing the research of the PI (Pulliam) and each of the CoPIs (Taylor and Wiegert)

## I. Introduction.

Land use change is a relatively understudied aspect of global change. In many cases, the impact of land use on plant and animal species may be far greater than the impact of climate change *per se*. As an integral part of our long-term studies of the response of animal populations to global change, we have focused on land use change as a dominant driving force. Climate change, no doubt, will also play a role in determining the future abundance and distribution of many species, but, for many species, the signal from climate change *per se* may be difficult to detect if we do not first understand the impact of land use change. This formed the dominant theme of the research by the PI (Pulliam). Both land use change and year to year climate change can directly affect other populations and two examples of this formed the focus of the remaining research, models of invertebrates in Carolina Bays (Taylor) and a model of a commercial estuarine population of blue crabs (Wiegert).

## II. Pulliam section.

MAP models, or models of Mobile Animal Populations, simulate long-term land use changes, population trends, and patterns of biological diversity on landscapes of $10^3$ to $10^5$ ha. MAP models can incorporate information about past land-use patterns and management practices and can project future patterns based on management plans. Our studies illustrate this approach with an example of how implementation of a Forest Service management plan at the Savannah River Site in South Carolina, U.S.A., might influence population trends of the 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, the Red-cockaded Woodpecker (Picoides borealis), may have a negative impact, at least in the short term, on another species of management concern, the Bachman's Sparrow.

### A. Population Dynamics in Spatially Heterogeneous Environments.

As a rule, birds leave their natal habitats and live most of their lives at some distance from where they were born.

Even comparatively sedentary species often move a few to many kilometers away from their natal sites when dispersing in search of mates or breeding habitat. The landscapes through which birds move are heterogeneous, and dispersing individuals encounter a

variety of habitats and may even settle in a different type of habitat than the one in which they were born. Dispersing birds may experience different mortality probabilities when dispersing through different types of habitat, and the type of habitat they choose for breeding can certainly affect their subsequent reproductive success and survival probability. As a consequence, the types of habitats available in a landscape and the positions
of the habitat patches can have a direct impact on avian population dynamics.

Many of the early attempts to model avian population dynamics ignored the spatial heterogeneity of the landscapes that populations inhabited. For the most part, populations were modeled as if they lived in spatially homogeneous environments in which they could instantaneously transport themselves to any suitable habitat that might be available. Such models have given us valuable insights into some of the ways in which population density and life-history characteristics, such as age-specific birth and death schedules, influence population growth and viability. These models have been useful in furthering our understanding of the most general features of population regulation and life-history evolution, but they have proven less useful when applied to the dynamics of particular populations in particular places.

Even in the absence of human activities, natural landscapes are heterogeneous, reflecting the physical variability associated with topographic relief and geological substrate plus witnessing the signatures of past natural disturbances such as fires, storms, and floods. Human activities have greatly altered the patterns of natural heterogeneity, generally having led to sharper landscape boundaries and more fragmented habitat patches. Consequent with these landscape changes, many animal and plant populations have declined in abundance and local extinctions appear to have greatly increased. As interest in the impact of such landscape changes has grown, ecologists have begun to develop new modeling approaches that directly incorporate habitat heterogeneity, in hope of projecting how future changes in landscapes might influence the organisms living in them.

The need to incorporate habitat heterogeneity into population models has been largely driven by the recognition that the dynamics of small populations in isolated patches of habitat are not independent of what is happening in surrounding patches of habitat. This has lead to the development of metapopulation models that explicitly incorporate the dynamics of clusters of habitat linked by immigration and emigration. The focus of such modeling efforts has been on how the number and size of habitat patches influences 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 imbedded 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, metapopulations are artificial constructs and it is usually not clear where the boundaries should be drawn.

## B. MAP Models.

MAP models, or models of Mobile Animal Populations, simulate the population dynamics of a mobile animal species on a heterogeneous landscape. Landscapes are typically represented in MAP models as large grids of hexagonal cells, each cell being the size of a single territory of the animal species being modeled. The landscapes may be totally artificial or may be close approximations to real landscapes. The landscapes may change through time and, when a real landscape is approximated, the changes in the landscape through time may be driven by a proposed management plan for the site.

A MAP simulation begins with a complete specification of location, shape and sizes 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 and only females are counted and located. If the information is known, the animal locations can be specified based on field surveys of the actual locations of censused individuals. If this information is not known, the initial distributions are determined by randomly assigning individuals to suitable habitat in the landscape.

The reproductive success and survivorship probability of 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 nonbreeding 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. If an adult dies, one of the juveniles produced in the previous breeding season is assumed to inherit its natal territory. All juveniles that survive the non-breeding season and who do not inherit a natal territory leave their natal territories in the spring in search of a new territory. Dispersing animals move across the landscape according to specified dispersal rules until they either find an unoccupied, suitable site in which to establish a territory or they die.

MAP models are typically run for 20 to 50 years and each year the landscape is updated. The initial landscape is usually based on a Geographic Information System (GIS) representation of the initial habitat configuration. Information about the size, shape, age, condition and location of each stand is preserved in the simulations. Stand age and condition are updated each simulation year based on landscape management plans. Patches of habitat may change simply due to succession or they may change due to management decisions. Habitat suitability is determined by stand type, age, and management history. For example, a species may only occupy pine stands that are greater than 80 years old or it may occupy younger stands if they have been thinned or burned. Since reproductive success and survival probability are habitat specific, reproductive success may be a function of management attributes such as the number of years since a stand was last burned or the basal area remaining after thinning. Whenever possible, such information should be based on a measured relationship between stand condition and field measurements of demographic conditions.

## C. Life History of the Bachman's Sparrow.

We illustrate the use of MAP models by describing a model that we have developed for Bachman's Sparrow (Aimophila aestivalis). This species is 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. The species is secretive, and little is known of its local population trends and requirements in many parts of its range. Because of these factors, Bachman's Sparrow is listed on many state lists of threatened and endangered fauna, and it is considered a species of management concern by agencies such as the U.S. Forest Service and U.S. Fish and Wildlife Service.

The 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. These conditions are found primarily in two age classes of pine forest, open, mature pine forest ( >80 yr old), and very young successional stages (1-7 yr old). Mature pine forest that is burned frequently generally has a dense ground layer of vegetation while tall shrubs are eliminated by the frequent fires. This is the habitat used by the endangered Red-cockaded Woodpecker (Picoides borealis) and state and federal agencies often manage some forest specifically to maintain older stands in this condition.

Young successional habitats, such as clearcuts in the first several years after timber harvest and replanting, also contain the required vegetation structures. These sites become less suitable for the sparrow as the planted pines and other trees grow into a dense shrub layer. The number of years that clearcuts are suitable depends on several factors that affect tree growth, including soil types and the species of pine planted. In the upper coastal plain of South Carolina, for instance, forest stands planted in the slow-growing longleaf pine (Pinus palustris) are in suitable condition for at least 7 years, while stands planted in the fast-growing loblolly pine (P. taeda) may become unsuitable in only 4 years.

Intermediate-aged forest is unsuitable for occupancy by the sparrow because it lacks the necessary vegetation conditions in the ground and understory layers. Young pine plantations (5-20 yr old) generally have a dense wall of young pines 2-5 m tall, while older stands with a closed canopy (20-70 yr old) allow little light to the ground layer and have little ground or shrub vegetation. 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.

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, Danielson and Watts, unpublished data). Clearcuts that are more than 0.5 km from other patches of suitable habitat support significantly lower numbers of sparrows. 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., manuscript in review). This observation, coupled with the fact that suitable patches are unoccupied throughout the species' range, suggests that the landscape distributions of suitable habitat patches may be important in the species' population decline. Thus, a MAP model for Bachman's Sparrow could be useful in determining how changes in the landscape could affect population dynamics of this species.

To build a MAP model for the 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. We compiled information on each of these phases from the literature and our field studies. BACHMAP is the name we have given to the version of the MAP model that has been specifically parameterized for Bachman's Sparrow.

Information on clutch size, nest mortality, and reproductive success was compiled from the literature. Bachman's Sparrows are territorial, mostly monogamous passerines and each pair may produce up to two successful clutches per breeding season. Territory sizes average 2.5 ha. Pairs average 3 fledglings per season, although several nesting attempts may be required to successfully rear young. We assumed the primary sex ratio to be 1:1, so in good habitat adult females produce on average 1.5 female offspring per season in our single-sex models. In poor habitats (primarily older clearcuts) we arbitrarily estimated that females produce on average 0.5 female offspring per season. This assumption decreased the average population density in older clearcuts to match the population declines seen in the field. Individual females were randomly assigned reproductive success values from a distribution that yielded the expected population average.

Little information is available on nonbreeding season mortality for this species. Bachman's Sparrows are extremely difficult to find in the winter as they are shy and almost completely unresponsive in this season to censusing aids such as tape recorded song. We surveyed the literature on mortality estimates for other species of sparrows to determine realistic adult and juvenile survivorship values. We used the following constraints suggested by the literature: maximum adult survivorship was $\leq 60\%$; juvenile survivorship was $\leq$ adult survivorship; and the selected survivorships allowed a population growth rate $\geq$ 1.0. This process identified feasible ranges of annual survivorship as 40-60% for adults and 27-60% for juveniles. For most simulations we used parameter values of 60% for adult survivorship and 40% for juvenile survivorship. We decreased these values in some simulations to show the impact of lower survivorship, because sensitivity analyses had determined that the model results were sensitive to survivorship parameters.

In general, dispersal information is even less available for terrestrial birds than is data on survivorship. We modeled dispersal as a series of steps where dispersing individuals move from cell to cell in the landscape searching for an unoccupied, suitable patch. Briefly, we assumed that a disperser chooses randomly among the adjacent, suitable patches and moves into one. If no adjacent patches are suitable, the disperser selects an adjacent patch at random, moves into it and then selects another patch from the new set of neighboring cells. In this way, a disperser moves across the landscape from cell to cell until it finds a unoccupied, suitable patch in which to settle, or until the disperser 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 moved into a new cell, it randomly drew a mortality value that determined whether it died. The mortality values were drawn from a distribution of mortalities that allowed 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.

A variety of other dispersal parameters can also be varied in the simulations. For instance, the dispersers could have different probabilities of moving in a straight line while dispersing, or could have the ability to remember their dispersal path and not re-enter previously searched cells. In our sensitivity analyses, the model proved to be less sensitive to variation in the dispersal parameters than it was to variation in reproductive success or survivorship.

As with all models, we have different levels of confidence for the different parameter values used in the simulations. The initial distribution of individuals and the patterns of habitat selection are based on local field studies we have conducted at our primary study site, 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, but 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 sparrow species. We feel that it is very unlikely that Bachman's Sparrow experiences survivorships greater than those used in our studies, and we have incorporated lower values in our simulations to determine their impacts. Finally, the dispersal parameters are based on the least amount of field data. However, the sensitivity analyses suggest that our models are not particularly sensitive to the exact values used. We are working on improving our understanding of dispersal in this species, and in models of this sort.

D. Projected Land-use Changes at the Savannah River Site.

MAP models can be used to project future population trends of bird species based on incorporating proposed management plans into a simulation model. We have done this for our study area at the Savannah River Site, a 770 $km^2$ US Department of Energy facility in Aiken and Barnwell counties, South Carolina. Our 5,000 ha study area in the southeastern portion of the Savannah River Site is almost totally forested, consisting of bottomland hardwood species in the riparian bottomlands and managed pine forest in the upland areas. The study area is divided into several hundred forest stands which are the basic management unit for the land management by the Forest Service. As explained earlier, Bachman's Sparrow is restricted to certain serial stages of the managed pine forest. Each tract of pines is dominated by a single age class of trees reflecting the planting date of the site. Since the Savannah River Site was established in the early 1950's, a majority (52%) of the pine stands are currently 31 to 40 years old.

The US Forest Service manages the forested lands at the Savannah River Site. The Forest Service has recently developed a long-term management plan called the "Savannah River Site Wildlife, Fisheries, and Botany Operation Plan" (1992). This management plan proposes a series of land manipulations over the next 50 years aimed at balancing timber production and the conservation of rare and endangered species. Although the management 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 manage the upland habitats to create more mature pine stands of the sort favored by the Red-cockaded Woodpecker (Picoides borealis).

We have attempted to incorporate the major components of the management plan (eg. harvesting, burning and thinning) into our simulation model in order to ask what impact the plan, largely designed to accommodate the habitat needs of a single endangered species, the Red-cockaded Woodpecker, would have on another species that the management plan was not specifically designed to accommodate. We were particularly interested in whether or not a management plan designed to improve habitat for one endangered spebIes e)ght degrade habitat for other species and potentially endanger them. To date we have only simulated the impact of the proposed management plan on the Bachman's Sparrow, but we are currently working to use the same approach on a number of other species of management concern.

The Operations Plan projects the age class distribution of pine stands on the Savannah River Site from 1991 to 2040. Under the plan, new clearcuts and young stands will initially decline because fewer older stands will be harvested each year 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. Over the earlier decades of the 21st century, however, habitat suitable for Bachman's Sparrow will gradually increase as stands that are currently 50 to 70 years old mature. Starting around the year 2030, this trend will accelerate as the stands currently 30 to 50 years old reach the minimum age (80 yrs.) required by Bachman's Sparrow.

Details of the simulation are beyond the scope of the present presentation but are presented in detail in Liu, Dunning, and Pulliam (in press). The "Savannah River Site Wildlife, Fisheries, and Botany Operation Plan" specifies how many stands of different age classes will be harvested each year but does not specify which individual stands will be harvested in each year. We compared the impacts of two different harvest options on Bachman's Sparrow population projections. The overall trends for the two options are quite similar, with populations initially declining dramatically and then slowly recovering.

We also compared the projected population trajectory to a "Minimum Objective" for Bachman's Sparrow. The Forest Service has 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 comprises about 10.5% of the entire Savannah River Site this corresponds to 115 pairs on our 5,000 ha study area. The simulations suggest that harvesting clusters of contiguous patches will lead to meeting the minimum objective of 115 pairs sooner than harvesting patches at random. This is because harvesting in clusters creates larger patches of suitable habitat and dispersing juveniles are less likely to die searching for suitable sites.

We are currently experimenting with a parallel processing version of the MAP models that we call METAMAP. In this version, a single landscape that would ordinarily be too large or detailed to be simulated on a single machine is subdivided into a number of smaller landscapes and each landscape in 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. Preliminary results show that populations in large preserves are less sensitive to changes in surrounding areas than are populations on smaller preserves.

## III. Taylor Section.

The general problem that we studied was the effect of environmental variation on the aquatic communities in wetland ponds. These ponds are common in the southeastern coastal plain, and 250-300 are found on the 780 $km^2$ area of the Savannah River Site in South Carolina. The ponds are typically shallow; most dry out annually. Hydroperiods very widely, among ponds and among years. The aquatic communities, including frogs, salamanders, insects, microcrustaceans, and other invertebrates, are extremely sensitive to weather and climate which govern initiation and duration of the hydroperiod. We pursued two lines of investigation, using various kinds of computer-based models. The first line concerned responses of representative pond species to variation in pond hydroperiod. The second line concerned more general properties of life history models in variable environments.

A wetland pond model incorporating the spatial structure of the basin was developed to investigate the relative success of zooplankton with differing life histories and cues for entering and breaking dormancy. For zooplankton, the dormant stage may be an egg or a juvenile. The physical and population models were based on data for Rainbow Bay, a well-studied pond on the SRS. Environmental variability included variability in timing and length of the hydroperiod.

Analytical models have shown that animals should switch to dormancy earlier as environmental variability increases. The model for Rainbow Bay supports these results. In variable environments, the life histories with earlier dormancy developed larger populations of dormant stages than those with later dormancy. The life histories with earlier dormancy were also less likely to go extinct in the most variable environments. Strategies with dormancy at a juvenile stage were more successful than those with dormancy as eggs. In all environments, strategies that did not rely on environmental cues were most successful, as measured by total numbers of nestings stages present after a century of simulated years. Environmentally cued strategies were more successful when duration, rather than timing, of the hydroperiod was varied. In those strategies that used an environmental cue to initiate dormancy, food availability was the most reliable cue, but water level was also effective.

Dormant animals or eggs in the sediments of the basin were an important source for recolonization to the simulated pond after years when populations failed to reproduce. Outer edges of the basin were important under dryer conditions, when the outer basin was inundated only occasionally. Strategies with overall poor success persisted in highly variable environments if a long season occurred even once or twice a century to restock the egg bank.

We also used a weather-driven empirical model for water level in Rainbow Bay (developed independently of this project by P.M. Dixon and others) to estimate frequency of successful reproduction for representative invertebrate and vertebrate taxa over the last sixty years. Results underscore the importance of adaptations to environmental variability in shaping these communities. For example, according to model, the calanoid copepod *Diaptomus stagnalis*, often an important member of the late winter-early spring pond community, reproduced successfully in only about half of the last sixty years.

The cladoceran *Daphnia* has provided a useful energetic model for studying life history strategies. With W. Gabriel (Max Planck Institute for Limnology), I extended analyses of optimal life histories for *Daphnia*, which we had previously studied in constant environments, to a seasonal environment. A temporary pond with variable hydroperiod inspired the model. The results point out limitations of predictions from theory that assumes constancy or equilibrium. The life history optimized to a temporary pond-like variable habitat shows typically earlier maturity but greater adult growth than the life history optimized for a constant habitat.

## IV. Wiegert section.

The primary responsibilities I assumed in the grant were 1) to prepare a detailed description of the range of generalized control functions that are useful in models of population responses to environmental perturbations and 2) to use current and past work by myself and my students to construct a detailed model of the response of the Georgia populations of the blue crab, **Callinectes sapidus**, to changing environmental conditions of land use and climate, affecting both coastal water temperature and salinity. Both of these tasks were accomplished (add paper descriptions).

### A. Generalized Control Functions.

From the earliest days of interest in theoretical ecology, practitioners have been interested in describing the behavior and growth of populations by reducing biological and ecological laws to sets of differential equations. Prior to the days of inexpensive, high-speed numerical integration, these equations of necessity had to be oversimplified and lacking the plethora of non-linearities and discontinuities (thresholds) found in the real world. Thus off-the-shelf simple control functions such as the Logistic and the Michaelis-Menten or hyperbolic were used routinely until the present day. The computational power now available, however, permits far greater latitude in matching the known rules of population behavior by realistic control functions. An example using the Logistic equation is illustrative of the approach used in Wiegert (199xa, ms. in prep.). In this example, the flow is from a resource (donor) compartment (X1) to a consumer (recipient) compartment. The control function is f(X2) or control by competition for shared space. The control is only of input, thus the control function must vary only between zero and unity. The subscript + indicates this constraint, i.e. the value within subscripted brackets can never fall below zero. In the example, loss by egestion is assumed zero, but this is assumed only to make the explanation clearer.

The logistic control function:

$$f(X2) = [1 - X2/K2]_{+} \qquad (1)$$

where:

K2 = the carrying capacity (f(X2)=1 when X2=K2)

Thus the flow form of the logistic is:

$$dX2/dt = X2*\{\tau*(1-\lambda/\tau)*f(X2)-\lambda\} \qquad (2)$$

Where:

$\tau$ = maximum input (and thus growth)
$\lambda$ = minimum losses under idealized conditions

Thus when f(X2)=1, input just balances losses and growth = 0. However, Eq. two has some serious limitations. First, it assumes that there is no threshold response density, i.e. a density below which there is no detectable competion for space and maximum input and population growth occur. Second, the function is assumed linear, i.e. the effect on input of adding a unit to X2 is the same, independent of the density of X2.

A more realistic, generalized form of the function was developed in part with support from this grant and is written:

$$f(X2) = [1 - (1 - \lambda/\tau)\{(\alpha-X2)_{+}/(\alpha-K2)\}_{+}]^{b} \qquad (3)$$

Where:

$\alpha$ = the response density threshold
b is an exponent determining the nature of the function

The exponent b permits fitting the function to any real data set on the relation between population input (whether food or movement of individuals) and net increase of the population. The function is generalized, but not at the expense of adding biologically undefincable (or measureable) parameters.

The same approach has been used to generalize a number of other controls functions, among them the Michaelis-Menten or hyperbolic function. Both of the commonly used forms of the latter have severe limitations, but they can be combined in a generalized form that will accomodate almost any set of data.

Several other forms of control are discussed and generalized in the paper being completed.

### B. The Model of a Blue Crab Population.

The commercial blue crab of the southeaster coast of the USA and the Gulf coast, **Callinectes sapidus**, has a life cycle that can be impacted greatly by conditions in its estuarine habitat, particularly changes in temperature and salinity. Temperature affects both crab activity and growth. Salinity changes can affect both the movement and survival of the immature stages.

The blue crab as a juvenile and adult spends most of its time (and makes all of its growth) in the tidal creeks and estuaries. After the final molt by the females, when they are impregnated by the males, the females migrate offshore, into high salinity ocean water, where the egg mass is produced and hatches into the first larval stage, the zooeal. The zooeal stage transforms into the megalopal stage and in this form the larval crabs reenter the estuary and tidal creek. They seek lower salinity water, where, having found a suitable substrate, they transform into the free-living juvenile crab. These feed in the estuaries and tidal creeks/marshes, beginning a series of molts that results in the adult.

For the past several years I and my students have studied blue crab populations with support from various sources, including the present grant. The focus of the work under this grant was to forge this information into a population model of the blue crab that would permit simulation of the effects of changing temperature and salinity on the populations dynamics. In particular, the megalopal and perhaps early juvenile stages are susceptable to salinity changes that result from drastic, drought-induced changes in river flow along the Georgia coast. The model is completed and is being incorporated into the larger ecosystem model of the salt marshes of the GA coast developed by Wiegert and coworkers during the past 20 years. Papers describing the models are in preparation.

Publications based on partial support from DOE grant.

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Liu, J., J. B. Dunning J. and H. R. Pulliam. 199x. Potential impacts of a forest management plan on Bachman's Sparrows Aimophila aestivalis): Linking a spatially-explicit model with GIS. Conservation Biology, in press.

Pulliam, H. R., Dunning, J.B., and Liu, J. 1992. Population dynamics in complex landscapes: a case study. Ecological Applications 2:165-177.

Manuscripts completed.

Taylor, B.E. and W. Gabriel. Optimal adult growth of *Daphnia* in a seasonal environment. Functional Ecology. (In review, revised version submitted)

Manuscripts in preparation.

(V. Medland has a manuscript in preparation.)

Three manuscripts are in preparation by Wiegert:
Wiegert, R.G. 199xa Generalized control functions in ecological models. (to be submitted in February, 1995 to Ecology)
Wiegert, R.G. A spatially-explicit model of a GA salt marsh and estuary. 199xb. To be sumitted to Ecological Modelling.
Wiegert, R.G. and Ting Dai. 199xc. A population model of the blue crab, **Callinectes sapidus**, in Georgia. To be submitted.

Published abstracts.

Taylor, B.E. and W. Gabriel. To grow or not to grow: optimal resource allocation for *Daphnia* in stable and variable environments. 7th Annual Southeastern Mathematical/Statistical Ecology Conference, Hickory Knob State Park, McCormick, South Carolina. April 1990.

Taylor, B.E. and W. Gabriel. Models for optimal growth and reproduction of *Daphnia*. Third Congress of the European Society for Evolutionary Biology, Debrecen, Hungary. September 1991. (Invited paper, Workshop on Optimal Energy Allocation)

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Medland, V.L. and B.E. Taylor. A model of the impact of climate variability on the success of life-history strategies of temporary pond crustaceans. American Society of Limnology and Oceanography Annual Meeting, Santa Fe, New Mexico. February 1992. (Poster)