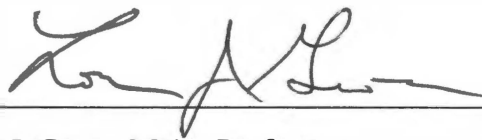


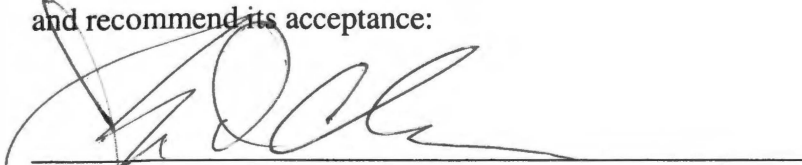
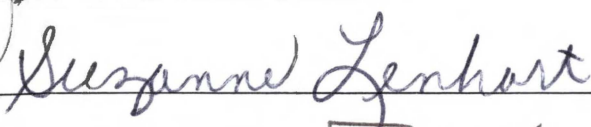
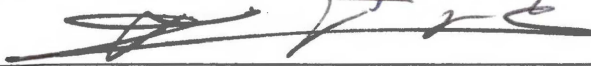
To the Graduate Council:

I am submitting herewith a dissertation written by René Armando Salinas entitled "Modeling the Effects of Harvesting on Black Bears in the Southern Appalachians". I have examined the final paper copy of this dissertation for form and content and recommend that it be accepted in partial fulfillment of the requirements for the degree of Doctor of Philosophy, with a major in Mathematics.

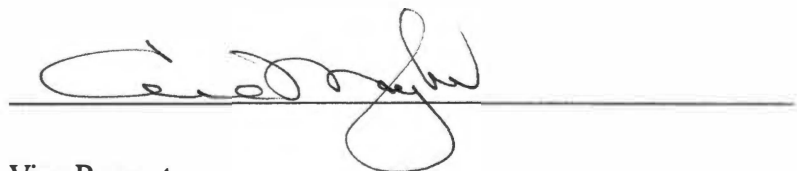


Louis J. Gross, Major Professor

We have read this dissertation
and recommend its acceptance:

Accepted for the Council:



Vice Provost
and Dean of Graduate Studies

Modeling the Effects of Harvesting on Black Bears in the Southern Appalachians

A Dissertation

Presented for the
Doctor of Philosophy
Degree

The University of Tennessee, Knoxville

René Armando Salinas

August, 2003

*Thesis
2003b
.S25*

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*...in accomplishing my dreams, I thank
my wife, Tracie, for sharing them,
my parents, Armando and Nancy, for the chance to pursue them, and
God for making it all possible...*

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Abstract

The black bear (*Ursus americanus*) population of the southern Appalachians is one of the most dense in North America. As a result, during fall mast failures an increasing number of nuisance bears may leave Great Smoky Mountains National Park and the surrounding national forest boundaries and enter human-populated areas. I developed two models to address several problems regarding this population: a metapopulation harvesting model and a spatially-explicit individual-based model.

The metapopulation model involved a coupled set of logistic-type growth models that included density-dependent immigration and emigration and harvesting. I applied Pontryagin's Maximum Principle to derive an optimal harvesting and reserve design strategy for the system. Model results suggested that a forest region's population could be maintained despite high harvest levels because of emigration from a connected, unharvested park region. The amount of shared border between the park and forest region was important in determining the optimal harvesting strategy.

The individual-based model used geographic information system (GIS) map layers of human density, bear sanctuaries and forest type to model the system. The model suggested that fall mast failures had a two-fold effect on the population. First, the lack of food caused bears to emigrate into unprotected areas and second, the lack of food caused females to enter denning with low caloric reserves. This resulted in high cub mortality. Various alternative harvesting scenarios were tested to determine the best harvesting regime and reserve design strategy for minimizing potential bear-human encounters and maintaining the population. The model provides the ability to analyze spatial rearrangements of sanctuaries in addition to alternative harvesting regulations.

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Chapter 1

Introduction

1.1 Black Bear Population

1.1.1 Background

Great Smoky Mountains National Park (GSMNP or Park) and surrounding national forests were established in the mid-1930s. National Park Service regulations eliminated hunting and timber harvest, which likely aided in the recovery of the black bear (*Ursus americanus*) population. New hunting regulations in the national forests established during the 1970s and the maturation of oak forests in the southern Appalachians advanced this recovery to what is now one of the most dense black bear populations in North America. Currently, the population is considered stable and healthy.

The last few decades also have seen an increase in the human population surrounding GSMNP and within the national forests. This human increase, coupled with black bear recovery, has elevated nuisance bear activity and bear-human encounters. In many cases, these increases are triggered by fall hard mast availability, which can affect bear movements. As managers maintain the black bear popula-

tion and the human population continues to increase, the incidence of bear-human encounters will likely increase as well. One primary concern for managers is that more encounters could increase the likelihood of a harmful encounter.

Currently, the only forms of control on the black bear population are hunting and euthanizing or translocating nuisance bears. Hunting is allowed on public lands that are not designated as bear sanctuaries. These sanctuaries, established in the 1970s, were designed to create local source populations throughout the region and minimize the threat of overharvesting. Tennessee has six of these sanctuaries spread across the Cherokee National Forest. North Carolina has 13 sanctuaries in Nantahala and Pisgah National Forests. GSMNP is the largest sanctuary and may serve as the primary source population in the southern Appalachians.

Managers would like to minimize nuisance activity but still provide bears for harvest. The usefulness of the sanctuaries must be considered when addressing the problem of minimizing nuisance bear activity. It is difficult for managers to predict how changes in the sanctuary design will affect the bear population. Managers must first understand the population dynamics of black bears in the southern Appalachians. The low reproductive rate of black bears makes long-term studies difficult to maintain. In this dissertation I develop models to address several of these issues.

1.1.2 Life History

Although the black bear population in the southern Appalachians is one of the longest studied large mammal populations, many questions remain. Gaps in the understanding of the population dynamics remain because of the difficulties associated with studying black bears and the highly stochastic nature of food resources [61].

The reproductive dynamics are perhaps the best understood aspects of the popu-

lation. Females mate during summer, have their cubs during late January and early February, and wean their cubs the following summer. Cubs typically stay with the female through the next fall and denning period and become independent by early summer. Thus, females typically have a two-year reproductive cycle. However, this cycle can be interrupted by the lack of fall hard mast.

The amount of hard mast (acorns, nuts, and other dry fruits) produced during the fall varies greatly from year to year. The mechanisms that cause these year-to-year fluctuations in fall mast are not well understood, but failures seem to occur every four to five years [33]. The intake of hard mast is vital for sustaining bears during hibernation, which lasts from December through March. During years in which fall mast production is low, gestating females are not able to attain enough fat reserves to feed lactating cubs, resulting in high cub mortality rates. When the breeding season starts in mid-June, females that previously lost their litter can enter estrus. This results in a disproportionately large number of gestating females, and produces a large cohort of cubs the following year. The observation of these spikes and troughs in reproductive success associated with fall mast failures has led to a better understanding of black bear population dynamics [27].

During hard mast failures bears may leave protected regions in search of food, thereby increasing the probability of entering human-populated areas. The magnitude of such movements, particularly from GSMNP, is not well understood and is of particular interest to Park managers. Understanding this aspect of the population requires an understanding of the bear density in the area. Because of sampling limitations, obtaining reliable densities has proven difficult [61]. Mark-recapture experiments have yielded estimates for small areas in the Park, but the large error associated with the Jolly-Seber model limits the usefulness of the data.

There is also little understanding of the effects of harvesting on the population. The GSMNP population is believed to act as a source population for the surround-

ing harvestable national forests [16]. The extent to which the Park contributes to the harvested population is unknown. The purpose of the sanctuaries is to provide local source populations to keep the overall population from being overharvested. The effectiveness of these bear sanctuaries within the national forests is also unknown. It is believed that the current harvest effort is saturated [89, 94], meaning that the removal of sanctuaries may not significantly affect the population level. Understanding the effects of various harvesting strategies may provide insight into the effectiveness of the current sanctuary design.

1.2 Objectives

The goal of my study was to develop a mathematical and computational model of the black bear population of the southern Appalachians and to derive harvesting strategies that minimize potential bear-human encounters, while maintaining the population at sustainable levels. I also used the models to gain insight into the effects of fall mast on the population dynamics.

1.2.1 Metapopulation Model

Optimal control models have been used in assessing the economic impacts of harvesting in fisheries for years [15]. The focus of those models is to maximize profit by deriving a maximum sustainable yield for harvesting. Because space typically is not incorporated into these fisheries models, there has been limited application to terrestrial systems where space often is the key element in the problem. Hastings and Botsford [36] developed a spatially-implicit model to show that marine reserves mixed with fisheries can increase yield. Recently, dynamic optimization techniques have been applied to metapopulation models in the context of marine

reserves [72, 86]. This shift in focus on spatial control problems is also evident in Hof and Bevers' book [6], *Spatial Optimization for Managed Ecosystems*.

In Chapter 2, a metapopulation model is described. It is a coupled, differential equation model that includes harvesting and migration between two populations. It is intended to represent the GSMNP black bear population and an adjoining, harvestable national forest population. The objective is to apply Pontryagin's Maximum Principle [62] to the system to derive an optimal harvesting and national forest design strategy to minimize potential bear-human encounters. Particular interest is placed on the proportion of the Park boundary that is connected with national forest areas. This connectivity is important because of the annual movement of bears out of the Park. Ideally, a harvestable buffer region completely surrounding the Park would control this movement, but because of tourism and other factors, this is not practical. The model explores how varying the connectivity may provide reasonable alternatives.

1.2.2 Individual-Based Model

With the development of geographic information system (GIS) landcover maps, spatially-explicit representations of managed systems are now possible. One of the most effective modeling techniques that can use these data is individual-based modeling (IBMs) [23]. By modeling the dynamics of individual entities, detailed effects of spatial variation can be analyzed. Because IBMs often are stochastic, rule-based computer simulations, analytic solutions for optimization are difficult and, in some cases, impossible to derive [34].

Chapter 3 describes a spatially-explicit individual-based model. The model is based on GIS maps for most of eastern Tennessee and western North Carolina. The objective is to provide a relative assessment of the effects of alternative harvesting

and bear sanctuary design strategies on the overall population size and annual potential bear-human encounters. Particularly, because the population has a positive growth rate, I test whether the removal of some sanctuaries is more beneficial in reducing encounters than costly in reducing the overall population. In chapter 4, the model is used to determine the effects of fall mast failures on various demographic elements of the population.

Chapter 2

Control of a Metapopulation

Harvesting Model

2.1 Abstract

Models that address spatial control of managed populations are gaining interest in ecology. This model is motivated by the black bear (*Ursus americanus*) in the southern Appalachians. Since logging and harvesting have been controlled, the population has grown to be one of the most dense in North America. As a result, there has been an increase in the number of nuisance bears that leave Great Smoky Mountains National Park and the surrounding national forest boundaries and enter human populated areas. I develop a metapopulation harvesting model that includes density-dependent immigration and emigration and apply Pontryagin's Maximum Principle to derive an optimal harvesting and reserve design strategy for this system. Model results suggest that a forest region's population can be maintained despite high harvest levels due to emigration from a connected, unharvested park region. The amount of shared border between the park and forest region is important in

determining the optimal harvesting strategy.

Key Phrases: black bear harvesting, metapopulation, optimal control, Pontryagin's maximum principle, reserve design

2.2 Introduction

I developed a model of the black bear population in the southern Appalachians. Since the late 1800s, this population has lost 80% of its range in the region [60]. Great Smoky Mountains National Park (GSMNP) was established in 1934. With its creation, bear hunting and timber harvesting were prohibited. Hunting is allowed in the surrounding national forests. Because the population has rebounded to such high levels and there has been an increase in human encroachment on the border of GSMNP, there has been an increase in bear-human encounters [55, 56]. One of the main reasons bears leave GSMNP is to obtain fall mast, e.g., nuts and acorns, which vary spatially from year to year. If a particular area has a mast failure, then bears may leave the region to find food elsewhere. The population can be viewed as a metapopulation with GSMNP and each national forest acting as a subpopulation. I developed a two-patch model for GSMNP and one adjacent national forest. The modeled populations were labeled Park and Forest.

A metapopulation is defined as a population consisting of many local populations [46]. These local populations are typically coupled by movement. Levins-type models, in which colonization and extinction in the local populations are modeled [35], are the most common type. Another common approach is the two-patch model. In this case, a population is divided between two habitat patches which may differ in quality for the species.

I developed an optimal harvesting strategy for the two populations that minimizes the number of bears that enter human-populated areas. In determining the

optimal strategy, various objectives were considered. Minimizing bear-human encounters is the central focus in this system. If this were the only element of the objective functional, the obvious solution would be to harvest the entire population. Therefore, other aspects of the population must be considered. Maintaining the population at sustainable levels was included in the objective functional to balance the effect of harvesting.

I assume that hunting regulations and mast variability affect the dynamics of the population differently in each patch. There are costs and benefits to harvesting. Not harvesting could lead to an increase in the number of bears that interact with humans, whereas overharvesting could lead to extinction of the local population.

Harvesting is not the only parameter that can be controlled in this system. I also examine how much of the border of GSMNP is connected with the national forest. Again there are trade-offs. Opening the entire border to harvesting would keep many of the bears out. However, many of the small tourist towns that border GSMNP cannot be opened for harvesting, which might result in nuisance bears entering these areas because of the abundance of food.

Because I am looking at the possibility of different harvesting strategies for two patches and changes in patch design, this problem can be considered as one of spatial control [6]. These types of problems involve applying control to biological systems from a spatial perspective. Bevers and Hof's recent book [6] illustrates the diversity of systems in which spatial considerations of control are important.

2.3 Methods

2.3.1 Model Description

I describe a system of two interacting populations with different harvesting parameters. I will use the following set of equations:

$$(2.1) \quad \frac{dP}{dt} = rP - r\frac{P^2}{K} + m_f \left(1 - \frac{P}{K}\right) r\frac{F^2}{K} - h_p P$$

$$(2.2) \quad \frac{dF}{dt} = rF - r\frac{F^2}{K} + m_p \left(1 - \frac{F}{K}\right) r\frac{P^2}{K} - h_f F$$

where:

- P = population size in the Park (Bear Density),
- F = population size in the Forest (Bear Density),
- r = population growth rate (*Proportion * Time⁻¹*),
- K = carrying capacity (Bear Density),
- m_p = proportion of Park boundary connected with the Forest,
- m_f = proportion of Forest boundary connected with the Park,
- h_p = harvesting level in the Park (*Proportion * Time⁻¹*), and
- h_f = harvesting level in the Forest (*Proportion * Time⁻¹*).

Each equation describes the following aspects of the population:

- rP , exponential growth,
 - $r\frac{P^2}{K}$, density-dependent emigration,
 - $m_f \left(1 - \frac{P}{K}\right) r\frac{F^2}{K}$, density-dependent immigration from the other population,
- and

- $h_p P$, harvesting, where h_p is the proportion of the population harvested.

2.3.2 Dynamics

Without loss of generality, I can non-dimensionalize eqs. (2.1) - (2.2) by letting $x = \frac{P}{K}$, $y = \frac{F}{K}$, and $\tau = tr$.

$$(2.3) \quad \dot{x} = (x + m_2 y^2)(1 - x) - h_1 x$$

$$(2.4) \quad \dot{y} = (y + m_1 x^2)(1 - y) - h_2 y$$

Where $\dot{} = \frac{d}{d\tau}$. The asymptotic dynamics of (2.3) - (2.4) are similar to the dynamics of the standard logistic growth plus harvesting model. There exist two non-negative equilibrium points, (0,0) and (x_{eq}, y_{eq}) . The non-trivial equilibrium point cannot be solved for analytically because it involves solving a fifth order polynomial. I can, however, write $x_{eq} = f(y_{eq}^2)$ and $y_{eq} = g(x_{eq}^2)$, in the form,

$$(2.5) \quad x_{eq} = \frac{1}{2} \left[(1 - m_2 y_{eq}^2 - h_1) + \sqrt{(1 - m_2 y_{eq}^2 - h_1)^2 + 4m_2 y_{eq}^2} \right]$$

$$(2.6) \quad y_{eq} = \frac{1}{2} \left[(1 - m_1 x_{eq}^2 - h_2) + \sqrt{(1 - m_1 x_{eq}^2 - h_2)^2 + 4m_1 x_{eq}^2} \right].$$

The trivial equilibrium point is unstable if harvesting is less than growth and immigration. The nontrivial equilibrium point is globally asymptotically stable in the region $D = (0, 1) \times (0, 1)$. To prove this I must first show that all the trajectories on the boundary of D flow into the set D .

Lemma 2.1. *In the system defined by eqs. (2.3) - (2.4) all the trajectories on $\tilde{D}$ flow into D for $0 \leq h_i < 1$.*

Proof:

For $x = 0$, $\dot{x} > 0$ and similarly when $y = 0$, $\dot{y} > 0$. When $x = 1$, $\dot{x} < 0$ and if $y = 1$, $\dot{y} < 0$. □

I next show that the nontrivial equilibrium point, (x_{eq}, y_{eq}) is globally asymptotically stable in D .

Theorem 2.2. *The nontrivial equilibrium point, (x_{eq}, y_{eq}) , is globally asymptotically stable in the set D for $0 \leq h_i < 1$, $i = 1, 2$.*

Proof:

I first define the Liapunov function:

$$(2.7) \quad V(x, y) = x - x_{eq} \ln \left(\frac{x}{x_{eq}} \right) + y - y_{eq} \ln \left(\frac{y}{y_{eq}} \right).$$

It is easily verified that $V(x, y) > 0 \forall (x, y) \in D$. Therefore V is positive definite.

I then have:

$$(2.8) \quad \dot{V}(x(\tau), y(\tau)) = \dot{x} \left(1 - \frac{x_{eq}}{x} \right) + \dot{y} \left(1 - \frac{y_{eq}}{y} \right).$$

By using eqs. (2.5) and (2.6), I now show that for $\bar{x} = x_{eq} + \varepsilon$ such that $x_{eq} < x_{eq} + \varepsilon \leq 1$, then $\dot{x} < 0$.

$$\begin{aligned} \dot{x}(\bar{x}, y) &= (x_{eq} + \varepsilon + m_2 y^2) (1 - (x_{eq} + \varepsilon)) - h_1 (x_{eq} + \varepsilon) \\ &= (x_{eq} + m_2 y^2) (1 - x_{eq}) - h_1 x_{eq} + \varepsilon (1 - x_{eq}) - \varepsilon (x_{eq} + m_2 y^2) - \varepsilon^2 - h_1 \varepsilon \\ &= -\varepsilon \left(\sqrt{(1 - m_2 y^2 - h_1)^2 + 4m_2 y^2} + \varepsilon \right) \\ &< 0 \end{aligned}$$

I next show that for $\bar{x} = x_{eq} - \varepsilon$ such that $0 < x_{eq} - \varepsilon < x_{eq}$, then $\dot{x} > 0$.

$$\begin{aligned}
\dot{x}(\bar{x}, y) &= (x_{eq} - \varepsilon + m_2 y^2) (1 - (x_{eq} - \varepsilon)) - h_1 (x_{eq} - \varepsilon) \\
&= (x_{eq} + m_2 y^2) (1 - x_{eq}) - h_1 x_{eq} - \varepsilon (1 - x_{eq}) + \varepsilon (x_{eq} + m_2 y^2) - \varepsilon^2 + h_1 \varepsilon \\
&= \sqrt{(1 - m_2 y^2 - h_1)^2 + 4m_2 y^2} - \varepsilon \\
&> 0, \text{ since } \sqrt{(1 - m_2 y^2 - h_1)^2 + 4m_2 y^2} > x_{eq} > \varepsilon.
\end{aligned}$$

The same relationship exists for $\dot{y}$. Therefore, $\dot{V}(x, y) < 0 \forall (x, y) \in D$, i.e. negative definite. Thus, the nontrivial equilibrium point, (x_{eq}, y_{eq}) , is globally asymptotically stable in D . $\square$

2.3.3 Optimal Control

I am interested in determining an optimal harvesting strategy over a relatively short time frame. I use Pontryagin's Maximum Principle (PMP) to determine the optimal strategies [62]. PMP provides necessary conditions for optimal control. These conditions lead to an optimality system that can be solved numerically. PMP gives a characterization of an optimal harvesting strategy in terms of the solution of an optimality system, the state system coupled with an adjoint system. This optimality system can be solved numerically and the effects of changing various parameters on the optimal strategy can be investigated. Other techniques have been used for similar systems; for example, Tuck et.al. [86] used Lagrangians for their discrete system of a marine reserve. Bhat and Lenhart [7] performed optimal control of partial differential equations in a harvest problem for beaver populations.

Note that the immigration terms in eqs.(2.1) and (2.2), $m_f (1 - \frac{P}{K}) r \frac{F_2}{K}$ and $m_p (1 - \frac{F}{K}) r \frac{P_2}{K}$, respectively, suggest that only a portion of the emigrating populations, $r \frac{P_2}{K}$ and $r \frac{F_2}{K}$, enters the other region. The portion of the population that does

not enter the other region can be described by the following equations:

- $(1 - m_p) r \frac{P^2}{K}$, the portion of the emigrating population from the Park that leave through a border that is not connected with the Forest population.
- $(1 - m_f) r \frac{F^2}{K}$, the portion of the emigrating population from the Forest that leave through a border that is not connected with the Park population.
- $\frac{F}{K} m_p r \frac{P^2}{K}$, the portion of the emigrating population from the Park that enters into the Forest region, but is forced to leave because of density-dependence.
- $\frac{P}{K} m_f r \frac{F^2}{K}$, the portion of the emigrating population from the Forest that enters into the Park region, but is forced to leave because of density-dependence.

These emigration components can be grouped into a general population O . The differential equation for the population in those areas outside the Park or Forest can then be written as:

$$(2.9) \quad \frac{dO}{dt} = (1 - m_p) r \frac{P^2}{K} + (1 - m_f) r \frac{F^2}{K} + \frac{P}{K} m_f r \frac{F^2}{K} + \frac{F}{K} m_p r \frac{P^2}{K}$$

This population is defined as the number of emigrators from each region that enter the “outside” region (Figure A.1) (Tables and Figures for Chapter 2 are located in Appendix A). Equation (2.9) simply keeps track of the number of the individuals and does not model their life history dynamics.

Now that the system is defined, I can derive the optimality system. In theory, one way to minimize the number of bears that enter the “outside” region is to find an optimal harvesting strategy for both populations. There is little chance that harvesting will be allowed in the Park. I can, however, vary the proportion of the border of the Park that is harvested, i.e., vary the proportion of the Park boundary that is connected to the Forest region. In this case I derive an optimal Forest boundary for

the Park, along with an optimal harvesting strategy for the Forest region. Recall that there is no harvesting in the “outside” region. I will develop an optimality system for both scenarios.

Harvesting Both Populations

I first define an objective functional:

$$(2.10) \quad J(h_p, h_f) = \int_0^T (O + c_p h_p^2 + c_f h_f^2) dt,$$

where the number of bears in the outside region, O , is balanced with the cost of harvesting in the two regions, represented by the quadratic terms. I use the O population as a metric for potential encounters. I want to keep this population level low. To avoid overharvesting, harvesting costs are added. The idea is not to associate these cost terms with a specific factor, but to view them in relative terms. A high cost of harvesting means that the removal of bears in that location could be detrimental to the population. In the Park, this could mean that it would affect the nature of the Park as a source for the population.

It is not possible for each term in equation (2.10) to be zero because zero harvesting would maximize O and O equal to zero is only possible via high harvest levels. Consequently, the functional should be minimized to find intermediate harvesting levels that will correspond to a sustainable population and low encounters. The constants c_p and c_f balance the weight of O against the cost of the two types of control.

The next step is to define the Hamiltonian of the system.

$$(2.11) \quad H = O + c_p h_p^2 + c_f h_f^2 + \lambda_1 \dot{P} + \lambda_2 \dot{F} + \lambda_3 \dot{O}$$

The Hamiltonian is then used to derive the optimality equations for harvesting by first taking the partial derivatives of H with respect to the harvesting terms:

$$(2.12) \quad \frac{\partial H}{\partial h_p} = 2c_p h_p - \lambda_1 P = 0$$

$$(2.13) \quad \frac{\partial H}{\partial h_f} = 2c_f h_f - \lambda_1 F = 0$$

Each equation is then set equal to zero and solved for h_i , resulting in an optimal pair (h_p^*, h_f^*) :

$$(2.14) \quad h_p^* = \frac{\lambda_1 P}{2c_p}$$

$$(2.15) \quad h_f^* = \frac{\lambda_1 F}{2c_f}.$$

The differential equations for the adjoints are:

$$(2.16) \quad \frac{d\lambda_1}{dt} = -\frac{\partial H}{\partial P} = -\lambda_1 \left[r \left(1 - \frac{P}{K} \right) - \left(\frac{rP + m_f r \frac{F^2}{K}}{K} \right) - h_p \right]$$

$$\begin{aligned} & -\lambda_2 \left[\left(\frac{2m_p r P}{K} \right) \left(1 - \frac{F}{K} \right) \right] \\ & -\lambda_3 \left[\frac{2(1-m_p)rP}{K} + \frac{m_f r F^2}{K^2} + \frac{2Fm_p r P}{K^2} \right] \end{aligned}$$

$$(2.17) \quad \frac{d\lambda_2}{dt} = -\frac{\partial H}{\partial F} = -\lambda_1 \left[\left(\frac{2m_f r F}{K} \right) \left(1 - \frac{N}{K} \right) \right]$$

$$-\lambda_2 \left[r \left(1 - \frac{F}{K} \right) - \left(\frac{rF + m_f r \frac{P^2}{K}}{K} \right) - h_f \right]$$

$$-\lambda_3 \left[\frac{2(1-m_f)rF}{K} + \frac{m_p r P^2}{K^2} + \frac{2Fm_f r P}{K^2} \right]$$

$$(2.18) \quad \frac{d\lambda_3}{dt} = -\frac{\partial H}{\partial O} = -1$$

with transversality condition:

$$(2.19) \quad \lambda_1(T) = \lambda_2(T) = \lambda_3(T) = 0.$$

Assumptions

Because of the complexity of the system, I make some simplifying assumptions. Without loss of generality, I normalize the maximum carrying capacity K . This keeps the population size in each region between $[0, 1]$. I also assume that the Park region is a square with unit area, whereas the Forest region can vary in shape to surround the Park, while still preserving the area assumption. This assumption results in m_f becoming a function of m_p . This will be used to simulate a dynamical Forest design in which the proportion of the border around the Park population that is harvestable can be adjusted from year to year. Figure A.2 illustrates this point. Table A.1 summarizes the resulting values and bounds used in the numerical computations. A numerical algorithm for Pontryagin's Maximum Principle can be summarized as follows:

1. choose time of run T ,
2. choose initial conditions for state equations (eqs.(2.1) and (2.2)),
3. let terminal condition for adjoints be $\lambda_i(T) = 0$,
4. choose initial harvest rates h_i ,

5. solve state equations forward in time,
6. use state values for P and F to solve adjoint equations backward in time,
7. use the new adjoints and state values to update the harvesting strategy (i.e., by using eqs. (2.14) and (2.15)), and
8. compare the previous state and adjoint values with those derived from 7. If they are not sufficiently close, repeat steps 5 - 7.

The system of differential equations is solved using a fourth-order Runge-Kutta method [9] and is written in C++. Similar “forward sweep - backward sweep” iteration algorithms have been used successfully for other systems [7, 29, 40].

Boundary Varying Case

I also wanted to find an optimal Forest boundary for the Park. A key assumption in the model is that the size and shape of the Park region are fixed; this assumption is realistic because national park boundaries are not likely to change. The model allows for the adjustment of a national forest region around the Park. This assumption has some merit in that the idea of creating buffer zones around national parks has been debated for many years [24, 47, 49, 67]. Many national parks have heavily traveled roads and towns adjacent to them, which makes establishing a buffer zone difficult in practice.

To model this phenomenon, I define a new objective functional:

$$(2.20) \quad J(m_p, h_f) = \int_0^T (O + c_m m_p^2 + c_f h_f^2) dt$$

In this system I assume that the Park cannot be harvested, but the boundary that the Park shares with the Forest can be altered (m_p) (Figure A.2). Recall that m_p is

defined as the proportion of the boundary that is connected to the Forest region.

The new optimality equation is:

$$(2.21) \quad \frac{\partial H}{\partial m_p} = 2c_m m_p - \lambda_2 F \frac{P^2}{K} \left(1 - \frac{F}{K}\right) + \lambda_3 \left(-rN^2 + \frac{FrP^2}{K^2}\right) = 0$$

which results in:

$$(2.22) \quad m_p^* = \frac{\lambda_2 F \frac{P^2}{K} \left(\frac{F}{K} - 1\right) + \lambda_3 r P^2 \left(1 - \frac{F}{K^2}\right)}{2c_m}$$

The adjoint equations are the same as eqs. (2.16) - (2.18).

Existence and Uniqueness

Since the solutions of the state and adjoint equations are *a priori* bounded, existence of an optimal control was determined using a result from Fleming et. al [30] (Theorem 4.1, pgs. 68-69). Analysis has also shown that the optimal control for each objective functional is unique under the condition that time is sufficiently small. This uniqueness is obtained by showing uniqueness of solutions to the optimality system. See Fister et. al. [29] for an example of a similar uniqueness result.

2.4 Results

Figure A.3 illustrates the optimal harvesting strategy assuming each population is of equal value and the cost of harvesting is minimal ($c_p = c_f = 1$). Both populations are harvested to extinction because the cost of having bears in region O is more “expensive” than not harvesting. For a more realistic motivating example, Figure A.4 shows a run in which the cost of harvesting the Park population is high ($c_p = 10,000$). The cost of harvesting the Forest population is still minimal

($c_f = 1$). The Park population, as expected, grows to carrying capacity whereas the Forest population is harvested. Note that the harvesting levels for the Forest population are similar to the harvesting levels in Figure A.3. This population does not go extinct because of the density-dependent emigration from the Park population. Because the Park population is not harvested, there is an increase in the number of bears in region O .

The first set of runs involved keeping the carrying capacity constant, $K = 1$. Because the black bear population is the motivation for this model, variations in carrying capacity were modeled to simulate mast fluctuations. K varied between 0.4 and 1 in a four-year cycle for 25 years (Figure A.5).

Figures A.6 and A.7 show the same runs as Figures A.3 and A.4, but with periodic carrying capacity. Figure A.7 suggests that the Park population fluctuates near the average carrying capacity. Note also that there is still enough emigration to sustain the Forest population.

For all previous runs, $m_p = 0.25$ and $m_f = 0.25$. The results are very different if the configuration of the regions is changed. Figure A.8 shows the same run as Figure A.4 but with different values of m_p and m_f . The dotted line represents the optimal harvesting strategy for $m_p = 0 = m_f$. Each successive solid line represents the resulting density from an increment of 0.1 on m_p . Note that despite an increase in harvesting, there is still an increase in the Forest population. This is due to the increase in immigration from the Park, which in turn results from an increase in m_p . This also leads to an increase in the O population.

In Figure A.9, the Park population was not harvested, the Forest population was harvested, and the Forest layout was allowed to vary temporally. Note the difference in the outside region compared with Figure A.4. Figure A.10 shows the results with periodic carrying capacity. I had previously assumed that the Park and Forest regions had the same variation in mast. In Figure A.11 mast variations

between the regions were asynchronous, meaning that the two regions are out of phase with each other. The peaks in the m_p plot correspond to mast failures in the Park.

2.5 Discussion

Limiting the movement of bears into human-populated areas is of great interest in the southern Appalachian region. The solution is not to simply harvest more bears everywhere, because the Great Smoky Mountain National Park population is an important source population for the entire region. To address this issue I developed a metapopulation model and used numerical techniques to find an optimal harvesting and region layout strategy. The model is to be considered a first approximation for the analysis of this type of system.

In the states of the southern Appalachians, the black bear is considered a game species. Although no bears can be harvested from GSMNP, the hunting seasons in the region provide an effective method to manage the population. Despite an estimated harvest rate in the region of about 12%, the population in the region is growing [60]. Simulation models suggest that harvesting reduces the number of bears entering human populated areas by 40% or more (Chapter 3).

Harvesting both Park and Forest populations resulted in reducing the populations to low levels, because there was no source population (Figure A.3). My results suggest that a population can be maintained in a Forest (buffer) region, despite high harvesting, if the central core population (GSMNP) is unharvested (Figure A.4). The level at which the overall population can be maintained is dependent on how much of a shared border the two regions have. Model results suggested a somewhat intuitive result in that the best strategy for the system would be to completely surround GSMNP with a harvested Forest region (Figure A.8). This allowed for

a maximum harvest rate in the Forest and a minimum number of bears entering human populated areas. However, in the case of GSMNP, it would be unlikely to completely surround the Park with a harvested Forest region because there are already many developed areas that immediately border the Park. I accounted for this with a boundary-varying case. This case allowed for variation in m_p , which was the proportion of the Park border that is shared with the Forest region. The boundary-varying case included a cost (c_m) associated with increasing m_p . The results show that it would be ideal to vary the proportion of border shared between the populations when there is variation in dispersal, e.g., variation in bear dispersal due to spatial heterogeneity in mast availability (Figures A.10 and A.11). This strategy would be difficult to apply, but simulation results suggest that increased harvesting during mast failure years would decrease the number of nuisance bears (Chapter 3).

As development near the Park boundary increases, it will become more difficult to implement a buffer region strategy. This would be equivalent to increasing the cost (c_m) of the border region, which results in a smaller optimal boundary design (smaller m_p) and more bears in the outside region.

The model is at best a first approximation of the dynamics of the system. Varying the growth rate, r , to simulate the effect of mast on cub mortality would be a logical extension. Having two different patch sizes also would be a worthwhile change. Including the dynamics of the population in the outer region, O , by including mortality and migration back into the Park and Forest regions also could yield different results. In reality, the outer region population is being harvested. Another interesting extension of this model would be a Leslie-type stage-structured model. Black bears are routinely divided into three demographic groups: cubs, sub-adults, and adults. In general, mast variations cause sub-adults to disperse from regions first. Harvesting would also be affected because it is limited to sub-adult and adult bears. Examining the interplay among these different age groups could provide

better insights into the sustainability of a population.

Chapter 3

Alternative Harvesting Strategies for the Control of Bear-Human Encounters: An Individual-Based Modeling Approach

3.1 Abstract

I describe a methodology to apply spatial control to harvesting of black bears (*Ursus americanus*) using an individual-based model that accounts for differences in gender, age, and size and how those factors affect movement, mating, and foraging rules. I specifically model the black bear population of the southern Appalachians, which consists of Great Smoky Mountains National Park (GSMNP), Cherokee, Pisgah, and Nantahala National Forests, and most of eastern Tennessee and western North Carolina. Increases in development around GSMNP and some national forests have increased the potential for bear-human encounters, which can be

detrimental to both. Hunting is prohibited in GSMNP and a mosaic of bear sanctuaries located within the national forests. Hunting pressure on bears interacts with environmental factors because years with low mast (mainly acorn) production lead to greater bear movement and generally higher harvests. Years with low mast production lead to low fecundity, affecting the demographics of the bear population for many years. Although these environmental factors cannot be controlled, the harvest season and location can be. I use the model to compare the effects of various alternative harvesting strategies on the demographics and distribution of the black bear population.

Key Phrases: alternative harvesting strategy, black bear, individual-based model, relative assessment

3.2 Introduction

The establishment of GSMNP in the mid-1930s created a protected environment for many over-exploited species. One of the species that benefited was the black bear, which now has one of the highest densities among black bear populations in North America. The population is near carrying capacity and acts as a source population for the surrounding region.

GSMNP is also one of the most visited national parks in the United States. Approximately nine million people visit each year, many with the hope of seeing a black bear. Located between Knoxville, Tennessee and Asheville, North Carolina (Figure C.1) (Tables and Figures for Chapter 3 are located in Appendix C), GSMNP lies adjacent to three national forests: Cherokee (CNF), Nantahala (NNF), and Pisgah (PNF) (Figure C.2). Each of the national forests also contains black bear populations, which are managed by harvesting. To prevent overharvesting, a mosaic of bear sanctuaries was established in the 1970s within the national forests.

Tennessee and North Carolina have different hunting seasons but the same restrictions (i.e., one bear bag limit, no weaning females, and sub-adult and adult bears only).

The human population surrounding GSMNP has been increasing, particularly during the last three decades. The Park is now surrounded by numerous small tourist towns and sprawling suburban areas. This change in human population and increase in the black bear population has led to an increase in bear-human encounters and nuisance incidents [56, 57]. Although most encounters are harmless, resource managers generally strive to reduce the frequency of such encounters and incidents.

There are two principal reasons bears leave the Park and other protected regions: establishing a home range and searching for food. Each summer, sub-adult bears must leave their mothers and find areas where they can establish home ranges. Females usually establish home ranges near the home ranges of their mother, whereas males are forced to disperse farther [88]. During the fall, bears may move greater distances searching for food to build up fat reserves for hibernation [13, 65, 68]. Their primary food source is hard mast [4, 10, 25], which can vary from year to year. During years of hard mast failure, bears may move out of the protected areas in search of sufficient food. Variations in hard mast also affect female reproductive success. If a female is unable to gain enough weight, lactation may be insufficient to feed her litter, resulting in cub mortality during the denning period [26].

The problem of humans encroaching on wildlife habitat is not unique to the southern Appalachians. All along the Appalachian range and in the western United States, the successful recovery of the black bear population, coupled with increased urban sprawl, has resulted in increased nuisance activity [81, 82, 32, 59, 84, 85]. In the western U.S., subdivisions have started encroaching on mountain lion (*Puma concolor*) habitat, increasing concerns over public safety [83]. The importance of

public opinion on wildlife management practices should not be underestimated. If the public perceives a species as dangerous, they may be less willing to promote conservation issues related to that species [59]. One option wildlife managers have at their disposal is to control wildlife populations through harvesting, thereby minimizing harmful interactions. However, information for optimal harvest strategies is lacking.

Bear-human encounters are of primary concern for resource managers when developing management strategies for black bears. For example, the recent plan for black bear management in Virginia has an entire section devoted to managing bear-human encounters [59]. Strategies to reduce such interactions include fertility control, issuing kill permits, supplemental feeding, repellents, and changes in regulated harvesting. Although it is possible for the model to simulate many of these control strategies, the focus of my analysis is on regulated harvesting.

Models are a powerful tool in the development of management strategies [51, 53, 73]. Most of the models that have addressed black bear management have been deterministic Leslie-type models [12, 51, 97]. However, such models are not able to address space explicitly and are therefore limited in their management implications. More recently, a simulation model was developed to determine the risk of extinction of brown bears (*Ursus arctos*) in Spain [96]. Although more detailed, this model did not include the intra-year dynamics of bears, which is vital to assess management strategies.

I addressed the issue of managing the black bear population by developing a spatially-explicit individual-based model (IBM) for the southern Appalachian region. IBMs involve modeling the life stages of each individual via a set of rules based on available data on the life history of the organism [23]. I used this model to explore the effects of fall mast variation on potential bear-human encounters. I also used the model to test various alternative harvesting strategies, including changing

sanctuary design, increasing harvesting effort, and harvesting in GSMNP. The objective was to determine how these alternative harvesting strategies affect potential encounters and the overall black bear population size. I hypothesized that removing the sanctuaries would not reduce the overall population to dangerously low levels, i.e., no risk of extinction. I tested this hypothesis and determined if harvesting could be an effective control on the population.

3.3 Model Description

The life cycle of black bears is driven by seasonal changes. In simplest terms, the population can be described by seasons: summer mating, fall foraging, winter denning and birthing, and spring emergence. In order to capture the within-season details that are important to understand the dynamics of the black bear population, I modeled the population with processes on two time scales. The daily time steps are shown in Figure C.3. Reproduction and denning were modeled as seasonal time-scale events because they occur across seasons.

The model ran on a daily time step for a user-defined length of time. The region was divided into 450 m x 450 m cells with an extent of 620 x 390 cells. That scale was chosen because it was large enough to reduce the effects of the low circuitous nature of bear movements [13, 65], yet small enough to capture day-to-day variation. The stochasticity in the model was driven by Monte Carlo tests throughout the various model procedures described below.

There were various map layers used in the model. The model was capable of subdividing the population into different sets, including state, GSMNP and forest regions, sanctuary and non-sanctuary, and human-populated. The human population map (Figure C.4) was obtained from the Oak Ridge National Lab LandScan Global Population Database [45]. The estimates of human population density were

based on data including landcover, landuse, nighttime lights, and U.S. census data. Because the data have not been groundtruthed for this area, I used GIS layers for roads, boundaries, and vegetation types to estimate the data fit. I assumed that these data overestimated human density because of the landuse data. For example, the human population points in GSMNP correspond to Cades Cove, which was once inhabited and cultivated. Where possible, I removed those points from the map. Because relative assessment analysis (discussed later) was used, this overestimate of human population did not drastically affect my results.

3.3.1 Daily Model Functions

Initialization

I assumed a June 1 start date for convenience in modeling reproduction; cubs who have been with their mothers for over a year become independent and estrous cycles have yet to begin. Individual bears were randomly placed in cells, within GSMNP and national forest boundaries, that had fewer than ten people per km^2 . I estimated initial densities for each region to match population estimates from the late 1970s, where data were available ($\frac{\text{bears}}{\text{cell}}$): 0.15 (*GSMNP*), 0.03 (*CNF*), 0.06 (*PNF*), and 0.08 (*NNF*) [52, 63].

The initial age distribution was estimated from McLean [52] and is shown in Figure C.5. Because the data used to calibrate the model were from the late 1970s and early 1980s and the most reliable empirical data on the population dynamics are from 1990 to the present, I started the model in 1980 but did not compile model results until 1990. The 10-year delay also ensured spatial and demographic heterogeneity in the population.

Mast Layer

Soft and hard mast are black bears' principal food sources for most of the year [4, 10, 25]. Soft mast, which includes berries and other fleshy fruits, provides most nutrition during summer. Hard mast, which includes acorns and other dry fruits, provides vital nutrition during the fall. Bears use hard mast to gain fat reserves for the denning period. Fall hard mast failures occur every four to five years [44]. It has been hypothesized that years of above average soft mast abundance can compensate for hard mast failures [41]. There are no data on the variability of soft mast in the region, so constant soft mast availability is assumed in the model.

Hard mast availability was simulated by using a vegetation map layer obtained from the Southern Appalachian Man and Biosphere project [78]. These data included nine forest types and one urban, non-forest type (Figure C.6). Kilocalories of available food throughout the year for each vegetation class were estimated using data derived for the northwestern section of GSMNP in 1995 [41]. The available kilocalories were updated every 2 weeks throughout the year. Because 1995 was an average fall mast year [41], the data were scaled to approximate maximum mast availability (Table C.1). Mast availability per cell was estimated as follows:

$$(3.1) \quad \text{Calories}(i, j)[t] = \text{Calories}(i, j)[t - 1] + \text{Cal}_{Max} * \text{Cal}_{Bears} * \text{Mast}_{level}$$

where:

- i, j designate the coordinates of the cell.
- $\text{Cal}_{Max} = \text{Calories}_{veg_type}[\text{month}_t]$, represents the number of kilocalories of the vegetation type in cell(i, j) for the month of time t . It is divided by 2 because mast is replaced every 14 days.
- Cal_{Bears} is the proportion of the kilocalories available to bears. Between 70

- 90% of mast is used by birds and small mammals [22, 41, 80]. For the summer, I assume 30% is available, whereas only 10% would be available during the fall.

- $Mast_{level} = \left(\frac{Mast_{year(t)} + random_{unif}}{10} \right)$ represents the mast index value for that year. Many mast indices have been developed to estimate the availability of food [41]. The model uses a 10-point scale in which 10 represents 100% of the possible mast is available. Because no data are available on soft mast variation during summer, I assume $Mast_{year(t)} = 3$. Over the last 20 years, the highest fall mast index was estimated at 3.6. For calibration purposes, the index was rescaled to the following discrete fall mast index values: 1.0, 2.0, 3.0, 4.0. An index value of 1.0 represents a complete failure and 4.0 is the best possible mast year. During a given masting event, not all trees produce the same amount of mast [33]. Therefore, to allow for spatial variability, the actual index value in each cell is uniformly distributed between $[Index - 0.5, Index + 0.5]$. The number is then divided by 10 to represent the value as a proportion.

Equation 3.1 does not represent the actual number of kilocalories in each cell. Instead, it is a metric for available food.

Movement

There are many approaches to modeling movement, and the proper approach depends on the behavioral characteristics of the organism to be modeled [87]. Bears have a hierarchical dominance structure in which older, larger males can acquire home ranges that include the best food resources [68]. Older females have a similar advantage over younger females. I modeled movement solely based on food availability and this hierarchical dominance structure.

The model assumed bears move to cells with the most food. In the case of adult males, a cell was available to be occupied if there were no older males within a one-cell radius. Adult females are the next level of dominance and could move to a cell if there were no adult males or older females in that cell. Sub-adult males could move into a cell if there were no adult males or females within a one-cell radius of the cell. Finally, sub-adult females could move into a cell if there were no other bears in that cell. The difference in this “tolerance” spacing between males (1-cell radius) and females (0-cell radius) is supported by data suggesting that females are more tolerant than males and often share home ranges with offspring [13, 65, 88].

Each bear searched outwardly from its current cell. Males could move as far as four cells in one day, whereas females were limited to two [13, 65]. If a bear was unable to find a suitable cell, it was randomly placed in one of the cells in its outer movement range. Because the cells are 450 m x 450 m, realistically more than one bear can occupy the same cell, at least temporarily. The movement rules allow for this since older bears can move to any cell despite the number of younger bears in it.

On June 1st and September 1st, positions of each sub-adult and adult were saved as a central location. As a bear was closer to its maximum distance (eight cells for males, five for females) away from this central location, the search region was skewed away from the maximum distance. For example, if a male was six cells east of its center, its search region in the x-direction was restricted to two cells to the east and four cells to the west (recall that a males have a maximum search range of four cells.). This implemented a restriction in uni-directional movement. When a bear reaches a point on its maximum distance, the central location is reset to that point to allow for long distance movement, which has been observed in telemetry data [88].

During the mating season, females enter estrus to attract males. In the model,

starting dates for estrus were assigned to non-weaning adult females on June 1st. The dates were distributed such that 30% started during the second half of June, 55% during the month of July and 15% during the first two weeks of August (approximated from [26]). Females were in estrus for 14 days [26] or until copulation took place. If a female was in estrus, the nearest adult male moved to her cell to copulate. Once copulation had occurred, they moved again to find food.

Update Food

The type of food bears eat during the year has been well studied [25], but the seasonal variation of the amount of food consumed is not as well documented. Nelson estimated the monthly variation in caloric intake [54]. A slightly modified version was used for the model (Table C.2). After movement, the corresponding amount of kilocalories was removed from the cell for each subadult and adult bear.

Update Food Reserve

Bear metabolic dynamics have been well documented [10, 28, 39, 50, 64, 66]. Because most of the data are on bears in the western United States, which have a more carnivorous diet, I do not attempt to model the weight of each bear. Fall caloric intake is vital for reproductive success; thus, the model collects the amount of kilocalories consumed during fall only. Calories were removed daily based on the following equation:

$$(3.2) \text{ } Cal_{total}(t) = Cal_{total}(t - 1) + 0.4 * intake(t) - (cost_{metabolic} + cost_{move}),$$

where $cost_{metabolic} = 142 \text{ kcal}$ [10, 25, 28, 64]. The value 0.4 corresponds to the proportion of the consumed kilocalories that are converted to stored fat, also in kilocalories. It should be emphasized that this was an approximation to capture the

general dynamics, not a specific estimate of actual kilocalories. Because of a lack of data on the actual metabolic cost of movement, I assumed $cost_{move} = 1000 \text{ kcal}$.

Mortality

There are numerous sources of mortality. Ideally, it would be best to explicitly model each type of mortality; however, limitations in understanding the mechanisms of these mortalities makes modeling them difficult. I restricted the model to three types of adult mortality: natural, harvest, and other.

Natural mortality included deaths due to illness and other non-interactive forms of mortality. This mortality was applied to every sub-adult and adult bear daily and was estimated to be 0.00002 per day [52]. Mortality due to old age was not assumed to be part of this type, therefore this natural mortality rate was constant for every individual. I assumed 20 years as a maximum age for bears and removed all bears that reached that age. This assumption was made based on limited data on the life expectancy of bears [89].

The “other” category incorporated poaching deaths plus other unknown sources of mortality. Poaching is difficult to estimate and was once considered to be a major source of mortality. However, poaching has likely declined in recent decades. The model assumed that the probability of poaching was greater outside federal lands. The probability was 0.0002 in GSMNP and national forests and 0.002 outside these areas (approximated from [52]). This mortality was implemented daily for all sub-adult and adult bears.

As mentioned previously, North Carolina and Tennessee have different hunting seasons. Each has a short bow season in the early fall that was not included because the harvest is negligible. Western North Carolina has a constant season across all counties, from late October into mid-November, followed by the last two weeks of

December. The Tennessee harvest season varies among counties, but I modeled the state season for all counties together; a one-week season at the end of September and a two-week season in early December.

Both states have a mosaic of bear sanctuaries where harvesting is prohibited (Figure C.7). Harvesting is also prohibited in GSMNP. Both states have a one bear bag limit per calendar year and only allow the harvesting of adult males and adult females without cubs [1, 17]. Each of these rules was incorporated into the model. Harvest rates were estimated at 12% for each state [52]. To estimate a daily harvest rate, I calculated the daily rate for each state corresponding to a 12% harvest. This resulted in harvest rates of 0.006 and 0.004 for Tennessee and North Carolina, respectively. These harvest rates were implemented daily during each of the respective hunting seasons.

Cubs were not subjected to the above mortalities. I assumed, however, that mortality of a mother would result in mortality of her cubs. Cub-specific mortality was modeled during the denning period and spring. If a female did not consume enough calories to endure the denning period and early spring, she lost her cubs. This was modeled by decreasing the stored calories during denning based on the following equation:

$$(3.3) \quad Cal(t) = Cal(t - 1) - cost_{metabolic} - 400 * cub_number,$$

where $cost_{metabolic} = 51 \text{ kcal}$. If $Cal(t) < 80,000 \text{ kcal}$, then all cubs were lost. As before, this equation was estimated from data [28], but it was used primarily to capture the dynamics of lactation costs of females.

Update State Variables

The update state variables function updated all the relevant state variables at the end of each day. These variables included age, denning days, estrous days, and weaning days. All the checks for timed variables occurred at this point. For example, if a female had mated, the gestation time was incremented by one. Once she reached the 220th day, she gave birth according to the probabilities mentioned in the next section.

3.3.2 Seasonal Life History Events

Denning

Hibernation is a common survival strategy employed by many large mammals to survive winters in which food is in low supply [95]. Winters in the southern Appalachian region are not as long or as harsh as in the western U.S., resulting in a short hibernation period of approximately three and a half months. Bears usually enter dens from early December through mid-January. Consequently, for the model, den-entry dates were randomly assigned so that 70% of females entered dens during the first two weeks of December and the remaining 30% during the last two weeks. Males entered uniformly from the last two weeks of December through the first half of January. Sensitivity analysis suggested that small deviations from these distributions did not affect the long-term population dynamics. The length of time bears den varies from year to year. In the model, females den for 110 days and males for 90 days [26]. These values were constant from year to year. Denning bears were not subject to harvesting or the “other” mortality function.

Some researchers have suggested that during years of hard mast failure, female bears will enter dens as early as mid-November. It has been hypothesized that they

do so because the metabolic cost of searching is greater than the cost of slowed metabolism during hibernation [42]. This phenomena was not modeled due to lack of data on what triggers this early denning.

Reproduction

Reproduction in black bears is characterized by three distinct phases: mating, birth, and weaning. Mating occurs during the summer between mid-July and early August. Primiparity in females is most commonly age three, although two-year-olds have been observed mating. Three years was the first age of reproduction in the model. Once copulation had occurred, a gestation timer was started for the pregnancy. A 220-day gestation was assumed [26] with all births occurring during the denning period.

There are conflicting data on the birth rate with two prevailing hypotheses:

- Females undergo delayed implantation; if they do not have enough fat reserves, fewer or no embryos implant in the uterus [68].
- All females give birth and the effects of low fat reserves (i.e., cub mortality) are manifested during the lactation period [91].

The latter was assumed, although the model can be parameterized to implement either scenario. There are other forms of cub mortality that are not well understood. To account for this additional mortality, the model assumed a 75% birth rate. Litter sizes varied from one to four cubs with the following probabilities: $P(1) = 0.2$, $P(2) = 0.4$, $P(3) = 0.3$, $P(4) = 0.1$ [26].

After den emergence, mothers weaned their cubs through the spring, summer, and the first part of fall. During the spring, the primary food source for bears are herbaceous plants, such as squawroot (*Conopholis americana*), which are generally

low in nutrition. Thus, spring is known as a negative foraging period [54]. Cub mortality via low calories available to their mothers was still considered during this time. Because mothers were not in hibernation, Equations 3.2 and 3.3 were used to account for the caloric decrease. Once summer began (June 1st), it was assumed there was enough food for cub survival and caloric intake was no longer recorded.

Cubs are with their mother throughout the year and den with their mothers the following fall. By this time, cubs are no longer weaning and have developed their own fat reserves, and therefore, are not a burden to their mothers during denning. To model this phenomena, cubs followed their mothers into denning and were abandoned the subsequent June 1st. These mothers were then assigned a new estrus date. All females that lost cubs, newborns or yearlings during the denning period (or spring) started estrus the following summer.

3.3.3 Model Implementation

The model was coded in C++ and compiled on a UNIX platform. The runtime for the model was approximately 20 minutes for a 23-year run. This was achieved on a Sun Enterprise 4500®, a 14 processor machine with 10 gigabytes of RAM. Due to the individual-based model design, runtime was dependent on the number of bears in the simulation. A typical model run involved 20 independent replications, each with different random number generator seeds. The resulting averages and 95% confidence intervals were used to present the data (except for the spatial maps in which one run was used to create the images). *PV – Wave*® visualization software was used to develop the graphs and images.

3.3.4 Alternative Management Strategies

Relative assessment analysis was developed by the Across Trophic Level System Simulation (ATLSS) research group to compare various model results for alternative hydrological scenarios for the Everglades restoration effort [21]. This involved developing a base scenario and comparing the model results for each alternative to that base. That method offers the potential to reduce the effects of uncertain model assumptions on the ranking of scenarios.

The base strategy for my analysis involved continuing the current harvest regime through the year 2023. I then compared those results to various alternative strategies outlined in Table C.3. Although not the only possible alternatives, they collectively address some of the management questions of interest in the area, which include the effectiveness of the sanctuaries, harvesting in GSMNP, and increasing harvest rates [89].

Each run started in 1980 and assumed current harvesting strategy through 2002. From 2003 - 2023 the alternative strategies were run. I resampled the mast data from the previous 20 years and chose a regime that captured enough variation to test the alternatives (Figure C.9); this is a projection to analyze the effects of the alternative strategies, not a prediction of future fall mast variation.

3.4 Results

3.4.1 Model Dynamics

Figure C.10 graph (A) shows the National Park Service (NPS) mast values from 1990 - 2002. There were two substantial mast failures, occurring in 1992 and 1997. Figure C.10 graph (B) shows model output for the total population of sub-adults and adults. The birth failures of 1992 and 1997 do not show up until two years later.

This is a result of only counting sub-adult and adult bears, as is standard practice in population estimation. High cub mortality in the fall of year (x) results in low cub survival in year ($x+1$). This cohort will not be seen in the data until it reaches subadult status in year ($x+2$).

Figure C.10 graph (C), cub mortality rate in GSMNP, shows the effects of mast failures on reproductive success. Figure C.10 graph (D) is the total number of potential bear-human encounters in a year. It was calculated by counting the number of bears in human populated cells each day from June through December. The peaks correspond to mast failure years, which cause bears to leave protected areas to find more food.

The model depicts the general dynamics of the system, not exact bear abundance estimates over time. However, the model values are similar to observed bear densities in the region. Figure C.11 shows comparisons between empirical data (dashed lines) and model output (solid lines). Graph (A) shows the GSMNP population. Model output compared favorably to Jolly-Seber model B [43, 74] estimates of the Park. In the model output there is a drop in the population immediately following each mast failure. This is due to the emigration of bears from the Park during the previous fall. The drop in the second year is the cohort effect described previously. Graph (B) compares Tennessee harvest data with the model. Because the model assumed a constant harvest rate, the model is not expected to capture all the dynamics associated with harvesting. The graph does suggest, however, that the model estimates the correct magnitude of the harvest. Peaks in the model data correspond to mast failure years because more bears would leave protected areas. The extremely high empirical harvest data in 1997 may be due to an increase in hunting effort [89]. Graph (C) shows a comparison with the western bear population in North Carolina. The data were obtained from the North Carolina Wildlife Resources Commission web page [17], which did not elaborate on estimation methods or provide error es-

timates. Therefore, I can only claim that the model suggests a similar growth rate as their data. Finally, graph (D) shows the model comparison with North Carolina harvest data. As with the Tennessee data, these harvest data have the same magnitude as the empirical data. Overall, I am confident that the model captures the general dynamics of the bear population in the region. A sensitivity analysis was performed on various parameters (Appendix B).

3.4.2 Scenario Comparisons

Figures C.12 and C.13 show the results of each scenario on the total population and potential bear-human encounters. Alt3 results in the greatest decrease in overall population size and the greatest reduction in potential bear-human encounters. Those results were expected because Alt3 involved the highest harvesting. Figure C.13 suggests that the five mast failure years result in the most potential encounters; therefore, I focused on those five years when comparing the scenarios. Table C.4 shows the numerical results of the total population at the end of the run and the potential encounters for the five fall mast failure years and their totals.

For a spatial perspective of the results, Figures C.14 - C.18 show a day in early November of a subregion of the model area. The subregion includes GSMNP, most of Nantahala National Forest, and the section of the Pisgah National Forest that is just west of Asheville, North Carolina, containing the Pisgah bear sanctuary. Figures C.14 and C.15 show the differences between an abundant mast year (2014) and a mast failure year (2016) with respect to bears in human populated areas (green regions). During the bad mast years, bears are immediately outside GSMNP. These are not meant to suggest exact numbers or locations of bears during mast failure years, only to represent a difference between abundant mast and mast failure years. Figure C.16 shows the effects of Alt2, harvesting in the sanctuaries and GSMNP,

for the same day in November and for the same mast failure year (2016). The double harvesting rate scenario, Alt3, results are shown in Figure C.17. Because this strategy continues to use the sanctuaries, their effect as source populations is more evident. Finally, Figure C.18 shows the results of the alternative sanctuary design scenario, Alt5. This alternative was the least effective in reducing overall potential bear-human encounters but did minimize the effects locally. For instance, there are fewer potential encounters near the Asheville area compared with the base scenario (Figure C.15).

Table C.5 shows the ranking of the alternative scenarios based on various objective functions. The first function ranks the alternatives based on their effects on the overall population. As a result, Alt5 provides the best strategy because it had the least effect. The second function is solely based on the effect on potential encounters. Alt3 ranks highest in this category because it most successfully reduced encounters. The third function compares the ratio of the percent difference in the overall population to the relative difference in potential encounters. This percentage-based approach results in the highest ranking for Alt5 with a one percent reduction in the overall population and seven percent reduction in encounters. Although this is the best ratio, the magnitude of the effects are not taken into account with this function. The last function accounts for the magnitude of the relative effects of the population by taking the difference of the relative differences. Alt6 provides the best scenario for that function.

3.5 Discussion

The objective functions given in Table C.5 are not the only possible criteria, but they do provide insight into the relationships among the different scenarios. Until computational techniques that allow for the determination of an optimal strategy

for IBMs are developed, it is best to test a variety of alternatives and objective functions. The information received from the various tests should be looked at collectively, and the best strategy (or strategies) should be analyzed further. Based on my results, Alt1, Alt2, and Alt6 varied the least between the rankings. Figures C.12 and C.13 suggest that these three alternatives are grouped relative to the others. If the goal is to find a balance between reducing potential bear-human encounters and reducing the overall population, these three scenarios potentially provide the best alternative harvesting strategies.

The practicality and ease of implementation of the strategies must also be considered. It is difficult to quantify such constraints, but they can be reasoned qualitatively. Alt2 requires the removal of bears from the GSMNP population every year and is, therefore, not practical. Alt6 requires the removal of bears from GSMNP only during mast failure years and a doubling of the harvest rate outside the Park. Because this would take place only a few times each decade, the removal of on the order of one hundred bears from the Park, not necessarily through harvesting, is possible. Outside of the Park, the actual implementation of an increased harvesting rate within a few weeks notice (fall mast availability can usually be estimated by mid-September) may be difficult. However, the concern of over-harvesting is minimized because that strategy maintains the sanctuaries during non-failure years. Alt1 would be the easiest to implement because it simply opens up the sanctuaries for harvesting. Although that strategy does not directly affect encounters resulting from the GSMNP population, it does address encounters in the other regions.

The importance of the local effects of potential encounters should be stressed. As in the case of Alt5, the overall decrease in encounters was minimal, but the local effects in the Pisgah bear sanctuary area were profound. Because the human population map has not been formally groundtruthed, I cannot make strategy decisions in specific towns or communities.

Various temporal variations of these scenarios might yield better results. The implementation of Alt3, for example, decreased the overall population too far to be considered, but it is possible that implementing Alt3 in 10-year cycles might be a possible strategy.

The two weakest elements in the model were movement and caloric dynamics. I did not attempt to model all bear movements explicitly. The movement rules in the model can be described as the effective movement dynamics for food consumption. Because there is substantial overlap in home ranges among black bears [88], the spacing limitations in the model seem to capture the general dynamics of movement.

The metabolic dynamics of reproductive females during fall are at best a generalization of the actual dynamics. The lack of data for black bears with similar diets and limitations in estimating mast availability required the simplifying assumptions. At some point between the onset of denning and early summer movements, substantial cub mortality can occur, especially after fall mast failures. The model seemed to capture the dynamics of this process. However, I could not determine when this mortality occurs, just the actual occurrence.

I have attempted to develop a methodology for comparing alternative management strategies using an individual-based model. The versatility of this modeling approach allowed for a variety of visualization options. The spatially-explicit nature of the model adds another powerful element to the comparisons of these strategies. The model framework is flexible enough to be adapted for other large, herbivorous or omnivorous mammalian species.

Chapter 4

What can Individual-Based Models Tell Us That We Don't Already Know: Insights for the Black Bear Population in Great Smoky Mountains National Park

4.1 Abstract

Gaps in data collection are one of the difficult issues wildlife biologists face in understanding the dynamics of species with long reproductive cycles and large ranges. Models, individual-based models (IBM) in particular, can be useful in giving insight into these gaps. IBMs involve modeling each individual organism throughout its life via a set of rules gathered from existing data. The advantage of this modeling technique is that one can output a multitude of information about the population. A

spatially-explicit IBM for the black bear population in the southern Appalachians is used to demonstrate some of the advantages of this methodology. Attention is focused on the Great Smoky Mountains National Park black bear population. One of the main environmental forces that affect black bears is fall mast. We demonstrate the ability of an IBM to give insight into the effects of mast from various demographic viewpoints. Many spatial and temporal representations of the population that cannot be developed empirically are displayed. We do not claim that IBMs can give accurate predictions, but rather they can provide researchers with a methodology to compare the importance of various factors and bring new insights into wildlife population dynamics.

Key Phrases: black bear, fall mast failures, Great Smoky Mountains National Park, individual-based models, wildlife population dynamics

4.2 Introduction

4.2.1 “All models are wrong, but some are useful” [8]

Box’s famous quote underscores much of the misunderstanding many wildlife biologists have regarding models. The benefits of modeling are only gradually being recognized in the field of wildlife biology. The issue of how useful model output is in obtaining reliable knowledge [69] has been a major concern in the wildlife community and has been debated for years [3, 58, 70, 75, 79]. Starfield [79] discussed many of the misconceptions of models, and since, there has been a slow trend towards greater acceptance of models as tools in wildlife management. Many models used in wildlife management have been developed to estimate intrinsic rates of growth and to make population projections [2, 5, 31, 38, 71]. Many of those models take the form of Leslie-type matrix models [14].

Modeling packages have given managers a user-friendly environment to experiment with modeling. These packages generally fall into two groups: population viability analysis software such as *RAMAS*[®] [76] and general dynamical modeling software such as *STELLA*[®] [77]. Although *RAMAS*[®] has been widely used in conservation biology, the source code is not available to users, which limits its flexibility [48]. *STELLA*[®] has established a strong base in ecology as an educational and research tool over the last 10 years [18, 19, 20]. Although it is useful for learning dynamical modeling, it has no explicit spatial utility. With the increase in the availability of GIS mapping tools, habitat index models have become more prevalent in the literature as well, but these fail to account for the population dynamics of the species [11, 90, 93].

The increase in computational power over the last decade has allowed the development of more sophisticated modeling techniques. One of those techniques is spatially-explicit individual-based modeling [23], which offers a methodology for incorporating GIS data and population dynamics. Spatially-explicit individual-based models can be used to expand the role of models from a tool to project population levels to one that helps fill gaps in data. I used this individual-based modeling technique to develop new hypotheses on the population dynamics of black bears by calculating population characteristics that are difficult or impossible to determine empirically. I present new insights on the Great Smoky Mountains National Park black bear population by using an IBM developed to analyze the effects of alternative harvesting strategies on potential bear-human encounters (chapter 3).

4.2.2 GSMNP Population

The black bear population of the southern Appalachians has one of the highest densities in North America. It is also one of the most studied large mammal pop-

ulations. For over 30 years, data have been collected on various aspects of the population [61]. Many insights have been gained from these data, particularly over the last 13 years. One of the key findings has been noting the magnitude of the effect of annual fall mast variation on reproductive success of females. It is hypothesized that during fall hard mast failures, females are not able to gain enough fat reserves to endure the cost of lactation. This causes significant decreases in cub production in years subsequent to fall mast failures.

Although other black bear populations in the U.S. feed on hard mast during the fall, not all are as dependent on its availability as the population in and around GSMNP. Bears in the western U.S. are able to consume large amounts of fish and other high protein content foods, whereas other populations in the eastern U.S. find corn and other crops on farm lands to compensate for a lack of mast. Southern Appalachian bears, however, must resort to campgrounds and encroaching suburban areas that surround GSMNP for alternatives to fall mast. Park officials have documented increased levels of nuisance bear activity during fall mast failures [57].

The question of a carrying capacity level for the black bear population in GSMNP also is of great interest [16, 89]. Because the GSMNP population cannot depend on other natural sources of food during fall, I hypothesized that fall mast variation dictates the carrying capacity of the population. As mast varies from year to year, so does the effective carrying capacity of the population. The model is also used to explore density-independent and -dependent relationships, which can lead to more effective population management.

4.2.3 Data Limitations

The collection of data on black bears is limited by many factors, including their shy and secretive nature, large home range sizes, rough terrain, and limited funding

[61]. These limitations affect both intra- and inter-year data collecting. I give three examples of how limited data affect our understanding of the black bear population in GSMNP.

One of the more important issues concerning the black bear population in the Park is determining population density. Current estimates are based on mark-recapture experiments that encompass approximately one-sixth of the Park area. The mark-recapture data have given some insight into the population density in the Park, but trap response biases are substantial. It is also believed that variations in fall mast impact subsequent summer sampling. Determining how these biases affect the data has yet to be explored.

The emigration of bears from GSMNP during fall mast failures causes significant problems for federal and state wildlife managers. Currently, nuisance bears are either translocated or euthanized. Determining emigration rates is of great interest to Park officials, but there are significant limitations to data collection. Radio telemetry has shown extensive fall movement of bears away from GSMNP, but the time and expense of collaring enough bears are prohibitive. Therefore, obtaining any reliable estimates of emigration rate is almost impossible. Along the same lines, bears marked during the summer mark-recapture sampling are occasionally harvested in Tennessee or North Carolina. This has re-enforced the hypothesis that GSMNP bears contribute to the harvest of each state. Again, because of a limitation in tagging opportunities, exact harvest rates for GSMNP bears cannot be easily obtained.

It would also be useful to have an understanding of the year-to-year fluctuations in population size. It has been shown that reproductive success is a function of fall mast variation [26]. Data on the reproductive dynamics of female black bears is limited by the times of the year in which field sampling can be done. Female bears are sampled during the denning period to establish reproductive status and

again in the summer during mark-recapture experiments. The den visits have been important to document the effects of mast failures on reproductive success. Those data have resulted in a firm understanding of the reproductive dynamics of female bears. Managers now know that mast failures tend to subsequently result in low cohort levels. However, it is not well understood how these demographic fluctuations affect the overall year-to-year population levels.

To capture these long-term, inter-year dynamics of the black bear population it is necessary to understand how the population responds to changes in fall mast [92]. The data available at present (1990 - 2002) reflect two hard mast failures, 1992 and 1997. Thirteen years of data and two mast failures limit the ability to make conclusions on the year-to-year fluctuations of the population, and it is impossible to perform empirical experiments of mast fluctuations over a large spatial scale. It would take many years of data to capture all the possible combinations of fall mast variability.

In this chapter, I use the individual-based model to address some of these issues. I compare the model to empirical data, estimate the native GSMNP bear harvest for each state, and analyze the within-year dynamics associated with mast. I also use the model to determine general principles of the effects of fall mast variation on population dynamics.

4.3 Methods

4.3.1 Model Description

The model area included the Great Smoky Mountains National Park (GSMNP), Cherokee, Pisgah, and Nantahala national forests, and most of eastern Tennessee and western North Carolina (Figures C.1 and C.2). The region was divided into

450 m x 450 m cells, which were labeled with a forest type (Figure C.6). Individual bears were modeled on a daily time step using a set of rules. A flow chart of the daily procedures is shown in Figure C.3. Individual bears were modeled throughout their lives, and various state variable information was recorded. State variables included age, sex, location, and denning and reproductive status. I included three types of mortality in the model: natural, harvest, and other. The “other” category included poaching and other unknown forms of mortality.

The dynamics of the black bear population in GSMNP were driven by fall mast variation. Fall mast failures occur every 4-6 years [44] and have a two-pronged effect on the population. First, the scarcity of mast during the fall foraging period causes an increase in emigration from the Park. The second effect is a decrease in female reproductive success due to a lack of nutrient reserves.

Movement in the model was based solely on food availability. During each time step, bears moved to the nearest cell with the most food. There was a maximum search distance for each day, and a maximum search range for each bear. If a bear reached its maximum range, it was recentered to that cell, which allowed long distance movements of bears across regions. The search distances and ranges were different for each sex with males able to search farther. The model assumed hierarchical movement rules: adult males had first choice in moving to a particular cell, adult females second, followed by sub-adult males and sub-adult females. If a bear could not find a “safe” cell, it was placed on a random cell at its maximum search distance.

Although cub survival during the denning period and early spring is dependent on the amount of fat reserves stored by females during fall, the mechanism by which this occurs is not well understood. One hypothesis is that bears undergo delayed implantation and do not implant the embryos if their fat reserves are too low [26]. Another is that most female bears give birth, and at some point during the

denning period, the cubs are lost [91]. Model assumptions were based on the latter mechanism, but both mechanisms can be parameterized to yield similar results.

Female fat reserves were modeled by calculating the amount of kilocalories mated females consume during fall, taking into account metabolic and movement costs. Mated females give birth during the early stages of denning. Once a female had cubs, kilocalories were removed from her stored reserves at rates estimated from data simulating lactation costs [28]. If, during the denning season or early spring, the reserve calories of a lactating female fell below a defined threshold, the entire litter of cubs died. This algorithm was designed to approximate the metabolic dynamics that occur during denning. I do not claim that I can predict the exact timing of cub mortality or the caloric dynamics of female black bears. Rather my intent was to capture the effects of fall mast variability on the dynamics of the black bear population in this region.

Although the model was designed to analyze the effects of alternative harvesting strategies on potential bear-human encounters for most of eastern Tennessee and western North Carolina, the model was well suited to specifically examine the GSMNP population. Because GIS map layers were used, I was able to focus on various subregions of the southern Appalachian region. That flexibility is one of the primary advantages of using spatially-explicit, individual-based models. The model was coded in C++ on a UNIX platform. For a more detailed description of the model, refer to Chapter 3.

4.4 Results

4.4.1 Model Comparisons to Data

Figure D.1 graph (A) (Tables and Figures for Chapter 4 are located in Appendix D) depicts the fall mast time series used for the comparison runs. The two mast failures in 1992 and 1997 are of particular interest. The model suggests a two-year effect of mast failures on the population (Graph (B)). Mast failures cause a substantial increase in the cub mortality rate (Graph (C)). One aspect of the black bear population that is of great importance in the region is the contribution of the GSMNP population to the other regions. Graph (D) shows the native GSMNP bears that have moved outside the Park. The spikes in 1993 and 1998 correspond to the emigration of bears from the Park due to mast failures. Not all these bears become nuisance bears; some move onto adjacent national forest land.

In addition to the model comparisons of Chapter 3 (Figure C.11), other, GSMNP specific, empirical data can be compared. Since 1981, National Park Service officials have conducted bait-station surveys to monitor black bear population trends. The survey consists of 30 lines with 10-15 bait stations. Each station consists of three cans of sardines, partially opened, left nailed or hanging on trees about 0.5 miles apart. All sites are checked exactly five days later to determine visitation by bears. Figure D.2 compares the model output for the GSMNP population and the proportion of bait stations that were visited by bears. Both suggest a two-year drop in the population following fall mast failures.

Figure D.3 compares model output to empirical estimates of female reproductive status during the denning period. These empirical data were collected during the latter end of the denning period and averaged eight samples per year. Because the model cannot accurately predict the exact timing of cub mortality and because

there are no available error estimates for the empirical data, I only expect the empirical data (*) to lie between the bars for each year.

When compared to available empirical data, the model seems to capture the general dynamics of the system. Comparisons of the model results with the Jolly-Seber model B [43, 74] estimates and the bait-station surveys indicate that the model produces a close approximation to the population abundance over time and a good fit to the dynamics.

4.4.2 Additional Output

Many of the hypotheses concerning the dynamics of the black bear population have been difficult to test empirically. Despite the lack of data, these hypotheses can be used as further tests of model performance. Likewise, model output can be used to test these hypotheses. In this sense, the model should be viewed as an experiment. Like any experiment, model results cannot conclusively determine the validity of any particular hypothesis.

Figure D.4 graph (A) depicts the GSMNP population at monthly intervals. Because the graphs represent sub-adult and adult bears, the spikes represent a new cohort of sub-adults entering the population. As expected, there is a two-year shift in the effect of mast on these cohorts. The mast failure in 1992 results in the lack of cubs in 1993, which, in turn, results in no sub-adults in 1994. Graph (B) shows the native GSMNP bear population outside the Park. The two large spikes represent the fall exodus of bears during the two mast failures. Graph (C) shows the total monthly movement (emigration - immigration) from the Park. The model suggests three major intra-annual movement events. The first spike represents the abandonment of yearling cubs in early summer and their subsequent search for safe areas away from older bears. The second spike represents the fall movements (note the

large peaks during the two failure years). The third event is a net immigration occurring during the spring.

The spatially-explicit format of the model allows for spatial images to be produced. Figures D.5 and D.6 show a spatial representation of bear locations. They depict snapshots of a day in early November of bear locations (cells with ≥ 1 bear) in an abundant mast year (1995) and a mast failure year (1992), respectively. The model clearly indicates an increase in emigration from the Park during fall mast failures as has been documented by Park officials [57]. The model can also be used to view the age structure of the population through time (Figure D.7). The graph suggests that mast failures in previous years can be inferred from low cohort levels.

Many managers are interested in knowing what proportion of the Tennessee and North Carolina harvests represent native GSMNP bears. Figure D.8 shows model results of harvest totals for each state and the number of native GSMNP bears that were harvested. Results suggest that approximately 20 percent of the state harvests include these emigrant GSMNP bears.

4.4.3 Generalized Mast Effects

I ran 30 iterations of 30-year runs with randomized mast index values that include a 20 percent chance of a failure (index = 1.0) and an 80% chance, uniformly distributed, for the other values (2.0, 3.0, and 4.0). The goal was to develop underlying principles about mast and various population characteristics that can be useful to managers.

Figure D.9 shows pooled data for each mast index value and the effects on GSMNP population size, change in population, cub mortality, and net annual movement (emigration - immigration) from GSMNP. Graph (A) shows the GSMNP population size as a function of the mast index of the previous year. With the exception

of a mast index of 2.0 vs. 3.0 ($p < 0.1$), each index value was significantly different from the others ($p < 0.005$). There also seemed to be a minimum carrying capacity for the population. Because fall mast failures do not mean zero mast levels, a minimum population size may be maintained [89]. Graph (B) suggests that the change in population can be negative or positive for each fall mast level with the largest reductions occurring during failures. Graph (C) suggests that cub mortality rates are high for failures and low for mast indices of 3.0 and 4.0, but index values of 2.0 encompass the entire spectrum. Graph (D) clearly shows a decrease in total annual movement from GSMNP as mast index values increase.

To explain the variance in graph (A) of Figure D.9, I ran the model with all abundant mast years (index value of 4.0) and all mast failure years (index value of 1.0) (Figure D.10). The graphs collectively suggest that after 3 successive mast failures, the population reaches a minimum carrying capacity of approximately 1,100 bears. The carrying capacity for the high mast index value appears to be near 3,800 bears. For continuous mast successes, it takes about 8-10 years to reach this level. One can infer that index values of 2.0 and 3.0 would correspond to carrying capacities between 1,100 and 3,800 bears.

I have shown why the maximum values for each index value in graph (A) of Figure D.9 are different, but to explain why the minimums are so similar, the year-to-year change in population size should be explored. Figure D.11 shows scatter plots of the data for each set of mast indices in graph (B) of Figure D.9. Graph (A) suggests a density-dependent effect on population change during mast failures. This accounts for the large variation in the data and explains why each of the minimum population sizes were so similar. We can also see that most of the negative change in population for higher mast index values is due to the effect of the index value of the previous year. This negative change is caused by a lack of new sub-adult cohorts entering the population.

For graph (C) of Figure D.9, I show a similar scatter plot as a function of population size (Figure D.12). Again, a density-dependent effect is apparent, especially in graph (B). This suggests that a mast index of 2.0 acts as a phase transition point for cub survival. By this I mean that cub mortality rates resulting from an index value of 2.0 are dependent on the population density. This phenomenon could be important in predicting cub mortality rates during years in which mast availability is average.

Finally, Figure D.13 represents the scatter plot of graph (D) in Figure D.9. As before, much of the variation is density-dependent, with the mast index of the previous year also playing a role. The linear relationship for mast failure years versus population size may provide managers with a metric to gauge the intensity of nuisance bear activity.

Variation in the results seems to be due to density-dependent (population size) and density-independent (previous mast year) effects. Although these plots cannot be used as exact predictors of mast effects on the population, they do provide an indication of relative changes in the population.

4.5 Discussion and Management Implications

The difficulties inherent in collecting data on secretive, K-selected species limits our understanding of population dynamics. The black bear population of GSMNP is one such species; only patchy knowledge exists of the dynamics of the black bear population in this region. In this chapter, I attempted to use a spatially-explicit, individual-based model to gain insight into the population dynamics of black bears.

Increases in computational power and availability of spatial data have allowed for the development of better models. One of the most powerful techniques is spatially-explicit individual-based modeling. The use of individual-based models

in wildlife biology is increasing as managers begin to understand their power and versatility.

The model's capacity for graphing various outputs was demonstrated by plotting regional harvest totals, age-structure, GSMNP emigration, and spatial location maps. The model suggested that 20% of the annual black bear harvest from each state included native Park bears. This value can be used as a benchmark for empirical studies.

The model has provided new insights into the relationship between fall mast variation and the dynamics of the black bear population. The model also demonstrated a two-year decrease in the population following fall mast failures. The model structure allowed a further analysis of the mechanisms behind this two-year effect. Fall emigration was responsible for the first year, whereas the lack of a new cohort resulted in the second-year decrease. This effect was suggested by bait-station surveys but not verified by Jolly-Seber population estimates, suggesting that the bait-station surveys may be capturing those dynamics better than the Jolly-Seber model. In future work, I will attempt to replicate the mark-recapture experiment in the model to determine what biases may occur in those estimates due to mast failures.

By replicating fall mast variation numerous times, I was able to develop relationships between fall mast and different aspects of the population, including population change, cub mortality rate, and annual net movement from the Park. The model provides managers with a method to estimate the possible effects of fall mast on the population from year to year.

The model structure lends itself to viewing various other demographic relationships that were not demonstrated in this paper. I hope to use the model to test various other hypotheses managers have proposed, such as the effects of soft mast variation. The model will answer other questions and spawn new ones. Although

complex, spatially-explicit individual-based models seem to offer a multitude of opportunities for wildlife management.

Unfortunately, conveying the usefulness of IBMs to managers will not be a trivial endeavor. The communication gap between modelers and managers is mostly due to the lack of user-friendly environments to demonstrate models. We chose the UNIX platform because of its efficiency. Twenty-three year runs currently take approximately 20 minutes to complete. However, many managers want PC-friendly graphical user interfaces (GUIs) to run these types of models. Many modeling packages give managers a false impression of the ease with which complex models can be adapted for commercial use. Often the limitations of these packages are not explained to managers, resulting in inappropriate development and application of models. Enhancing the communication between modelers and managers will be crucial before the models can be effectively applied in wildlife management.

Chapter 5

Conclusions and Future Directions

5.1 Metapopulation Model

The metapopulation model yielded interesting results with respect to how a protected national park and harvested national forest areas interact. The best solution for minimizing the flow of bears into the outer region was to harvest both the park and forest, irrespective of their degree of connectivity. In reality, this would be impossible to implement. When the park population was considered unharvestable, the interplay between the regions' connectivity and forest harvesting became evident. The optimal solution suggested that the forest population could be sustained with high harvest rates due to the flow of bears from the park population. When the connectivity of the two populations was placed in the objective functional and carrying capacity was allowed to vary periodically, the optimal solution was to vary the connectivity with the changes in carrying capacity.

There are many inherent limitations when attempting to describe a population with a single state variable. The advantage is the relative ease with which analytic expressions of optimal control in terms of ordinary differential equations can be

derived. Increasing the realism in the model also increases the complexity of the solutions. Computational power and an array of numerical techniques offers the ability to solve more complex sets of differential equations and other types of dynamical systems. Numerical simulations can be used to make the metapopulation model more realistic and offer more detailed conclusions about the system. The life history patterns of the black bear population suggest that a stage-structured population model or partial differential equation model would be appropriate alternatives. A cub, sub-adult, adult structure could lead to additional insights into the demographic effects of mast variation.

The spatial assumptions in the model were implemented for analytical convenience. It is not clear how changing the area-preserving assumptions on the forest population would affect the results. Given that the population was acting as a reservoir for emigrating bears from the park, removing the area restriction may just increase the optimal harvesting effort. Developing a more spatially realistic representation of the system to include the network of other sanctuaries can also be implemented numerically. This approach could give new insight into the effectiveness of the distance between and size of the sanctuaries.

5.2 Individual-Based Model

In general, the model performed well in capturing the dynamics of the system. Results of the IBM verified my hypothesis that removing the sanctuaries would be more beneficial in reducing potential encounters than costly in terms of reduction in the overall population. The model was able to provide insights on many of the unknown aspects of the population. The model suggested that two-year drops in the GSMNP population occur following mast failures. This phenomenon had not been captured by the Jolly-Seber estimates, but was suggested in the bait-station surveys.

The model may be used to reconcile the discrepancies between the bait-station survey data and the Jolly-Seber population estimates. In future work, I intend to use the model to replicate the mark-recapture experiments and attempt to evaluate potential biases associated with the Jolly-Seber technique.

Two of the weakest components of the model are movement and the corresponding feeding dynamics. Of the various components of bear movements, including home range surveying and simple random meandering, I only modeled the movement components associated with feeding. This assumption is simplistic, but the comparison with bait-station surveys suggests that the model may have captured the dynamics of the system remarkably well. Thus, the movement rules in place may be good enough that the increased computational effort and potential error associated with incorporating additional movement rules may not be warranted. The caloric dynamics that were developed to simulate the mechanism by which cub mortality occurs during denning also fit well with empirical data.

Many of the weaknesses of IBMs are associated with the lack of data on specific elements of the populations. These limitations result in mechanistic assumptions that can drastically affect the dynamics of the model. One weakness of the black bear data is the effect of soft mast variation. It has long been suspected that soft mast affects the population, but empirical studies have not been performed. A possible example of how soft mast can affect the system is provided by the empirical data from 1997. The harvest totals were nearly twice the normal levels in both States and have yet to reach those levels again. The summer of 1997 was a soft mast failure, which caused a disproportionate increase in the capture rate during the mark-recapture experiment, thus inflating the population estimates. I hypothesize that during that summer a larger number of bears left the Park and other protected areas. The fall happened to be a hard mast failure and resulted in additional movement into harvestable areas. This resulted in a greater than usual number of bears

available for harvest. The model can be adapted to test this hypothesis, and this is a goal for future work.

Currently the model is not easily implemented by other users. The trade-off with the efficiency of running on UNIX is that wildlife managers are unlikely to be familiar with the platform. It would be a worthwhile task to develop a user-friendly version of this code that can run under a *Windows*® platform and produce spreadsheet or *Arc View*® formatted output.

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Appendices

Appendix A

Chapter 2 Figures and Tables

Table A.1: Parameter values and bounds used in numerical results.

Parameter	Value/Bounds
P, F	$[0, 1]$
K	$(0, 1]$
r	0.15
m_p	$[0, 1]$
m_f	$[0, \sqrt{2} - 1]$
h_p	$[0, 1]$
h_f	$[0, 1]$
T	25

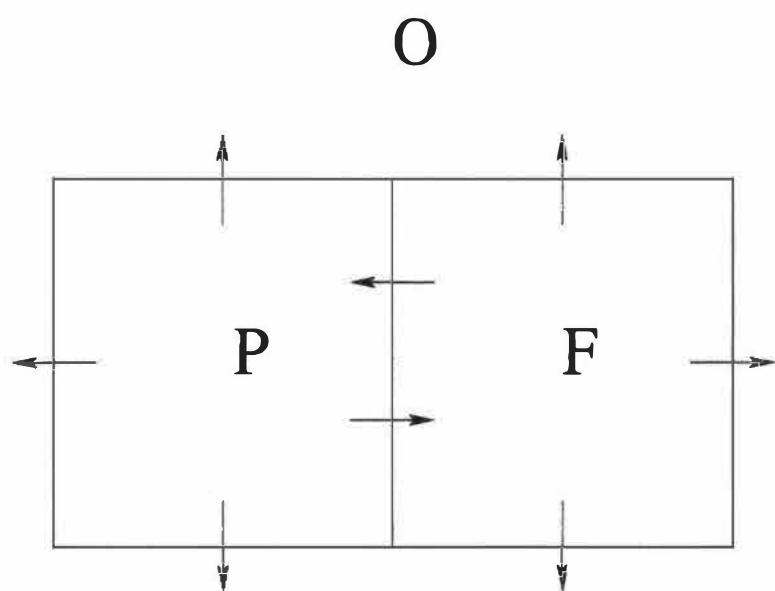
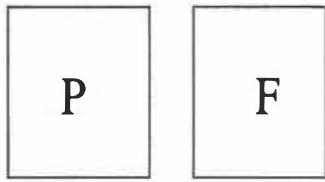
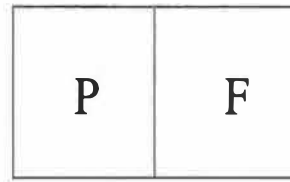


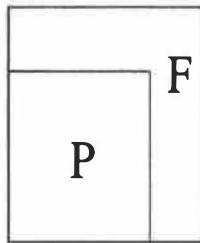
Figure A.1: Schematic representation of modeled regions.



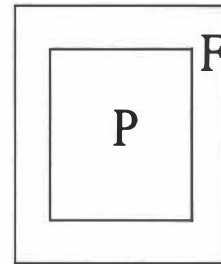
A) $m_p = 0 = m_f$



B) $m_p = 0.25 = m_f$



C) $m_p = 0.5, m_f = 0.353$



D) $m_p = 1, m_f = 0.453$

Figure A.2: Examples of region orientations given geometrical assumptions.

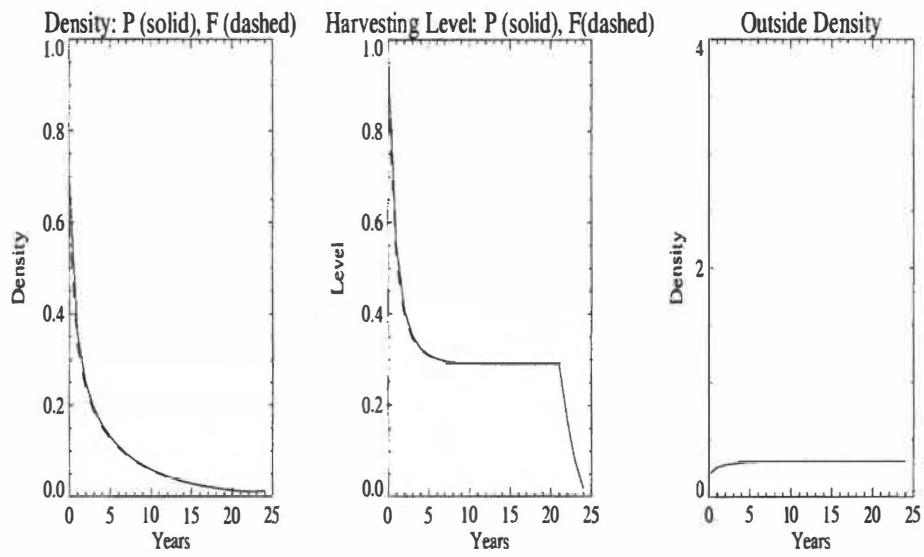


Figure A.3: Optimal harvesting strategy with $c_p = c_f = 1$ for both populations. In the first two plots, the solid line indicates the Park population and the dashed line indicates the Forest population.

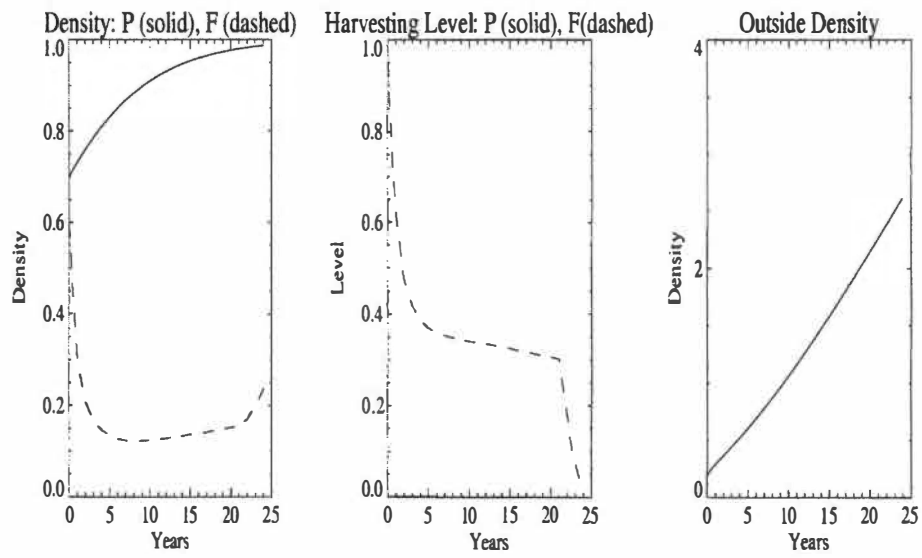


Figure A.4: Optimal harvesting strategy with $c_p = 10,000$ and $c_f = 1$. In the first two plots, the solid line indicates the Park population and the dashed line indicates the Forest population.

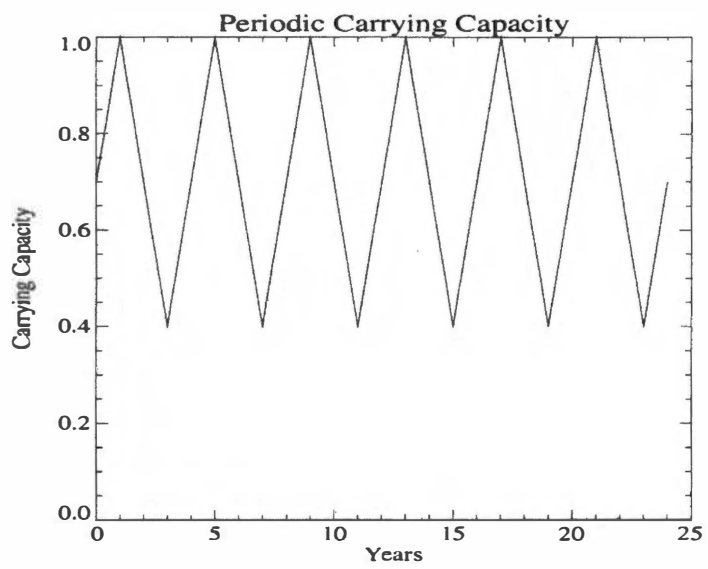


Figure A.5: Time series variation in carrying capacity.

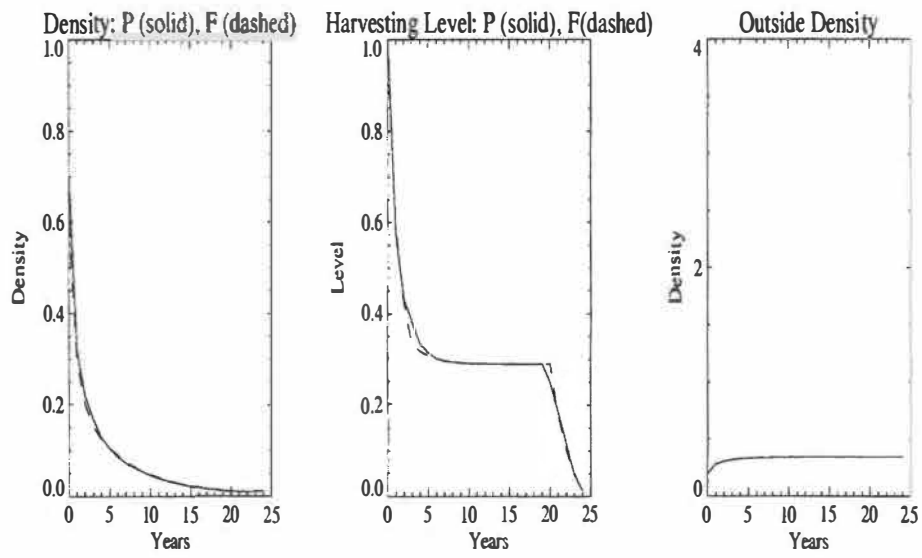


Figure A.6: Optimal harvesting strategy with varying carrying capacity and $c_p = c_f = 1$. In the first two plots, the solid line indicates the Park population and the dashed line indicates the Forest population.

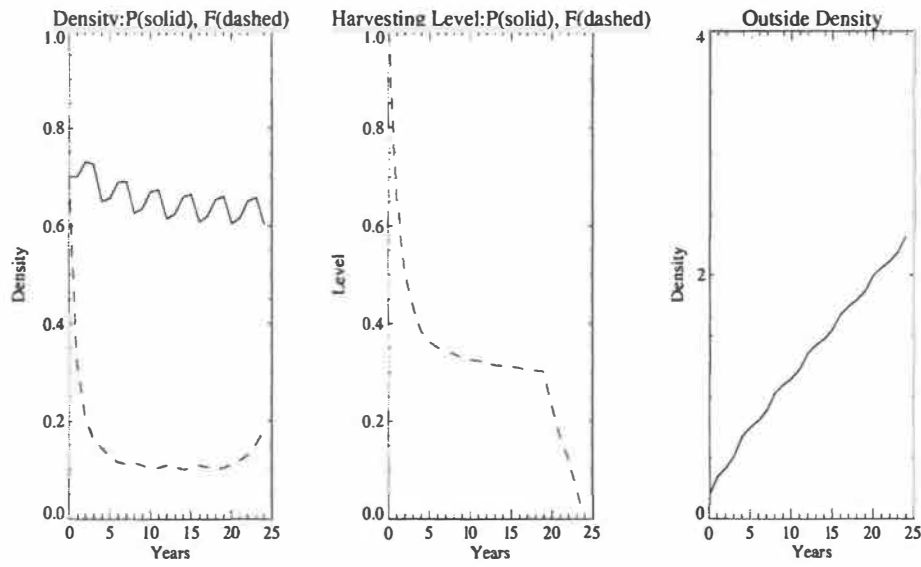


Figure A.7: Optimal harvesting strategy with varying carrying capacity and $c_p = 10.000$ and $c_f = 1$. In the first two plots, the solid line indicates the Park population and the dashed line indicates the Forest population.

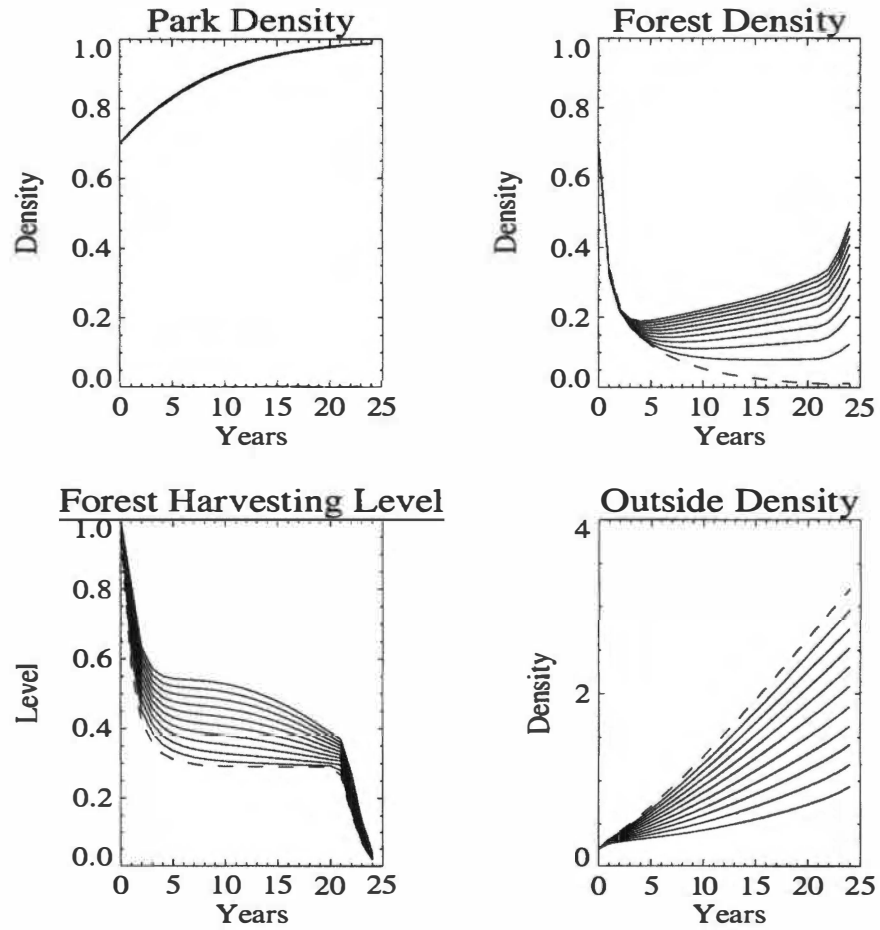


Figure A.8: Optimal harvesting strategy for different values of m_p . Dotted line is $m_p = 0$. Each successive solid line is an increment of 0.1 ($c_p = 10,000$ and $c_f = 1$).

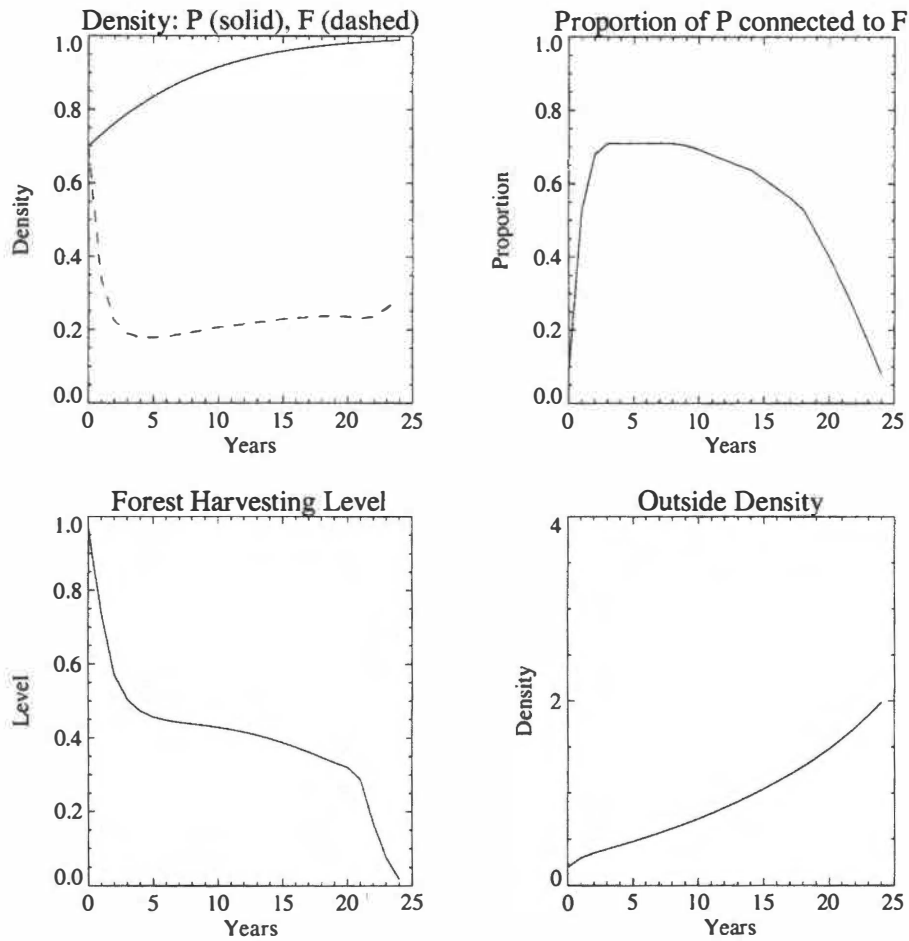


Figure A.9: Optimal harvesting and forest layout strategy ($c_m = c_f = 1$). Dashed line in upper left graph represents the Forest population.

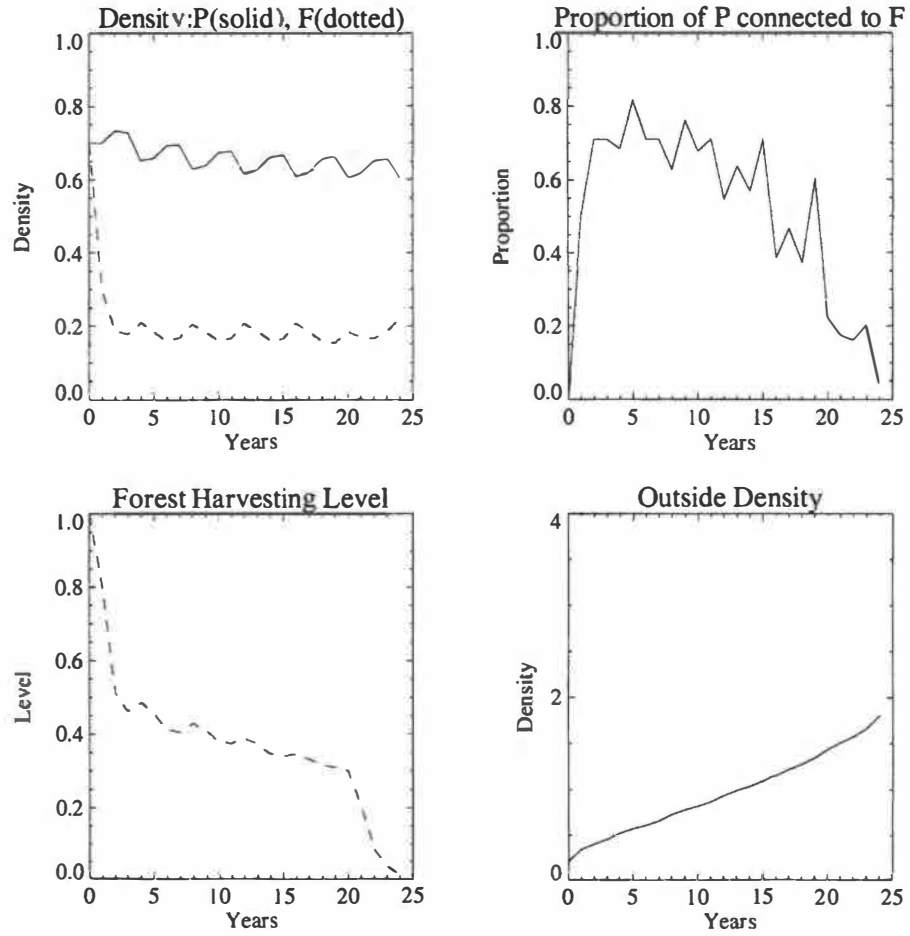


Figure A.10: Optimal harvesting and forest layout strategy with varying, synchronous carrying capacity ($c_m = c_f = 1$). Dashed line in upper left graph represents the Forest population.

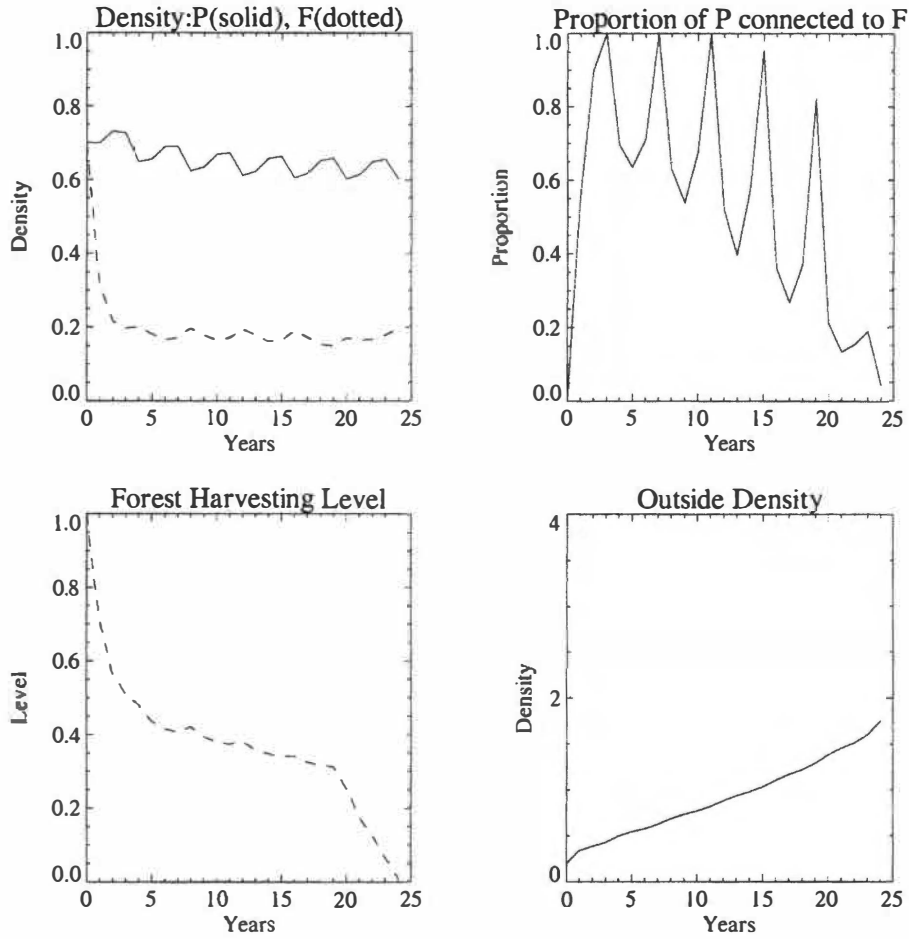


Figure A.11: Optimal harvesting and forest layout strategy with varying, asynchronous carrying capacity between regions ($c_m = c_f = 1$). Dashed line in upper left graph represents the Forest population.

Appendix B

Individual-Based Model Sensitivity Analysis

For each analysis, 20 replications with different random number generator seeds were run. I used the GSMNP population size to compare parameter sensitivity. Average relative error (described in figure legends) was used to determine the magnitude of sensitivity.

B.1 Initial Population Size

The IBM starts with an initial population size of approximately 1,250 bears. The model was run with initial population sizes of 1,000 and 1,500 bears and compared with the default value in Figure B.1. Over the 13-year period (1990 - 2002) in which data were collected, the alternative initial conditions resulted in less than a 5% change in the population. The dynamics of the population were not affected.

B.2 Birth Rate

Because births occur early in the denning period, empirical data are difficult to obtain. A conservative birth probability of 0.75 is used in the model. It is assumed this value takes into account all cub mortality not due to female Caloric status. Figure B.2 shows a comparison with a probability of birth equal to 1.0. This resulted in an approximately 10% increase in the population, but similar dynamics.

B.3 Energetics

In modeling the effects of fall mast failures on the reproductive success of females, a metric was established to track female Caloric reserves. Although the daily consumption and metabolic and lactation costs were based on published data, some of the data were based on approximations. In particular, the daily consumption rates

by Nelson [54] are controversial [37]. Figure B.3 tests the sensitivity of the model to different consumption values. The default daily consumption rates for fall are shown in Table C.2. These rates correspond to an average of approximately 11,000 $\frac{\text{Cal}}{\text{day}}$. The model was run with four other rates: 9,000, 10,000, 11,000, and 15,000. It was assumed that the rates were constant throughout the fall. The results show that 9,000 $\frac{\text{Cal}}{\text{day}}$ leads to an essentially constant but low population size in which fall mast does not determine the population size. Also, a constant consumption rate of 11,000 $\frac{\text{Cal}}{\text{day}}$ was indistinguishable from the default rates. A counter-intuitive result occurred with a consumption rate of 15,000 $\frac{\text{Cal}}{\text{day}}$. The population decreased, on average, by 2%. This decrease was due to density-dependent effects on the population because of greater cohort levels.

The female Caloric reserve threshold value used to determine cub mortality during lactation was not based on empirical data. I assumed a threshold value of 80,000 kcal. Figure B.4 shows results with 60,000 and 100,000 kcal threshold values. The results show an almost uniform effect on the population. Because the dynamics of the population were not affected by relatively large changes of this threshold value, the cub mortality mechanism in the model may be considered robust.

B.4 Movement

Movements in the individual-based model were based only on food availability. Bears moved to the nearest cell with the most food. There are two major components to this movement: daily movement range and interspecific interactions.

The default values for movement range were a 4-cell radius for males and a 2-cell radius for females. Figure B.5 compares the default values to 3 other sets of ranges. The effects of the changes were only seen during the mast failure of

1992. This was the first failure in which the population size was large enough to be significantly affected. Female movement range was the most sensitive parameter. After the 1992 mast failure, the population of female bears was reset to a density that was “stable” for the new movement parameters. The effects of mast variation were still present.

In modeling interspecific interactions the model assumed a “safe” cell radius in which a bear can move into a cell. Figure B.6 compares the default values with two other spacing scenarios. The figure suggests that the model is highly sensitive to the female interaction value. There was a 25% drop in the population when the female interaction value was equal to 1. This increased spacing forced more females to emigrate from the park. This reduction in female bears resulted in a decreased effect of mast variation on the population. Because data supports the smaller territorial association of female bears, the default assumptions seem to provide good representations of the system.

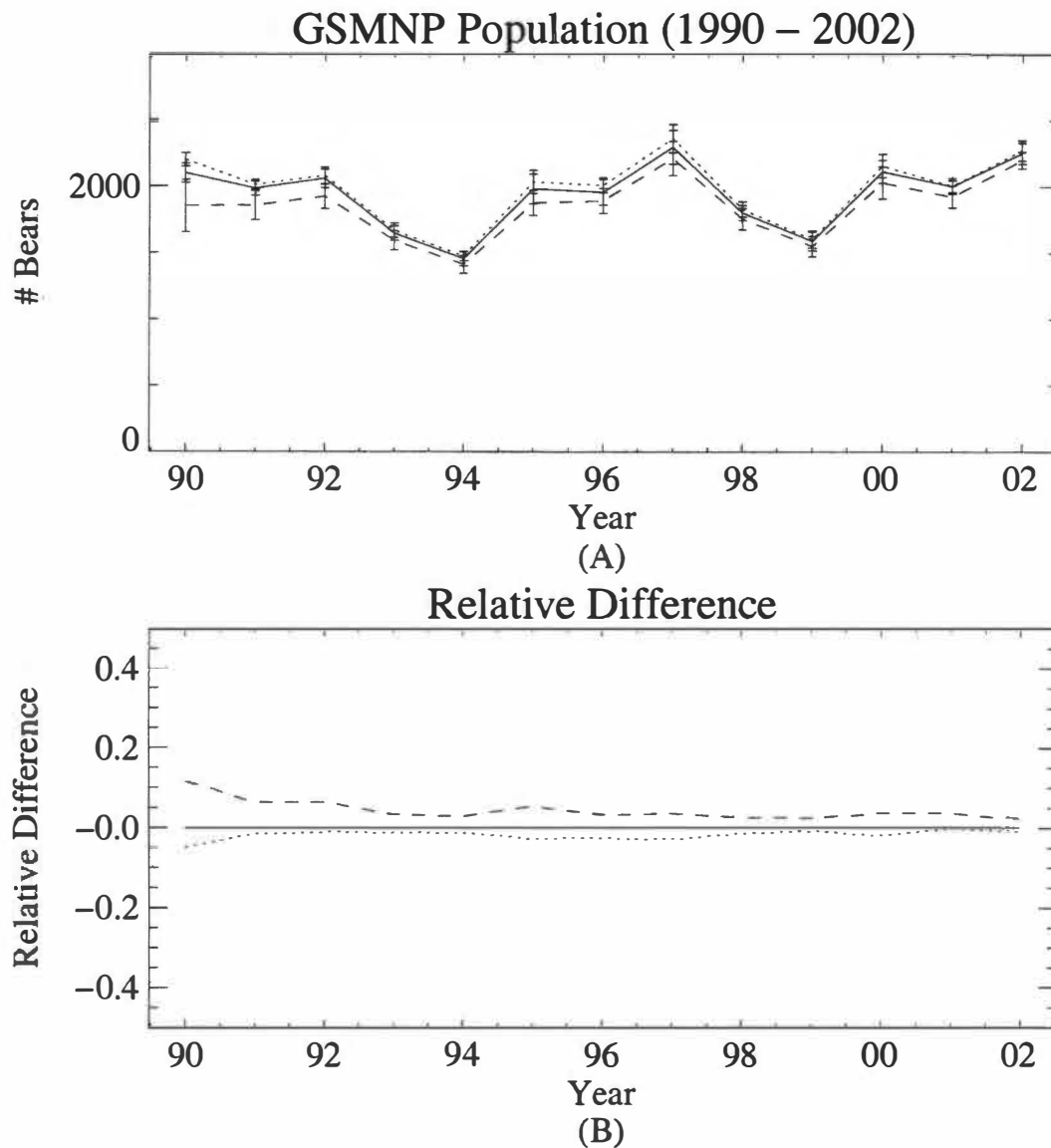


Figure B.1: Sensitivity analysis for initial population size (solid line indicates default model value): 1,000 (- - -), 1,250 (—), and 1,500 (····). (A) GSMNP population, error bars indicate 95% confidence intervals. (B) Relative difference for each different value compared with the default value $\left(\frac{\text{default} - \text{change}}{\text{default}}\right)$. Average relative difference: 0.045 (- - -), -0.018 (····).

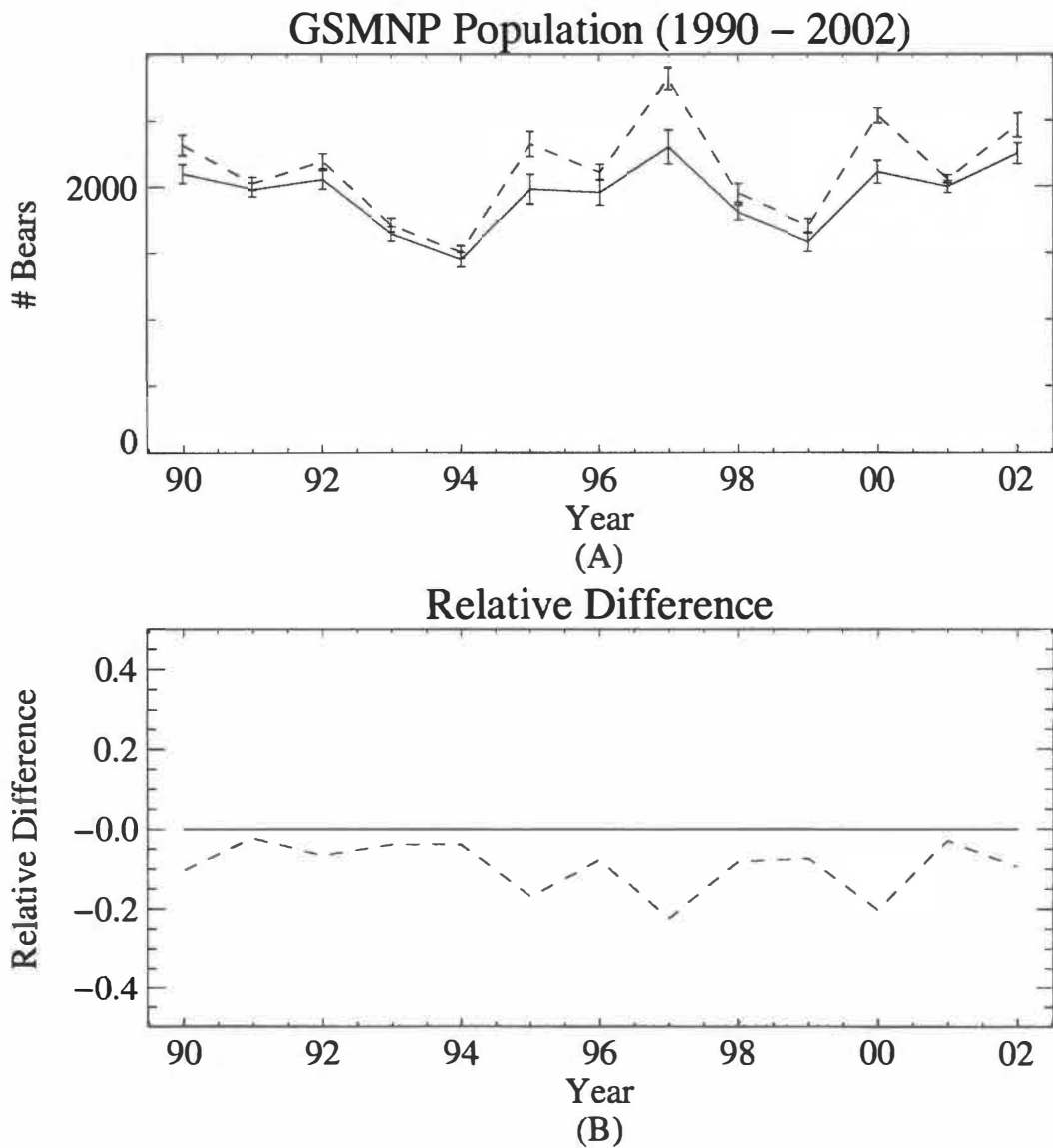


Figure B.2: Sensitivity analysis of successful birth probabilities (solid line indicates default model value): 0.75 (—) and 1.00 (- - -). (A) GSMNP population, error bars indicate 95% confidence intervals. (B) Relative difference for each different value compared with the default value ($\frac{\text{default} - \text{change}}{\text{default}}$). Average relative difference: -0.094 (- - -).

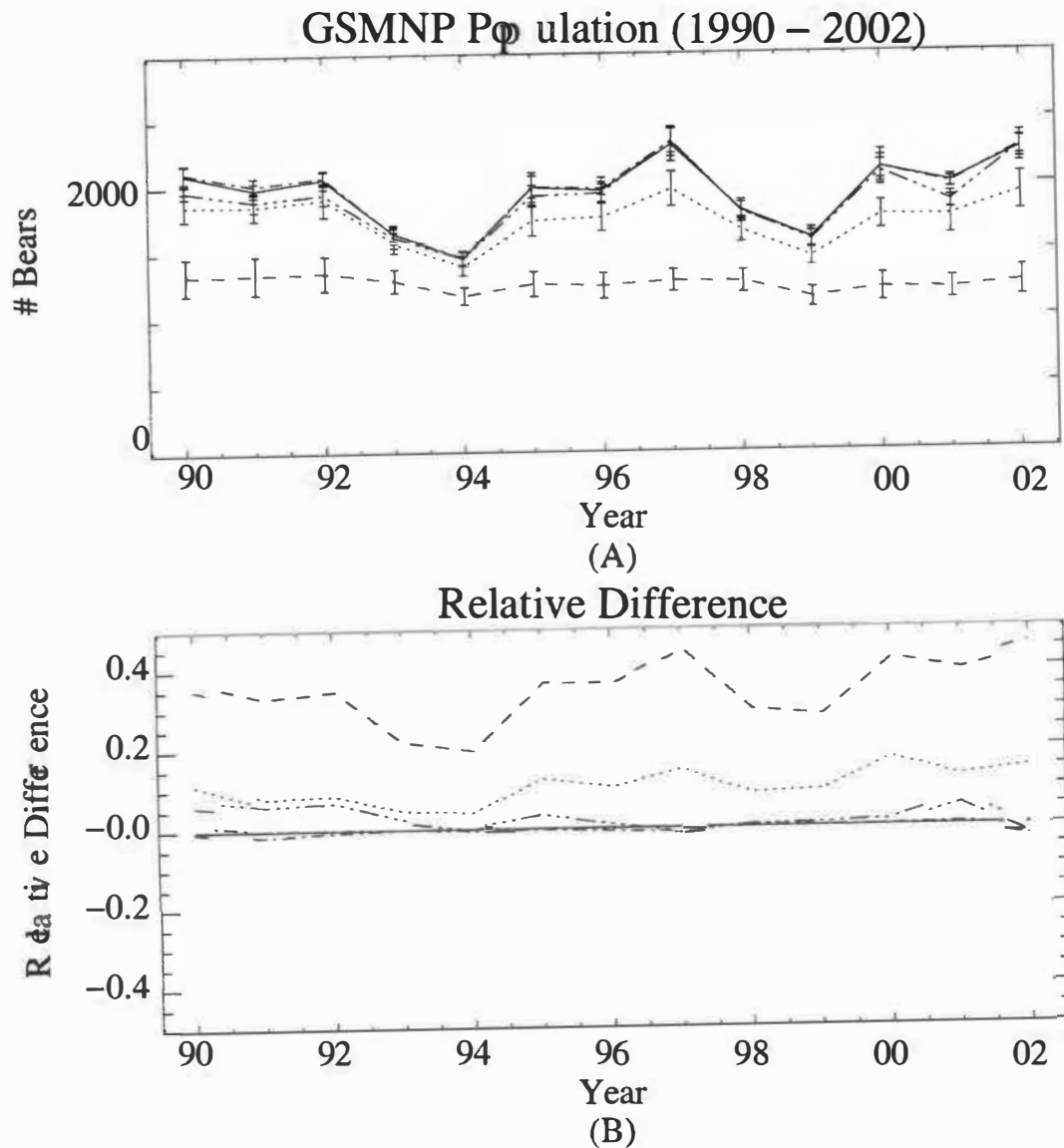


Figure B.3: Sensitivity analysis of fall feeding rates ($\frac{Cal}{day}$). Default feeding rates (—) are: Sept. = 8,000, Oct. = 10,000, Nov. = 15,000, and Dec. = 10,000. Other runs assume constant feeding rate throughout fall: 9,000 (---), 10,000 (····), 11,000 (- · - ·), and 15,000 (- · · · -). (A) GSMNP population, error bars indicate 95% confidence intervals. (B) Relative difference for each different value compared with the default value ($\frac{d \text{ population}}{d \text{ feeding rate}}$). Average relative difference: 0.344 (---), 0.100 (····), 0.004 (- · - ·), and 0.023 (- · · · -).

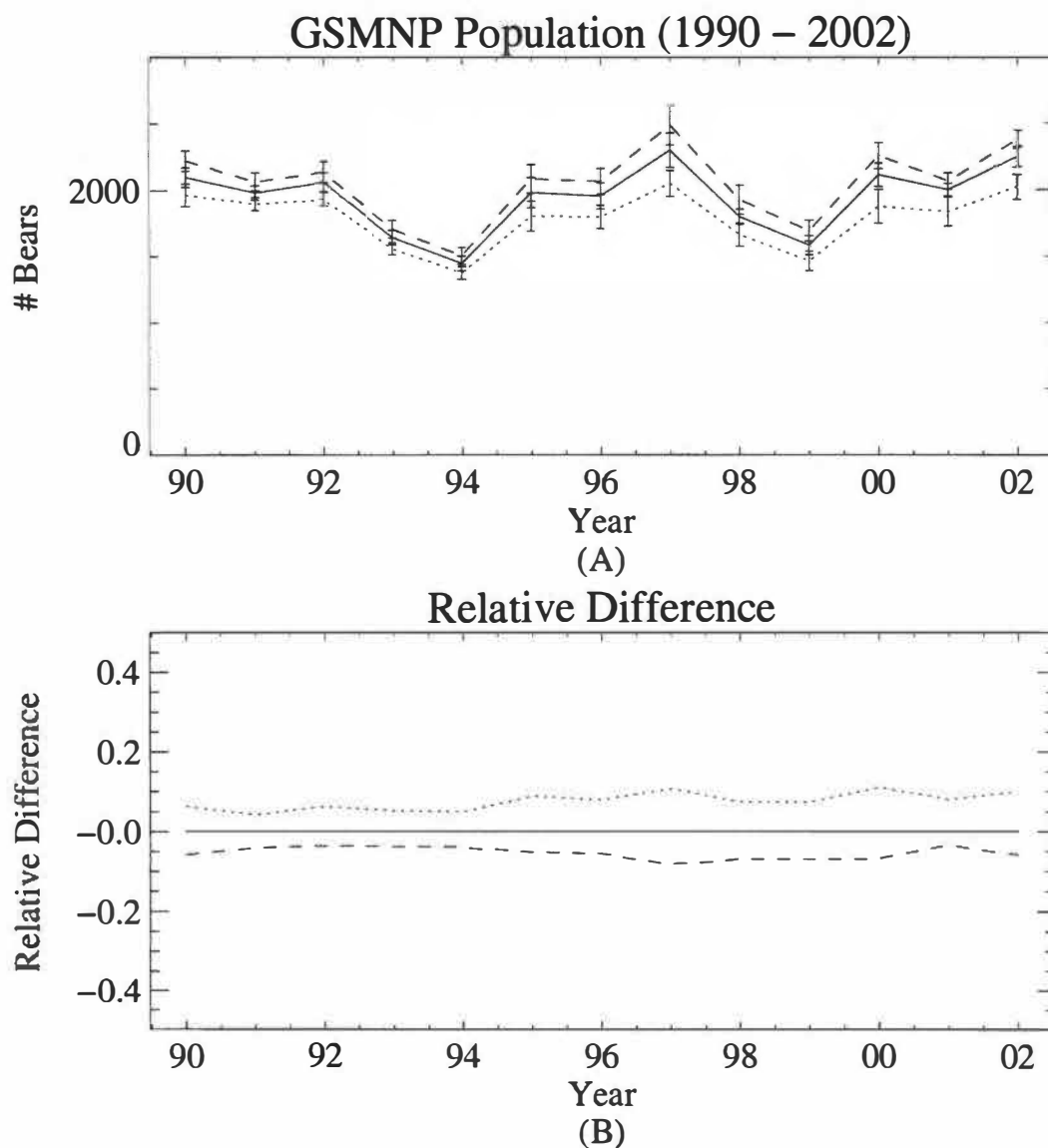


Figure B.4: Sensitivity analysis of female caloric reserve threshold (solid line indicates default model value): 60,000 (---), 80,000 (—), and 100,000 (····). (A) GSMNP population, error bars indicate 95% confidence intervals. (B) Relative difference for each different value compared with the default value $\left(\frac{\text{default}-\text{change}}{\text{default}}\right)$. Average relative difference: -0.054 (---), 0.076 (····).

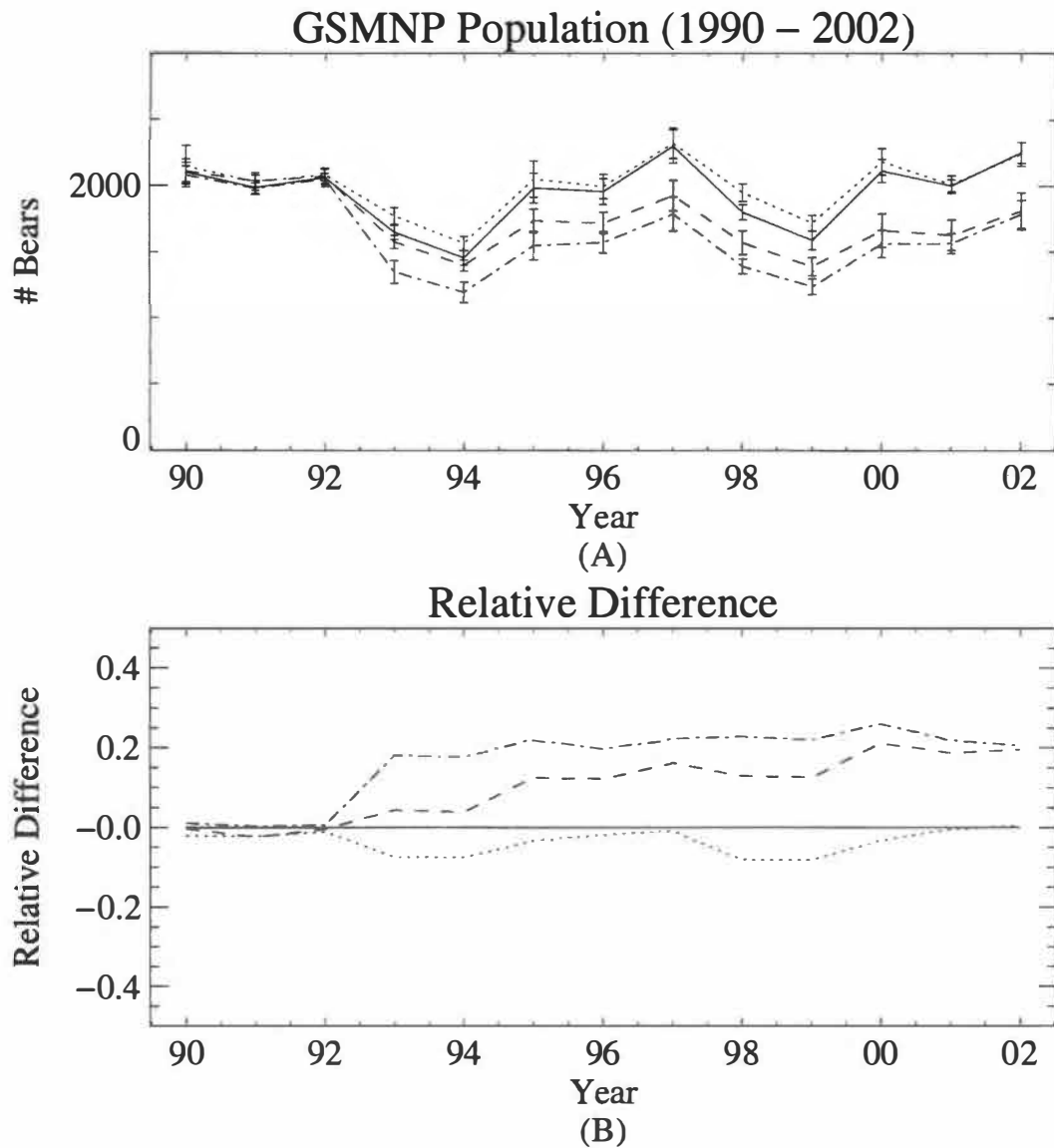


Figure B.5: Sensitivity analysis of daily movement ranges (solid line indicates default model values): Male = 4/Female = 2 (—), Male = 2/Female = 4 (- - -), Both = 2 (····), and Both = 4 (- · - ·). (A) GSMNP population, error bars indicate 95% confidence intervals. (B) Relative difference for each different value compared with the default value $\left(\frac{\text{default} - \text{change}}{\text{default}}\right)$. Average relative difference: 0.100 (- - -), -0.036 (····), and 0.165 (- · - ·).

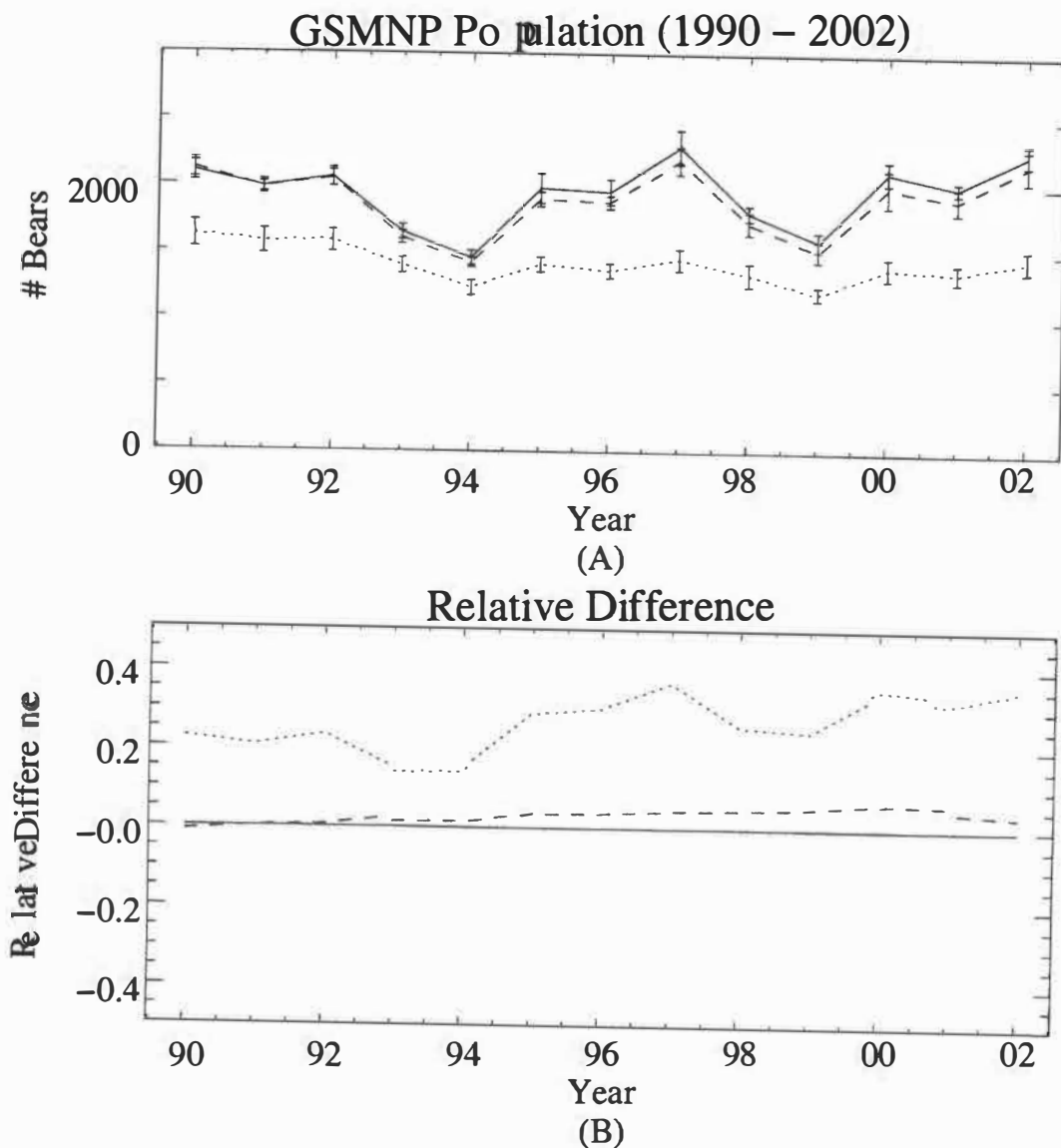


Figure B.6: Sensitivity analysis of interaction conditions. Values correspond to “safe” cell radius from dominant bears (solid line indicates default model values): Male = 1/Female = 0 (—), Both = 0 (---), and Both = 1 (····). (A) GSMNP population, error bars indicate 95% confidence intervals. (B) Relative difference for each different value compared with the default value $\left(\frac{\text{default} - \text{change}}{\text{default}}\right)$. Average relative difference: 0.031 (---) and 0.264 (····).

Appendix C

Chapter 3 Figures and Tables

Table C.1: Maximum calories (x1,000) available per cell for each month and vegetation type.												
Veg. Type	Jan.	Feb.	Mar.	Apr.	May	Jun.	Jul.	Aug.	Sep.	Oct.	Nov.	Dec.
None	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Spruce Fir	0.00	0.00	100	100	100	0.00	0.00	891	3,080	607	0.00	0.00
N. Hardwood	0.0.0	0.00	100	100	100	0.00	81.0	526	1,880	769	547	344
C. Hardwood	0.00	0.00	100	100	100	6480	830	324	5,060	5,630	4,780	3,360
Mesic Oak	0.00	0.00	100	100	100	81.0	283	405	3,680	4,050	202	0.00
Mix. Mes. Hardwood	0.00	0.00	100	100	100	486	405	445	4,330	4,620	3,640	2,430
Tulip Pop.	0.00	0.00	100	100	100	324	101	182	1,090	1,540	1,300	810
Xeric Oak	0.00	0.00	100	100	100	162	405	405	2,100	2,790	1,860	972
Oak-Pine	0.00	0.00	100	100	100	162	562	567	1,540	1,780	1,380	648
Pine	0.00	0.00	100	100	100	324	324	324	1,820	2,390	1,620	963

Table C.2: Rate of consumption of black bears for each month of the year.

Month	Rate of Consumption ($\frac{\text{Cal}}{\text{day}}$) per Bear
Jan.	0
Feb.	0
Mar.	0
Apr.	1,000
May	2,000
Jun.	4,000
Jul.	5,000
Aug.	6,000
Sep.	8,000
Oct.	10,000
Nov.	15,000
Dec.	10,000

Table C.3: Alternative harvesting strategies.

Scenario	Description
Base	Current harvesting regulations and sanctuaries
Alt1	Current harvesting rules, but with no sanctuaries (except GSMNP)
Alt2	Same as Alt2, but with addition of GSMNP hunting season
Alt3	Doubling of harvest rate with original sanctuaries
Alt4	Current harvesting rules, but with sanctuary harvest during fall mast failure years
Alt5	Current harvesting rules, but with a different sanctuary design (Figure C.8)
Alt6	Similar to Alt4 with the exception that during years of fall mast failures: (1) the harvesting rate is doubled and (2) the GSMNP season in Alt2 is added

Table C.4: Comparison of outputs for each scenario including: Total population at the end of the run and the number of potential bear-human encounters for each of the mast failure years. Superscripts indicate level of significant difference between the base scenario and each alternative.

Scenario	Total Pop. in 2023	Potential Bear/Human Encounters for Mast Failure Years (x1,000)					
		2004	2010	2011	2016	2022	Total
Base	13,300 ± 464	32.5 ± 4.6	54.4 ± 3.8	40.8 ± 3.1	49.2 ± 4.9	66.6 ± 5.5	244 ± 10
Alt1	11,100 [†] ± 443	30* ± 4.7	40.3 [†] ± 6.3	31.2 [†] ± 5.7	34.0 [†] ± 3.3	44.8 [†] ± 4.8	180 [†] ± 11.3
Alt2	9,680 [†] ± 449	28.5 [°] ± 4.9	34.9 [†] ± 6.6	27.4 [†] ± 3.9	28.6 [†] ± 3.9	36.3 [†] ± 4.1	156 [†] ± 10.8
Alt3	7,740 [†] ± 263	26.3 [†] ± 3.7	26.8 [†] ± 3.8	18.0 [†] ± 2.8	19.2 [†] ± 2.3	23.6 [†] ± 2.9	114 [†] ± 7
Alt4	12,600 [†] ± 323	30.5 ± 5.4	50.1 [°] ± 6.3	36.0 [†] ± 3.7	42.8 [†] ± 3.3	59.1 [†] ± 5.3	218 [†] ± 11.2
Alt5	13,000* ± 302	30.2* ± 4.9	49.7 [°] ± 7.0	38.8* ± 4.5	46.2* ± 5.4	62.1 [°] ± 2.1	227 [†] ± 11.8
Alt6	10,700 [†] ± 329	28.4 [°] ± 4.5	42.5 [†] ± 3.6	23.2 [†] ± 2.5	26.4 [†] ± 2.3	39.8 [†] ± 4.3	160 [†] ± 7.8

* = $p < 0.05$, ° = $p < 0.005$, † = $p < 0.0005$ (when compared to the base scenario)

Table C.5: Various rankings of the alternative harvesting scenarios. $\% \Delta P$ = relative change in population size between the base ($Base$) and each alternative (Pop_{Alt_i}), $i = 1..6$. $\% \Delta E$ = relative change in potential encounters between the base (Enc_{Base}) and each alternative (Enc_{Alt_i}), $i = 1..6$.

Rank	Objective Functions			
	Max. Pop.	Min. Enc.	Min. ($\% \Delta P : \% \Delta E$)	Max. ($\% \Delta E - \% \Delta P$)
1	Alt5	Alt3	Alt5 (0.01:0.07)	Alt6 (0.15)
2	Alt4	Alt2	Alt4 (0.04:0.10)	Alt3 (0.12)
3	Alt1	Alt6	Alt6 (0.19:0.34)	Alt1 (0.11)
4	Alt6	Alt1	Alt1 (0.15:0.26)	Alt2 (0.10)
5	Alt2	Alt4	Alt2 (0.26:0.36)	Alt4 (0.06)
6	Alt3	Alt5	Alt3 (0.41:0.53)	Alt5 (0.05)
$\% \Delta P = \left(\frac{Pop_{Base} - Pop_{Alt_i}}{Pop_{Base}} \right)$ and $\% \Delta E = \left(\frac{Enc_{Base} - Enc_{Alt_i}}{Enc_{Base}} \right)$				

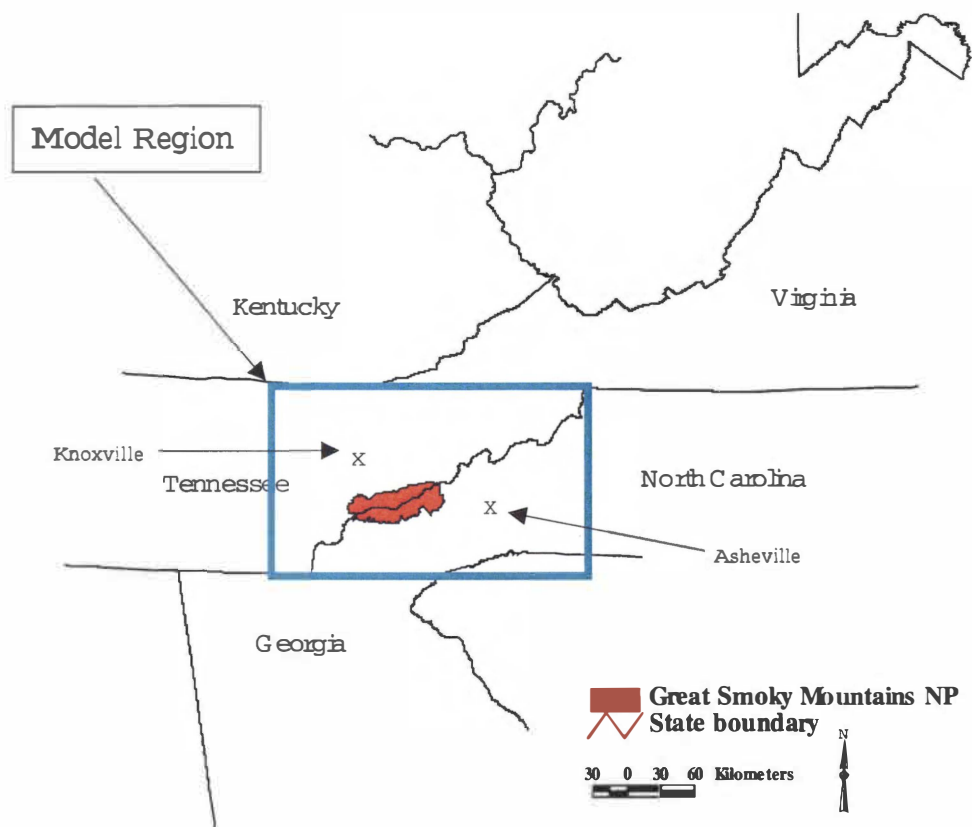


Figure C.1: Study region for the individual-based model.

Region Map

Great Smoky Mountains National Park

Cherokee National Forest

Pisgah National Forest

Nantahala National Forest

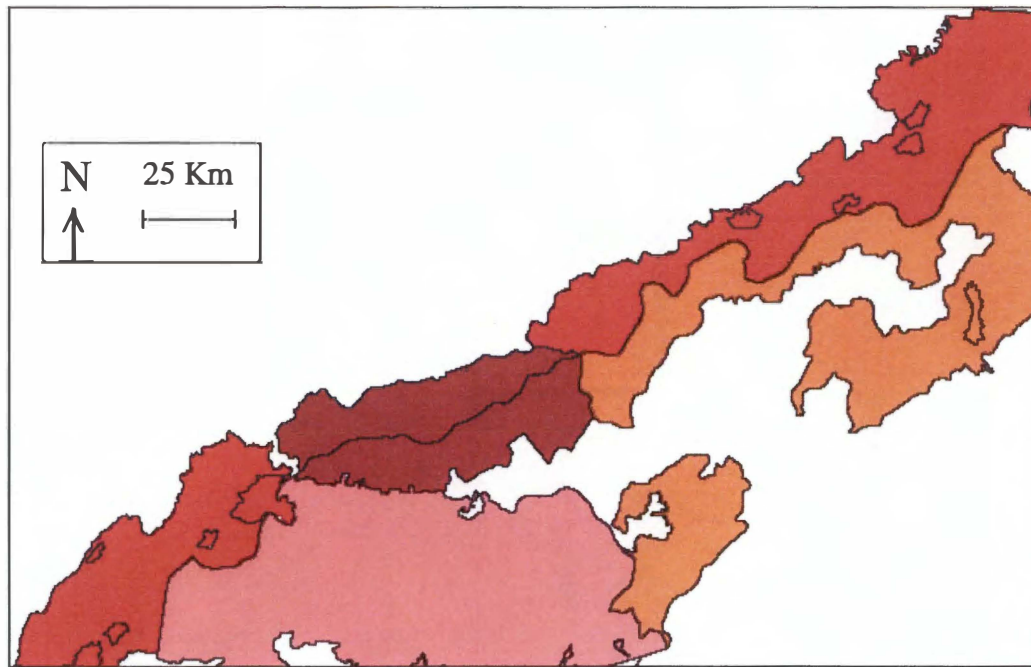


Figure C.2: Region map for the southern Appalachian region.

Daily Model Functions

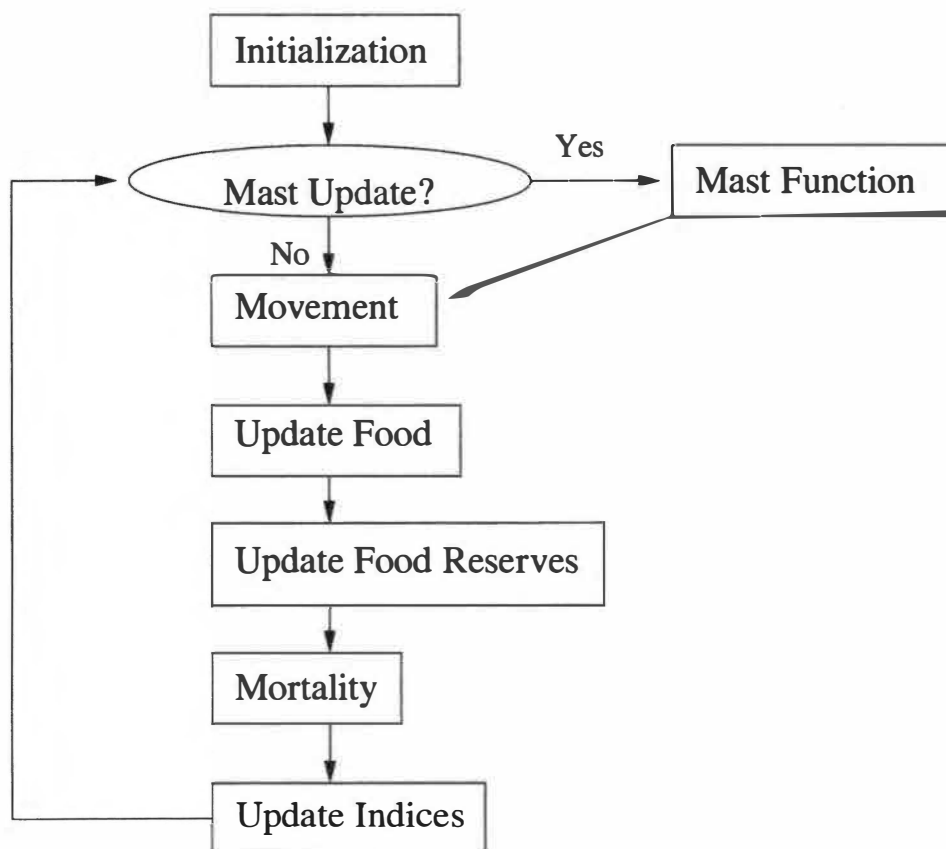


Figure C.3: Daily model functions.

Human Population Map

People/Km² < 10 and/or Bear Sanctuaries

11 < People/Km² < 20

Major Roads in white

21 < People/Km² < 100

Park/Forest Boundaries in black

People/Km² > 101

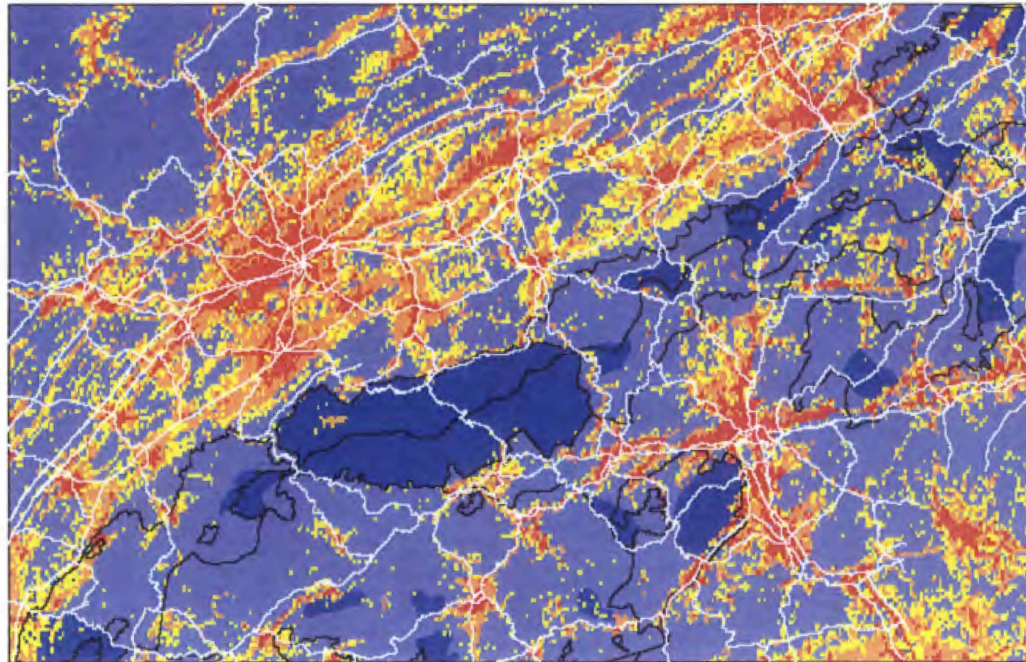


Figure C.4: Human density in the southern Appalachian region.

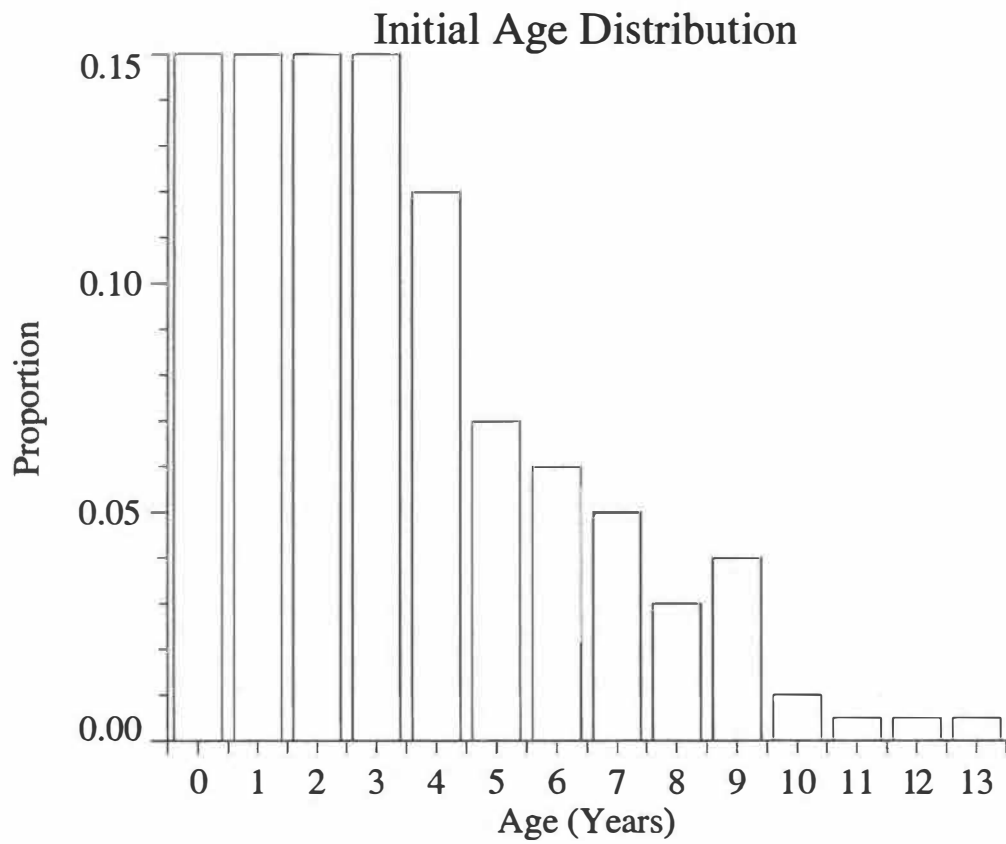


Figure C.5: Black bear initial age distribution used for the model.

Vegetation Map

Spruce Fir

Northern Hardwood

Cove Hardwood

Mesic Oak

Mixed Mesic Hardwood

Tulip Poplar

Xeric Oak

Oak – Pine

Pine

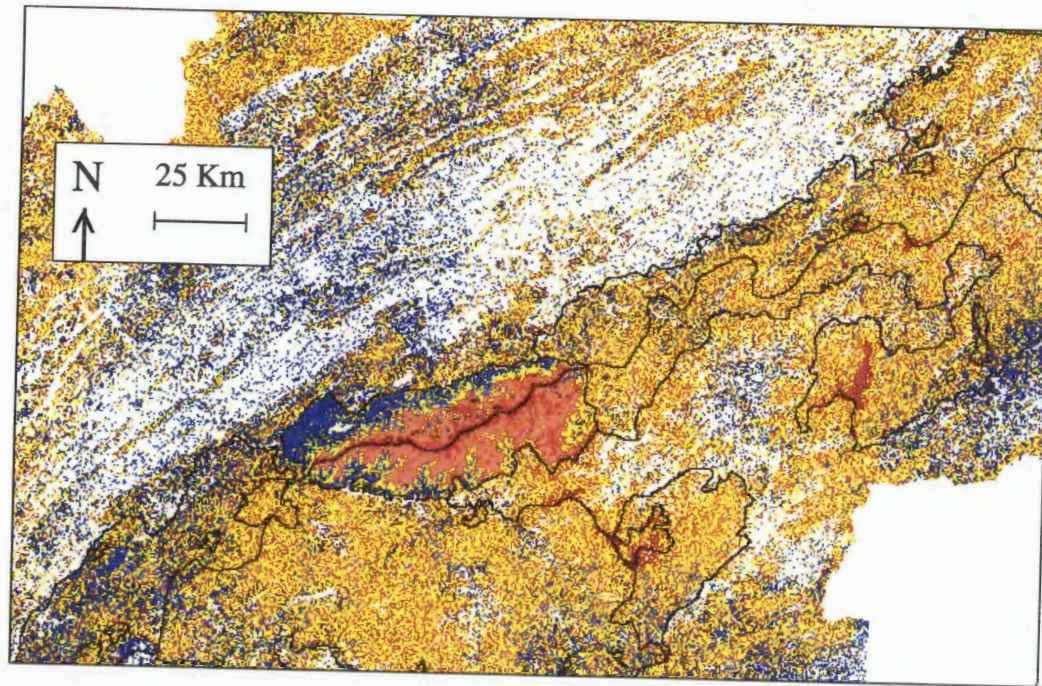


Figure C.6: Forest types for the southern Appalachian region

Black Bear Sanctuaries

Tennessee Areas

North Carolina Areas

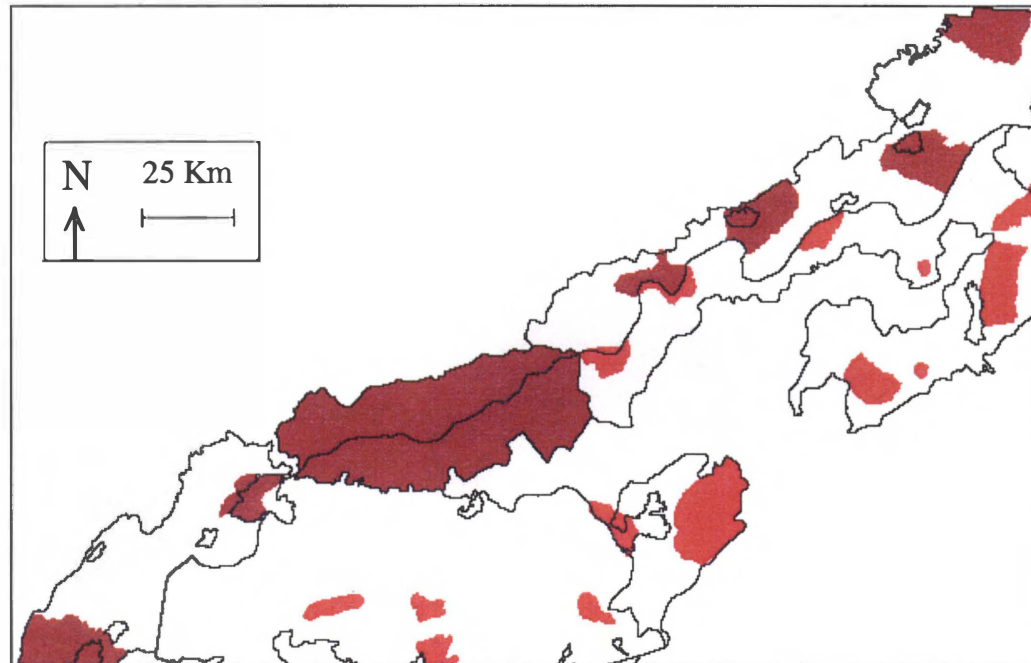


Figure C.7: Black bear sanctuaries in the southern Appalachian region.

Black Bear Sanctuaries for Alt 5

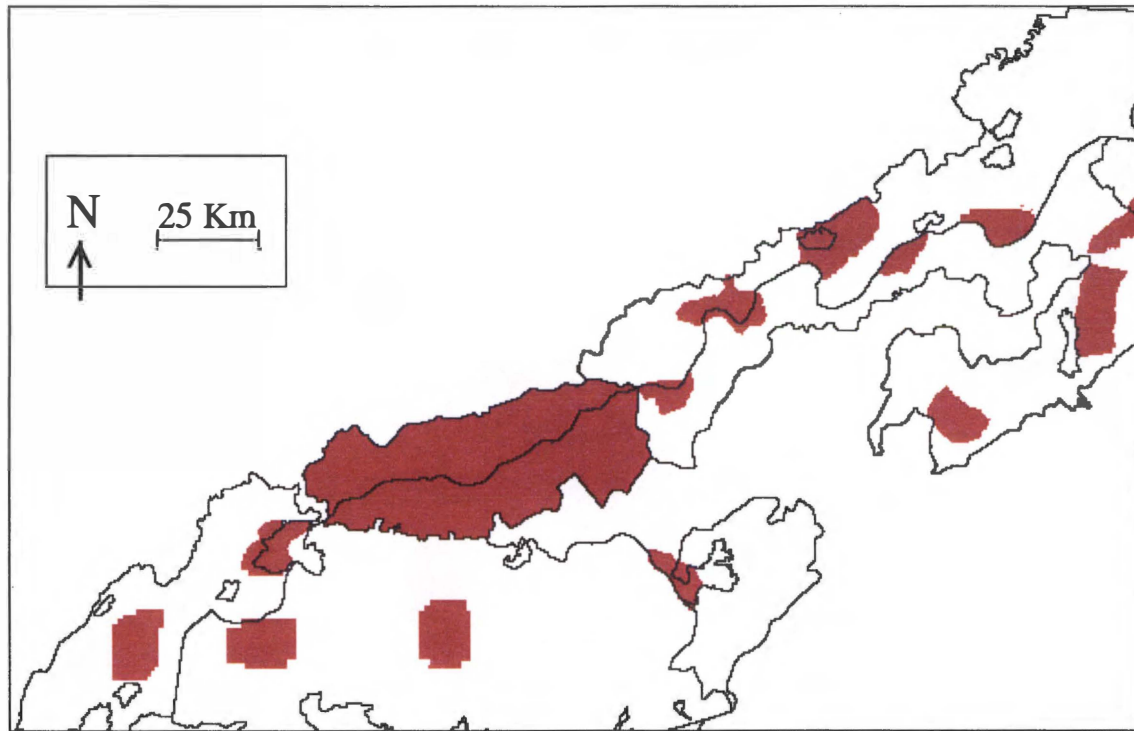


Figure C.8: Alternative black bear sanctuaries used for Alt 5.

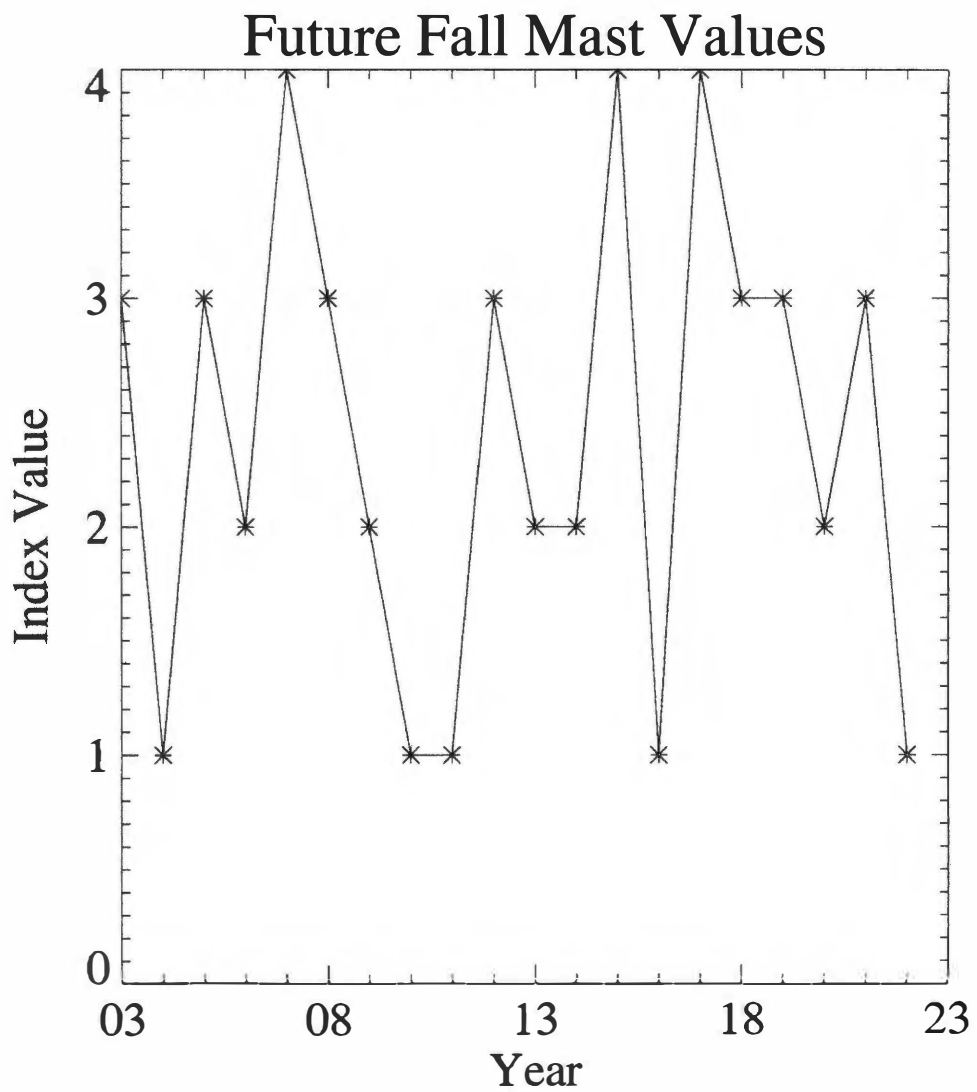


Figure C.9: Future fall mast values used in testing the alternative strategies.

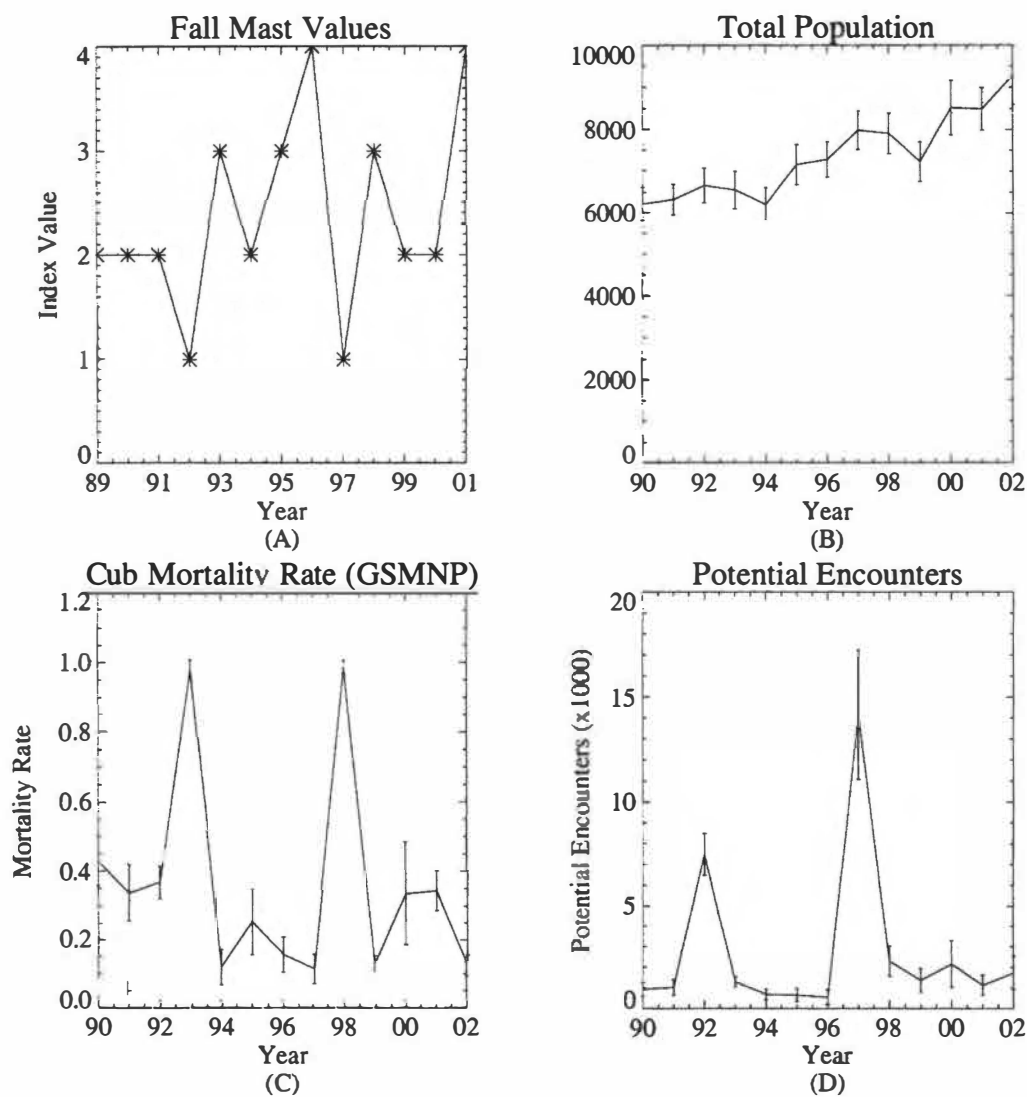


Figure C.10: Model output for: (A) Fall mast indices and the modeled response of (B) total population, (C) cub mortality rates, and (D) potential bear-human encounters. Error bars indicate 95% confidence intervals.

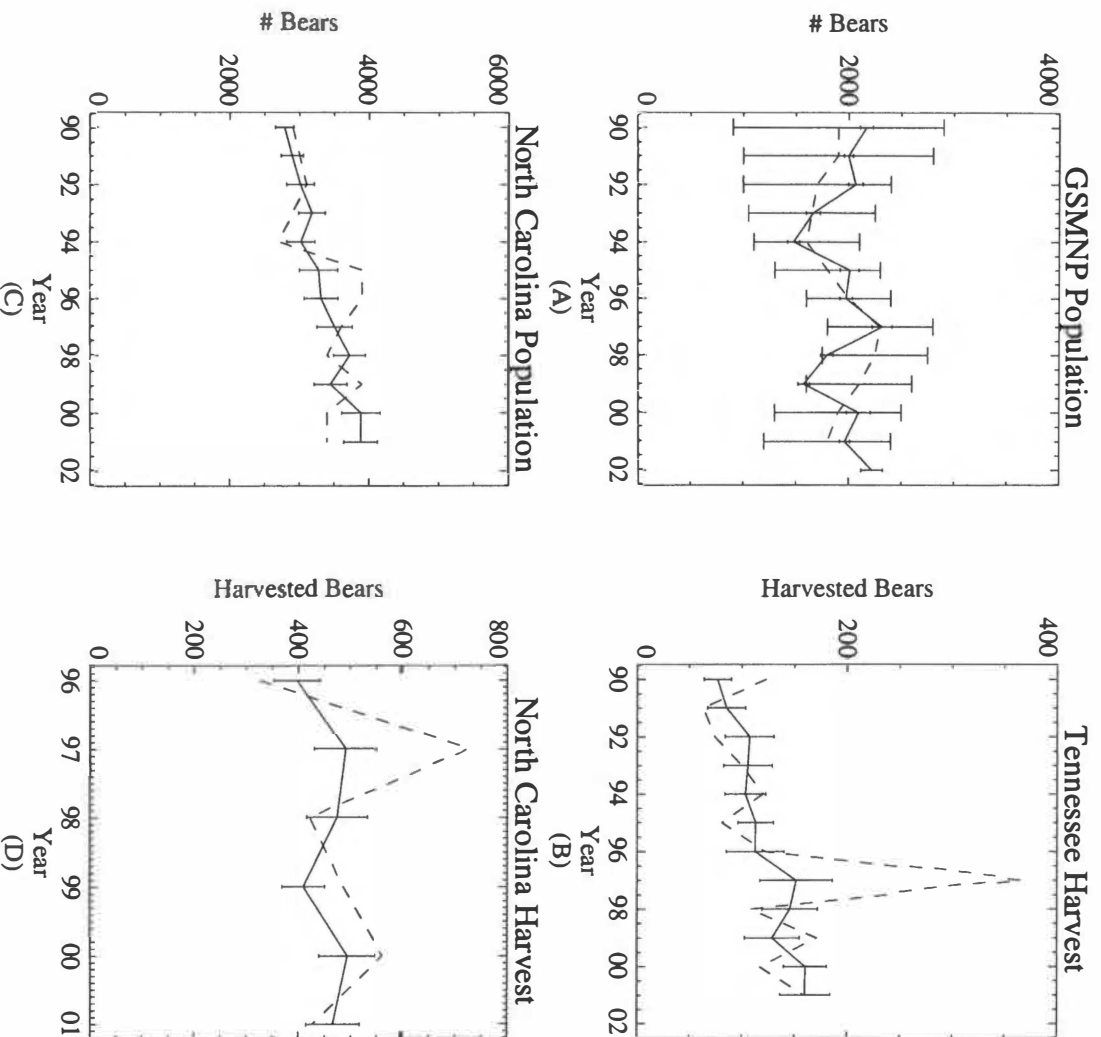


Figure C.11: Model comparisons to empirical data (IBM (—), data (---)): (A) GSMNP population vs. three-year running average Jolly-Seber estimates (large error bars correspond to 95% confidence interval for empirical data), (B) Tennessee harvest data, (C) Western North Carolina population, and (D) Western North Carolina harvest data. Error bars correspond to 95% confidence intervals for model results. Error estimates for the empirical data in (B), (C), and (D) were not available.

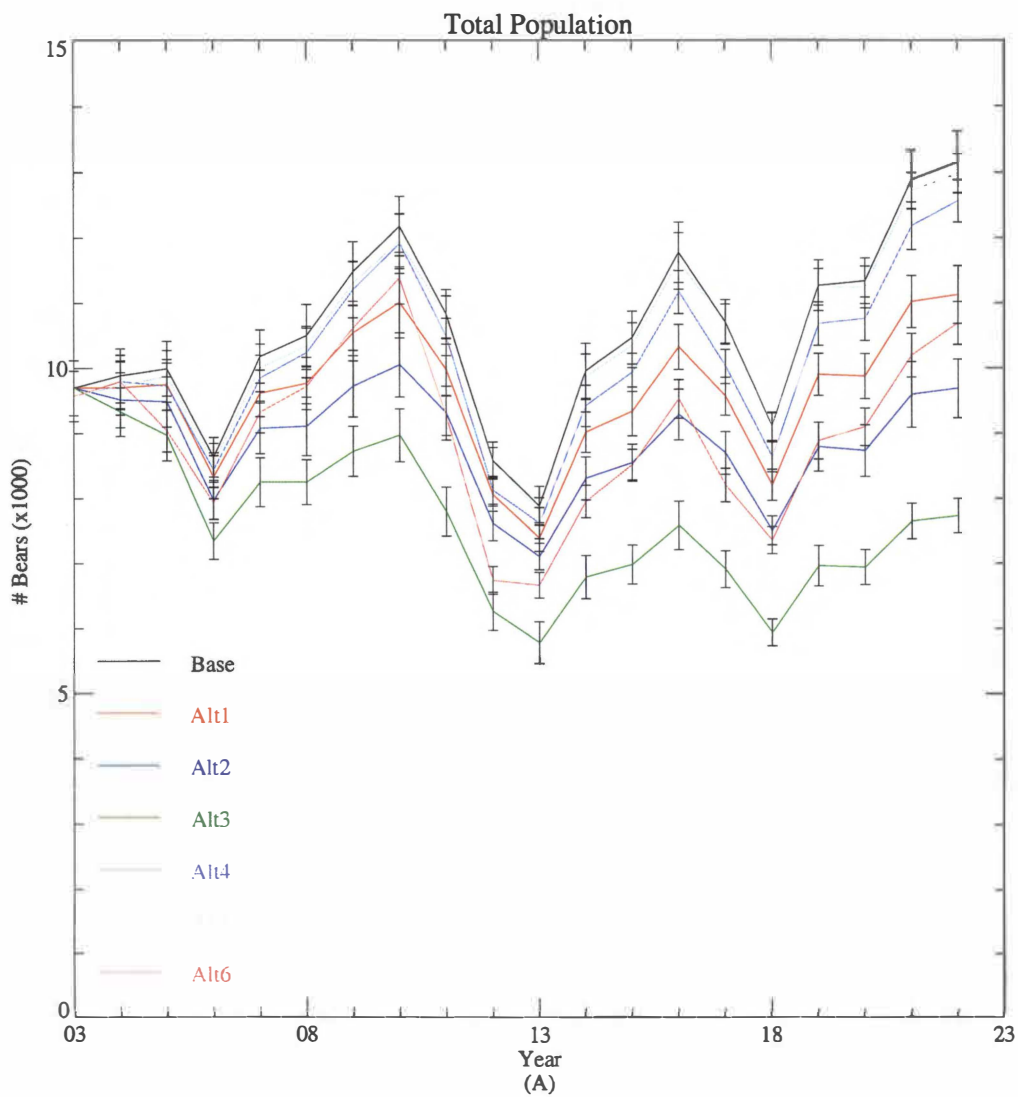


Figure C.12: Total population time series for each scenario (See Table C.3 for a description of each scenario). Error bars indicate 95% confidence intervals.

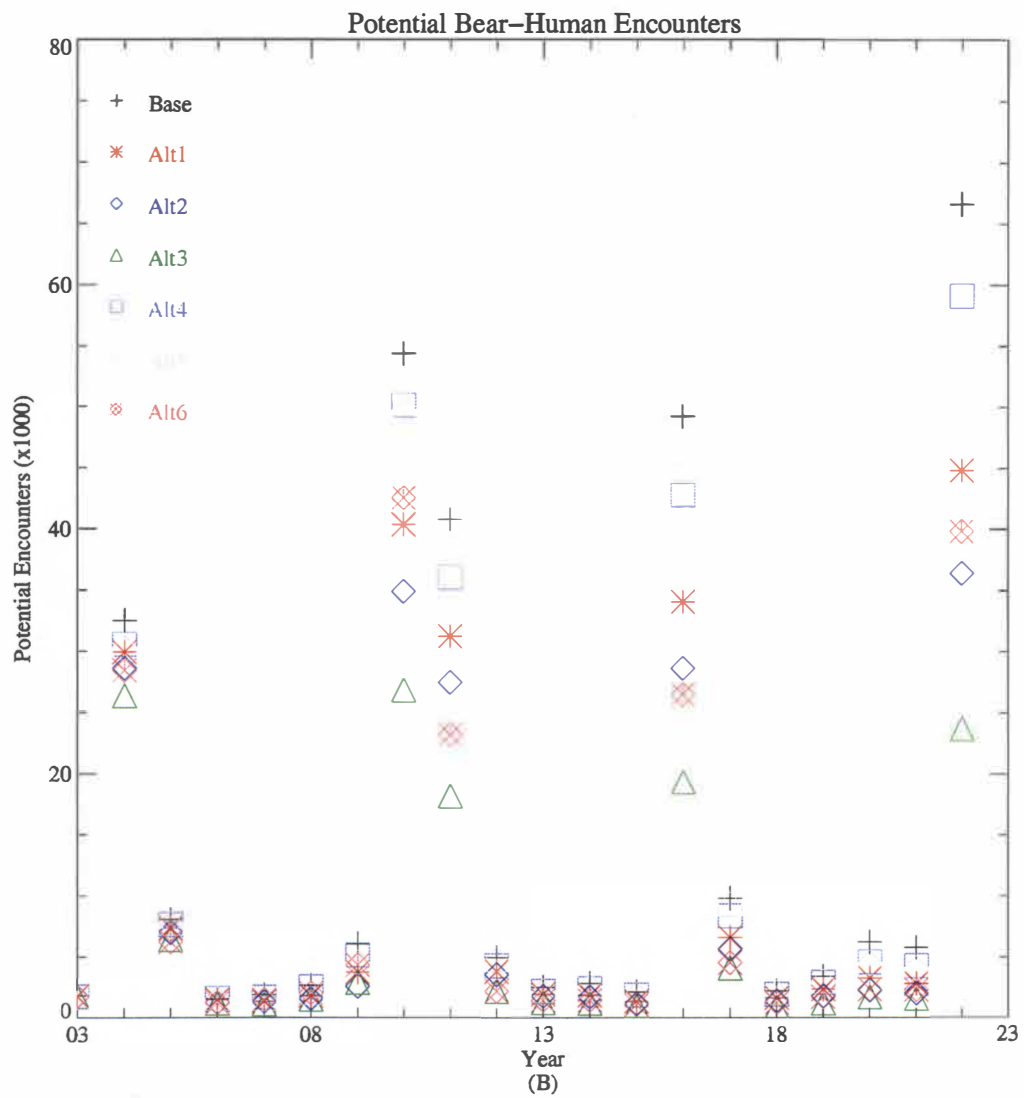


Figure C.13: Potential bear-human encounters for each scenario (See Table C.3 for a description of each scenario).

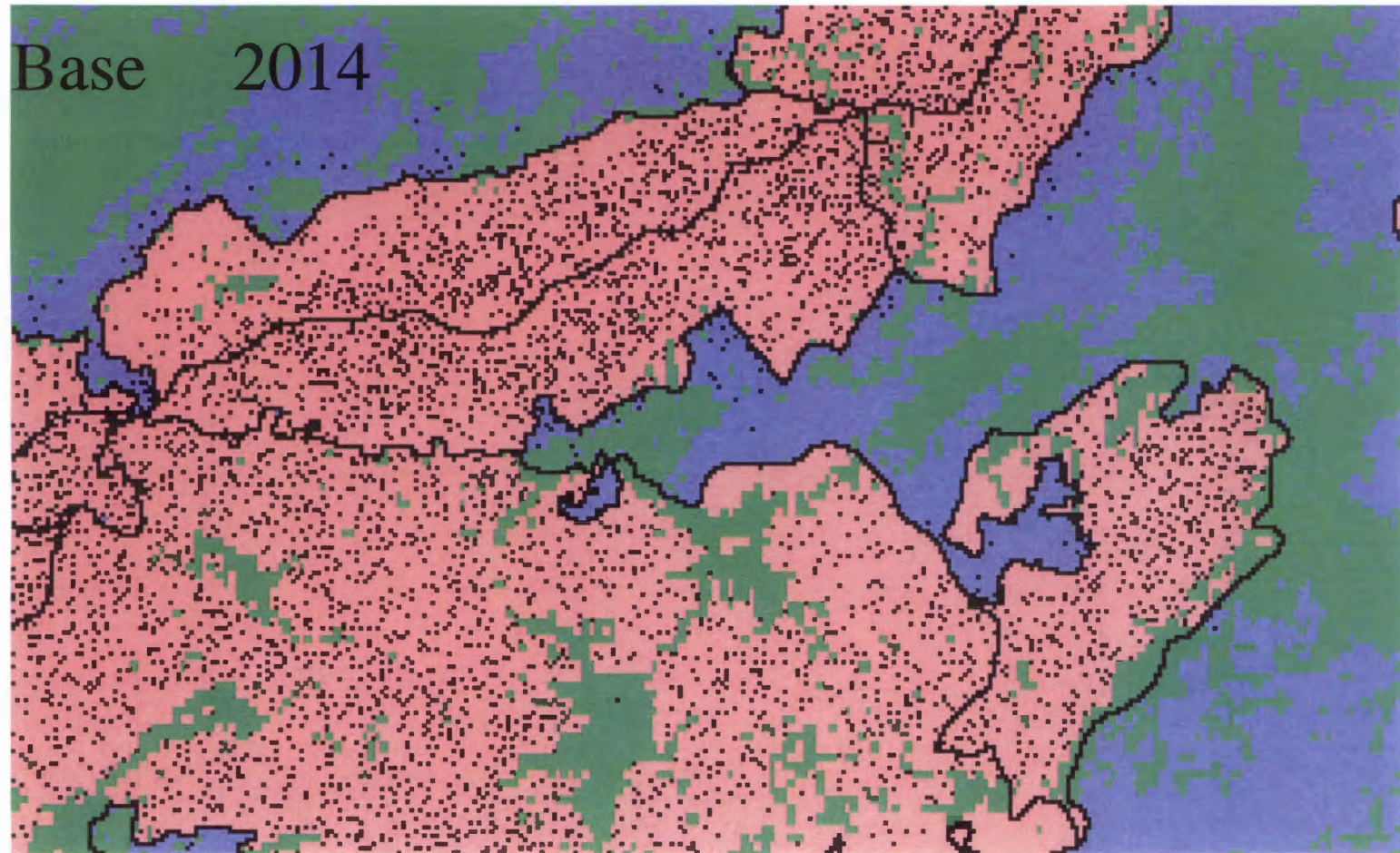


Figure C.14: Base scenario one day snapshot of bears in early November in a good mast year (2014). Black dots indicate cells with at least one bear, and green indicates human populated cells.

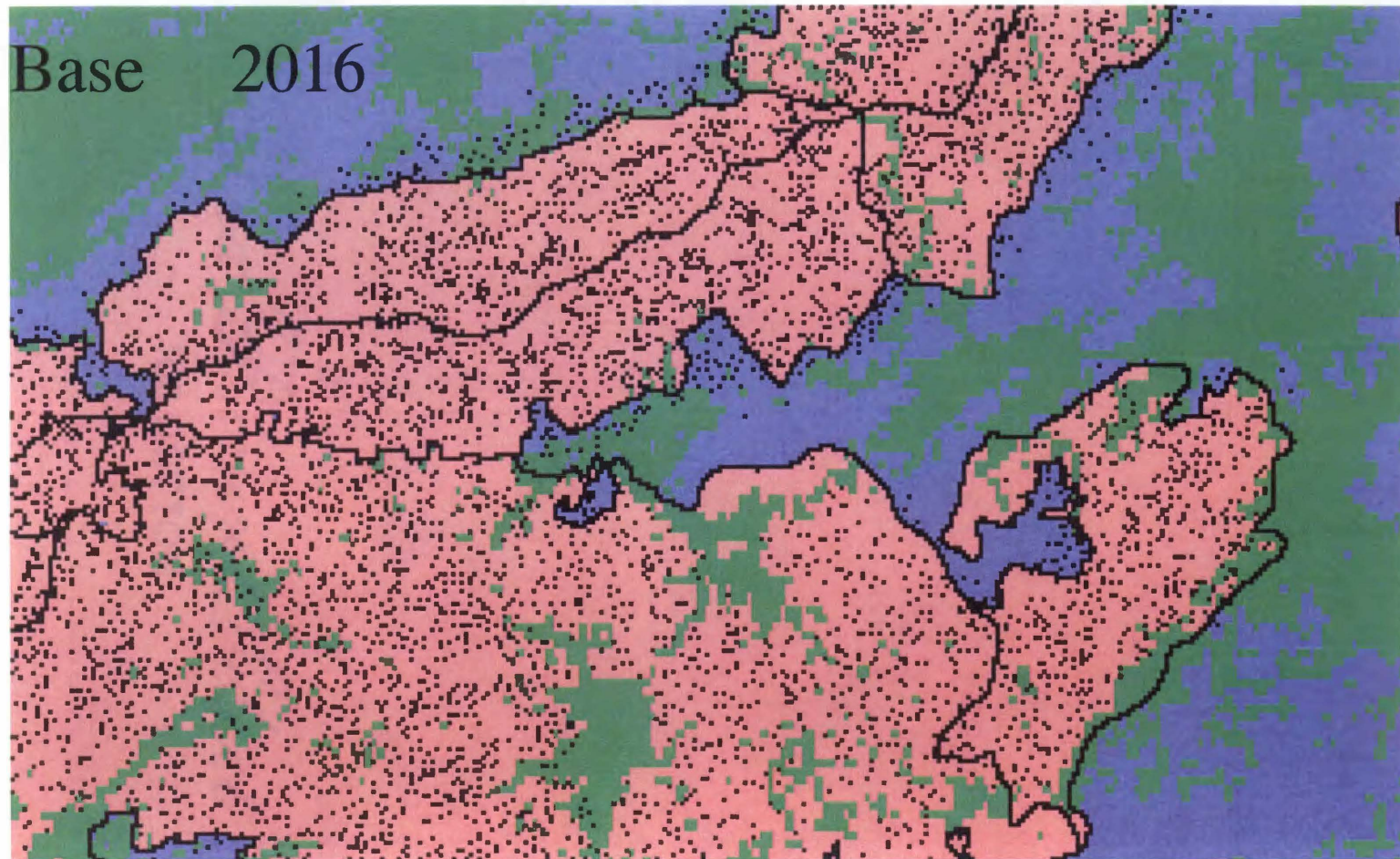


Figure C.15: Base scenario one day snapshot of bears in early November in a bad mast year (2016). Black dots indicate cells with at least one bear, and green indicates human populated cells.

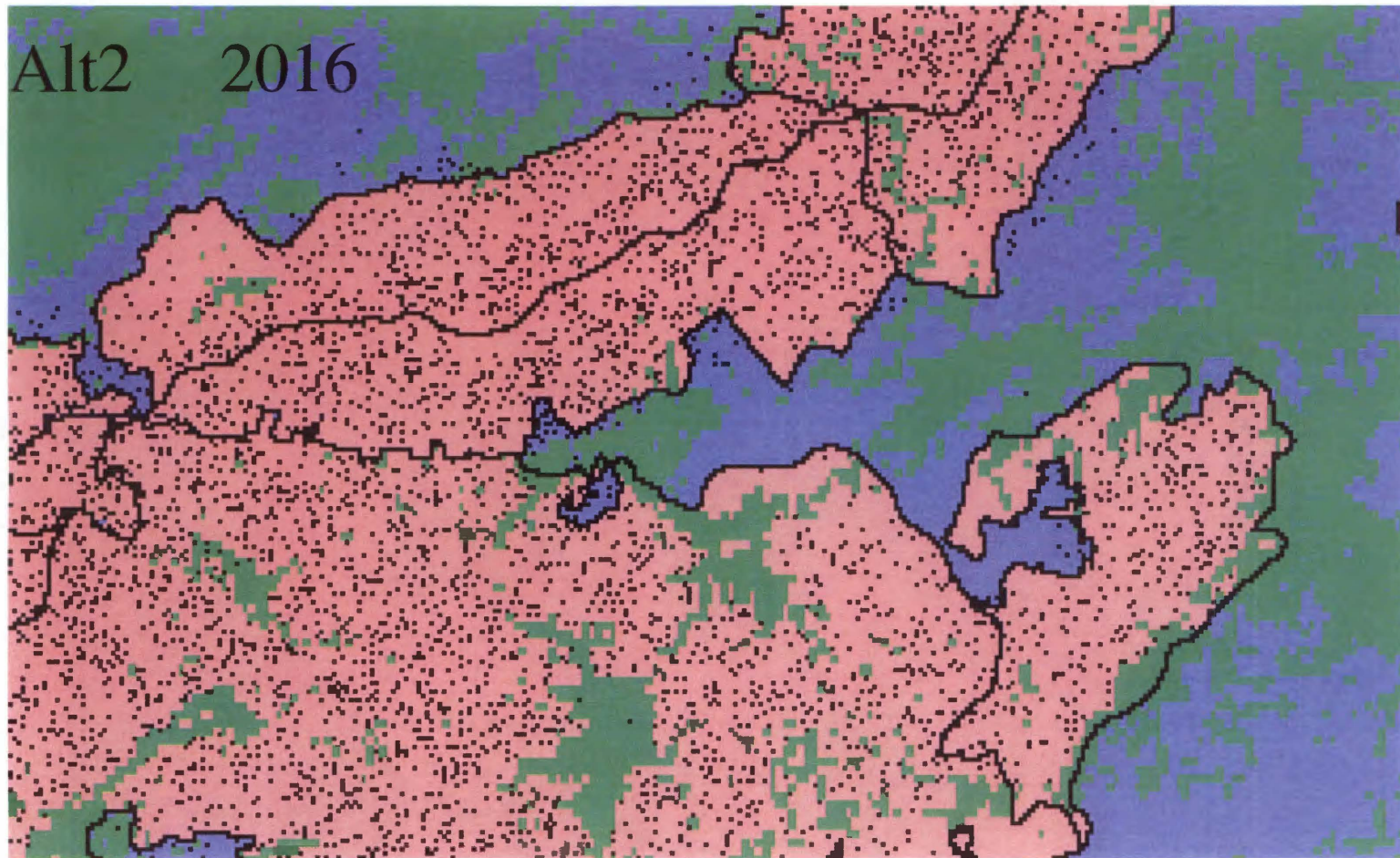


Figure C.16: Alt2 scenario one day snapshot of bears in early November in a bad mast year (2016). Black dots indicate cells with at least one bear, and green indicates human populated cells.

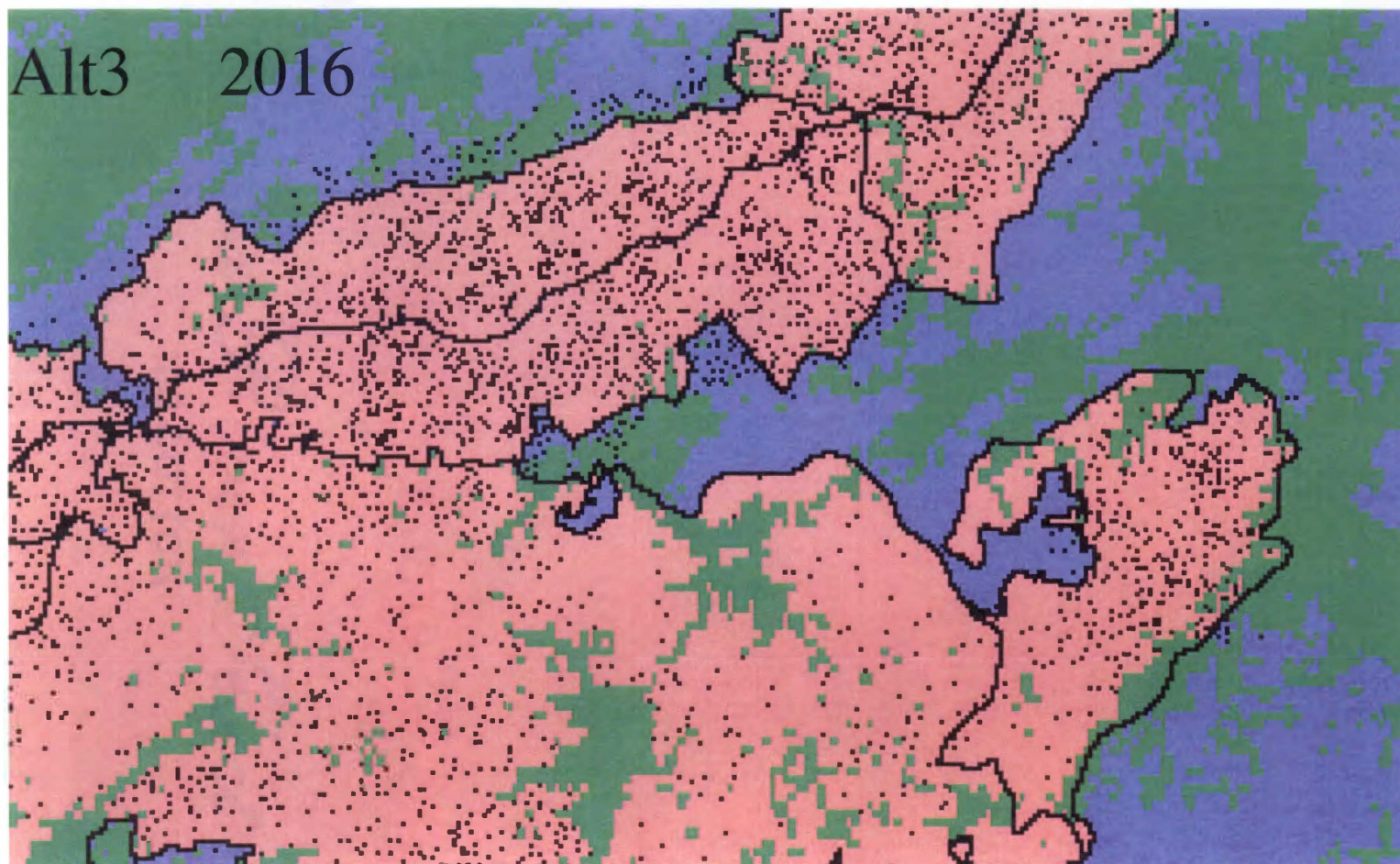


Figure C.17: Alt3 scenario one day snapshot of bears in early November in a bad mast year (2016). Black dots indicate cells with at least one bear, and green indicates human populated cells.

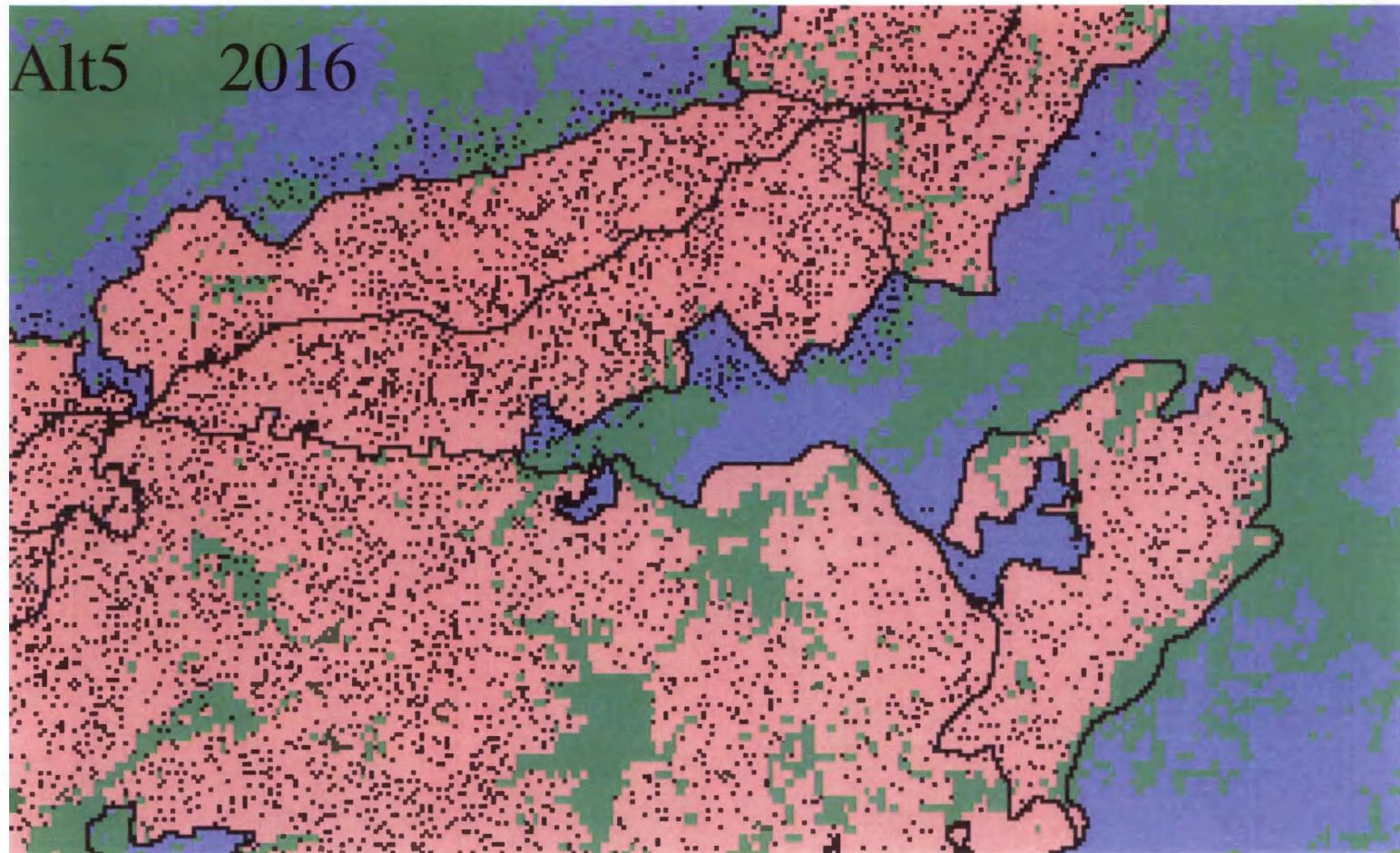


Figure C.18: Alt6 scenario one day snapshot of bears in early November in a bad mast year (2016). Black dots indicate cells with at least one bear, and green indicates human populated cells.

Appendix D

Chapter 4 Figures

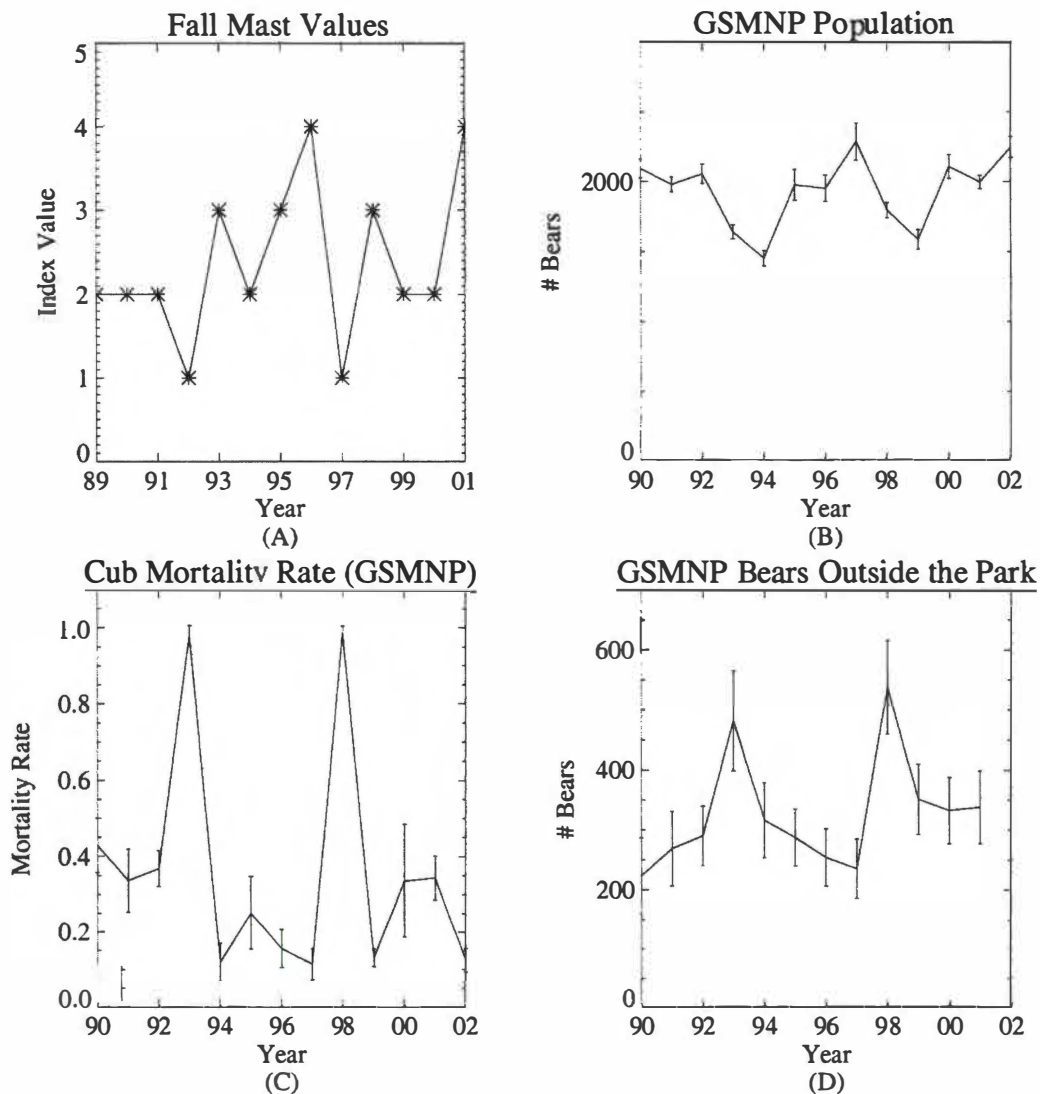


Figure D.1: IBM results for the GSMNP: (A) fall mast index values, (B) GSMNP summer population, (C) cub mortality rate, and (D) native GSMNP bears located outside the park (summer). Error bars indicate 95% confidence intervals.

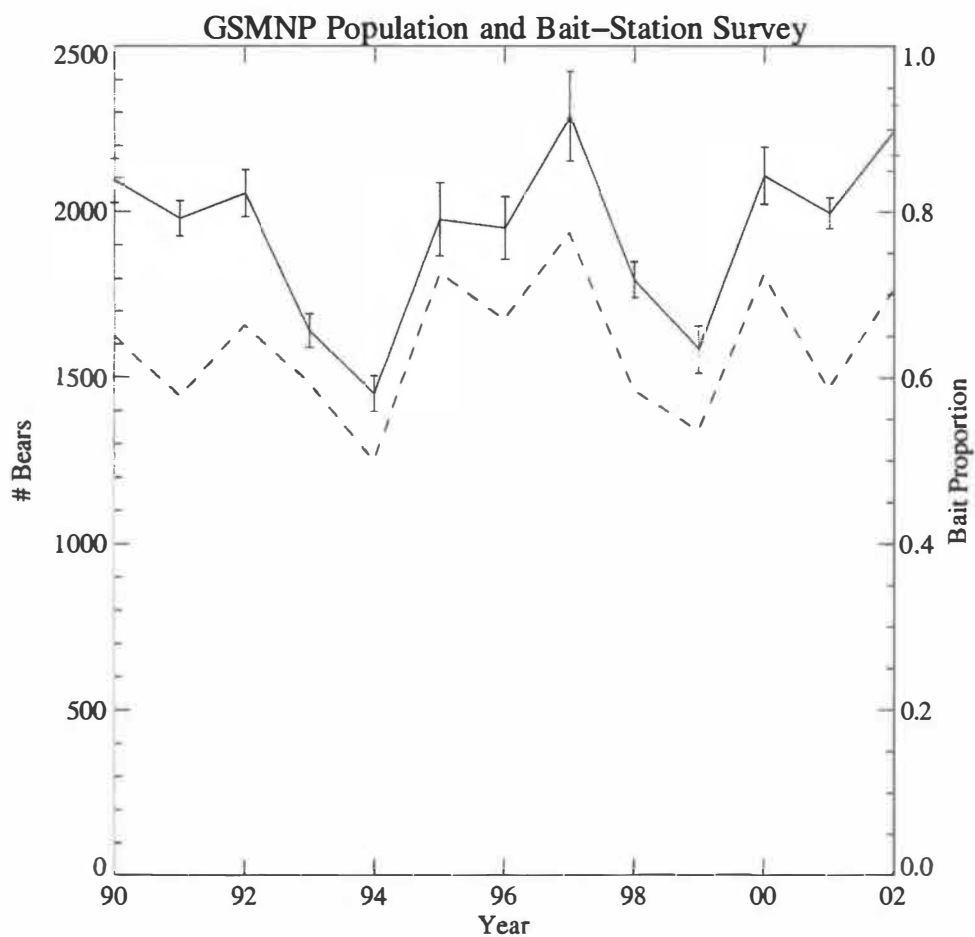


Figure D.2: Model output for GSMNP population (solid line, left axis) compared to bait-station surveys (dashed line, right axis). Error bars indicate 95% confidence intervals.

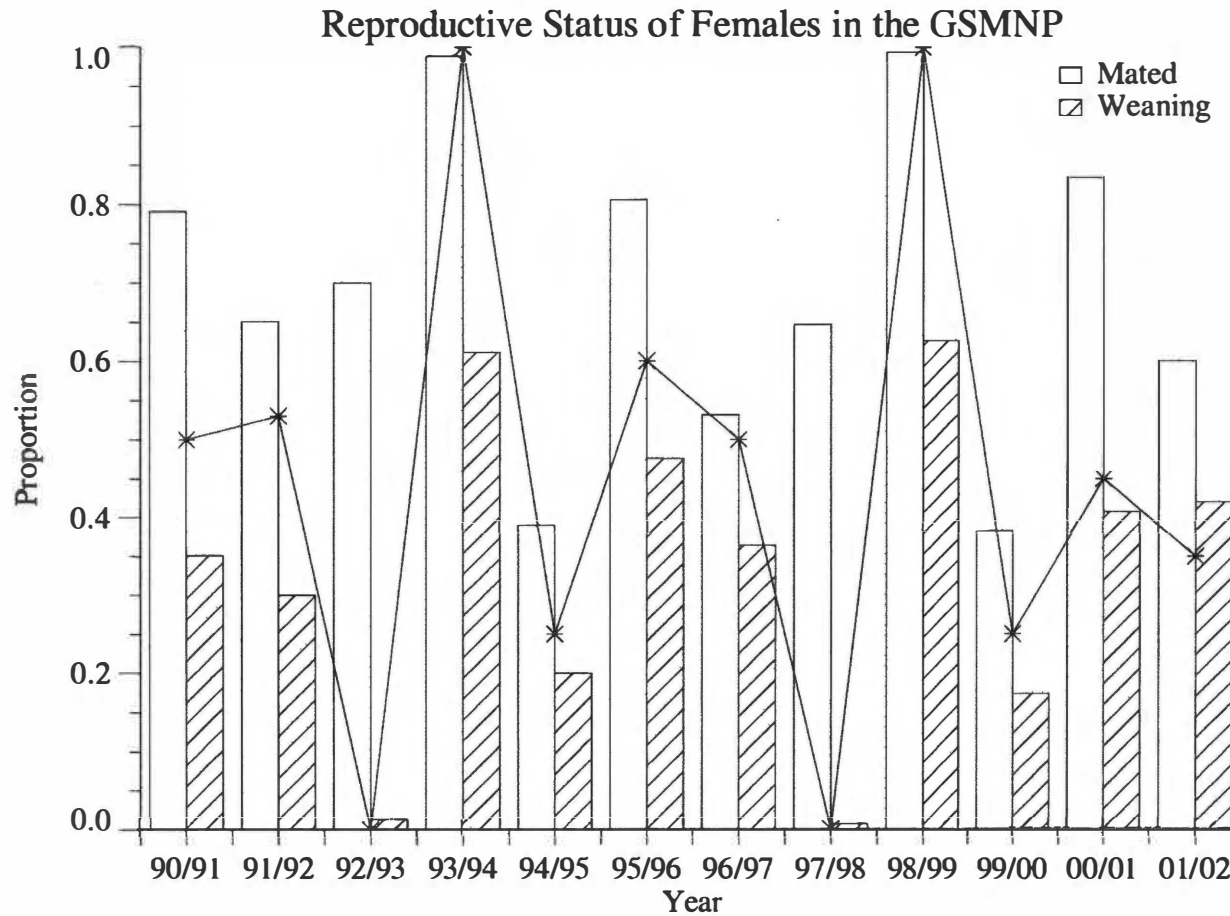


Figure D.3: Model output of proportion of females bear that have mated during the onset of denning (solid), proportion of female bears weaning by early summer (slashed), and empirical den survey proportions conducted towards the end of the denning season (*).

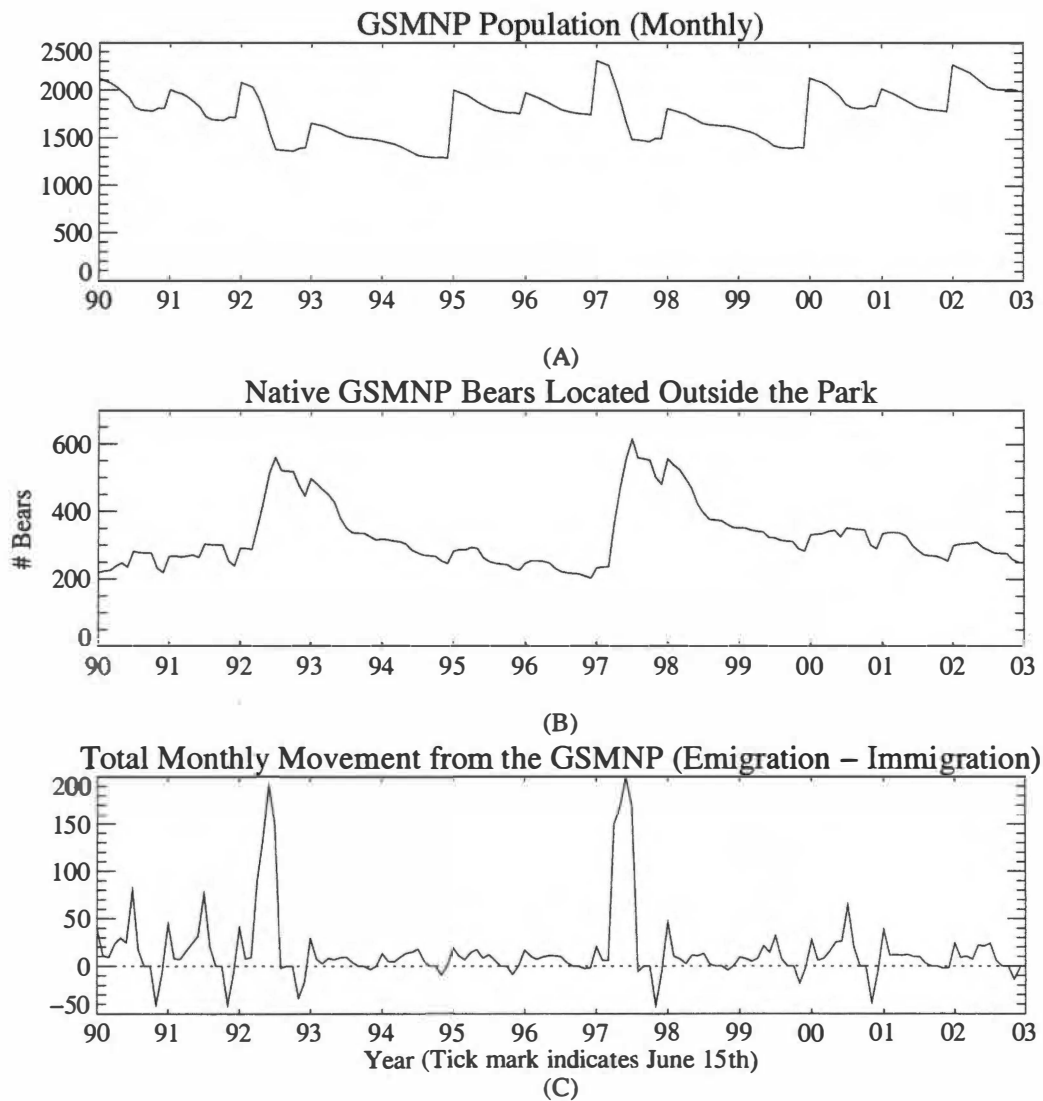


Figure D.4: Monthly time series for: (A) GSMNP population, (B) number of native GSMNP bears not in the park, and (C) monthly sum of net movement (emigration - immigration).

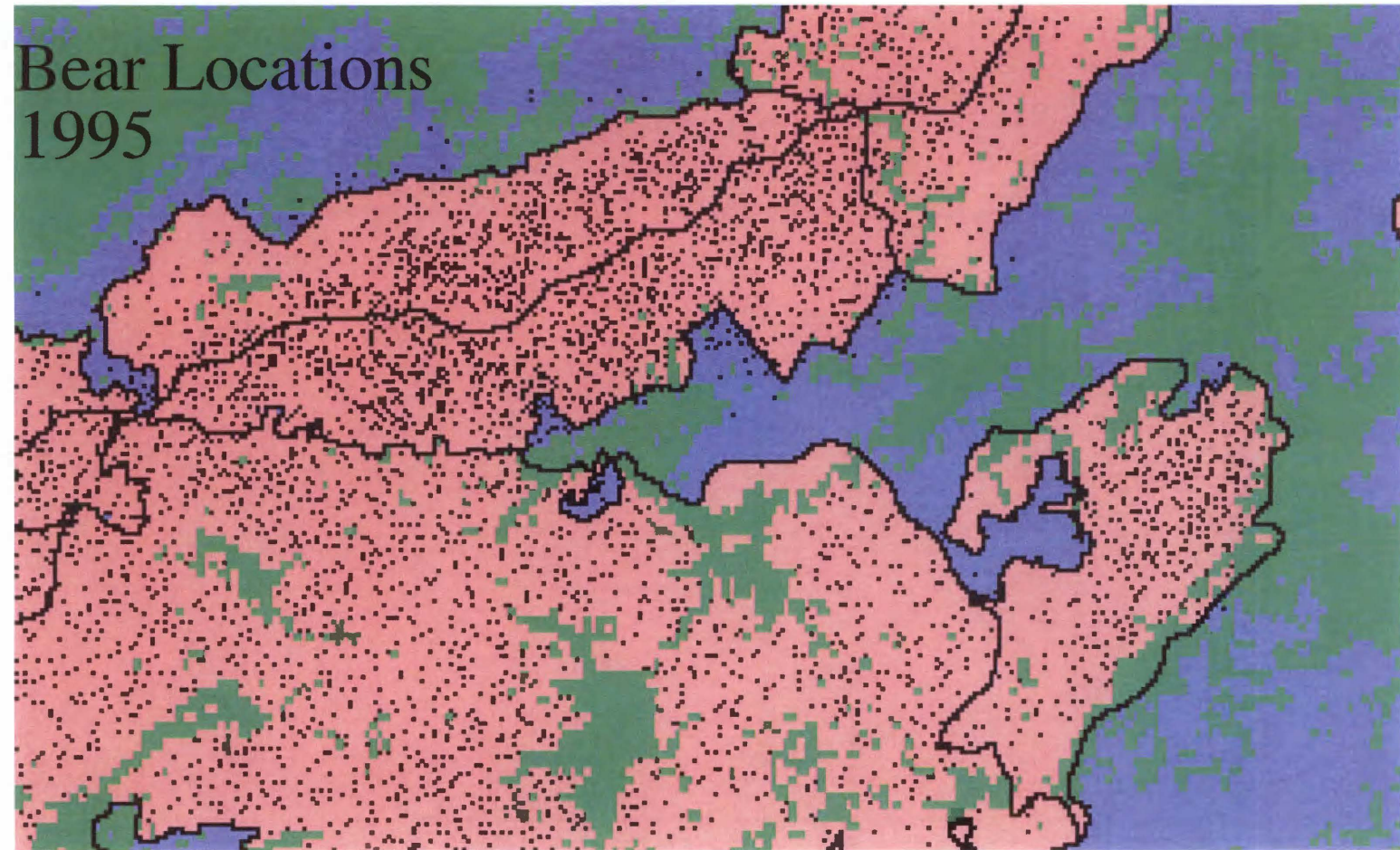
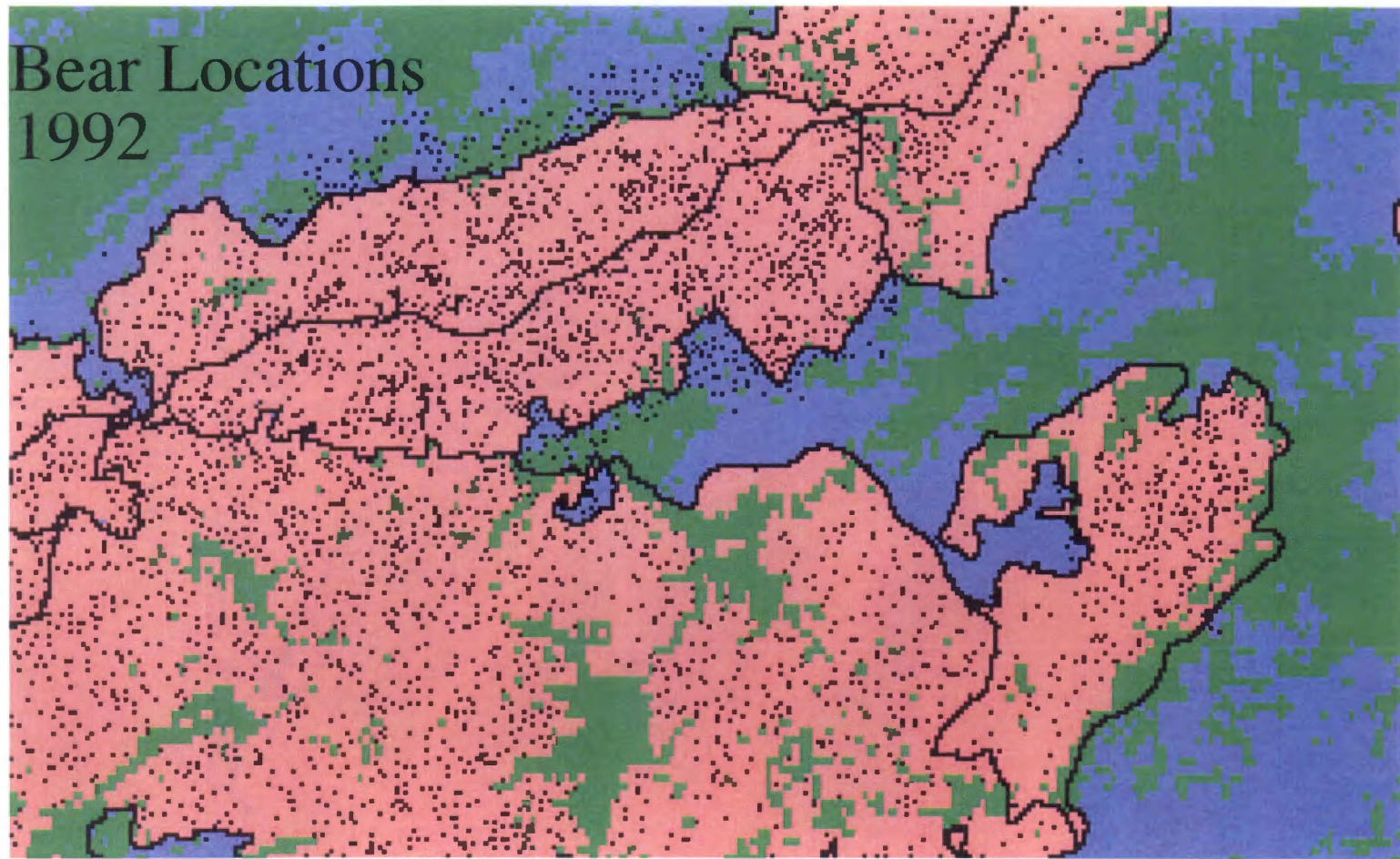


Figure D.5: One-day snapshot of bears in early November in a good mast year (1995). Black dots indicate cells with at least one bear, and green indicates human populated cells.



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Figure D.6: One-day snapshot of bears in early November in a bad mast year (1992). Black dots indicate cells with at least one bear, and green indicates human populated cells.

Black Bear Age Structure in GSMNP

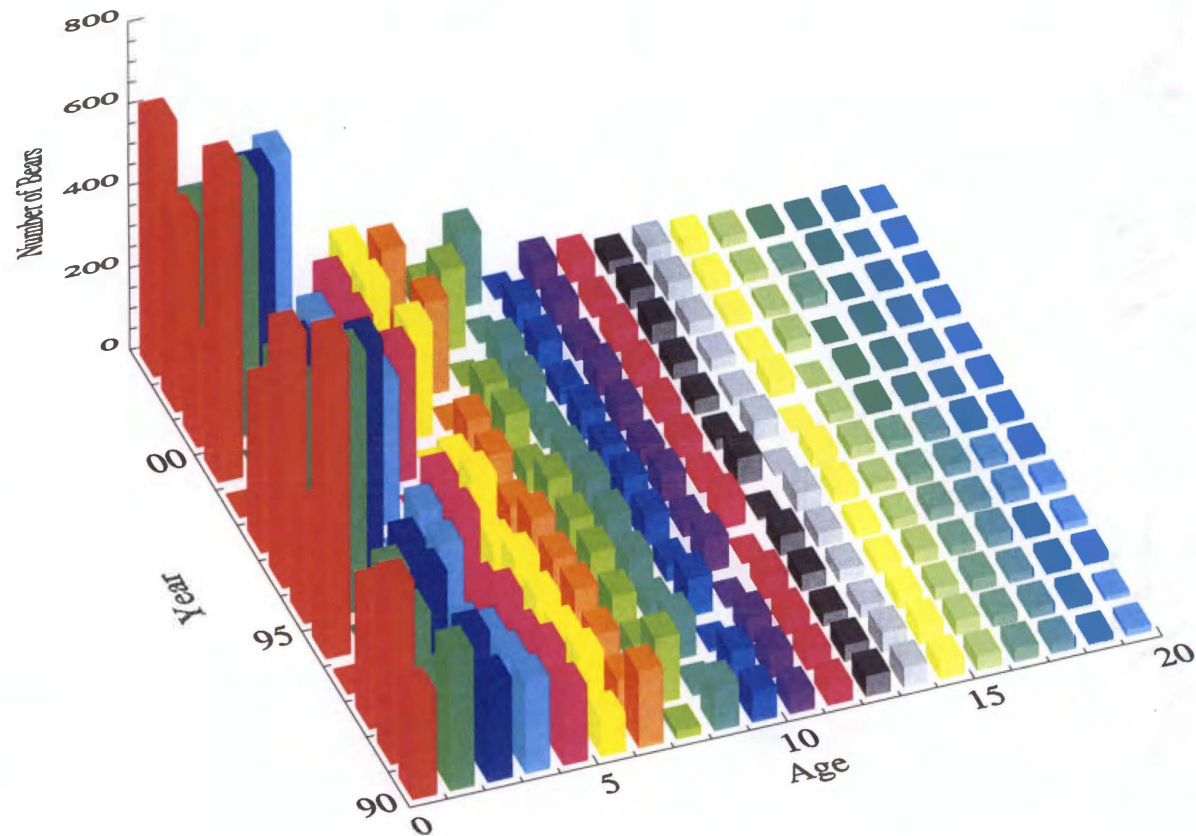


Figure D.7: Age-structure for the black bear population of the GSMNP from 1990 - 2002.

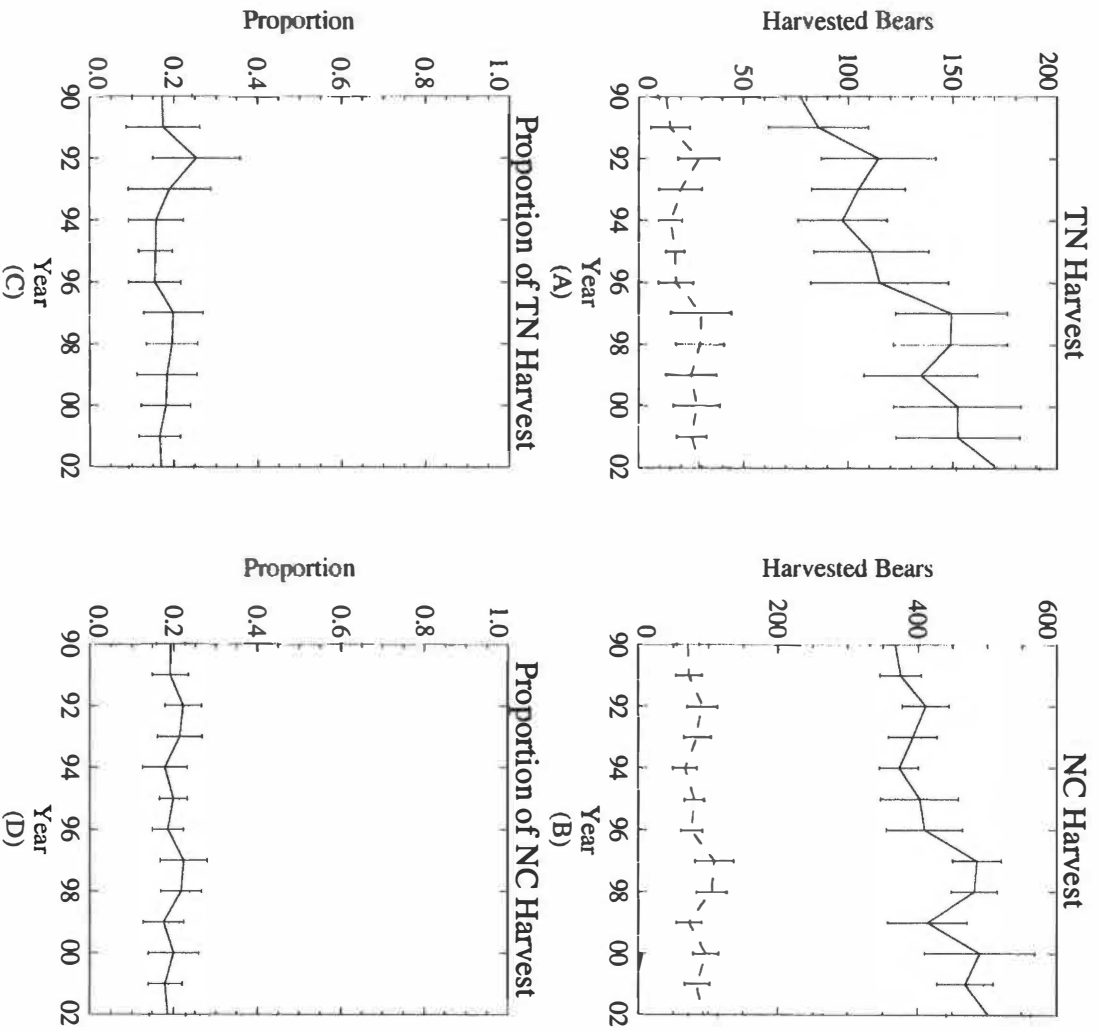


Figure D.8: GSMNP bear contribution to harvesting. (Total (solid), GSMNP natives (dashed)): (A) Tennessee, (B) Western North Carolina, (C) proportion of TN harvest, and (D) proportion of NC harvest. Error bars indicate 95% confidence intervals.

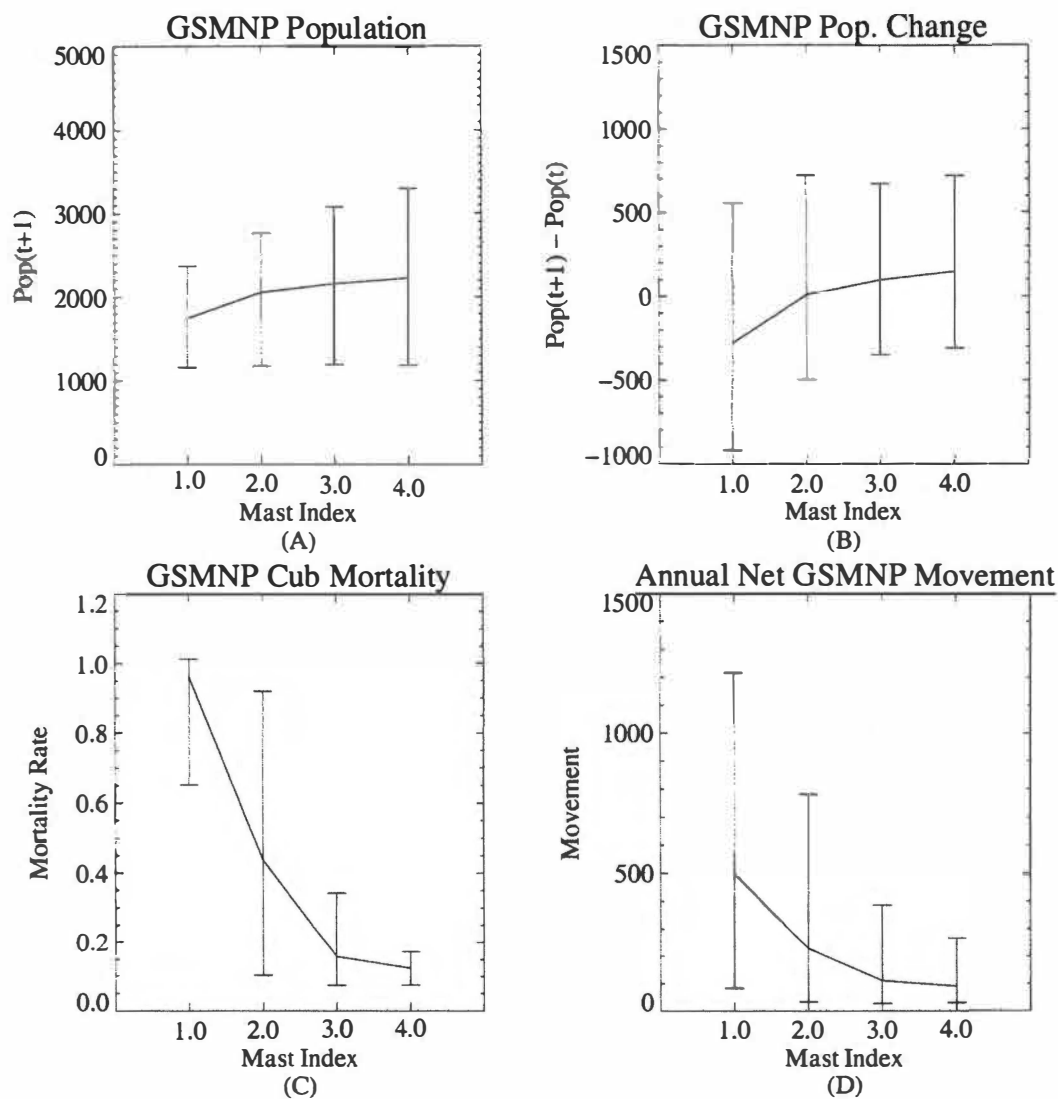


Figure D.9: Mast effects on the modeled GSMNP population using random sequences of mast data (see text): (A) population size, (B) change in population, (C) cub mortality, and (D) total annual net movement (emigration - immigration) from the GSMNP. Error bars indicate the range of the data.

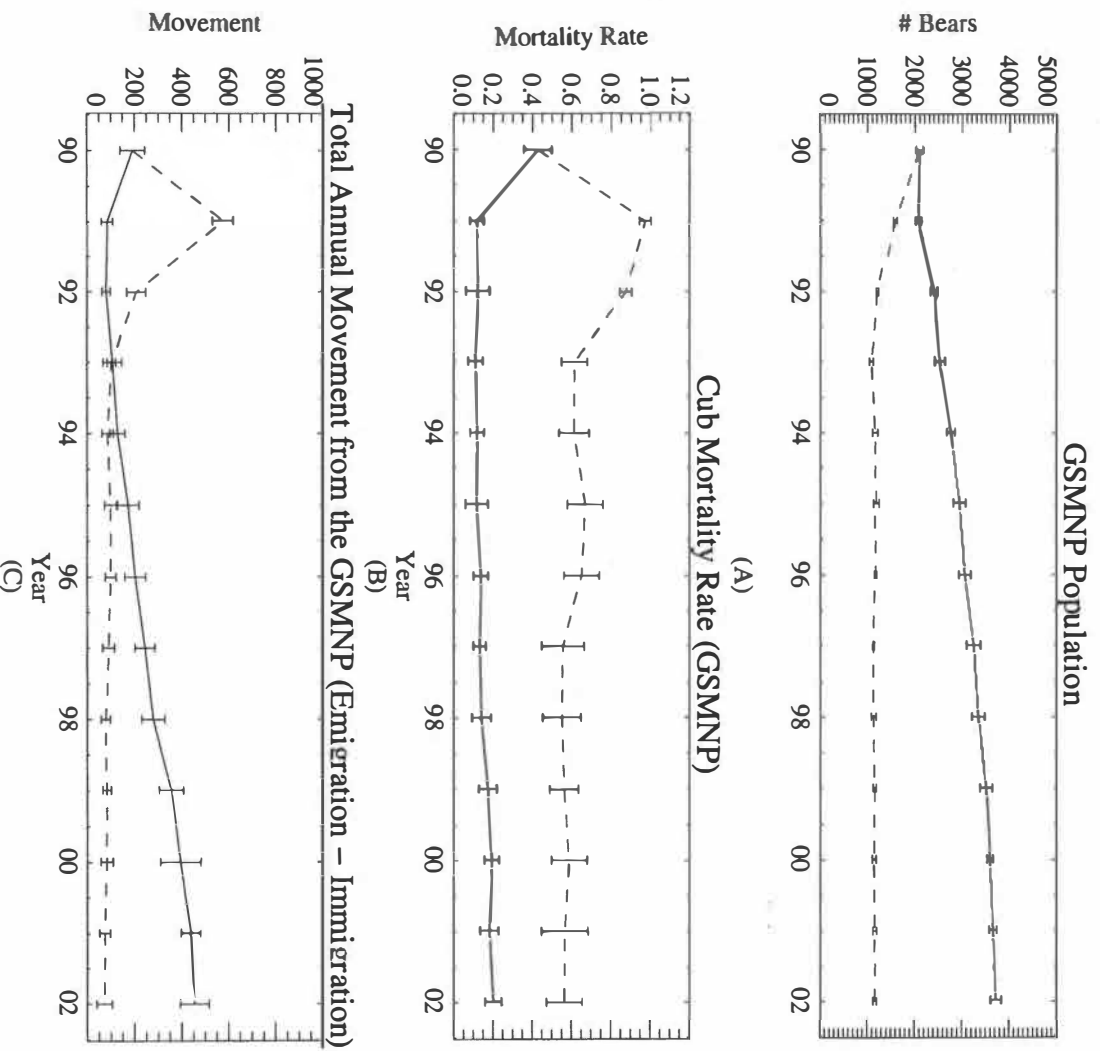


Figure D.10: Asymptotic GSMNP population dynamics with all good mast (4.0) years (solid) and all mast failure (1.0) years (dashed): (A) GSMNP population, (B) cub mortality rate, and (C) annual net movement.

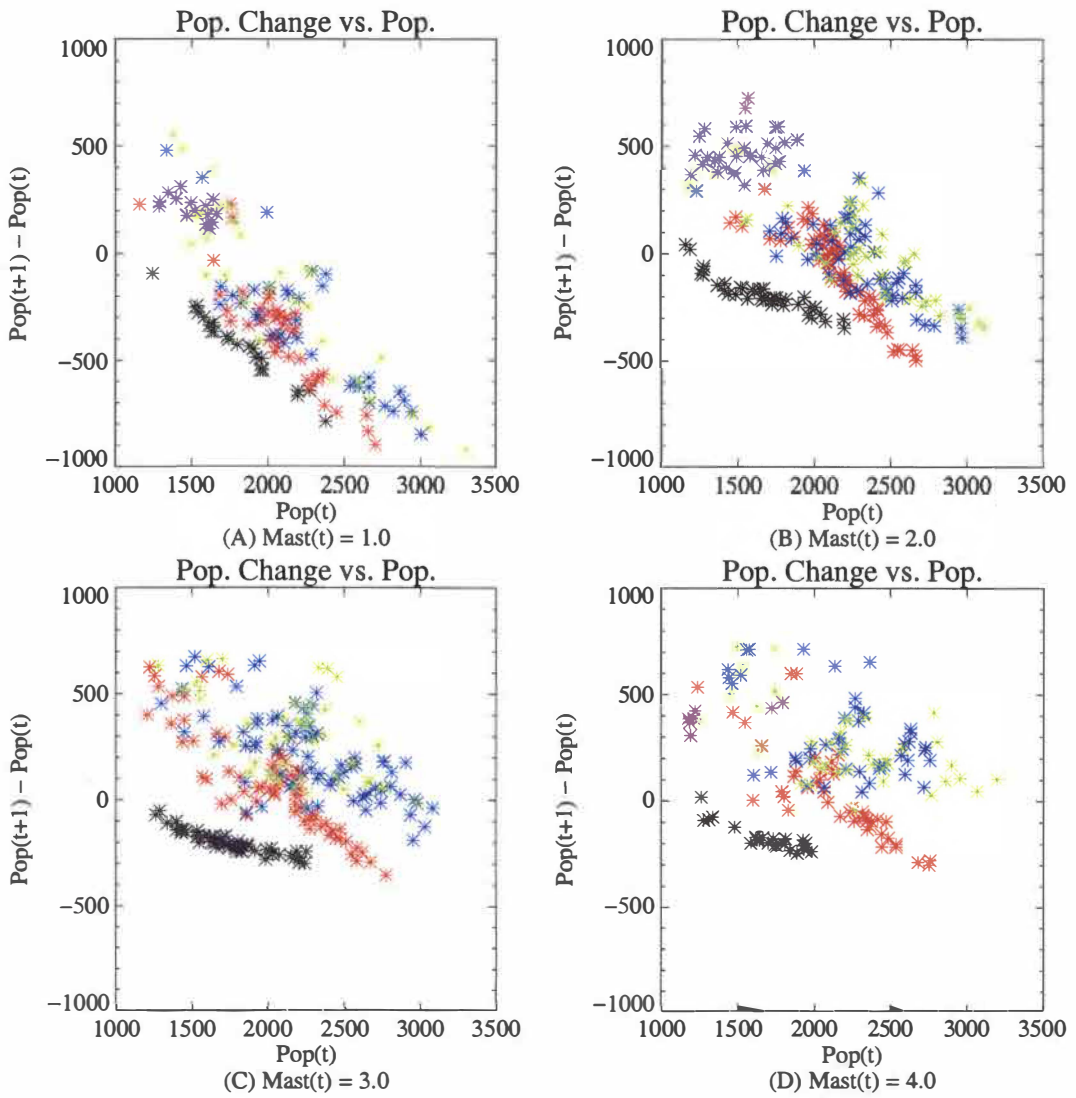


Figure D.11: Scatter plot of change in population size as a function of population size for each mast index value. Colors depict mast index for the previous year: 1.0 (black), 2.0 (red), 3.0 (blue), and 4.0 (green).

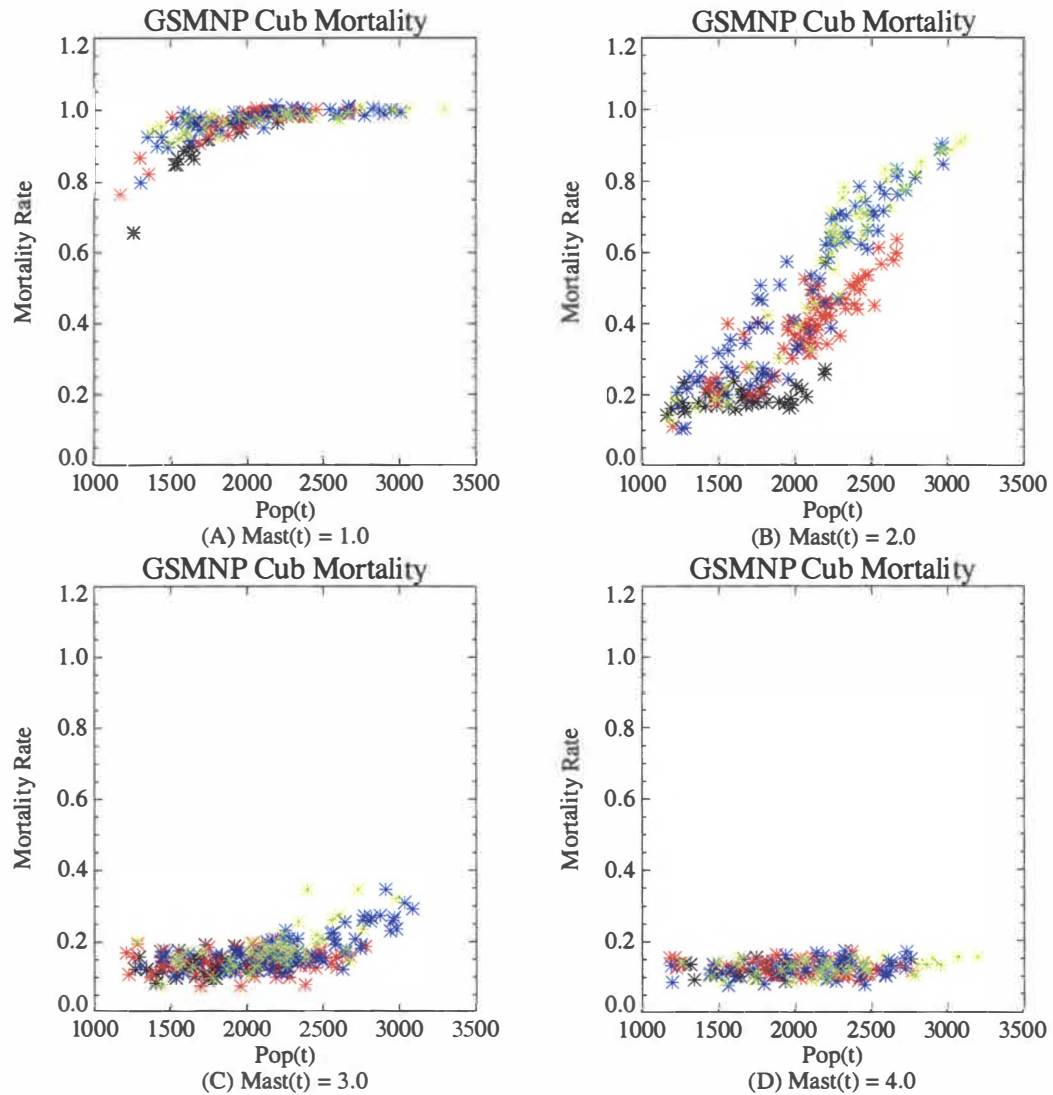


Figure D.12: Scatter plot of cub mortality rate as a function of population size for each fall mast index level. Colors depict mast index for the previous year: 1.0 (black), 2.0 (red), 3.0 (blue), and 4.0 (green).

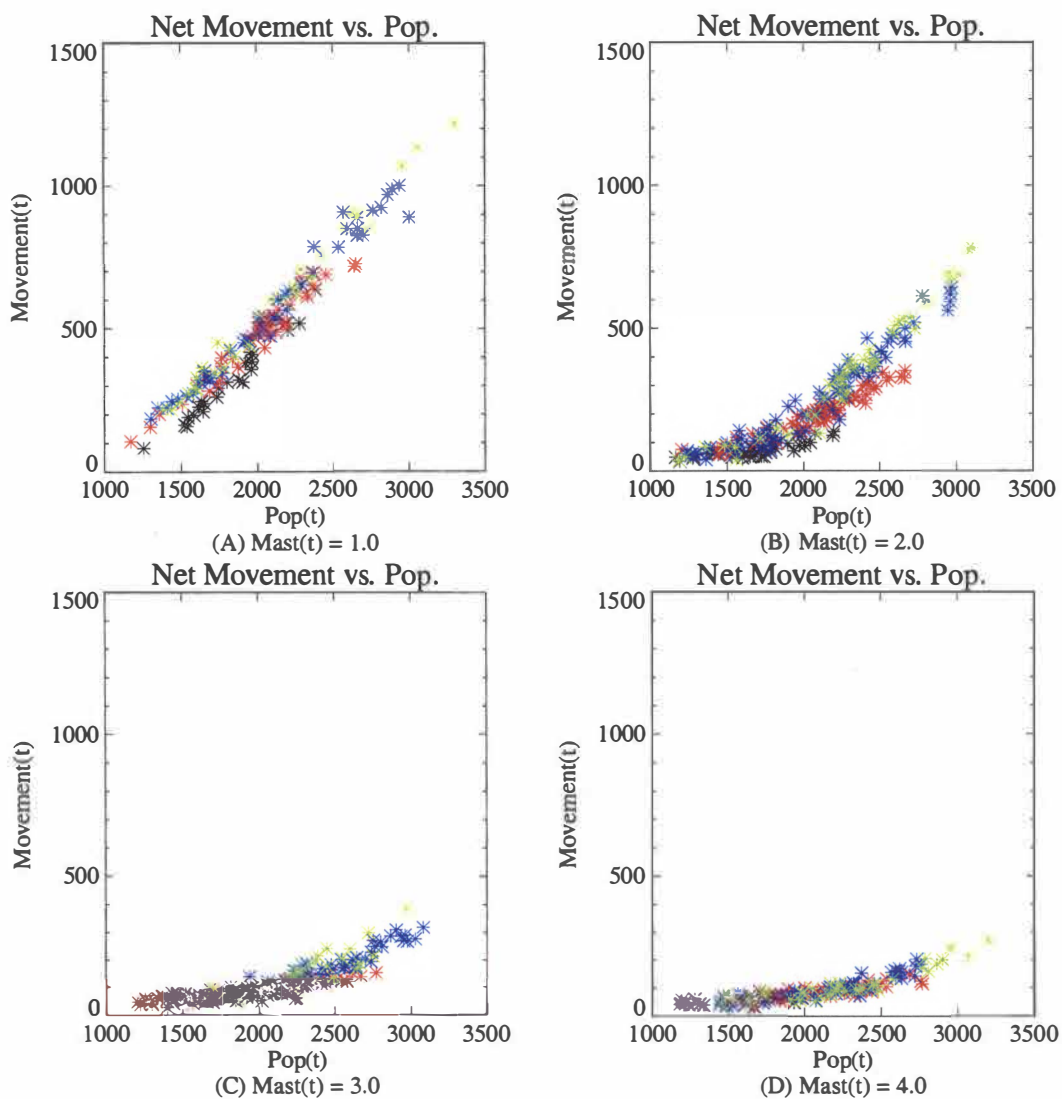


Figure D.13: Scatter plot of net movement (emigration - immigration) from the GSMNP as a function of population size for each mast index value. Colors depict mast index for the previous year: 1.0 (black), 2.0 (red), 3.0 (blue), and 4.0 (green).

Vita

René Armando Salinas was born in Alice, Texas, on August 31, 1974. He attended Alice High School and graduated in May 1992. He received a Bachelor of Science degree Biology and a Bachelor of Science degree Physics in May 1996 from Texas A&M University at Kingsville. In August 1996, he was accepted in the graduate program of the Mathematics Department at the University of Tennessee, Knoxville. In August 2003 he graduated with a Doctor of Philosophy degree with a major in Mathematics and an emphasis in Mathematical Ecology.

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