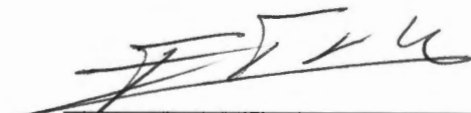


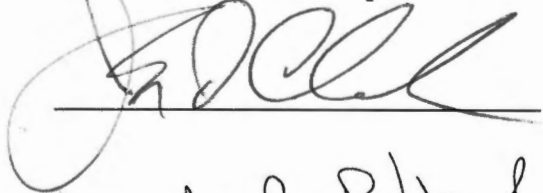
To the Graduate Council:

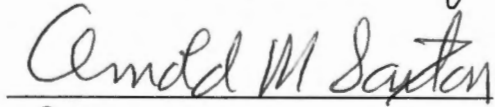
I am submitting herewith a thesis written by Jennifer L. Murrow entitled "A Black Bear Metapopulation Analysis for the southern Appalachians". I have examined the final copy of this thesis for form, content, and quality and recommend that it be accepted in partial fulfillment of the requirements for the degree of Master of Science, with a major in Wildlife and Fisheries Science.

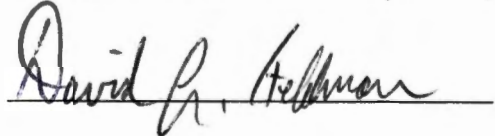


Frank van Manen, Major Professor

We have read this thesis
and recommend its acceptance:

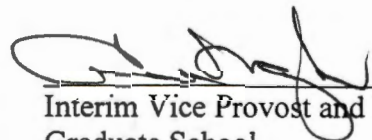


Michael R. Vaughan


Arnold M. Saxton


David R. Helman

Accepted for the Council:



Interim Vice Provost and Dean of the
Graduate School

**A BLACK BEAR METAPOPULATION ANALYSIS FOR THE
SOUTHERN APPALACHIANS**

A Thesis

Submitted for the

Master of Science

Degree

The University of Tennessee, Knoxville

Jennifer Lynn Murrow

May 2001

Thesis
2001
.M88

AO-VET-MED

ACKNOWLEDGMENTS

Financial support for this study was provided by the U.S. Fish and Wildlife Service; U.S. Geological Survey, Biological Resources Division; and the University of Tennessee, Knoxville.

I would like to recognize the many people who helped make this thesis possible. First and foremost, I would like to thank my major advisor and mentor, Dr. Frank van Manen. He has been a teacher and a friend. My committee members, Dr. Joseph Clark, Dr. Michael Vaughan, Dr. Arnold Saxton, and Dr. David Feldman have all supported me throughout this scientific process.

I have been lucky enough to form some lasting friendships because of this thesis, and my appreciation is due to Andy Edwards, Carrie Schumacher, Jaime McNutt, Donny Martorello, Mark Boersen, Meghan Carr, Brandon Wear, and who could forget Steven Dobey. Thank you all for your support, understanding, and advice.

Lastly, I must commend all my family. They have stood beside me with unwavering support. So, this is for you mama and Frank, daddy and Kay, Mark, and Granny and Pop-pop. Never let it be said that a community cannot raise a child.

I am so thankful for the opportunity to earn a degree in such an honorable profession that plays a vital role in the future of our children.

ABSTRACT

Black bears (*Ursus americanus*) once were found throughout the southern Appalachians, but because of overexploitation and habitat loss, their range was reduced by approximately two-thirds. Anthropogenic changes on the southern Appalachian landscape during the last 100 years have resulted in a patchy distribution of forest habitats and fragmented black bear populations. Consequently, bears in the southern Appalachians may exist as a metapopulation, i.e., localized populations that interact through periodic local extinctions and recolonizations. My objective was to determine whether classic metapopulation theory, with local extinction and recolonization rates being dependent on patch size and isolation, explains occupancy of black bear habitat patches in the southern Appalachians. I tested this hypothesis by using >10,000 black bear radiotelemetry locations from studies conducted in North Carolina, Tennessee, and Virginia to delineate habitat patches at various spatial scales and resolutions. These patch aggregates were generated by resampling the original habitat grid at increasingly coarser resolutions. Occupancy of each patch was determined based on recent black bear distribution data. Using a metapopulation developed by Hanski (1993) and nonlinear regression, I estimated 3 extinction and colonization parameters for each patch aggregate. The regression analyses produced significant models ($P < 0.001$, $R^2 = 0.691\text{--}0.896$) for the 4 spatial scales that I examined. Consistent with metapopulation theory, as patch area increased and isolation decreased, the probability of occupancy increased. My results suggest that metapopulation theory is useful in explaining the spatial distribution of black bears in the southern Appalachians and that these models can be used to predict bear

distribution based on future conditions. My results suggest that isolation, rather than patch area, is the major impediment to black bear range expansion. The utility of the model was demonstrated by the removal of several large patches. The probability of black bear occurrence decreased in many remaining patches. Also, I illustrated the effect of bear reintroductions as a conservation tool, by simulating colonization of several patches. Depending on which patches were targeted for reintroduction, probabilities of colonization in surrounding patches increased by as much as 56%. My study suggests that the degree of isolation may warrant more consideration when making regional management decisions. This may be particularly important for isolated bear populations where long-term population persistence may be dependent on immigration or for unoccupied patches with suitable habitat that are too isolated for natural recolonization.

TABLE OF CONTENTS

CHAPTER	PAGE
I. INTRODUCTION	1
II. THEORETICAL BACKGROUND.....	5
METAPOPOPULATION MODELS.....	5
SPATIALLY IMPLICIT MODELS	6
Patch Models.....	6
Structured Models.....	7
SPATIALLY EXPLICIT MODELS.....	8
n-Population Simulation Models	8
NEW MODELING METHODS.....	8
III. STUDY AREA	10
IV. METHODS	16
STUDY AREA AND BUFFER DELINEATION.....	16
BLACK BEAR DISTRIBUTION DATA	16
HABITAT PATCH IDENTIFICATION	18
PATCH ANALYSIS.....	22
METAPOPOPULATION ANALYSIS	28
SIMULATIONS	32
Source-Sink Dynamics.....	32
Reintroductions	33
V. RESULTS	34
METAPOPOPULATION ANALYSIS	34
SIMULATIONS	42
Source-Sink Dynamics.....	42
Patch Aggregate 1: 298.6 km ²	42
Patch Aggregate 2: 74.7 km ²	47
Reintroductions	51
Reintroduction Sites.....	51
Keystone Patches	55
VI. DISCUSSION	58
MODEL ASSUMPTIONS	59
PARAMETER ESTIMATES	61
AREA AND ISOLATION.....	63
SIMULATIONS	64

	Source-Sink Dynamics.....	65
	Reintroductions.....	66
VII.	MANAGEMENT AND RESEARCH IMPLICATIONS.....	67
	MANAGEMENT NEEDS.....	67
	METAPOPULATION MODELING.....	69
	LITERATURE CITED.....	71
	APPENDIX - Terminology.....	76
	VITA.....	79

LIST OF FIGURES

FIGURE		PAGE
1.	Current distribution of the American black bear (<i>Ursus americanus</i>) in the southeastern United States (from Pelton and van Manen 1997).	3
2.	The Southern Appalachian Assessment area (modified from SAMAB 1996).	11
3.	Ecological regions of the southern Appalachian region (modified from SAMAB 1996).	13
4.	Study area to determine black bear metapopulation dynamics in the southern Appalachian region, 2000.	17
5.	Suitable black bear habitat (deciduous, evergreen, and mixed forest) based on black bear telemetry locations in the southern Appalachian region, 2000	21
6.	Black bear habitat patches with spatial scale representing a small local breeding population, southern Appalachian region, 2000.	24
7.	Black bear habitat patches with spatial scale representing a large male home range, southern Appalachian region, 2000.	25
8.	Black bear habitat patches with spatial scale representing an average male home range, southern Appalachian region, 2000.	26
9.	Black bear habitat patches with spatial scale representing a female home range, southern Appalachian region, 2000.	27
10.	An illustration of centroid distances (dashed lines) versus edge distances (straight lines).	29
11.	Current black bear distribution in the southern Appalachian region, 2000.	35
12.	Model 1 (298.6-km ² patch scale): patch area, patch isolation, and patch occupancy for black bears in the southern Appalachian region, 2000. The units of area and isolation are 0.1 km ² and 1 km, respectively. J_i = predicted probability of patch occupancy.	38

13.	Model 2 (74.7-km ² patch scale): patch area, patch isolation, and patch occupancy for black bears in the southern Appalachian region, 2000. The units of area and isolation are 0.1 km ² and 1 km, respectively. J_i = predicted probability of patch occupancy.	39
14.	Model 3 (18.7-km ² patch scale): patch area, patch isolation, and patch occupancy for black bears in the southern Appalachian region, 2000. The units of area and isolation are 0.1 km ² and 1 km, respectively. J_i = predicted probability of patch occupancy.	40
15.	Model 4 (4.7-km ² patch scale): patch area, patch isolation, and patch occupancy for black bears in the southern Appalachians region, 2000. The units of area and isolation are 0.1 km ² and 1 km, respectively. J_i = predicted probability of patch occupancy	41
16.	Model 1 (298.6-km ² patch scale): patch areas, patch isolation, and patch occupancies for black bears based on edge-to-edge distances, southern Appalachian region, 2000. The units of area and isolation are 0.1 km ² and 1 km, respectively. J_i = predicted probability of patch occupancy	44
17.	Model 2 (74.7-km ² patch scale): patch areas, patch isolation, and patch occupancies for black bears based on edge-to-edge distances, southern Appalachian region, 2000. The units of area and isolation are 0.1 km ² and 1 km, respectively. J_i = predicted probability of patch occupancy	45
18.	Model 1 (298.6-km ² patch scale): black bear habitat patches in the southern Appalachian region and probability of occupancy, 2000.....	48
19.	Model 1 (298.6-km ² patch scale): black bear habitat patches in the southern Appalachian region and annual colonization probability, 2000.....	49
20.	Model 2 (74.7-km ² patch scale): black bear habitat patches in the southern Appalachian region and probability of occupancy, 2000.....	52
21.	Model 2 (74.7-km ² patch scale): black bear habitat patches in the southern Appalachian region and annual colonization probability, 2000.....	53

FIGURE	PAGE
22. Model 2 (74.7-km ² patch scale): currently unoccupied black bear habitat patch networks that represent potential reintroduction sites in the southern Appalachian region, 2000	54
23. Model 2 (74.7-km ² patch scale): annual colonization probabilities of habitat patches surrounding Big South Fork National River and Recreation Area, Kentucky/Tennessee, following a hypothetical colonization. Initial annual colonization probabilities for surrounding patches were 0.00	56
24. Model 2 (74.7-km ² patch scale): keystone patches within 2 local networks of unoccupied black bear habitat in the southern Appalachian region, 2000	57

LIST OF TABLES

TABLE		PAGE
1.	Distribution of the Southern Appalachian Assessment area by ownership (SAMAB 1996).....	12
2.	Dominant forest types, area, and total percentage within the Southern Appalachian Assessment area (SAMAB 1996).	15
3.	Frequency of black bear locations by land-cover type, southern Appalachian region, 1976–1990.	20
4.	Number of patches and size of grid cells associated with 4 patch aggregates, southern Appalachian region, 2000.	23
5.	Two methods of calculating the distance to the nearest occupied patch for patch aggregate 1 (298.6-km ² scale), southern Appalachian region, 2000.	30
6.	R^2 value, model P -value, and parameter estimates, with approximate standard errors in parentheses, for nonlinear regression models, based on Hanski's (1993) incidence function model, for black bears in the southern Appalachians, 2000.	36
7.	Correct prediction rates of patch occupancy for metapopulation models for black bears in the southern Appalachians, 2000. J_i is the actual occupancy and P is the predicted occupancy from Hanski's (1993) incidence function model.	37
8.	R^2 value, model P -value, and parameter estimates, with approximate standard error in parentheses, for nonlinear regression models, based on Hanski's (1993) incidence function model, for black bears in the southern Appalachians after removal of the 2 largest habitat patches, 2000.	43
9.	Predicted probability of occupancy (J_i) by black bears for Model 1 (298.6-km ² scale), based on edge distance calculations and given removal of selected habitat patches, southern Appalachian region, 2000. J_i values calculated using Hanski's (1993) incidence function model.	46

TABLE

PAGE

10. Annual colonization probability (C_i) of black bears for Model 1 (298.6-km² scale) based on edge distance calculations and given removal of selected habitat patches, southern Appalachian region, 2000. J_i values calculated using Hanski's (1993) incidence function model. 50

CHAPTER I

INTRODUCTION

The study of ecology seeks to explain how ecosystems function in space and time. To better understand how populations and their ecosystems operate, a communion must be made between population biology and ecology. The evolution of this new way of looking at populations and their ecology has led researchers to question many basic ecological principles. For example, a paradigm existed from the 1930s through the 1950s that wildlife populations maintained a state of equilibrium regulated by births and deaths (Begon and Mortimer 1986). More recently, it was recognized that population regulation was more chaotic than first thought, and the concept of an “unstable” equilibrium has gained popularity (Turchin 1998). Organizational patterns that allow for persistence despite such spatial and temporal variations in the environment have since been recognized for many species (Hanski 1990).

One such pattern is referred to as a metapopulation. The term *metapopulation* was first used by Levins (1970) to describe an aggregate of local populations connected by dispersal. A metapopulation is a population consisting of small, localized sub-populations that interact through periodic local extinctions and recolonizations in 1 or several habitat patches. Metapopulation theory is used to assess the dynamic interplay between periodic patch extinctions and recolonizations (Hanski 1996). These local population extinctions and recolonizations within the individual habitat patches define persistence of the local population and throughout the metapopulation.

Black bears (*Ursus americanus*) historically ranged throughout North America, but overexploitation and habitat loss has reduced that range by 38% (Pelton and van Manen 1994). In the Southeast, loss has been greater, with the species now occupying approximately 20% of its former range (Fig. 1; Pelton and van Manen 1997). Habitat fragmentation may have exacerbated this decline. Fragmentation may limit demographic exchange among populations and may make otherwise suitable habitat unavailable to bears. Bears are particularly susceptible to habitat fragmentation because females are poor colonizers (Bunnell and Tait 1981, Rogers 1977). Furthermore, because fragmentation often is patchy and occurs gradually, the cumulative effects are difficult to assess. Therefore, it is crucial that long-term, regional black bear management strategies are developed to address this dilemma.

Black bear populations in the southern Appalachians may exist as a metapopulation. If so, it is essential that managers have a good understanding of the underlying mechanisms that govern local colonizations and extinctions along with the factors most influential to the metapopulation dynamics. By identifying black bear habitat patches and analyzing the relationships between patch characteristics and occupancy of habitat patches, it may be possible to develop a black bear metapopulation model. Such a model could then be used to predict the occupancy of habitat patches and probability of population persistence in response to different scenarios of future landscape conditions. Given the removal of patches, source-sink dynamics can be interpreted and the role certain patches play in the metapopulation can be determined. Therefore, the objective of my study was to create a metapopulation model for black bears in the southern Appalachian region to test the following null hypothesis:

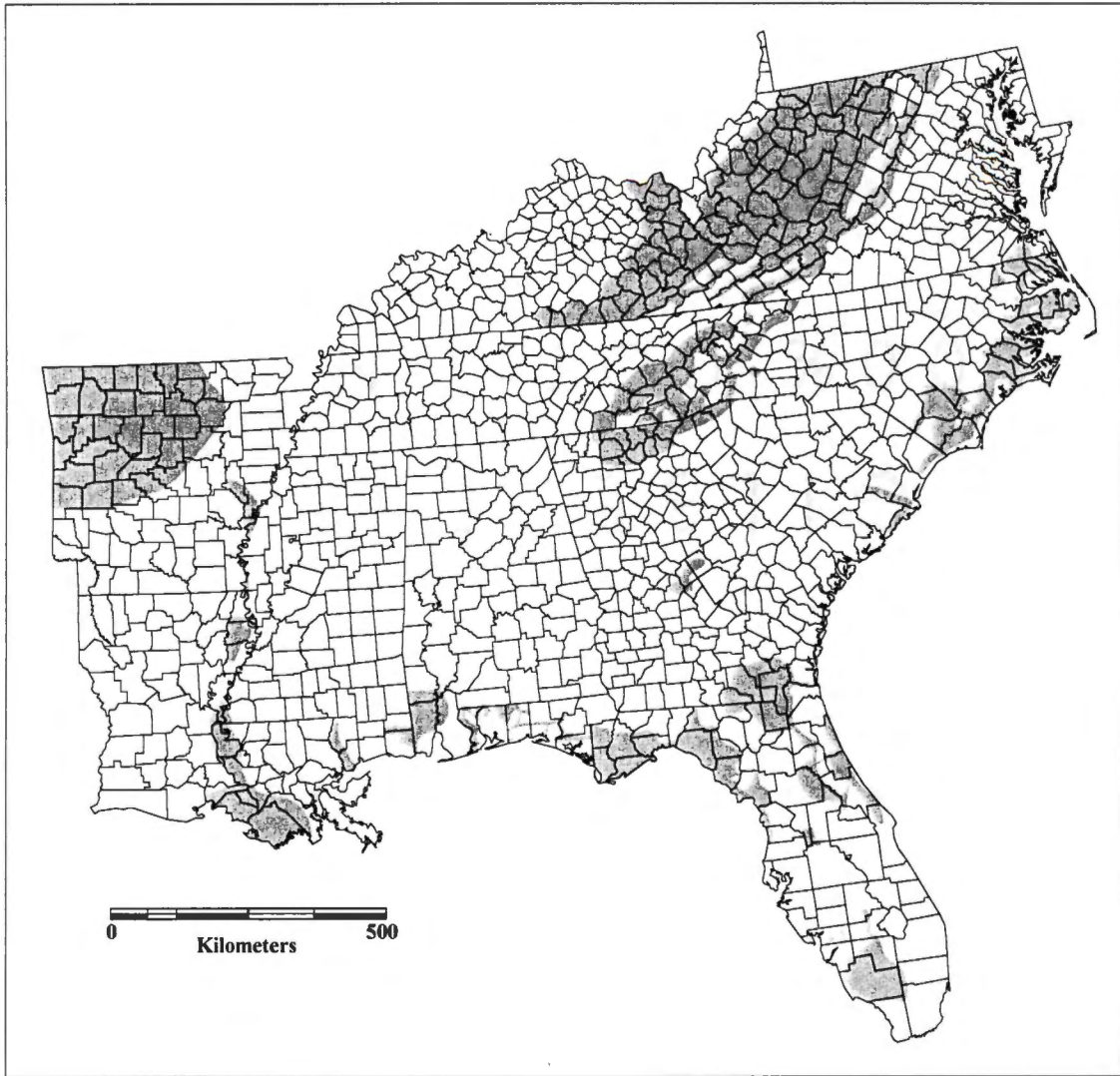


Fig. 1. Current distribution of the American black bear (*Ursus americanus*) in the southeastern United States (from Pelton and van Manen 1997).

H_0 : The probability of habitat patch occupancy by black bears does not decrease with decreasing patch area and increasing patch isolation.

CHAPTER II

THEORETICAL BACKGROUND

METAPOPULATION MODELS

Metapopulation analysis incorporates concepts from conservation biology and island biogeography theory. The well-known equilibrium theory of island biogeography from MacArthur and Wilson (1967) predicted the total number of species on islands given a certain island size and isolation as:

$$\hat{s} = \frac{IP}{E + I}, \quad (1)$$

where $\hat{s}$ is the number of species at equilibrium, I is the immigration rate, P is the number of species capable of immigrating to the island, and E is the extinction rate. The metapopulation concept is a special case of this theory; when only 1 species is considered, the population organization is extended to situations where no mainland exists, and colonizations are due to dispersal from occupied habitat patches (Hanski 1996). Single-species metapopulation analysis considers habitat patch isolation and size, evolutionary changes in colonization ability, and heterogeneity among patches (Hanski 1991).

Most metapopulation models have been conceptual, and ecologists are now trying to make models more reflective of the dynamic nature of metapopulations (Hanski 1990). Because of the complexity and multitude of models, only those models that have contributed to metapopulation theory and are relevant to my study are discussed.

One type of metapopulation model is the mainland-island model. In general, these models assume a large core population exists on a “mainland” or large habitat patch where the probability of species extinction is extremely low. Habitat patches are not assumed to be equal in size, and individuals migrate from the mainland to smaller habitat patches or “islands”, which have populations that vary in size. These models, as all single-species metapopulation models, have traditionally been classified as either spatially implicit or spatially explicit (Hanski and Gyllenburg 1993). Spatially implicit models are based on the assumption that all local populations are equally connected. Spatially implicit models usually require a permanent number of equally sized local populations and concentrate on the effects of emigration and immigration on local population abundance and stability. Spatially explicit models are based on the assumption that dispersal is density-dependent. Also, particular areas, spatial locations, and other attributes can be assigned to habitat patches using spatially explicit models (Hanski 1996).

SPATIALLY IMPLICIT MODELS

Patch Models

Patch models ignore local population size and attempt to mimic the fraction of patches occupied within the metapopulation. Levins (1970) formulated a classic example of a spatially implicit patch model, which laid the groundwork for current advances in metapopulation theory. This model was based on the notion that species can exist regionally in a network of habitat patches with an independent probability of extinction for each local population. The Levins model,

$$\frac{dp}{dt} = mp(1 - p) - ep, \quad (2)$$

estimates the rate of change in metapopulation size, p . Levins created 2 parameters that incorporated individual and population processes; e is the rate of local extinction, and m is the rate of local colonization. This simple model has been modified to describe relationships for competitive species, predator-prey interaction, and single-species metapopulation dynamics (Hanski and Gyllenberg 1993). The practicality of applying Levins' model to conservation management has been questioned (Harrison 1994); a major assumption is that a subset of local populations characterized by instability may still represent a metapopulation that is regionally stable (Sjögren-Gulve and Ray 1996). This assumption may prevent the model from identifying a metapopulation that is gradually going extinct, thereby reducing the model's value for conservation planning.

Structured Models

Structured models incorporate the effects of local dynamics and dispersal on population growth rates, whereas the assumption of equal patch size is relaxed (Hastings 1991, Gyllenburg and Hanski 1992, Hanski and Gyllenburg 1993). These types of models can also be used to characterize density-dependent dispersal and to estimate density-dependent extinction risk (Hanski and Gyllenburg 1993). Structured models are relatively general and assume that all local populations are equally connected. For example, Hanski and Gyllenburg (1993) formulated a model that incorporates both environmental heterogeneity and internal patch dynamics. The advantages of this model are that it incorporates spatial variation in patch size and the effects of migration on local

populations. It also allows for the existence of empty habitat patches regardless of a continuous flow of dispersers among the patches, as opposed to dispersal strictly between a mainland and an island.

SPATIALLY EXPLICIT MODELS

n-Population Simulation Models

Models of 2 populations can be developed by extending the single population Levins' model. However, when the model is further extended to n populations connected by dispersal, mathematical difficulties arise. In such cases, simulation techniques can be used to incorporate other aspects of dispersal, population spatial location, and stochasticity that otherwise would have been neglected (Hanski 1996). Such simulation models have the potential to answer many questions of interest, but simulation techniques have led to increased problems with interpretation, unreasonable assumptions, parameters that are difficult to estimate, and increasing specificity needed in empirical data (Hanski and Thomas 1994).

NEW MODELING METHODS

In response to the shortcomings of the metapopulation models discussed previously, scientists have tried to more accurately model the true complexity of the dynamics of local, interacting populations. Hanski (1993) developed a model that combines the advantages of structured modeling with simulation modeling. His model is based on a single-species version of MacArthur and Wilson's (1967) mainland-island equation. This model can be fit to empirical presence/absence data from identified

habitat patches with known areas and isolations by use of nonlinear regression (Hanski 1996). The structure of this model is relatively simple because it focuses only on the effects of patch area and isolation. I selected this simple metapopulation model to determine how the probability of black bear habitat patch occupancy responds to changing patch area and patch isolation in the southern Appalachians.

CHAPTER III

STUDY AREA

At the beginning of the nineteenth century the natural resources of the southern Appalachian region were heavily exploited. Erosion, deforestation, and depleted soil nutrients were the results, and this habitat degradation influenced the formation of national forests and parks in the southern Appalachian region. Currently, the southern Appalachians contain the largest concentration of federal lands in the eastern United States consisting of 7 national forests and 3 national parks. The study area was the southern Appalachian region as defined by the Southern Appalachian Assessment (SAA) and a 75-km buffer area (see Methods; Hermann 1996; Southern Appalachian Man and Biosphere (SAMAB) 1996).

The SAA covers 150,000 km² and is located within portions of Alabama, Georgia, North Carolina, South Carolina, Tennessee, West Virginia, and Virginia (Fig. 2). Over the past 20 years, human development has continued to increase as the population within this area has expanded. Over 80% of the study area is privately owned, and national parks and forests comprise over 14% of the remaining land (Table 1; SAMAB 1996).

The southern Appalachian Mountains extend northeast to southwest through the study area. The region is considered one of the most ecologically diverse temperate areas in North America, containing 10 different ecological regions (Fig. 3; SAMAB 1996). The Blue Ridge Mountains dominate the eastern portion of the study area with the



Legend

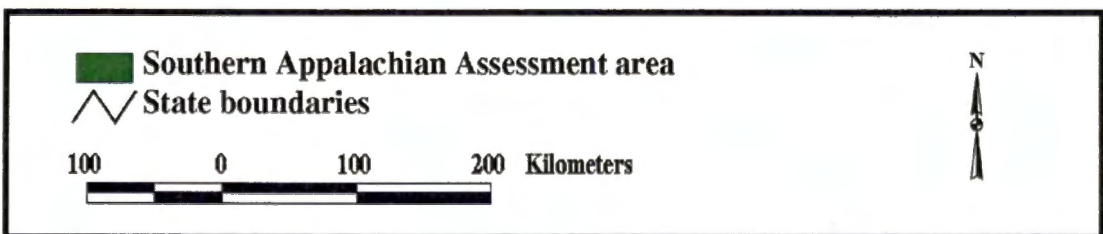
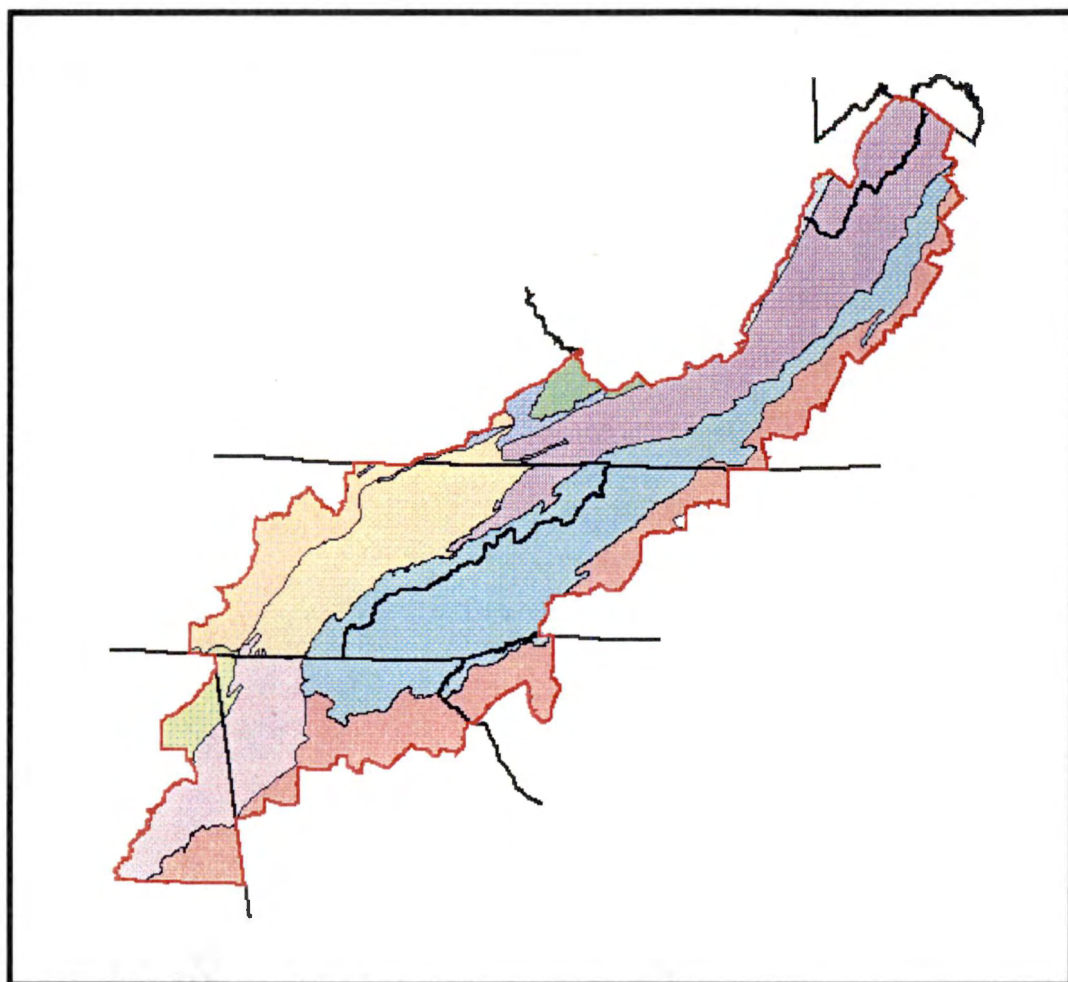


Fig. 2. The Southern Appalachian Assessment area (modified from SAMAB 1996).

Table 1. Distribution of the Southern Appalachian Assessment area by ownership (SAMAB 1996).

Land Ownership	Area (ha)	%
Cherokee Reservation	18,402	0.1
National Forests	1,844,223	12.2
National Parks	340,478	2.2
Other Federal	43,211	0.3
Private	12,571,241	83.7
State Owned	232,722	1.5



Legend

Ecoregions

- Allegheny Mountains Section
- Blue Ridge Mountains Section
- Central Ridge and Valley Section
- Northern Cumberland Mountains Section
- Northern Cumberland Plateau Section
- Northern Ridge & Valley Section
- Southern Appalachian Piedmont Section
- Southern Cumberland Mountains Section
- Southern Cumberland Plateau Section
- Southern Ridge and Valley Section

Southern Appalachian Assessment area

State boundaries

100 0 100 200 Kilometers



Fig. 3. Ecological regions of the southern Appalachian region (modified from SAMAB 1996).

Cumberland Plateau and the Central and Northern Ridge and Valley Province dominating the western portion. The Blue Ridge Mountains contain the highest peaks in the eastern United States with elevations as high as 1,829 m. Deciduous and coniferous forests covered 70% of the study area with oak (*Quercus* spp.)-hickory (*Carya* spp.) forests at lower elevations and spruce (*Picea* spp.)-fir (*Abies* spp.) forests at higher elevations. Designated wilderness and roadless lands constituted 4% of the study area, pastures made up 17.4% of the study area, 3.4% of the land was in crops, and human development covered 3.1% of the land (SAMAB 1996).

Variation in topography and climate and the presence of 9 major riverine systems have resulted in great diversity of plant and animal species within the study area. Most physiographic provinces within the southern Appalachians had a greater area of forested land than non-forested land, except for the Central Ridge and Valley areas. Deciduous forest types were dominant: oak forests, northern hardwoods, mixed mesophytic hardwoods, and bottomland hardwoods (Table 2). Approximately 80 species of amphibians and reptiles, 175 bird species, 65 mammalian species, and 2,250 vascular plant species exist in the southern Appalachians (Hamel 1992, U.S. Forest Service 1993, Boone and Aplet 1994).

Table 2. Dominant forest types, area, and total percentage within the Southern Appalachian Assessment area (SAMAB 1996).

Forest Type	Area (ha)	%
Deciduous Forest	7,136,867	47.1
Northern Hardwood	249,077	1.6
Mixed Mesophytic Hardwood	1,266,080	8.4
Oak	5,438,293	35.9
Bottomland Hardwood	183,418	1.2
Evergreen Forest	1,828,471	12.1
White Pine (<i>Pinus strobus</i>)-Hemlock (<i>Tsuga</i> spp.)	269,700	1.8
Montane Spruce-Fir	36,491	0.2
Southern Yellow Pine (<i>Pinus</i> spp.)	1,522,280	10.1
Mixed Forest	1,634,476	10.8
White Pine-Hemlock-Hardwood	336,379	2.2
Mixed Pine-Hardwood	1,298,115	8.6
Total Forest Area	21,199,647	70

CHAPTER IV

METHODS

I tested the research hypothesis by the following 3 general steps:

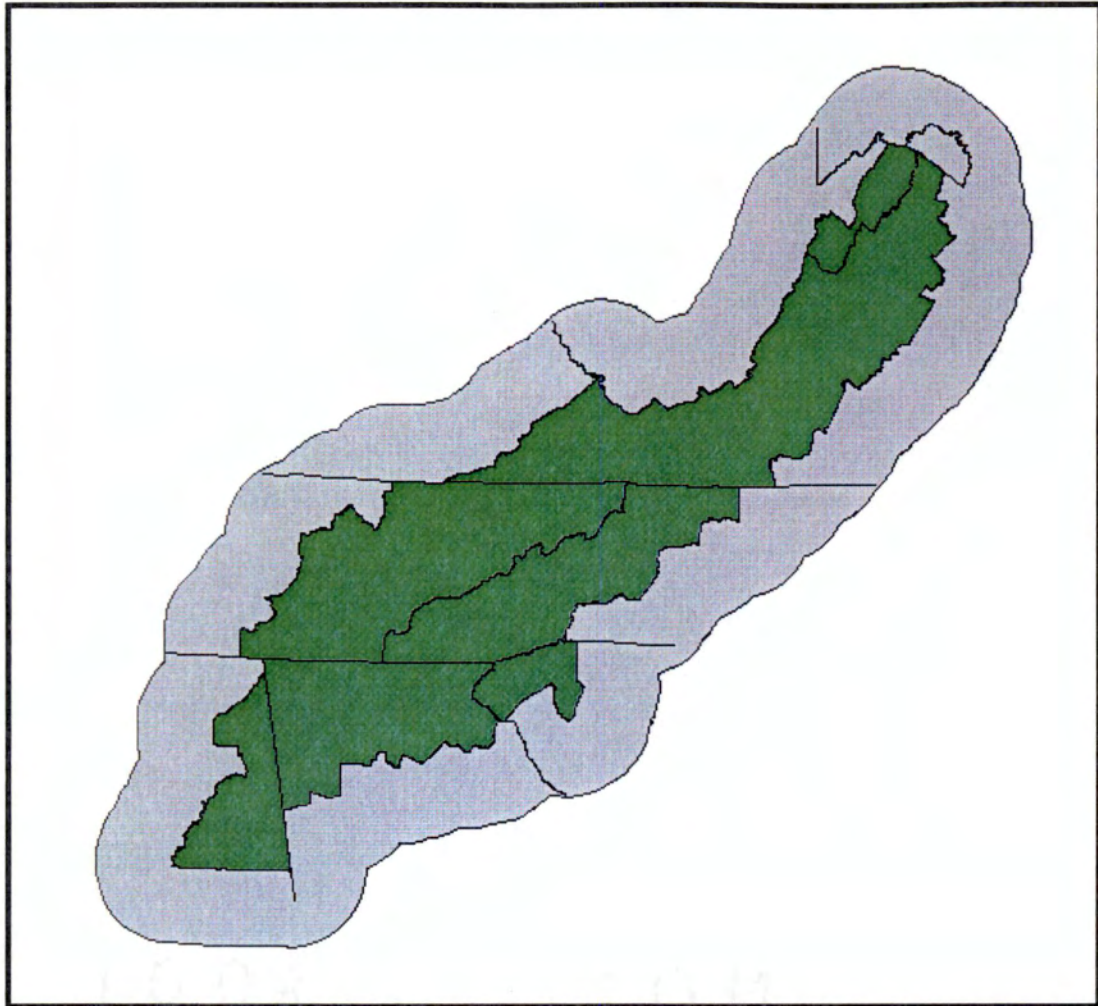
- (1) identify potential patches of black bear habitat in the southern Appalachians,
- (2) characterize each patch by area, isolation, and black bear presence, and
- (3) apply the patch characteristics to Hanski's metapopulation model (1993, 1996) to determine if a good fit could be achieved.

STUDY AREA AND BUFFER DELINEATION

A buffer area was needed to ensure that habitat patches outside the SAA were considered when determining the distance to the closest occupied patch and to account for bear dispersal. A reasonable dispersal distance for male black bears was assumed to be 75 km (Rogers 1977). Therefore, a 75-km buffer was created around the SAA boundary (Fig. 4). The resulting study area was 360,207 km² in size and incorporated the majority of the known bear distribution in the southern Appalachians.

BLACK BEAR DISTRIBUTION DATA

Occupancy of each patch was determined by updating the most recent (1993) black bear distribution data (Pelton and van Manen 1994). I received information from state and federal biologists to update range maps. I defined occupied range as areas with reproducing female bears. I digitized the new bear distribution in ArcView[®] GIS and



Legend

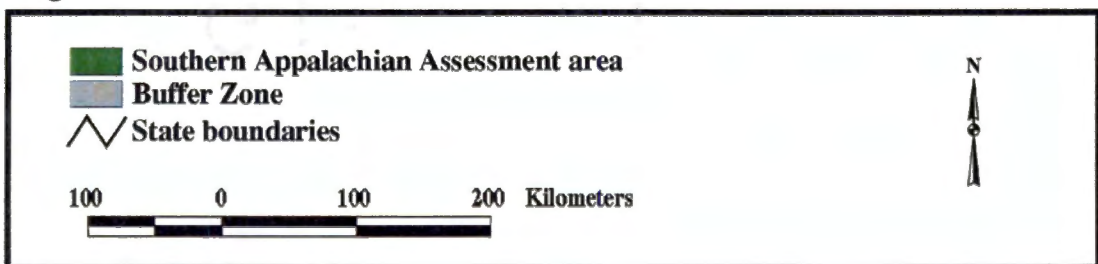


Fig. 4. Study area to determine black bear metapopulation dynamics in the southern Appalachian region, 2000.

used it to determine whether identified patches of suitable habitat were occupied or unoccupied. Habitat patches had to have at least 50% occupancy by area to be considered occupied.

HABITAT PATCH IDENTIFICATION

I used 10,113 telemetry locations to develop a habitat model that defined potential black bear habitat. Bear telemetry data were obtained from studies conducted in North Carolina and Tennessee (M. Pelton and F. van Manen, University of Tennessee), and Virginia (M. Vaughan, Virginia Polytechnic Institute and State University). Telemetry locations were selected for analysis based on the following criteria: a minimum sample of 50 locations per individual, bears had to be adults (≥ 3 years of age), and locations of each bear were collected during all 3 active seasons (April–December). The minimum sample size was used to reduce the effect of location outliers; the age requirement was used to eliminate exploratory movements of dispersing juveniles; and all 3 active seasons had to be represented to account for variance in habitat use during the year.

I wanted to identify every cell, the smallest unit of area in a set of spatial data, that had the potential to be used by a bear, regardless of what habitat surrounded that cell. I used land-cover as the primary variable to avoid biases associated with other types of data. For example, had I included a variable such as road density, telemetry locations would have a bias because many were from national parks and forests, where road densities are relatively low. Moreover, had I mapped potential bear habitat including the road density variable, many habitat patches may not have been considered because of high road density nearby. Yet, these patches may provide suitable habitat but are not

occupied because they are too small or too isolated; therefore, exclusion of such patches would ignore an important aspect of metapopulation dynamics.

The telemetry locations were overlaid with Multi-Resolution Land Cover (MRLC; Vogelmann et. al. 1998*a, b*) data (30- x 30-m cell resolution) in ARC/Info® GIS to obtain the land-cover values associated with each location. Locations of individual bears were pooled because variation among individuals was low (Table 3). The majority of locations fell within deciduous forest, evergreen forest, and mixed forest habitat types (Table 3).

Potential bear habitat was determined using the Mahalanobis distance statistic (D^2):

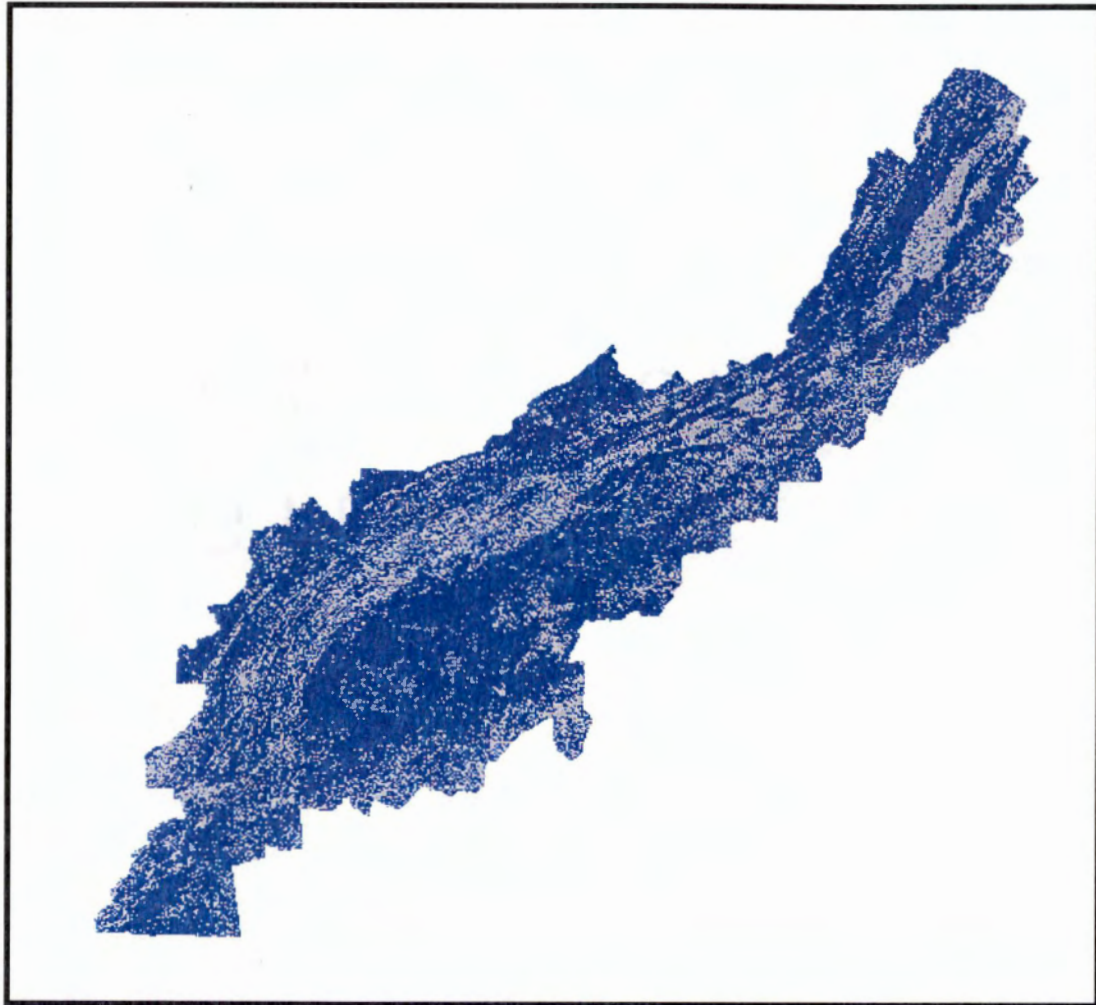
$$D^2 = (\underline{x} - \underline{\bar{u}})' \bar{\Sigma}^{-1} (\underline{x} - \underline{\bar{u}}), \quad (3)$$

where $\underline{x}$ is a vector of habitat variables associated with each cell, such as land cover type; $\underline{\bar{u}}$ is a mean vector of habitat variables estimated from the set of telemetry locations; and $\bar{\Sigma}$ is the inverse of the estimated covariance matrix, also calculated from the telemetry locations (Rao 1952, Morrison 1976:241). This statistic measures the dissimilarity between “ideal” habitat and a set of sample variates (Clark et al. 1993). Mahalanobis distance values were calculated for each 30-m cell within the study area with ARC/Info® GIS. Low values indicated habitat conditions similar to the habitat characteristics of the original bear locations. Cells with low Mahalanobis distance values (i.e., a value range that contained 75% of all bear locations) were considered suitable bear habitat. The Mahalanobis distance statistic supported classifying deciduous, evergreen, and mixed forest types as suitable habitat. These 3 habitat types were combined into a single type to delineate potential bear habitat within the study area (Fig. 5).

Table 3. Frequency of black bear locations by land-cover type^a, southern Appalachian region, 1976–1990.

Habitat Type (MRLC Code)	<i>n</i>	%
Open Water (11)	2	0.02
Developed: Low Intensity Residential (21)	3	0.03
Developed: Commercial/Industrial/Transportation (23)	8	0.08
Barren: Transitional (33)	8	0.08
Deciduous Forest (41)	6,098	60.30
Evergreen Forest (42)	1,873	18.52
Mixed Forest (43)	2,092	20.69
Pasture/Hay (81)	25	0.25
Row Crops (82)	4	0.04

^a Land-cover type based on Multi-Resolution Land Cover data (Vogelmann et al. 1998a, Vogelmann et al. 1998b).



Legend

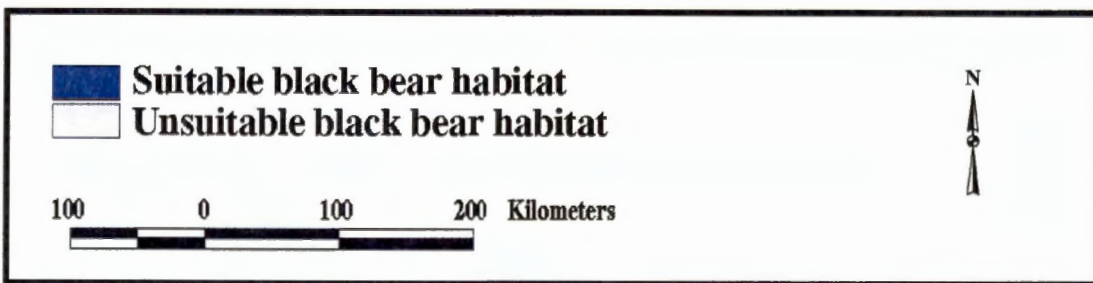


Fig. 5. Suitable black bear habitat (deciduous, evergreen, and mixed forest) based on black bear telemetry locations in the southern Appalachian region, 2000.

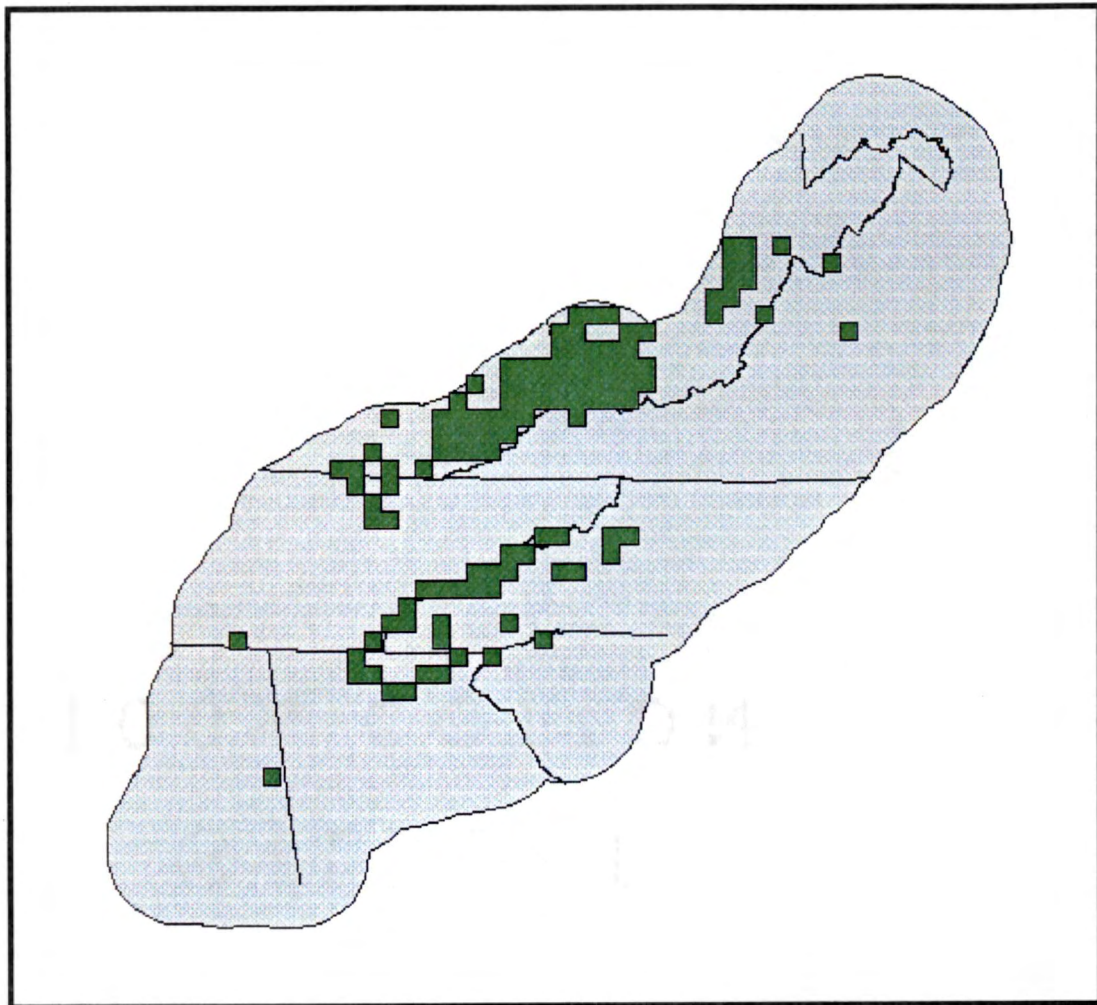
PATCH ANALYSIS

The GIS coverage of potential black bear habitat was used to define habitat patches. Patches were defined at 4 different scales with a single patch block measuring 298.6 km² (scale 1), 74.7 km² (scale 2), 18.7 km² (scale 3), and 4.7 km² (scale 4) in size. These scales were chosen based on my estimates of the area occupied by a minimum local breeding population (scale 1) and several scales representing various levels of individual male and female home ranges (scales 2–4; van Manen 1994). Patches were identified in Arc/Info[®] GIS by overlaying a square of each of the 4 scale sizes (Table 4) on the 30-m land-cover grid. If 95% of the 30-m grid cells within the larger square were suitable bear habitat, the entire square received a value of 1 (suitable bear habitat). Otherwise, a value of 0 (unsuitable bear habitat) would be assigned to the cell. I choose the 95% criterion to maintain a conservative definition of habitat patch. Also, the 95% criterion captured the largest amount of forested area while maintaining an adequate sample size of patches; the greater percentage resulted in too few patches for analysis whereas a lower percentage increased the number of patches beyond computational capabilities.

Once the 4 patch aggregates were created by manipulating scale and resolution (Table 4), a GIS coverage was created for each. Each coverage contained unique patch numbers, the area of each patch, and the coordinates of the centroid of each patch (Figs. 6–9). The distance to the nearest occupied patch was calculated for each patch using 2 techniques. I used PROC VARIOGRAM in SAS (SAS Institute, Inc. 1989) to calculate the distance from each patch centroid to the centroid of every occupied patch. The smallest distance was then selected for the analysis. These centroid distances can be

Table 4. Number of patches and size of grid cells associated with 4 patch aggregates, southern Appalachian region, 2000.

Patch Aggregate	<i>n</i>	Resolution (m)	Scale (km ²)
1	29	17,280	298.6
2	90	8,640	74.7
3	424	4,320	18.7
4	1,810	2,160	4.7



Legend

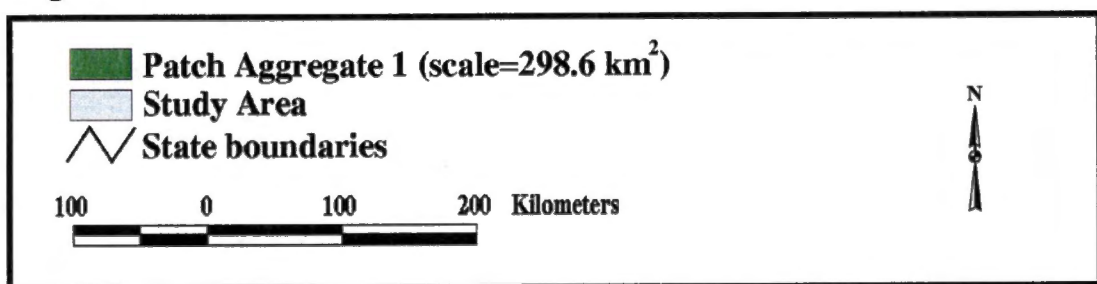
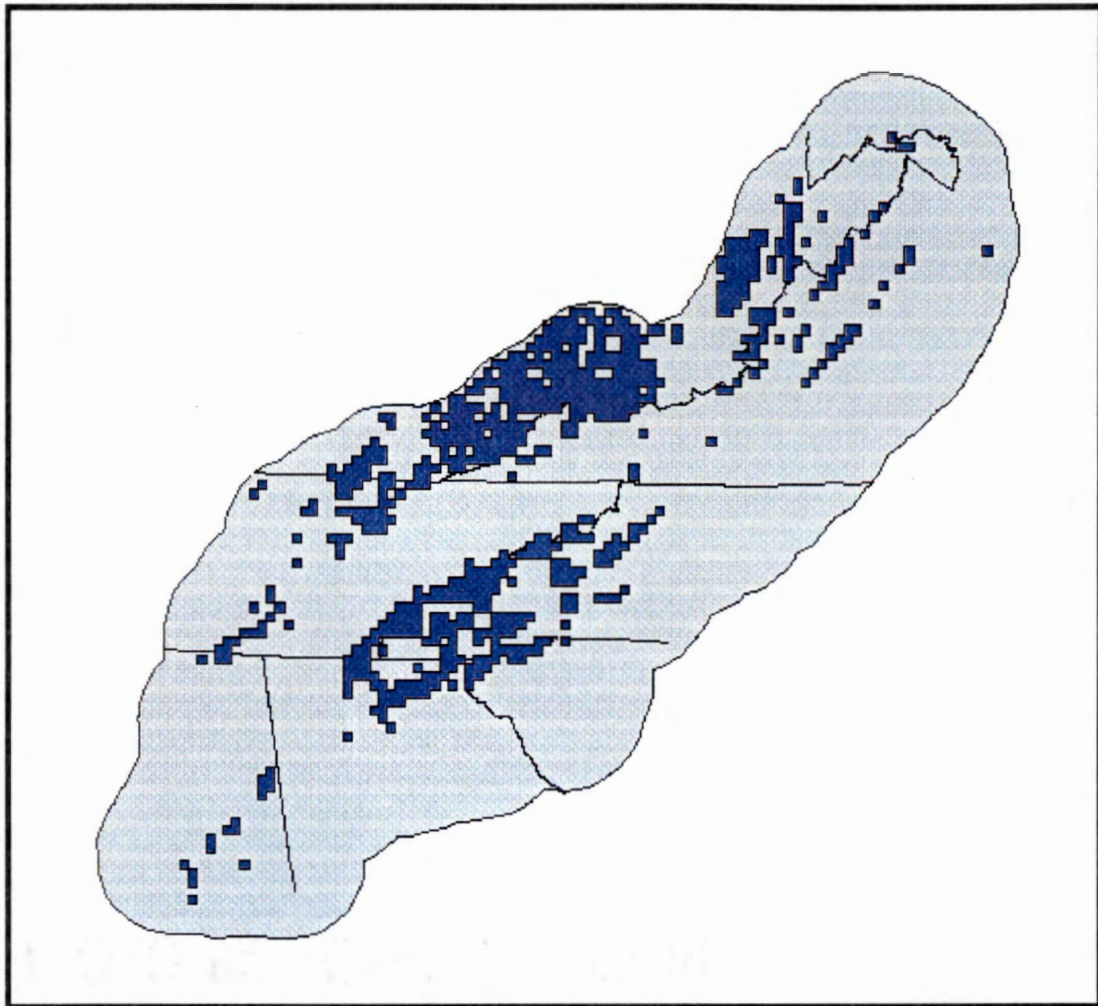


Fig. 6. Black bear habitat patches with spatial scale representing a small local breeding population, southern Appalachian region, 2000.



Legend

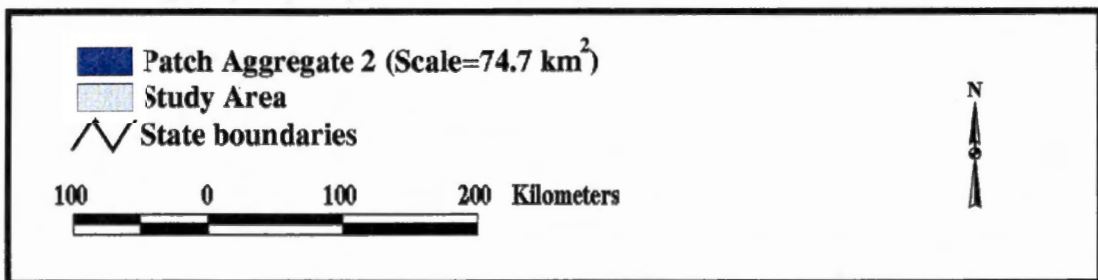
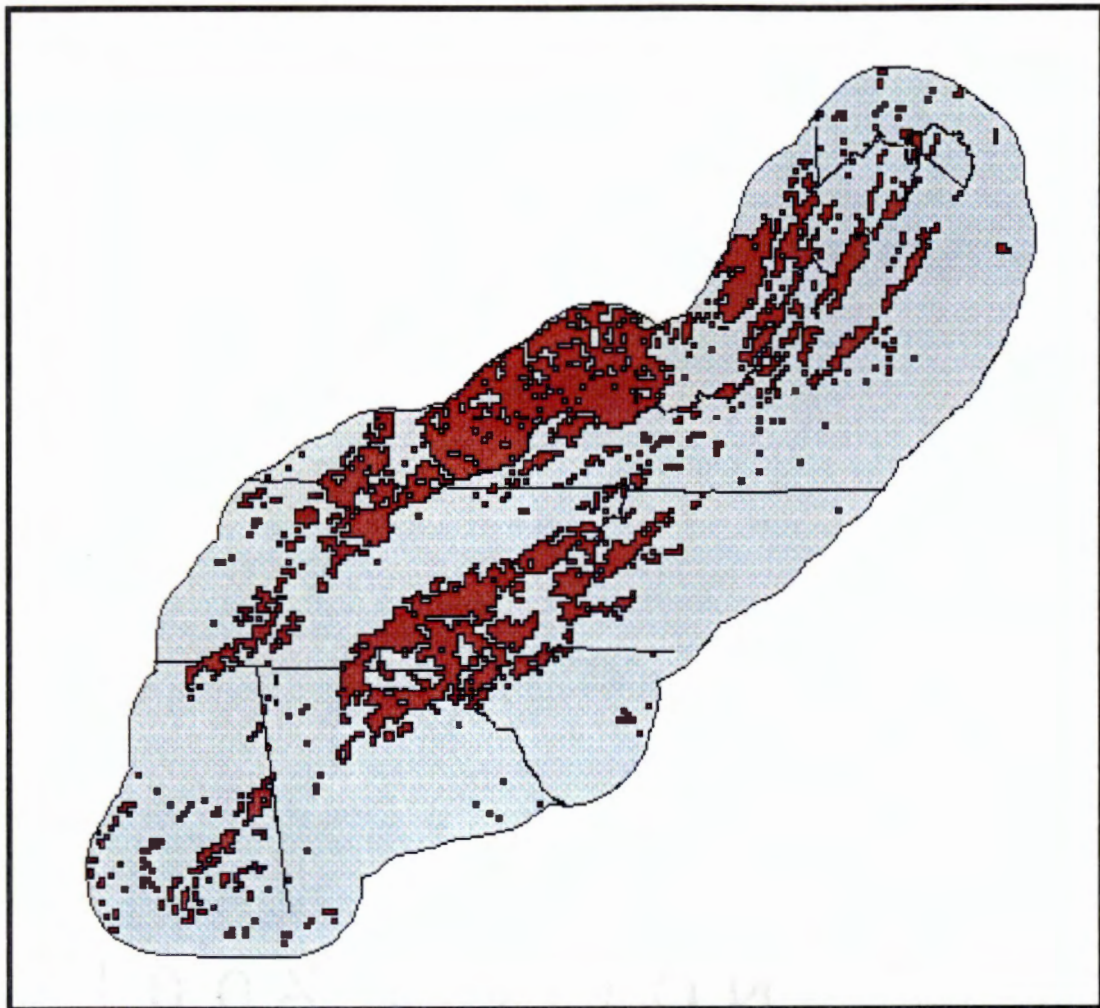


Fig. 7. Black bear habitat patches with spatial scale representing a large male home range, southern Appalachian region, 2000.



Legend

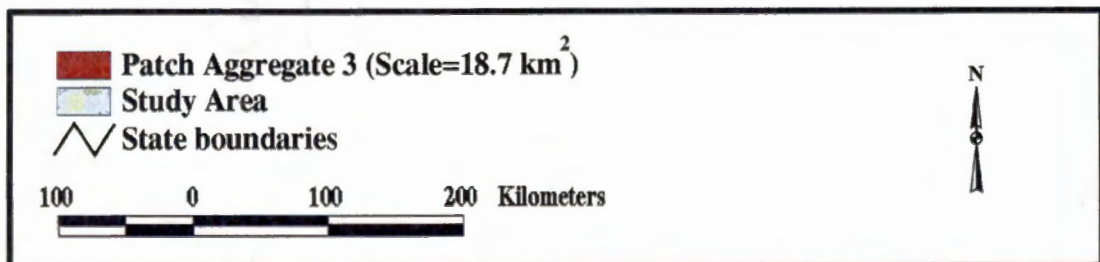
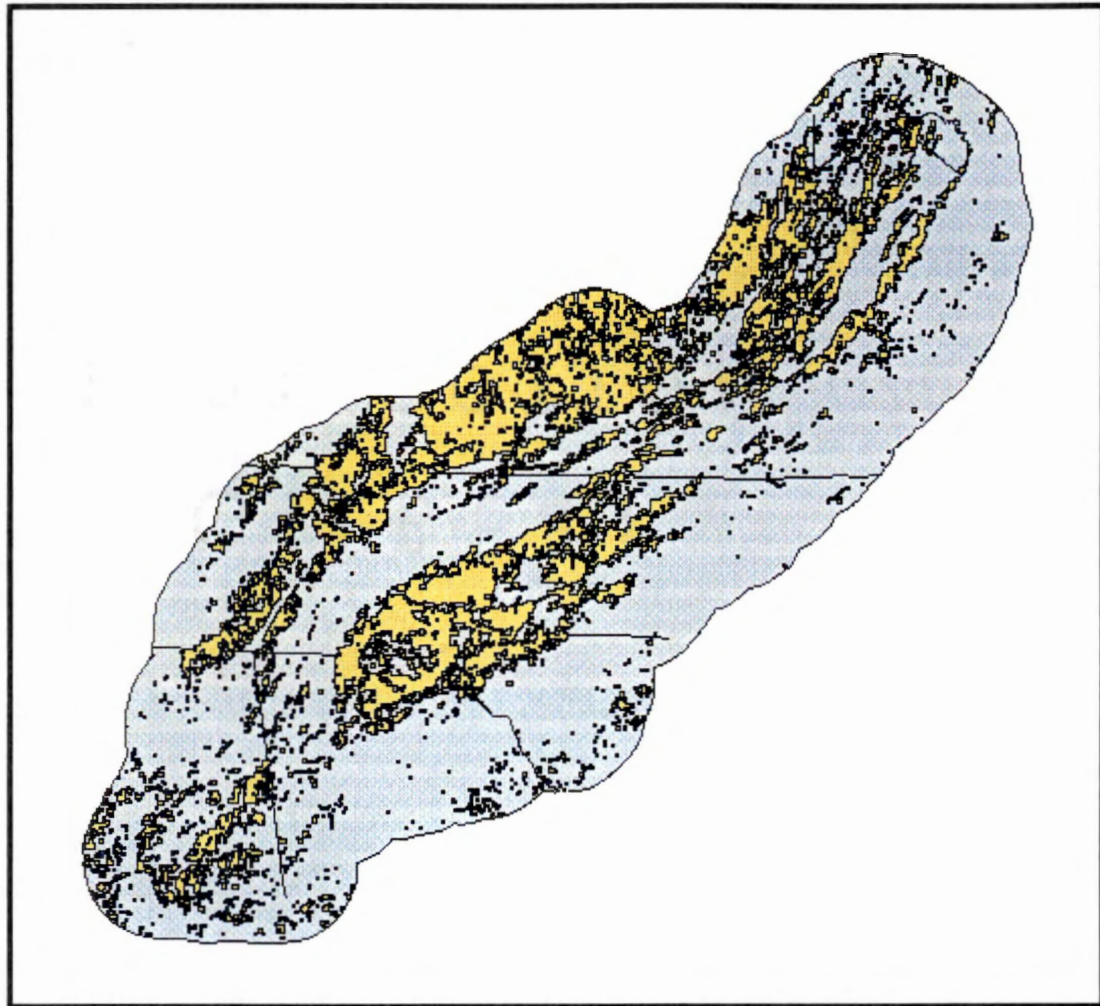


Fig. 8. Black bear habitat patches with spatial scale representing an average male home range, southern Appalachian region, 2000.



Legend

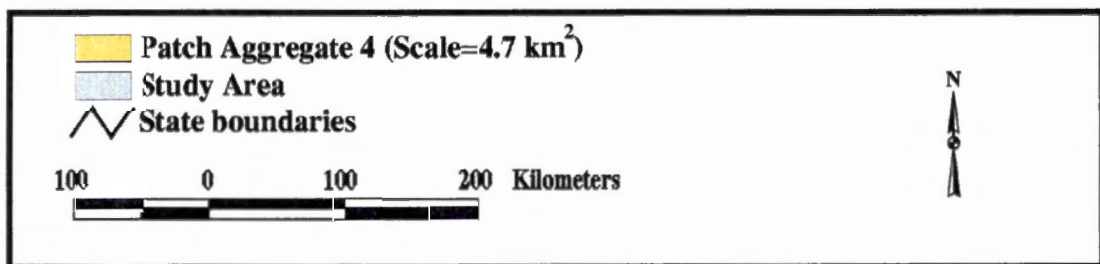


Fig. 9. Black bear habitat patches with spatial scale representing a female home range, southern Appalachian region, 2000.

biased because of patch size, so I also calculated distances between the nearest edge of each polygon pair for scales 1 and 2 in ArcView® GIS using the Pythagorean theorem (Fig. 10 and Table 5).

METAPOPULATION ANALYSIS

I used a simple mainland-island incidence function model (Hanski 1993) to determine if patch isolation and area could explain occupancy of habitat patches by black bears. The model is based on the assumption that there is a mainland population where population extinction does not occur. Several large occupied patches (e.g., Great Smoky Mountains National Park and eastern Kentucky) may serve as mainlands within the southern Appalachian landscape. However, given the stringent requirements of patch allocation (95% forest) and bear distribution (reproducing females) and the presence of stable to slightly increasing populations in the southern Appalachians (Pelton et al. 1999), most occupied patches are assumed to serve as mainlands. Therefore, the distance to the nearest occupied patch was substituted for the isolation from the mainland although occupied patches are still assumed to have some probability of extinction, especially given limited female dispersal capabilities.

Hanski (1993, 1996) found that the following parameters can be estimated if presence/absence data exist for patches of habitat: the risk of extinction of a population living in a certain patch, the decline in extinction risk with increasing patch area, and the decline of the colonization probability with increasing isolation. I used the black bear distribution data and the identified habitat patches for the southern Appalachians to employ the following metapopulation model (Hanski 1993),

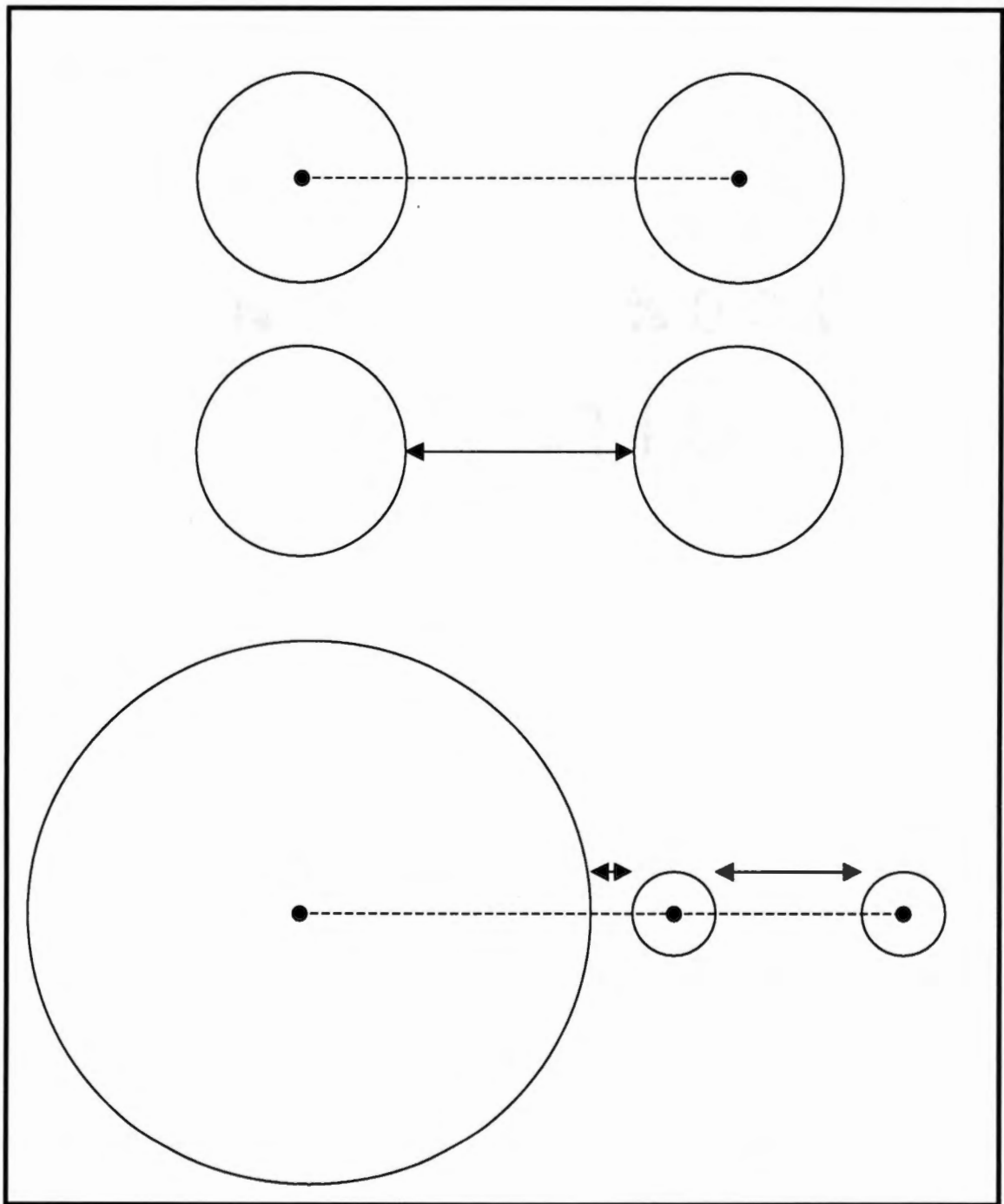


Fig. 10. An illustration of centroid distances (dashed lines) versus edge distances (straight lines).

Table 5. Two methods of calculating the distance to the nearest occupied patch for patch aggregate 1 (298.6-km² scale), southern Appalachian region, 2000.

Patch ID	Area (km ²)	Isolation: Centroid (km)	Isolation: Edge (km)
2	2,690	49	17
3	300	55	17
4	300	55	35
5	16,420	156	52
6	300	49	17
8	300	71	52
9	300	69	9
10	300	159	35
11	300	159	52
12	900	148	69
14	600	128	35
15	300	116	9
16	900	105	55
17	600	39	9
18	900	58	17
19	2,990	62	9
20	600	39	17
21	900	37	9
22	600	31	9
23	300	39	17
24	300	132	104
25	300	27	9
26	300	39	17
27	900	27	9
28	300	31	9
29	300	35	17
30	600	31	9
31	600	39	9
32	300	147	111

$$J_i = \frac{1}{1 + \frac{\beta\mu e^{\alpha D_i}}{A_i^x}}, \quad (4)$$

where J_i is the incidence of species presence in patch i , D_i is the isolation of a habitat patch in distance units, β is the probability of colonization of an empty patch with no isolation ($D_i = 0$), μ is the risk of extinction per unit time of a population living in a patch of unit size, x is the rate of decline in extinction risk with increasing patch area, α determines how rapidly the colonization probability declines with increasing isolation, and A is the area of a patch. The unknown incidence of J_i was replaced by p_i , the presence ($p = 1$) or the absence ($p = 0$) of bears in patch i (Hanski 1996).

This model is based on several assumptions:

- (1) patches are correctly classified as occupied or unoccupied,
- (2) habitat patches must be small, discrete, and make up a small portion of the landscape ($\leq 20\%$),
- (3) there must be substantial variation in patch size and isolation,
- (4) a mainland with no significant probability of extinction is present in the patch network, and
- (5) extinction and colonization are functions of patch area and isolation, respectively.

I also assumed that $\beta = 1$; given the mobility of black bears (Rogers 1987), a habitat patch with no isolation from other occupied patches will likely be occupied as well.

The parameters μ , x , and α were then estimated from the metapopulation model with nonlinear regression (Hanski 1993). This nonlinear regression model allows for the

combination of multiple parameters that have a nonlinear relationship. The nonlinear regression analysis determines the values of such parameters from an equation of specified form that result in the best fit to a set of data values. The percent of variation explained by the models (R^2) was calculated by

$$R^2 = 1 - \frac{RSS}{TSS}, \quad (5)$$

where RSS is the residual sum of squares and TSS is the corrected total sum of squares (A. Saxton, University of Tennessee, USA, personal communication).

The annual colonization probability C_i was calculated using the following equation:

$$C_i = \beta e(-\alpha d_i), \quad (6)$$

where α , estimated by nonlinear regression (Equation 4), determines how rapidly the colonization probability declines with increasing isolation and d_i is the distance to the nearest occupied patch. Again, I assumed that $\beta = 1$ for black bears. I also assumed that for an unoccupied patch, the nearest occupied patch would act as a mainland population.

SIMULATIONS

Source-Sink Dynamics

I defined the relationships between the probability of occupancy and certain landscape characteristics associated with each patch to estimate the effects of landscape changes on the persistence of black bear populations. To do so, I assessed large patch source-sink dynamics by assuming that the 2 largest patches were not occupied in the 2

largest patch aggregates (scales 298.6 km² and 74.7 km²). I then calculated isolation based on edge-to-edge distances after removing the patches containing Great Smoky Mountains National Park and eastern Kentucky (the 2 largest patches in each patch network) and subsequently recalculated the probability of species occurrence and colonization. Eastern Kentucky and Great Smoky Mountains National Park were removed separately and then together.

Reintroductions

A better understanding of the effects of bear reintroductions on the probability of occurrence in surrounding areas is critical. To illustrate this, I identified potential reintroduction sites and hypothetically colonized ($J_i = 1$) them to represent a successful reintroduction. These areas were identified based on an area ≥ 300 km² and isolation such that bears are not likely to be able to successfully colonize the area within the next 25 years. Isolations were calculated using the standard centroid method, and resultant changes in annual colonization probabilities were recalculated. In so doing, the best potential release sites were identified by determining which patches, if recolonized, would facilitate the highest increase in the annual colonization probability of surrounding patches. This was done by “colonizing” individual patches with all other patches remaining unoccupied and recalculating annual colonization probabilities. This process was continued, patch by patch, until I identified the patch that caused the highest overall increase in annual colonization probability of adjacent patches.

CHAPTER V

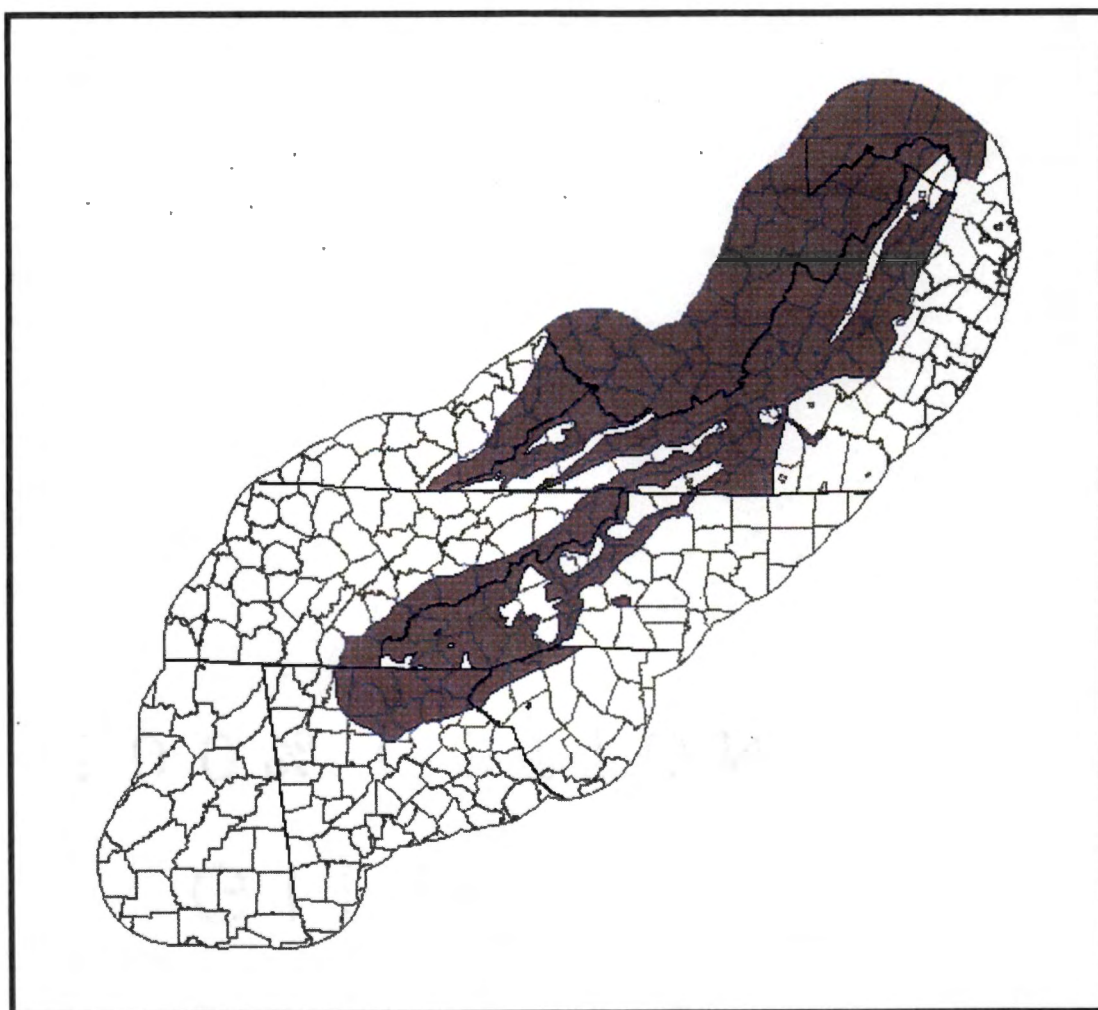
RESULTS

METAPOPULATION ANALYSIS

The current black bear distribution in the southern Appalachians comprised 34% of the study area (Fig. 11). Alabama was the only state without occupied black bear habitat within the study area.

Four different scales were examined using Hanski's (1993) incidence function model. Application of the nonlinear regression models resulted in statistical significance for all models ($P < 0.001$, $R^2 = 0.69$ – 0.90) and all 4 models had high rates of correctly classified predictions of occupancy (Tables 6 and 7). Model 1, with a scale of approximately 300 km^2 , explained the most variation ($R^2 = 0.90$). However, standard errors of the parameter estimates were high ($SE = 0.093$ – 34.779), which likely was related to the small sample size ($n = 29$ patches). Model 2 also explained much variation ($R^2 = 0.81$), and the standard errors of the parameter estimates were smaller than those of model 1 ($SE = 0.015$ – 0.409). The lowest amount of variation was explained by model 3 ($R^2 = 0.69$) and standard errors were similar to model 2. Model 4 explained 75% of the variation in the data ($R^2 = 0.75$), and had the lowest standard errors ($SE = 0.002$ – 0.080).

Isocline graphs for the 4 models illustrated the relationship between patch area and isolation in relation to patch occupancy at 3 probabilities of occurrence ($J_i = 90\%$, 50% , and 10% ; Figs. 12–15). These graphs indicate that patch occupancy was shown to be influenced by patch area and, particularly, patch isolation. Therefore, I rejected the



Legend

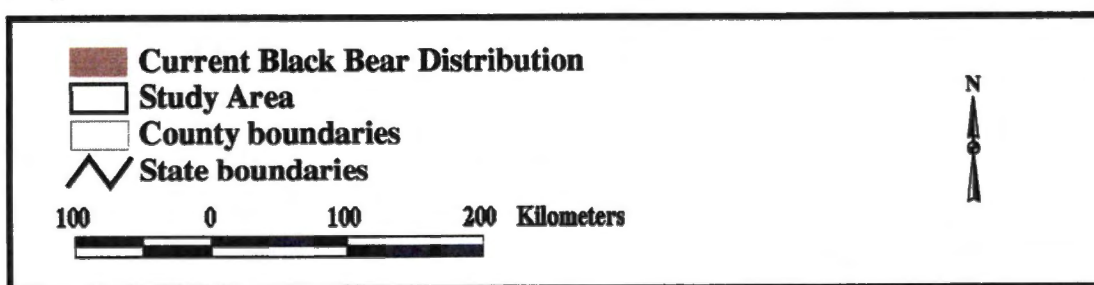


Fig. 11. Current black bear distribution in the southern Appalachian region, 2000.

Table 6. R^2 value, model P -value, and parameter estimates, with approximate standard errors in parentheses, for nonlinear regression models, based on Hanski's (1993) incidence function model, for black bears in the southern Appalachians, 2000

Model	R^2	Prob.	μ^a (SE)	χ^b (SE)	α^c (SE)
1	0.90	<0.001	16.322 (34.780)	4.983 (2.234)	0.203 (0.093)
2	0.81	<0.001	0.036 (0.040)	0.494 (0.409)	0.067 (0.015)
3	0.69	<0.001	0.113 (0.032)	0.985 (0.243)	0.123 (0.016)
4	0.75	<0.001	0.011 (0.002)	0.847 (0.080)	0.383 (0.022)

^a μ = Risk of extinction per unit time of a population living in a patch of unit size.

^b χ = Rate of decline in extinction risk with increasing patch area.

^c α = A parameter that determines how rapidly the colonization probability declines with increasing isolation.

Table 7. Correct prediction rates of patch occupancy for metapopulation models for black bears in the southern Appalachians, 2000. J_i is the actual occupancy and P is the predicted occupancy from Hanski's (1993) incidence function model.

Classification	Model 1	Model 2	Model 3	Model 4
$J_i = 1 \ P_i = 1$ Correct Presence	95 %	98 %	96 %	93 %
$J_i = 0 \ P_i = 0$ Correct Absence	89 %	88 %	82 %	92 %

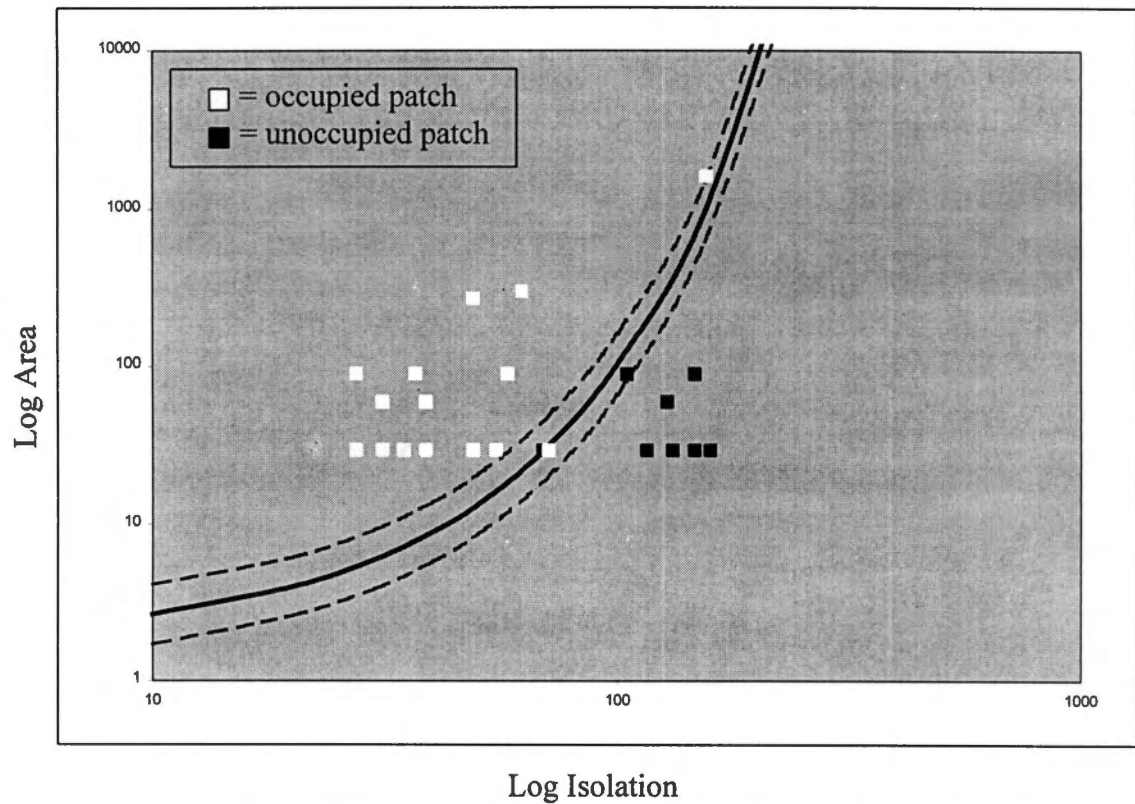


Fig. 12. Model 1 (298.6-km² patch scale): patch area, patch isolation, and patch occupancy for black bears in southern Appalachian region, 2000. The units of area and isolation are 0.1 km² and 1 km, respectively. J_i = predicted probability of patch occupancy.

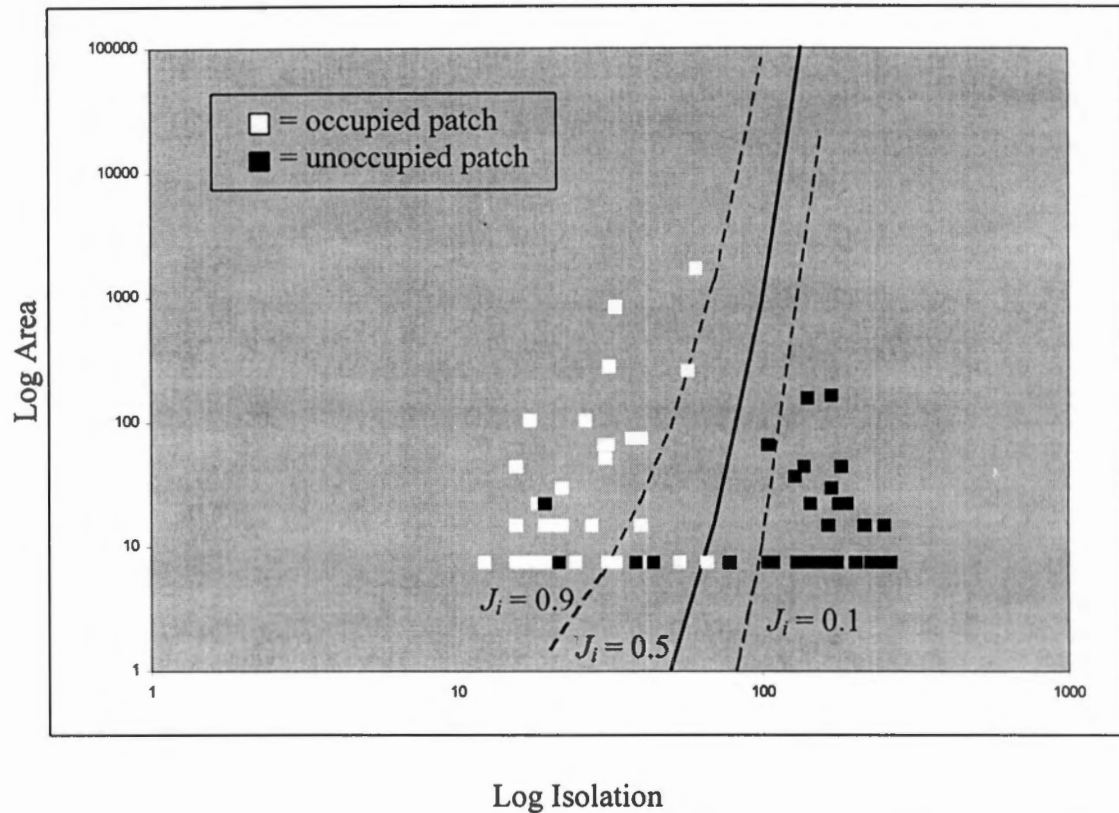


Fig. 13. Model 2 (74.7-km² patch scale): patch area, patch isolation, and patch occupancy for black bears in southern Appalachian region, 2000. The units of area and isolation are 0.1 km² and 1 km, respectively. J_i = predicted probability of patch occupancy.

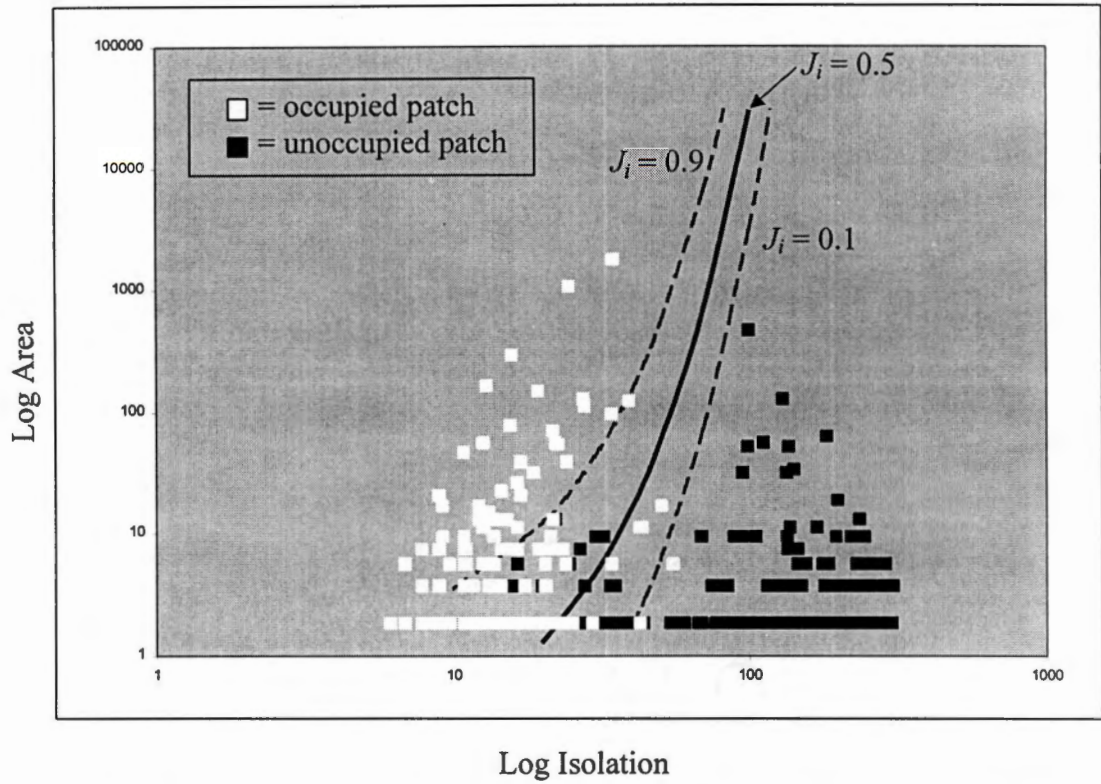


Fig. 14. Model 3 (18.7-km^2 patch scale): patch area, patch isolation, and patch occupancy for black bears in southern Appalachian region, 2000. The units of area and isolation are 0.1 km^2 and 1 km , respectively. J_i = predicted probability of patch occupancy.

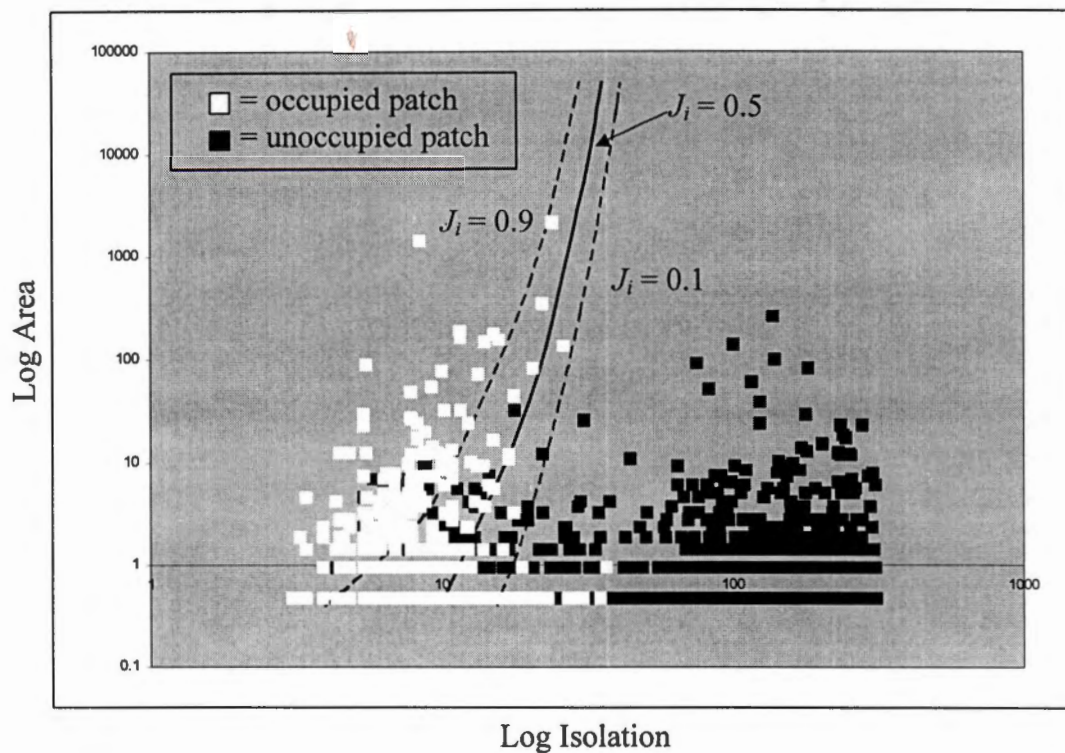


Fig. 15. Model 4 (4.7-km² patch scale): patch area, patch isolation, and patch occupancy for black bears in southern Appalachian region, 2000. The units of area and isolation are 0.1 km² and 1 km, respectively. J_i = predicted probability of patch occupancy.

null hypothesis that decreasing patch area and increasing patch isolation does not decrease the probability of habitat patch occupancy by black bears.

SIMULATIONS

Source-Sink Dynamics

Patch aggregates 1 and 2 were chosen for patch removal and recalculation of the probability of species occurrence. Parameter estimates were recalculated (Table 8) for these 2 patch aggregates based on edge-to-edge isolation distances. Models 1 and 2 had lower R^2 values (0.43 and 0.64, respectively) and greater standard errors of the parameter estimates than the models based on centroid distances. Model 1 had the smallest sample size ($n = 29$), and because of my assumption that all occupied patches can act as mainlands, a few small and unoccupied patches near large patches had more influence on the model. Neither model predicted occupancy as well as the models based on centroid distances. However, isocline trends were similar for both centroid and edge-to-edge isolation calculations (Figs. 16 and 17).

Patch Aggregate 1: 298.6 km².—When Great Smoky Mountains National Park was removed to determine what source-sink role it may play, 7.1% of the patches experienced a decrease in probability of occupancy (Table 9). Assuming that a probability ≥ 0.50 represents occupancy, none of these patches changed from occupied to unoccupied. Removing eastern Kentucky resulted in a decrease in probability of occupancy for 21.4% of the patches (Table 9). Fifty percent of those patches had values predicting a change from occupied to unoccupied. When both Great Smoky Mountains National Park and eastern Kentucky were removed, 29.6% of the patches experienced a

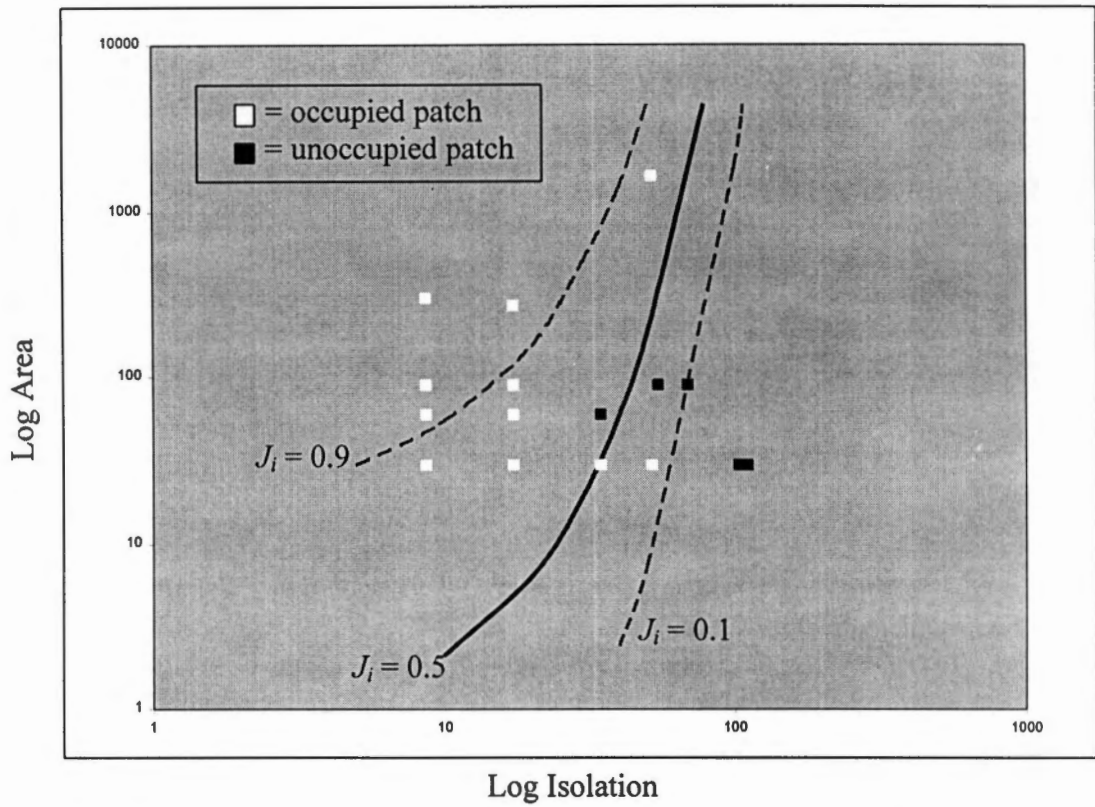
Table 8. R^2 value, model P -value, and parameter estimates, with approximate standard error in parentheses, for nonlinear regression models, based on Hanski's (1993) incidence function model, for black bears in the southern Appalachians after removal of the 2 largest habitat patches, 2000.

Model	R^2	Prob.	μ^a (SE)	χ^b (SE)	α^c (SE)
1	0.43	<0.001	0.784 (1.720)	0.690 (0.601)	0.076 (0.033)
2	0.64	<0.001	0.043 (0.059)	0.245 (0.583)	0.168 (0.051)

^a μ = Risk of extinction per unit time of a population living in a patch of unit size.

^b χ = Rate of decline in extinction risk with increasing patch area.

^c α = A parameter that determines how rapidly the colonization probability declines with increasing isolation.



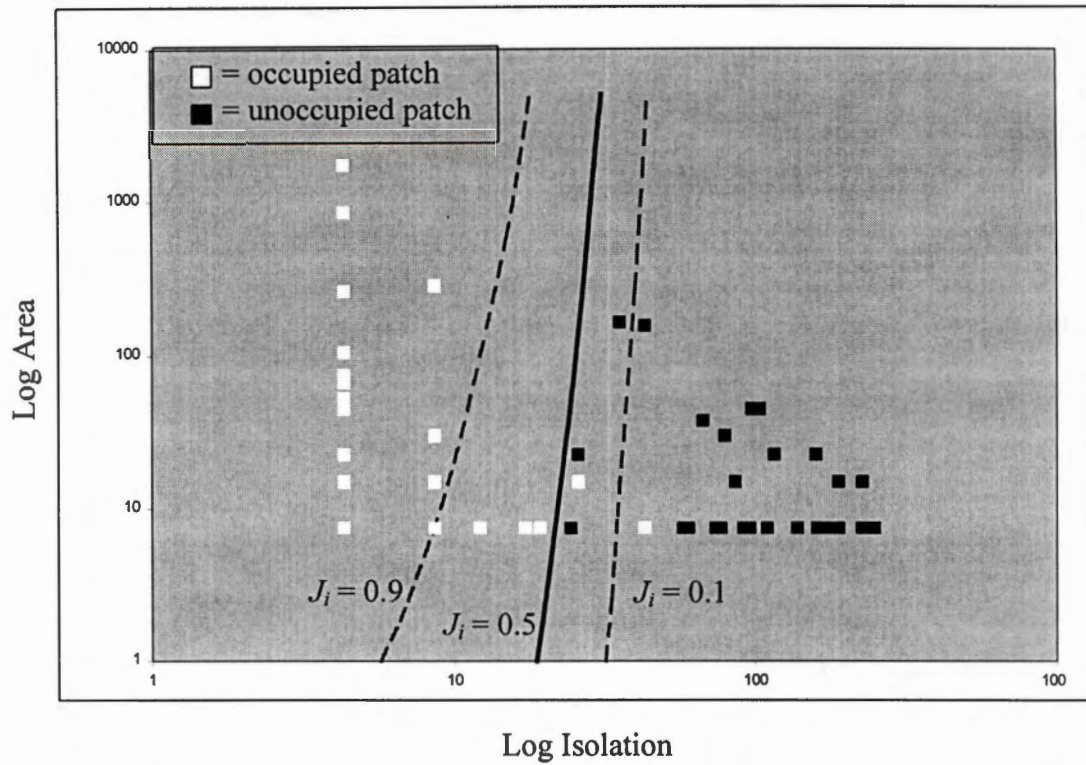


Fig. 17. Model 2 (74.7-km² patch scale): patch areas, patch isolation, and patch occupancies for black bears based on edge-to-edge distances, southern Appalachian region, 2000. The units of area and isolation are 0.1 km² and 1 km, respectively. J_i = predicted probability of patch occupancy.

Table 9. Predicted probability of occupancy (J_i) by black bears for Model 1 (298.6-km² scale), based on edge distance calculations and given removal of selected habitat patches, southern Appalachian region, 2000. J_i values calculated based on Hanski's (1993) incidence function model.

Patch ID	J_i (all)	J_i (GSMNP ^a removed)	J_i (KY removed)	J_i (GSMNP and KY removed)
2	0.94	0.94	0.94	0.94
3	0.78	0.78	0.78	0.78
4	0.49	0.49	0.49	0.49
5	0.80	0.80	removed	removed
6	0.78	0.78	0.78	0.78
8	0.20	0.20	0.20	0.20
9 ^b	0.87	0.87	0.00	0.00
10 ^b	0.49	0.49	0.00	0.00
11 ^b	0.20	0.20	0.00	0.00
12 ^b	0.13	0.13	0.02	0.01
14 ^b	0.61	0.61	0.03	0.01
15 ^b	0.87	0.87	0.01	0.00
16 ^b	0.31	0.20	0.31	0.13
17 ^b	0.92	0.85	0.92	0.85
18	0.88	0.88	0.88	0.88
19	0.97	removed	0.97	removed
20	0.85	0.85	0.85	0.85
21	0.94	0.94	0.94	0.94
22	0.92	0.92	0.92	0.92
23	0.78	0.78	0.78	0.78
24	0.01	0.01	0.01	0.01
25	0.87	0.87	0.87	0.87
26	0.78	0.78	0.78	0.78
27	0.94	0.94	0.94	0.94
28	0.87	0.87	0.87	0.87
29	0.78	0.78	0.78	0.78
30	0.92	0.92	0.92	0.92
31	0.92	0.92	0.92	0.92
32	0.00	0.00	0.00	0.00

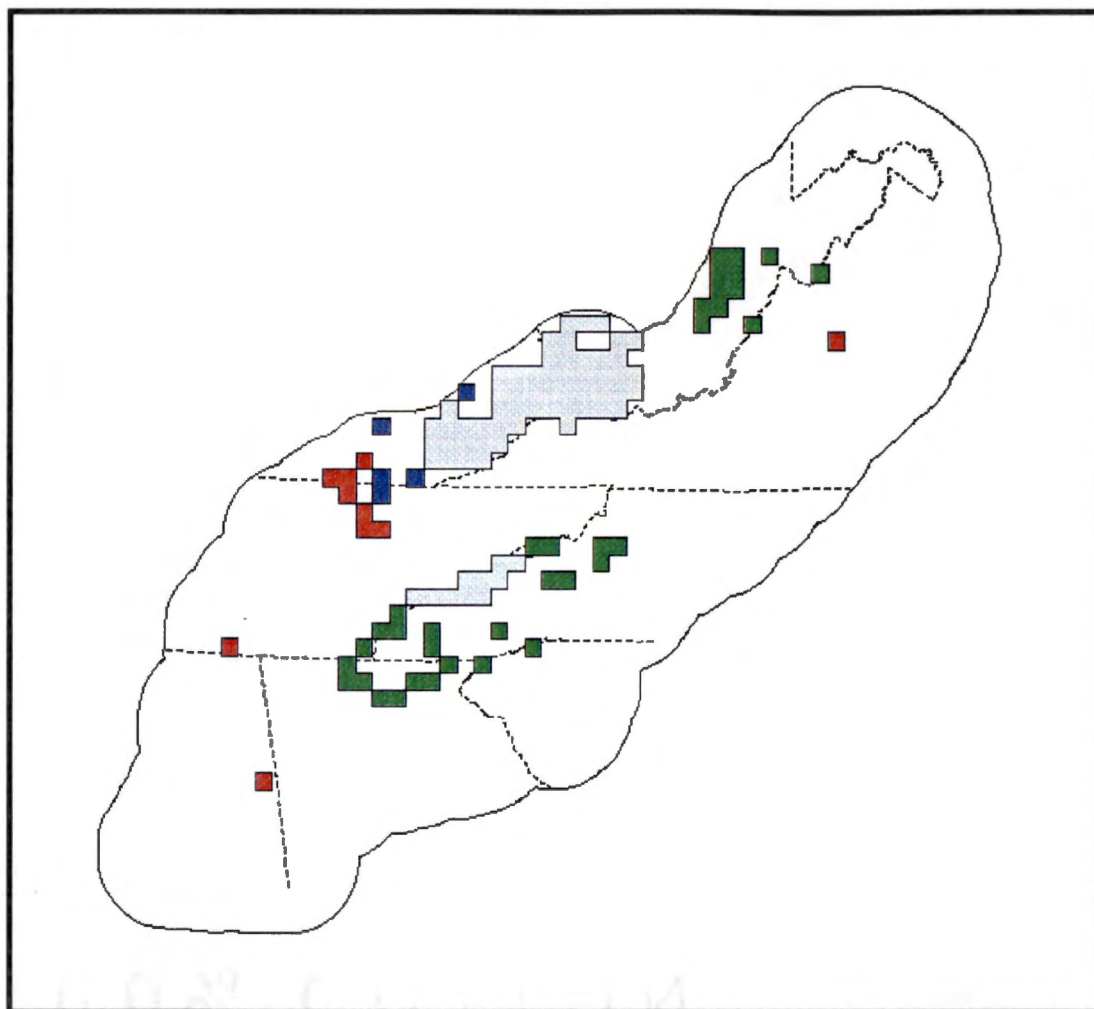
^a GSMNP = Great Smoky Mountains National Park.

^b Patches experiencing noticeable changes in probability of occurrence (>0.025).

decrease in probability of occupancy (Table 9). Of those patches, 38% had values that predicted a change from occupied to unoccupied habitat (Fig. 18). Colonization probabilities for model 1 followed a similar pattern as the probabilities of occupancy (Fig. 19). After Great Smoky Mountains National Park was removed, 3.6% of the remaining patches experienced a decrease in the annual colonization probability to <0.25 (Table 10). When eastern Kentucky was removed, the probability of colonization decreased for 21.5% of the patches. Thirty-three percent of those patches had values that changed prediction from above to below 25% (Table 10). When both Great Smoky Mountains National Park and eastern Kentucky were removed, 26% of the remaining patches experienced a significant decrease in colonization probability. Forty-three percent of those patches experienced a decrease in annual colonization probability from above to below 0.25 (Table 10).

Overall, when patches representing Great Smoky Mountains National Park and eastern Kentucky were removed from models 1 and 2, nearby patches experienced some decrease in the probability of occurrence. This decrease usually was small, except when remaining occupied patches were great distances away (e.g., Table 9: patch ID# 14). Colonization probabilities only decreased slightly unless occupied patches were separated by great distances.

Patch Aggregate 2: 74.7 km².—Removing Great Smoky Mountains National Park resulted in a decrease in probability of occupancy in 7.9% of the remaining patches. Forty-three percent of those patches had values that changed prediction from occupied ($J_i \geq 0.50$) to unoccupied ($J_i < 0.50$). When eastern Kentucky was removed, the probability of occupancy decreased for 10.1% of the patches. Forty-four percent of those patches



Legend

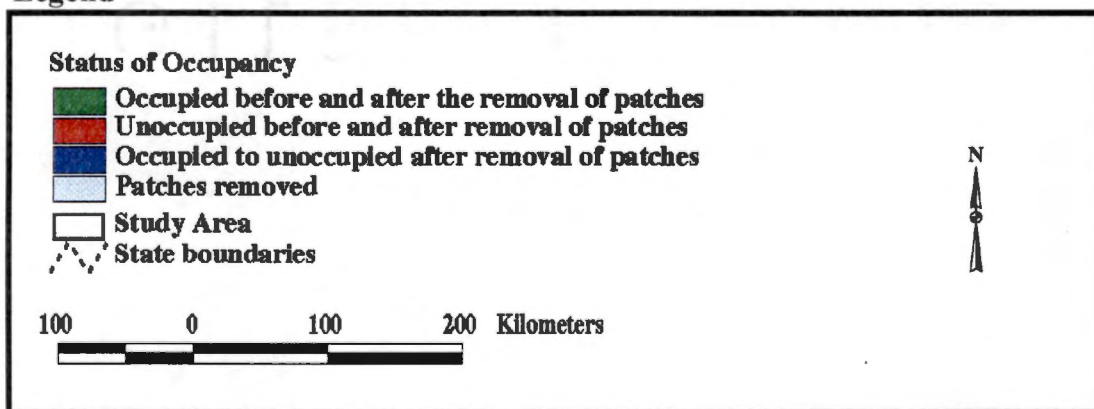
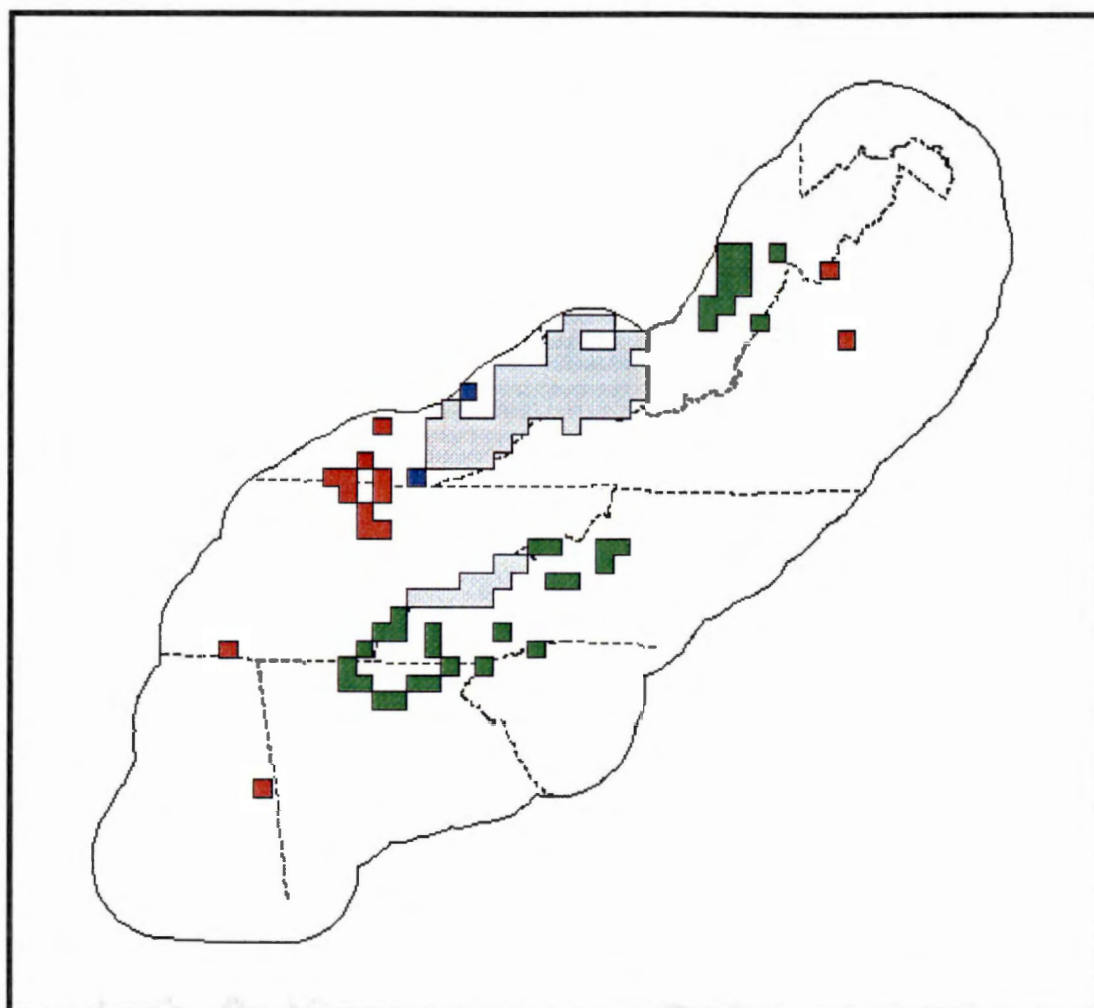


Fig. 18. Model 1 (298.6-km² patch scale): black bear habitat patches in the southern Appalachian region and probability of occupancy, 2000.



Legend

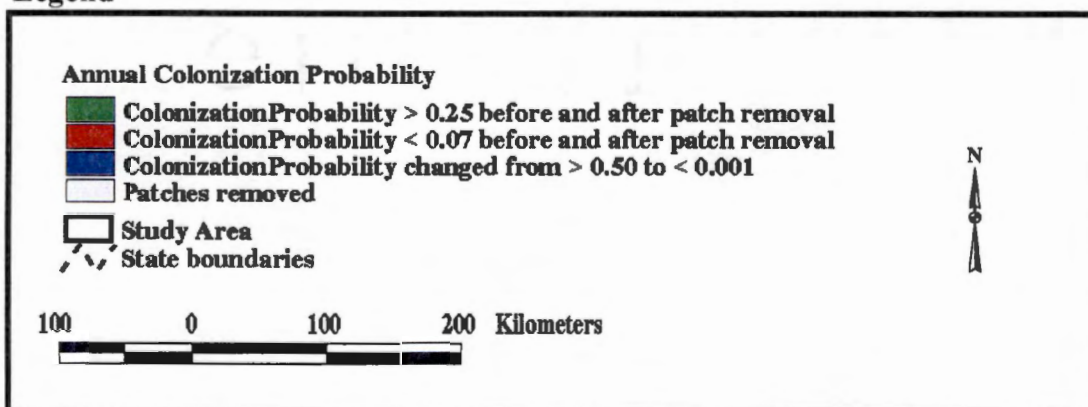


Fig. 19. Model 1 (298.6-km² patch scale): black bear habitat patches in the southern Appalachian region and annual colonization probability, 2000.

Table 10. Annual colonization probability (C_i) of black bears for Model 1 (298.6-km² scale) based on edge distance calculations and given removal of selected habitat patches, southern Appalachian region, 2000. J_i values calculated based on Hanski's (1993) incidence function model.

Patch ID	C_i (all)	C_i (no GSMNP ^a)	C_i (no KY)	C_i (no GSMNP or KY)
2	0.27	0.27	0.27	0.27
3	0.27	0.27	0.27	0.27
4	0.07	0.07	0.07	0.07
5	0.02	0.02	removed	removed
6	0.27	0.27	0.27	0.27
8	0.02	0.02	0.02	0.02
9 ^a	0.52	0.52	0.00	0.00
10 ^b	0.07	0.07	0.00	0.00
11 ^b	0.02	0.02	0.00	0.00
12	0.01	0.01	0.00	0.00
14 ^b	0.07	0.07	0.00	0.00
15 ^b	0.52	0.52	0.00	0.00
16 ^b	0.02	0.01	0.02	0.01
17 ^b	0.52	0.27	0.52	0.27
18	0.27	0.27	0.27	0.27
19	0.52	removed	0.52	removed
20	0.27	0.27	0.27	0.27
21	0.52	0.52	0.52	0.52
22	0.52	0.52	0.52	0.52
23	0.27	0.27	0.27	0.27
24	0.00	0.00	0.00	0.00
25	0.52	0.52	0.52	0.52
26	0.27	0.27	0.27	0.27
27	0.52	0.52	0.52	0.52
28	0.52	0.52	0.52	0.52
29	0.27	0.27	0.27	0.27
30	0.52	0.52	0.52	0.52
31	0.52	0.52	0.52	0.52
32	0.00	0.00	0.00	0.00

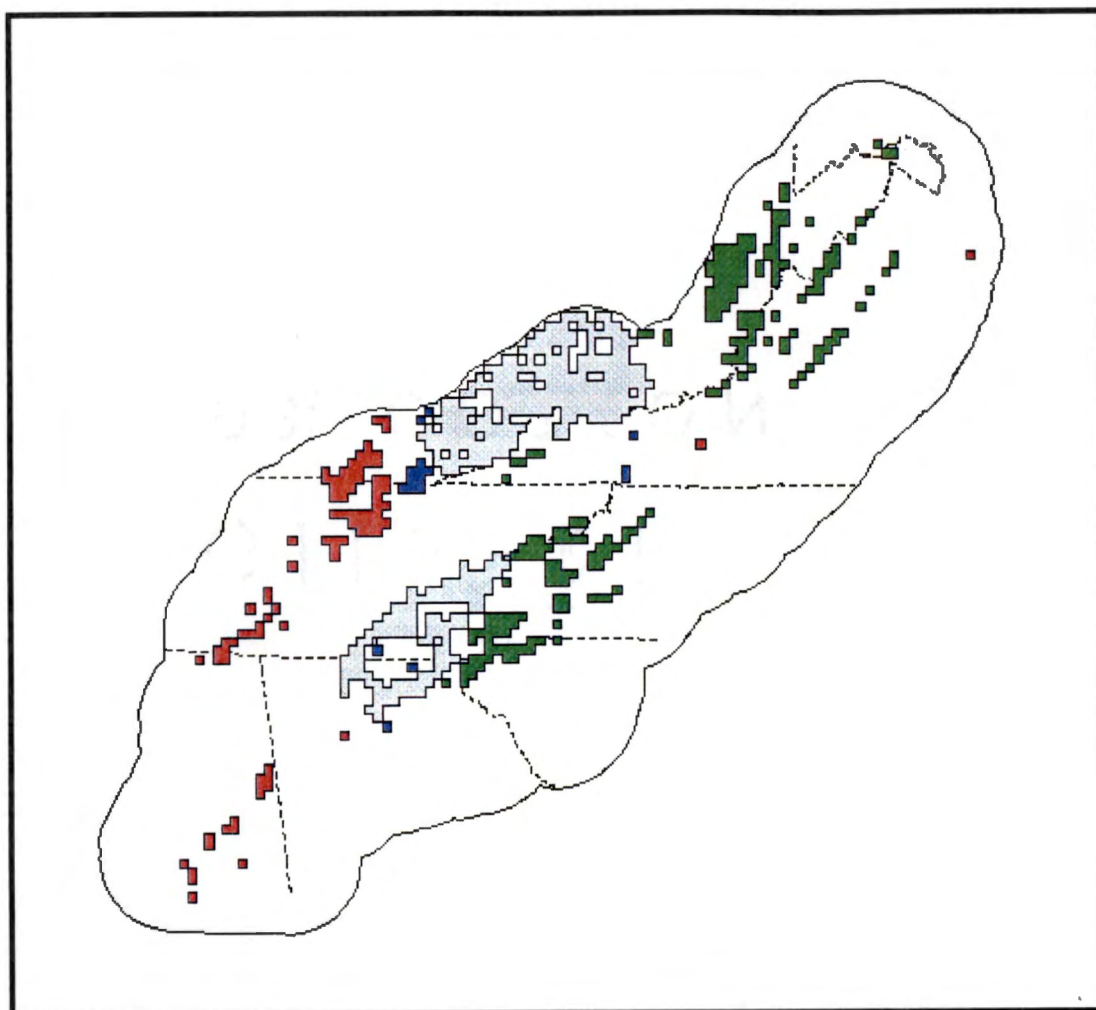
^a GSMNP = Great Smoky Mountains National Park.

^b Patches experiencing noticeable changes in colonization probability (>0.025).

had values that changed prediction from occupied to unoccupied. Eliminating both Great Smoky Mountains National Park and eastern Kentucky resulted in a decrease in probability of occupancy for 18.2% of the patches. Forty-four percent of those patches had values that changed from occupied to unoccupied (Fig. 20). Changes in colonization probabilities were smaller than the changes in probabilities of occupancy for model 2 (Fig. 21). When Great Smoky Mountains National Park was removed, 6.7% of the remaining patches experienced a decrease in the annual colonization probability. Eighty-three percent of those patches had values that experienced a decrease to below 0.25 probability of annual colonization. After removing eastern Kentucky from patch aggregate 2, the probability of colonization decreased for 5.6% of the patches. Annual colonization probabilities changed from above to below 0.25 for 80% of those patches. When both Great Smoky Mountains National Park and eastern Kentucky were removed, 12.4% of the remaining patches experienced a significant decrease in colonization probability. Eighty-two percent of those patches experienced a decrease in annual colonization probability from above to below 0.25.

Reintroductions

Reintroduction Sites.—I identified 3 areas from patch aggregate 2 (scale = 74.7 km²) that may be potential reintroduction sites in the southern Appalachian region (Fig. 22). Big South Fork area in Kentucky and Tennessee, Morgan, Scott, and Cumberland counties in Tennessee and Catoosa Wildlife Management Area (4,050 km²); the area west of Chattanooga in Franklin county Tennessee and Jackson county Alabama (1,275 km²); and Talladega National Forest in east-central Alabama (1,200 km²). Black bears were



Legend

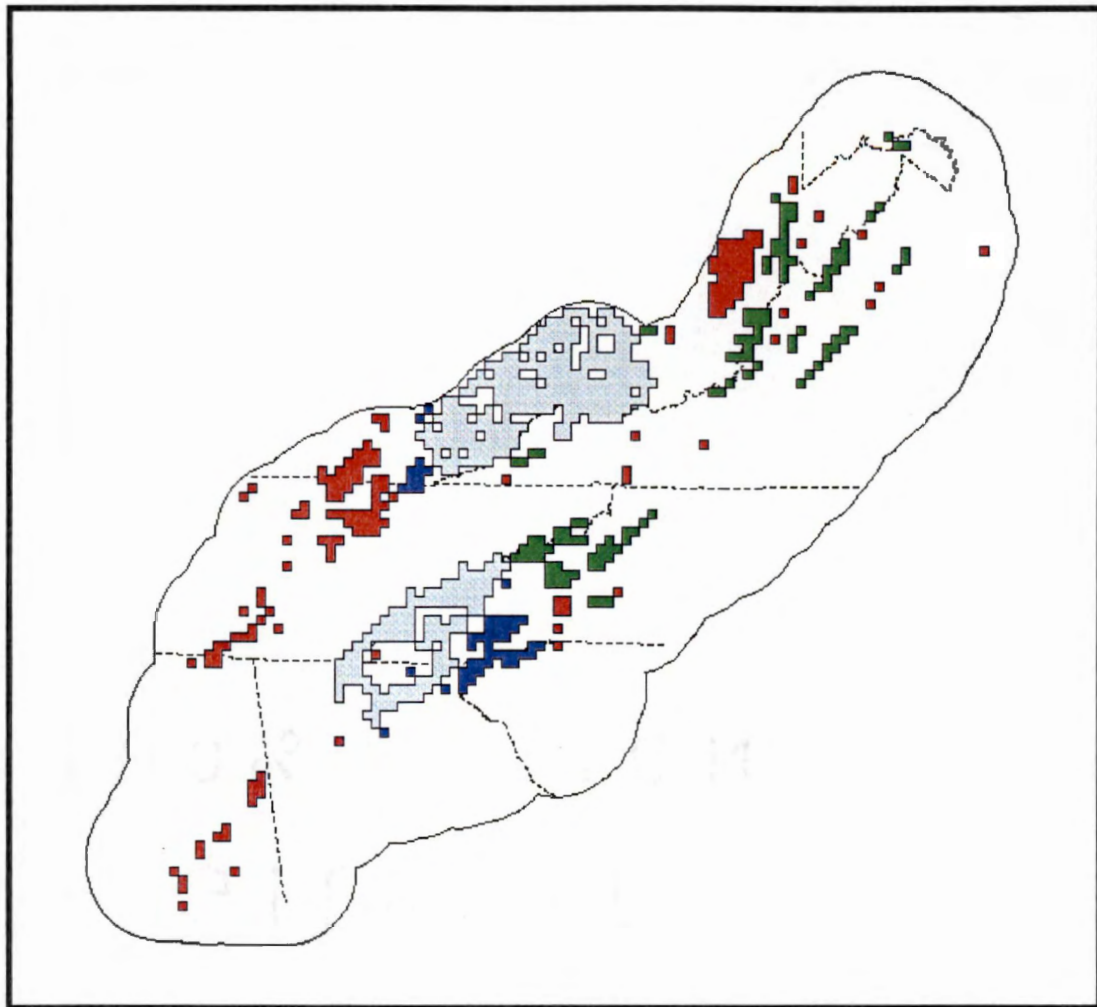
Status of Occupancy

- Occupied before and after patch removal
- Unoccupied before and after patch removal
- Occupied to unoccupied after patch removal
- Patches removed
- Study Area
- State boundaries

100 0 100 200 Kilometers



Fig. 20. Model 2 (74.7-km² patch scale): black bear habitat patches in the southern Appalachian region and probability of occupancy, 2000.



Legend

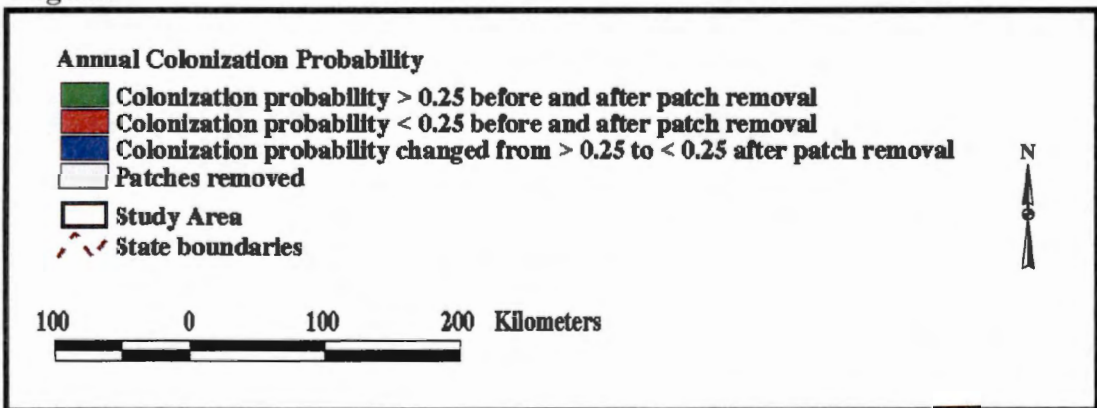
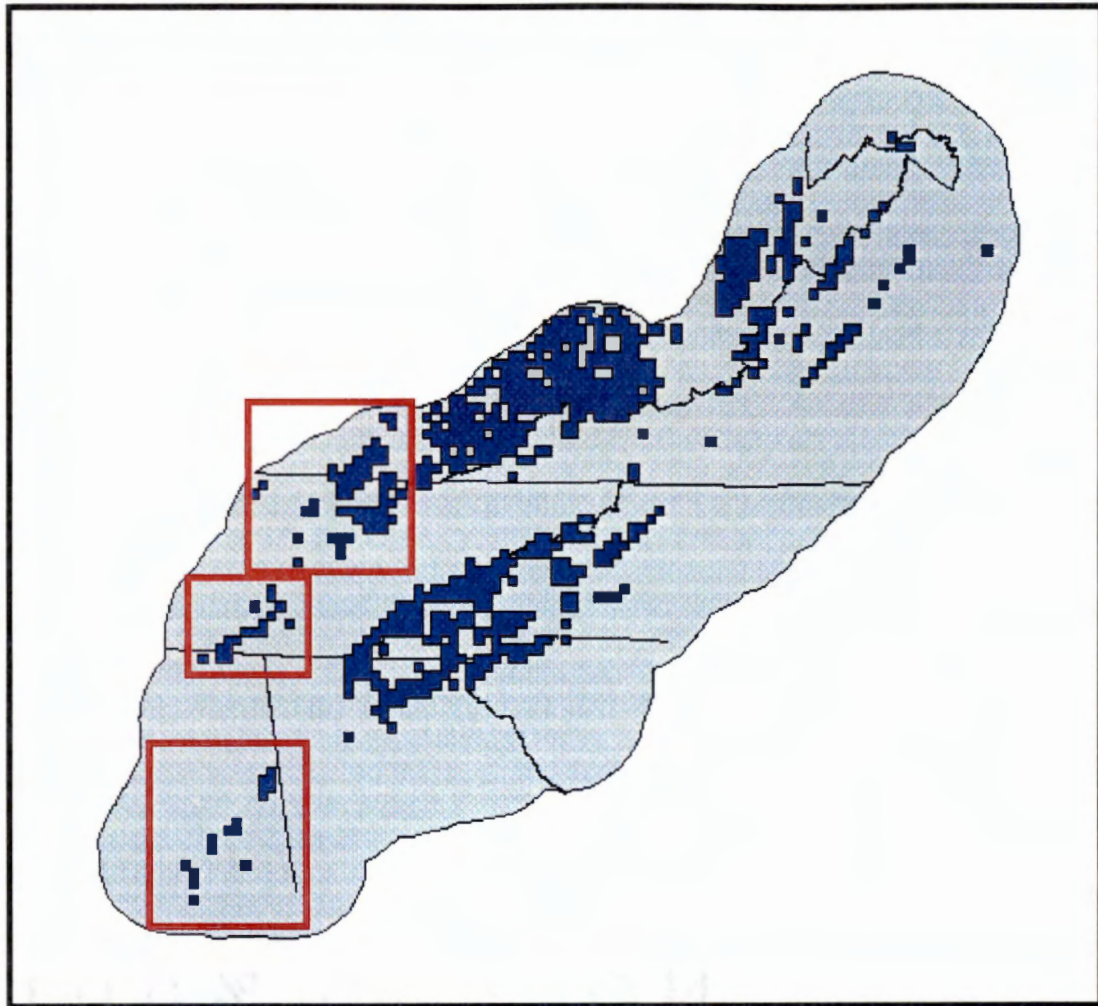


Fig. 21. Model 2 (74.7-km² patch scale): black bear habitat patches in the southern Appalachian region and annual colonization probability, 2000.



Legend

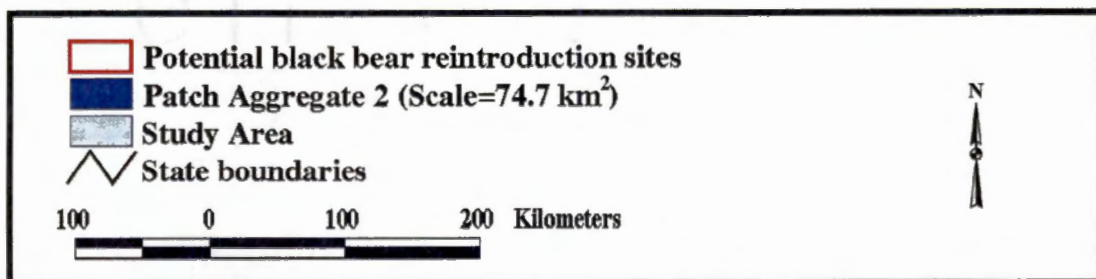
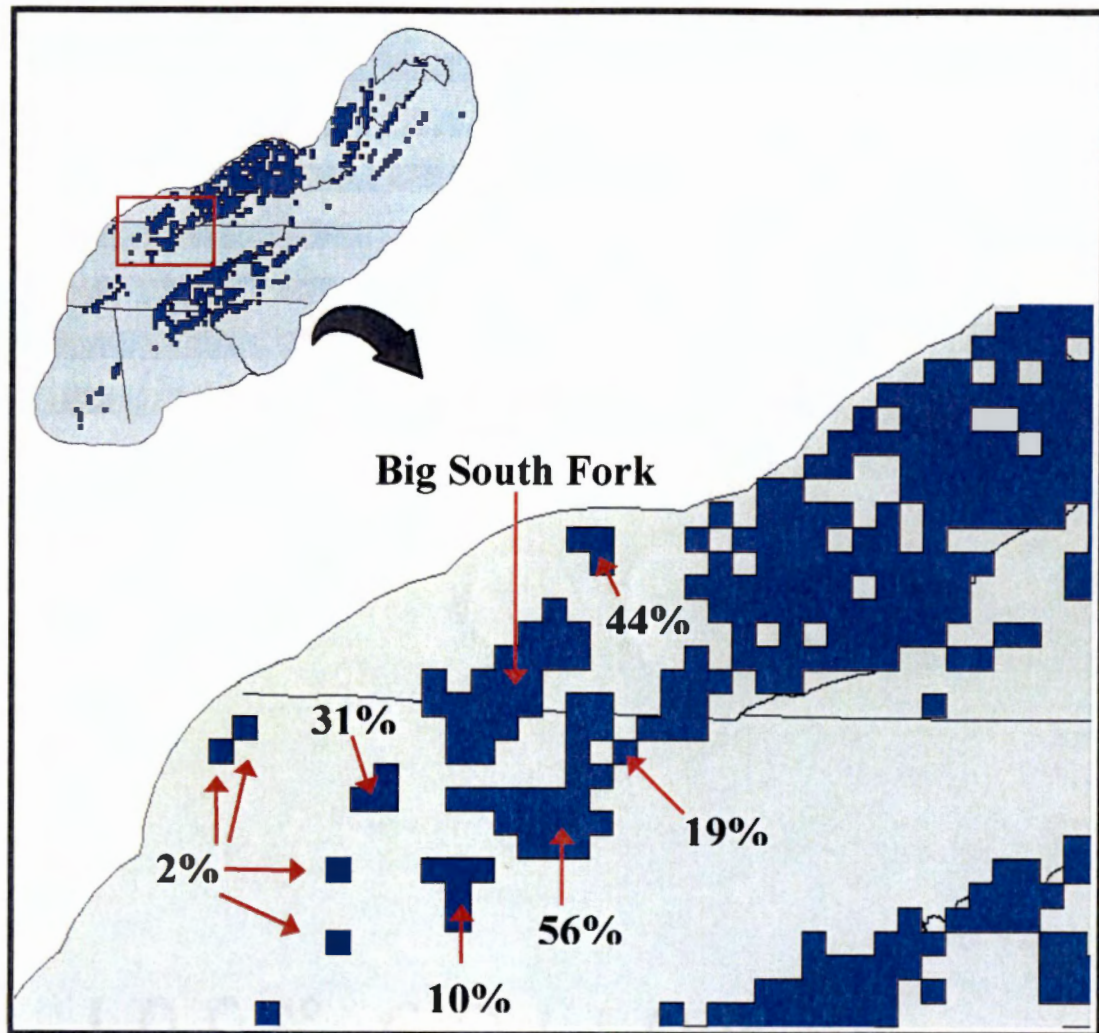


Fig. 22. Model 2 (74.7-km² patch scale): currently unoccupied black bear habitat patch networks that represent potential reintroduction sites in the southern Appalachian region, 2000.

actually reintroduced to the Big South Fork area in 1997-1998 (Eastridge 2000) and, if the colonization effort is successful, the annual probability of colonization of surrounding unoccupied patches increases from 0% to as much as 56% (Fig. 23).

Keystone Patches.—I identified “keystone” patches for the area west of Chattanooga in Tennessee and Talladega National Forest in east-central Alabama (Fig. 24). These were identified as patches with the greatest potential to facilitate the colonization of surrounding patches. As with the previous analyses, patch isolation was a more important factor than patch size. Patches with the greatest potential to impact adjacent patches were more centrally located, but the most central location was not always obvious.



Legend

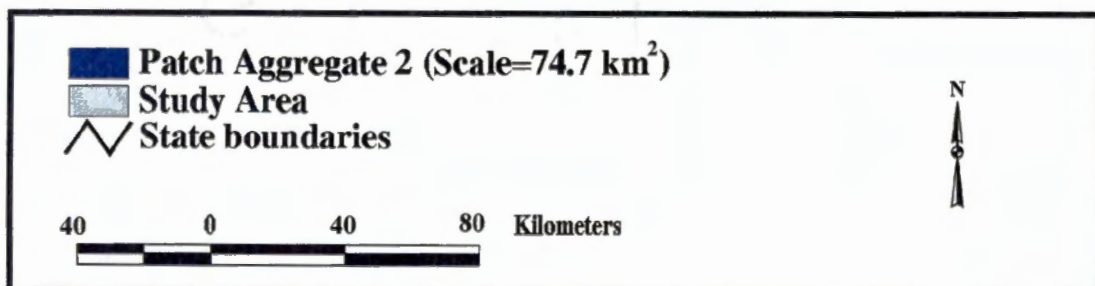
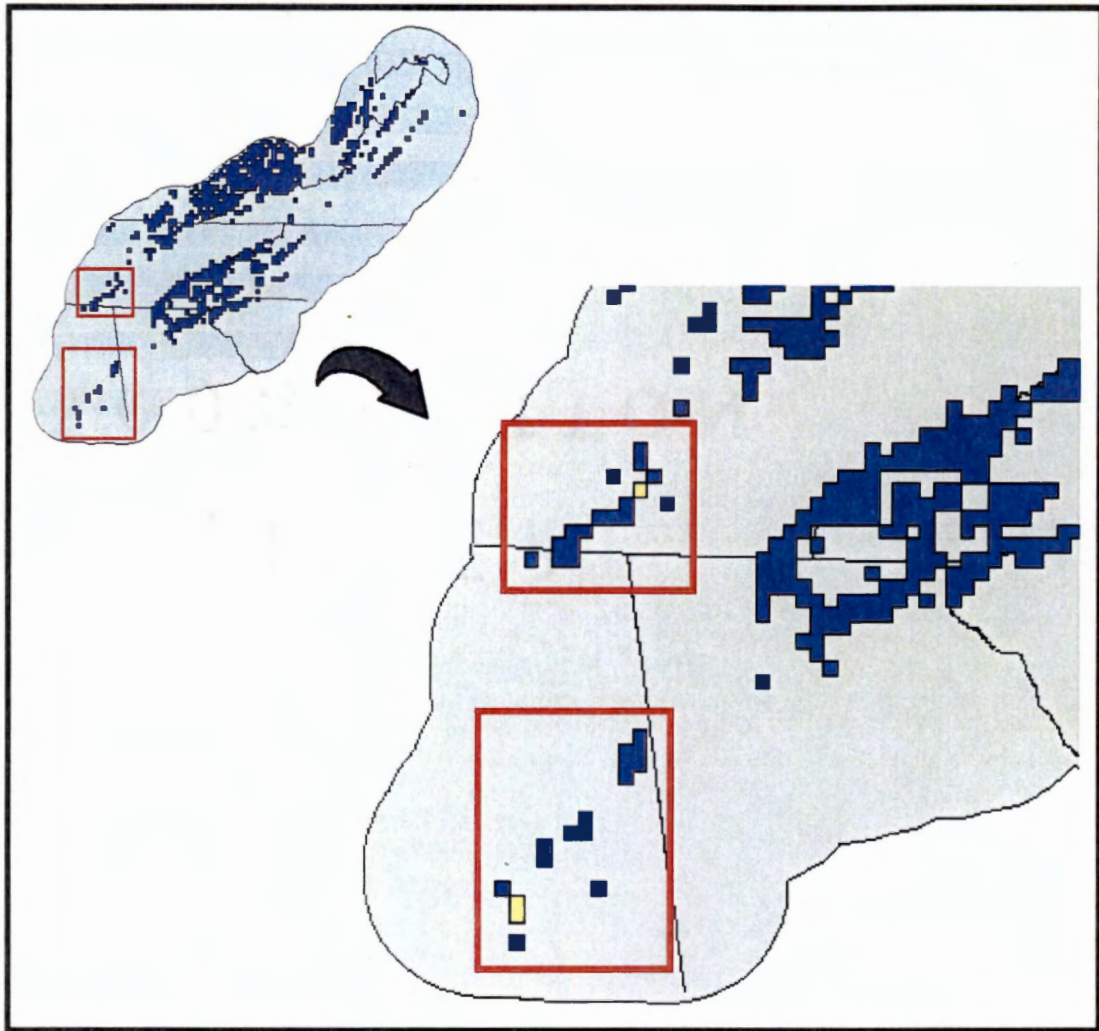


Fig. 23. Model 2 (74.7-km² patch scale): annual colonization probabilities of habitat patches surrounding Big South Fork National River and Recreation Area, Kentucky/Tennessee, following a hypothetical colonization. Initial annual colonization probabilities for surrounding patches were 0.00.



Legend

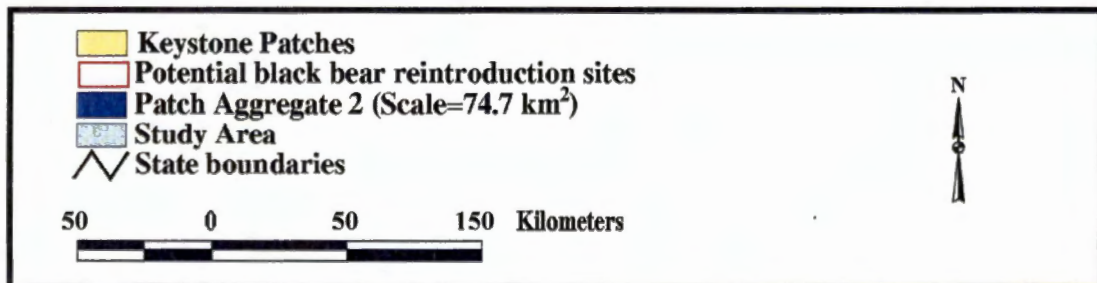


Fig. 24. Model 2 (74.7-km² patch scale): keystone patches within 2 local networks of unoccupied black bear habitat in the southern Appalachian region, 2000.

CHAPTER VI

DISCUSSION

Classic metapopulations naturally occur in discrete habitat patches that usually constitute a small, distinct portion of the landscape. The pool frog (*Rana lessonae*) has been described as existing as such a metapopulation (Hanski 1994, 1999). This frog is well known from 60 Scandinavian localities, all of which consist of permanent ponds along the Baltic coast of east-central Sweden (Sjögren-Gulve and Ray 1996). Another good example of a classic metapopulation is the American pika (*Ochotona princeps*). Pikas occur in spatially distinct habitat patches, which are made up of rock outcrops adjoining vegetation suitable for foraging (Moilanen et al. 1998). Both species occur in habitat patches that are separate and distinct within the landscape. However, black bear habitat in the southeastern United States was once equivalent to the landscape itself; human-induced fragmentation may have caused the bear population to now function as a metapopulation.

Since the introduction of Levins' model, metapopulation models have become more applicable to management. The conceptual and mathematical basis for metapopulation theory has gradually changed to better capture the complex dynamics of metapopulations. Depending on the system being studied and questions being asked, certain models may be more appropriate than others. However, no single model can describe the metapopulation dynamics of all systems of local populations.

MODEL ASSUMPTIONS

The model I used is an incidence function model and describes a relatively simple metapopulation. The model assumes correct classification of patch occupancy status (Hanski 1999). In my study it was possible to have bear distribution where no habitat patches existed, because patches were stringently defined ($\geq 95\%$ forest cover) and bear habitat may actually occur at a lower level of forest cover. Consequently, potential patches may have been excluded from the patch network, but all occupied patches were most likely correctly classified. Habitat patches had to have $>50\%$ bear distribution by area to be classified as occupied, thus eliminating patches from being categorized as occupied when only a small portion of the patch fell within the distribution. It was more conservative to classify those patches as unoccupied.

The incidence function model ignores patch shape, but required discrete patches that jointly constitute approximately 20% or less of the landscape. Patch aggregates 1–4 constituted approximately 10%, 14%, 19%, and 25% of the study area landscape, respectively. If centroid distances are used as the isolation distance, the model requires that the distance between the centroids of the patches approximates pair-wise isolations (distance between 2 patches). Therefore, this model applies best to a highly fragmented landscape without large patches. The centroid distance from a small patch to a large patch becomes more biased with closer proximity. This bias results because the distance from the edge of the larger patch to its centroid inflates the actual distance to the centroid of the other patch (Fig. 10). All models had several relatively large patches, e.g., Great Smoky Mountains National Park and eastern Kentucky (approximately 2,092 km² and

16,500 km², respectively), and the centroid distances did not always accurately approximate pair-wise isolations. Therefore, I also calculated edge distances for the 2 patch aggregates that were used for patch removal.

For better parameter estimation, substantial variation in patch size and isolation must be present in the metapopulation (Hanski 1999). All 4 models were based on a wide array of patch sizes and isolation. Because I established a minimum size aggregate of forest to build patches, there were many patches with the minimum patch size. However, this large number of small patches was not a restrictive condition for the models.

The model I applied works best with several years of data so that changes in patch occupancy over time can be incorporated. However, it is possible to obtain parameter estimates from a single period of patch occupation (Hanski 1999). I based my analysis on black bear distribution data from 2000, because multiple years of occupancy data were not available. The 1993 bear distribution data (Pelton and van Manen 1994) were not based on the range of reproducing females, so it was not appropriate to use as an initial record of occupancy. Also, given the biology of black bears, a much wider time span between periods would be needed to view population turnover. With only 1 time period available, parameter estimates can result in unrealistically high extinction and colonization rates (Hanski 1999). In my analysis, the number of patches that experienced extinction, given removal of certain patches, was relatively small. Therefore, the parameter estimates did not seem to be overly sensitive to this effect (Hanski 1999).

Finally, the model assumes that animal movements occur only between the habitat

patch islands and the mainland. The assumption of no exchange among non-mainland patches may not be reasonable for the southern Appalachians. This assumption would make the model more conservative (a bias toward extinction) than a model that takes a continuous flow of animals among patches into account. If a habitat patch has immigration of animals from multiple islands, those islands could act as a buffer if 1 goes extinct. On the other hand, if exchange only occurs between 2 patches and 1 temporarily goes extinct, the remaining patch would have a much higher probability of extinction. Considering the assumptions, the incidence function model seemed an appropriate first step for a basic metapopulation analysis of black bears in the southern Appalachians.

PARAMETER ESTIMATES

Interpretability of parameter estimates was variable among models. Because scale and resolution change, it was also difficult to directly compare parameter estimates among models. Parameter estimation was performed with nonlinear regression, but the plausibility of the estimates had to be established within biological limits, especially because only 1 time period of occupancy was considered. I used Hanski's (1999) method of individually estimating parameters to determine whether the estimated parameters were feasible. Because E_i cannot exceed 1 and if one knows or can estimate X , a minimum value of μ could be determined given the equation for extinction probability, $E_i = \mu / A^x$ (Hanski 1992). The smallest patch area is known, and I assumed the nonlinear regression estimated a reasonable value for X . The parameter estimates for all models

(Table 6) produced values of μ that did not exceed the minimum patch area raised to the power of X ; therefore, estimates of μ seemed biologically reasonable.

The parameter X describes the relationship between patch area and extinction and indicates whether extinction events are influenced more by environmental stochasticity, such as extreme weather events, or demographic stochasticity, such as reproductive fluctuations. Understanding environmental stochasticity and how the extinction probability of local populations depends on population size has practical value. For example, if $X > 1$, the time to extinction increases exponentially with increasing population size, as expected from models of demographic stochasticity (Goodman 1987). If $X < 1$, the time to extinction increases approximately logarithmically with increasing population size, a relationship associated with environmental stochasticity (Goodman 1987). All species are affected by demographic stochasticity to a certain degree, but some species are much more susceptible to environmental stochasticity than others. Given the large standard errors (Table 6), the actual value of X may have been above or below 1 for each model. Therefore, no strong inferences can be made about the relationship between environmental stochasticity and extinction rate across all scales.

The last parameter, α , is related to dispersal distance. The average dispersal distance of an individual leaving its natal area and dispersing to a new local population is approximately equal to $1/\alpha$ (I. Hanski, University of Helsinki, Finland, personal communication). I used this equation to determine whether the α values were reasonable. The parameter estimates for α suggest an average dispersal distance between 3 and 15 km (Table 6). These dispersal rates seemed reasonable given that the analyses were

based on the distribution of reproducing females. Yearling females have been documented dispersing to a smaller portion of their mother's territory, resulting in relatively low dispersal distances (Rogers 1987).

AREA AND ISOLATION

The relationships of occupancy, area, and isolation illustrate the importance of patch isolation (Figs. 12–17). The isoclines of isolation versus area would be relatively flat if area was limiting, exhibiting an asymptotic relationship with area. Conversely, if isolation was limiting, the isoclines would be steeper, exhibiting an asymptotic relationship with isolation. If isolation and area were equally important, there would be no asymptotic relationship or limiting threshold. All isoclines exhibited an asymptotic relationship with isolation, indicating that isolation was the primary factor influencing patch occupancy. Therefore, certain thresholds of isolation may exist that are important for bear occupancy and colonization (Figs. 12–17), and the isolation thresholds decrease as the models decrease in scale. Although isolation seems to be the most influential of the 2 axes for all 4 models, the isoclines for model 1 (Fig. 12) have a slightly flatter slope, indicating a stronger influence of patch area than the other models. This influence of patch area may be expressed more because the scale is that of a local population. At larger scales, the population may maintain itself more so than smaller scales, where occupancy is more dependent on colonization. Therefore, area has relatively more influence on occupancy in model 1 than in other models.

Establishment of a new breeding population usually entails females dispersing

and establishing new breeding home ranges. However, female black bears exhibit limited dispersal movements (Rogers 1987). My results suggest that habitat patches need to be relatively close or well connected for effective colonization. Two studies investigating the population ecology of black bears in fragmented habitat in northeast Louisiana support these findings (Anderson 1997, Beausoleil 1999). Beausoleil (1999) found that female movements between habitat patches did not occur unless patches were connected by corridors or the habitat patches were <0.5 km apart. In those studies, 2 sites, the Deltic study area and the Tensas River National Wildlife Refuge, were approximately 5 km apart. However, there has been only 1 documented bear movement between the 2 areas during the last decade (Anderson 1997). This distance is shorter than the isolation threshold supported in my metapopulation analysis, but a 4-lane highway separates the 2 Louisiana study sites, likely increasing the isolation effect. My analysis does not directly consider how highways and urban areas may increase isolation, which may account for a portion of the unexplained variation. Such travel impediments may result in underestimation of extinction probabilities and overestimation of colonization probabilities for patches with short isolation distance but a difficult traveling environment, e.g., roads.

SIMULATIONS

Simulations of habitat patch removal were based on calculating isolation distances between the edges of 2 patches. Calculating the distance to the nearest edge of an occupied patch provided a more realistic model of patch occupancy. However, the R^2

values of the resulting models were lower compared with the centroid distance models because of the spatial configuration of the patch network (Table 8). In models 1 and 2, several small unoccupied patches were close to the 2 largest patches. Based on the centroid distances, these patches were more isolated (Fig. 10). When the edge distances were used, the isolation was reduced to a more accurate estimate (Table 5). The nonlinear regression models using edge-to-edge distances were not as effective at predicting occupancy because these small, unoccupied patches were only slightly isolated.

Given the large standard errors (Table 8), again the value of X may fall above or below 1 for the 2 models with edge-to-edge isolations. Therefore, again no strong inferences can be made about the relationship between environmental stochasticity and extinction rate. The parameter α would suggest an average dispersal rate at these scales of 6–13 km, which is similar to the centroid method parameter estimates.

Source-Sink Dynamics

Removal of large occupied patches caused changes in the isolation distance associated with remaining patches. Patches that were only slightly isolated had higher annual probabilities of colonization (Table 10). I expected to find the patterns shown in Figs. 18–21 because well-connected patches are likely to be similarly classified, either occupied or unoccupied (Hanski 1999). Patches near Great Smoky Mountains National Park were occupied and tended to stay occupied with high colonization rates regardless of the removal of Great Smoky Mountains National Park because there were smaller

networks of occupied patches close together. Likewise, unoccupied patches grouped great distances from occupied habitat tended to stay unoccupied and have low colonization rates, regardless of the presence or absence of large patches. Great Smoky Mountains National Park and Kentucky were mainly important for groups of unoccupied patches that were relatively close, which was to be expected given my assumption of occupied patches acting as mainlands. Because isolation seems to have such a strong influence on occupancy, patches that were closer to those 2 large patches experienced more unoccupancy when those large patches were removed, and were predicted to be occupied when those patches were present. The importance of connectivity may be emphasized through these large patches because they only benefit nearby habitat and did not seem to play a major “source” role. Therefore, regardless of large patches, bears may not be able to reach other habitat patches unless there are accessible habitat connections.

Reintroductions

This model identified areas that could serve as potential reintroduction sites. The model suggests that these areas are currently unoccupied because they are extremely isolated. Although males can disperse long distances, females are poor colonizers, and therefore, even small isolations may restrict successful colonization. The changes in colonization probabilities, illustrated by my hypothetical colonizations, illustrate the potential conservation value of reintroductions and population augmentation. Moreover, the results of my study can be used to identify where reintroductions may be most effective.

CHAPTER VII

MANAGEMENT AND RESEARCH IMPLICATIONS

MANAGEMENT NEEDS

The results of my study suggest that landscape connectivity is important to the integrity of black bear populations in the southern Appalachians. If viable bear populations are desired, managers need to consider the potential impacts of fragmentation on the dynamics of the metapopulation. Cooperative efforts among private, state, and federal agencies may promote management at the regional level and increase the potential for protecting corridor areas among fragmented bear populations via improved landscape planning.

My study suggests that habitat isolation may be the major impediment to range expansion of black bears. Establishing connectivity among patches is important for long-term population persistence. Reintroductions can be effective when such connections do not exist. Three black bear reintroductions have occurred in the southern United States during the last 10 years: the Big South Fork Area in southeastern Kentucky and northeastern Tennessee (Eastridge 2000), Felsenthal National Wildlife Refuge in southern Arkansas (J. D. Clark, U.S. Geological Survey, personal communication), and the Interior Highlands of Arkansas (Ozark and Ouachita mountains; Smith and Clark 1994). Bears were extirpated from these 3 areas during the early 1900s. Reintroduction efforts essentially counteracted the isolation factor and may be effective in establishing

black bear populations where natural dispersal cannot (Smith and Clark 1994). For example, black bears have been absent from the Big South Fork Area for almost 100 years. Until recently the area had been isolated from the nearest occupied bear habitat by approximately 100 km. I inferred from the values of α (Model 2, Table 6) that the per-year colonization probability of a habitat patch 100 km from the main bear distribution is 0.001. This protected area is approximately 30 years old; based on the parameter estimates, the isolated habitat patch would only have a 3% probability of occupancy in 30 years. This example illustrates the potential effectiveness of reintroductions when unoccupied patches with suitable habitat are too isolated for natural recolonization. Furthermore, given the importance of isolation, the effectiveness of population augmentations is supported when long-term population persistence may be dependent on immigration. Furthermore, the cumulative effects of fragmentation are difficult to assess. Therefore, understanding the underlying mechanisms that govern local colonizations and extinctions, such as isolation, and identifying primary and potential habitat corridors and important “keystone” habitat patches are crucial to the regional management of the black bear population in the southern Appalachians. The results of my study can be used to assess the biological importance of certain patches (source-sink dynamics), identify areas for potential reintroduction, determine whether isolation among patches within potential reintroduction areas is suitable for dispersal, and identify the best release site within those areas (keystone patches).

METAPOPULATION MODELING

There are aspects of metapopulation modeling that make this technique difficult to apply to wildlife management. This type of modeling often requires extensive field data and modeling capabilities. The predictions of simpler models are easier to test and interpret, but they may not accurately represent the dynamic interactions among local populations. Ecologists continue to formulate more complex models to better represent metapopulation dynamics. However, such models are difficult to develop and apply because spatial, temporal, and demographic variables influence extinction and colonization rates. The Levins model has yet to be expanded to a general model that is suitable for metapopulations with more complex dynamics.

Sjögren-Gulve (1994) and Sjögren-Gulve and Ray (1996) combined empirical data, logistic regression, and Monte Carlo simulations to model metapopulation dynamics. From these analyses, probabilities of patch extinction and colonization can be determined using a stochastic, discrete-time metapopulation model; colonization and extinction can depend on several variables, which may differ temporally and spatially (Sjögren-Gulve and Ray 1996). When colonization and extinction are held constant the model is equivalent to Levins' model (1969). Such analyses were useful to understand metapopulation dynamics and guiding conservation efforts for the pool frog (*Rana lessonae*) (Sjögren-Gulve and Ray 1996) and seems to be the next logical step for black bears in the southern Appalachians. This type of analysis would indicate whether colonization and extinction depends on variables other than patch area and isolation (e.g.,

demographic parameters or other patch characteristics), providing better insight into the metapopulation dynamics of black bears in the southern Appalachians.

LITERATURE CITED

LITERATURE CITED

- Anderson, D. R. 1997. Corridor use, feeding ecology, and habitat relationships of black bears in a fragmented landscape in Louisiana. Thesis, University of Tennessee, Knoxville, Tennessee, USA.
- Beausoleil, R. A. 1999. Population and spatial ecology of the Louisiana black bear in a fragmented bottomland hardwood forest. Thesis, University of Tennessee, Knoxville, Tennessee, USA.
- Begon, M., and M. Mortimer. 1986. Population ecology. Sinauer Associates, Sunderland, Massachusetts, USA.
- Boone, D., and G. Aplet. 1994. Sustaining biodiversity in the southern Appalachians. The Wilderness Society, Washington DC, USA.
- Bunnell, F. L., and D. E. N. Tait. 1981. Population dynamics of bears-implications. Pages 75-98 in C. W. Fowler and T. D. Smith, eds. Dynamics of large mammal populations. John Wiley and Sons, New York, New York, USA.
- Clark, J. D., J. E. Dunn, and K. G. Smith. 1993. A multivariate model of female black bear habitat use for a geographic information system. *Journal of Wildlife Management* 57:519-526.
- Eastridge, R. 2000. Experimental repatriation of black bears to the Big South Fork area of Kentucky and Tennessee. Thesis, University of Tennessee, Knoxville, Tennessee, USA.
- Goodman, D. 1987. The demography of chance extinctions. Pages 11-34 in M. E. Soulé, editors. Viable populations for conservation. Cambridge University Press, Cambridge, England.
- Gyllenburg, M., and I. Hanski. 1992. Single-species metapopulation dynamics: a structural model. *Theoretical Population Biology* 42:35-61.
- Hamel, P. 1992. The land managers guide to birds of the South. The Nature Conservancy. Chapel Hill, North Carolina, USA.
- Hanski, I. 1990. Density dependence, regulation, and variability in animal populations. Pages 141-150 in M. P. Hassell and R. M. May, editors. Population Regulation and Dynamics. The Royal Society, London, England.

- _____. 1991. Single-species metapopulation dynamics: concepts, models, and observations. *Biological Journal of the Linnean Society* 42:17–38.
- _____. 1992. Inferences from ecological incidence functions. *American Naturalist* 139: 657–662.
- _____. 1993. Dynamics of small mammals on islands. *Ecography* 16(4):372–375.
- _____. 1994. Metapopulation structure and migration in the butterfly *Melitaea cinxia*. *Ecology* 75(3):747–762.
- _____. 1996. Metapopulation ecology. Pages 13–43 in O. E. Rhodes, R. K. Chesser, and M. H. Smith, editors. *Population Dynamics in Ecological Space and Time*. The University of Chicago press, Chicago, Illinois, USA.
- _____. 1999. *Metapopulation ecology*. Oxford University press, New York, New York, USA.
- _____, and M. Gyllenburg. 1993. Two general metapopulation models and the core-satellite species hypothesis. *American Naturalist* 142(1):17–41.
- _____, and C. D. Thomas. 1994. Metapopulation dynamics and conservation: a spatially explicit model applied to butterflies. *Biological Conservation* 68:167–180.
- Harrison, S. 1994. Metapopulations and conservation. Pages 111–128 in P. J. Edwards, R. M. May, and N. R. Webbs, editors. *Large-scale Ecology and Conservation Biology*. Blackwell publishers, Oxford, England.
- Hastings, A. 1991. Structured models of metapopulation dynamics. Pages 57–71 in M. Gilpin and I. Hanksi, editors. *Metapopulation Dynamics*. Academic Press, London, England.
- Hermann, K.A. 1996. The Southern Appalachian Assessment GIS database CD ROM set. The Southern Appalachian Man and Biosphere Program. Gatlinburg, Tennessee, USA.
- Levins, R. 1969. Some genetic and demographic consequences of environmental heterogeneity for biological control. *Bulletin of the Entomological Society of America* 15:237–240.
- _____. 1970. Extinction. Pages 77–107 in M. Gerstenhaber, editor. *Some Mathematical Questions*. American Mathematical Society, Providence, Rhode Island, USA.

- MacArthur, R. H., and E. O. Wilson. 1967. The theory of island biogeography. Princeton University Press, Princeton, New Jersey, USA.
- Moilanen, A., A. T. Smith, and I. Hanski. 1998. Long-term dynamics in a metapopulation of the american pika. *American Naturalist* 152(4):530–542.
- Morrison, D. F. 1976. Multivariate statistical methods. McGraw-Hill Book Co., New York, New York, USA.
- Pelton, M. R., and F. T. van Manen. 1994. Distribution of black bears in North America. *Eastern Workshop on Black Bear Research and Management* 12:133–138.
- _____, and _____. 1997. Status of Black Bears in the Southeastern United States. Pages 31–44 in A. L. Gaski and D. F. Williamson, editors. *Proceedings of the Second International Symposium on the Trade of Bear Parts*. Traffic USA/World Wildlife Fund, Washington D.C., USA.
- _____, A. B. Coley, T. H. Eason, D. L. Doan Martinez, J. A. Pederson, F. T. van Manen, and K. M. Weaver. 1999. American black bear conservation action plan. Pages 144–156 in C. Servheen, S. Herrero, and B. Peyton, eds. *Bears: status survey and conservation action plan*. IUCN/SSC Bear and Polar Bear Specialist Groups. IUCN, Gland, Switzerland and Cambridge, UK.
- Rao, C. R. 1952. *Statistical methods in biometric research*. John Wiley and Sons, New York, New York, USA.
- Rogers, L. L. 1977. Social relationships, movements, and population dynamics of black bears in northeastern Minnesota. Dissertation, University of Minnesota, St. Paul, Minnesota, USA.
- _____. 1987. Effects of food supply and kinship on social behavior, movements, and population growth of black bears in northeastern Minnesota. *Wildlife Monographs* 97.
- SAS Institute, Inc. 1989. *SAS/STAT User's Guide, Version 6, 4th edition, Volumes 1 and 2*. SAS Institute Inc., Cary, North Carolina, USA.
- Sjögren-Gulve, P. 1994. Distribution and extinction patterns within a northern metapopulation of the pool frog *Rana lessonae*. *Ecology* 75:1357–1367.
- _____, and C. Ray. 1996. Using logistic regression to model metapopulation dynamics: large-scale forestry extirpates the pool frog. Pages 111–137 in D. R. McCullough, editor. *Metapopulations and Wildlife Conservation*. The Wildlife Society Meeting, Albuquerque, New Mexico, USA.

- Smith, K. G. and J. D. Clark. 1994. Black bears in Arkansas: characteristics of a successful translocation. *Journal of Mammology* 75(2):309–320.
- Southern Appalachian Man and the Biosphere (SAMAB). 1996. The Southern Appalachian Assessment Summary Report. Report 1 of 5. U.S. Department of Agriculture, Forest Service, Southern Region. Atlanta, Georgia, USA.
- Turchin, P. 1998. Quantitative analysis of movement: measuring and modeling population redistribution in animals and plants. Sinauer Associates, Sunderland, Massachusetts, USA.
- U.S. Forest Service. 1993. ECOMAP-National hierarchical framework of ecological units. U.S. Department of Agriculture, Forest Service, Washington, D.C., USA.
- van Manen, F. T. 1994. Black bear habitat use in Great Smoky Mountains National Park. Dissertation, University of Tennessee, Knoxville, Tennessee, USA.
- Vogelmann, J. E., Sohl, T., Campbell, P. V., and D. M. Shaw. 1998*a*. Regional land cover characterization using Landsat Thematic Mapper data and ancillary sources. *Environmental Monitoring and Assessment* 51:415–428.
- _____, _____, and S. M. Howard. 1998*b*. Regional characterization of land cover using multiple sources of data. *Photographic Engineering and Remote Sensing* 64:45–57.

NOV 200 4001

61819

APPENDIX

Terminology

APPENDIX

GLOSSARY OF TERMS

Alpha (α) — characterizes the rate of decline in colonization probability with increasing isolation (Hanski 1993)

Beta (β) — the probability of colonization of an empty patch with no isolation ($D_i = 0$) or of 2 adjacent patches (Hanski 1993)

Centroid isolation — an isolation measurement based on the straight-line distance between the centroids of 2 patches

Colonization — enough immigration occurs into a habitat patch that will sustain it for several generations with no additional immigration (Hanski 1993)

Distribution — the range of reproducing female black bears reported by state and federal biologists

Edge-to-edge isolation — an isolation measurement based on the straight-line distance between the 2 closest edges of 2 patches

Incidence function model — a model of $J_i(t)$, the probability of patch i being occupied in generation (year) t , generally assumed to be a function of the size and isolation of patch I (Hanski 1996)

Isolation (D_i) — a straight-line distance measurement between a habitat patch and the nearest occupied patch

Probability of occupancy (J_i) — the incidence of species presence in patch I (Hanski 1993)

Metapopulation — an aggregate of local populations connected by dispersal. A population consisting of small, localized sub-populations that interact through periodic local extinctions and recolonizations, although not all local populations in a metapopulation necessarily interact (Hanski 1996)

Mu (μ) — the risk of extinction per unit time of a population living in a patch of unit size (Hanski 1993)

Nonlinear regression — a statistical technique that allows for the combination of multiple parameters that have a nonlinear relationship

Occupancy — bear distribution occupies 50% or more of a patch by area

Patch — an area of space within which a species lives or could live or a homogenous habitat that is distinct from the surrounding habitat (Hanski 1996)

Patch aggregate — an output (assembly of patches) created by resampling the input (forest coverage) at a coarser resolution based on specific criteria (ARC/Info[®] GIS)

Spatially explicit models — model in which dispersal is distance-dependent, often restricted to the nearest habitat patch (Hanski 1996)

Spatially implicit models — model in which all local populations are equally connected.

X — the rate of decline in extinction risk with increasing patch area (Hanski 1996)

VITA

Jennifer Lynn Murrow is the daughter of Charlotte Murrow Taylor and Linwood Murrow. She was born in Charleston, South Carolina on 28 August 1976. She graduated from Bishop England High School in 1994. She received a degree of Bachelor of Science with a major in Wildlife and Fisheries Biology in 1998 from Clemson University, South Carolina. She entered the graduate program at the University of Tennessee, Knoxville in 1998, and received a degree of Master of Science with a major in Wildlife and Fisheries Science and minors in Statistics and Environmental Policy in May 2001.

9932 7513 5
09-20-01 MAB