5-2004

Relationships Between Spatial Enviromental Variability and Black Bear Occurrence in the Continental United States of America

Donald Alfonso Martorello
University of Tennessee - Knoxville

To the Graduate Council:

I am submitting herewith a dissertation written by Donald Alfonso Martorello entitled "Relationships Between Spatial Enviromental Variability and Black Bear Occurrence in the Continental United States of America." I have examined the final electronic copy of this dissertation for form and content and recommend that it be accepted in partial fulfillment of the requirements for the degree of Doctor of Philosophy, with a major in Ecology and Evolutionary Biology.

Michael R. Pelton, Major Professor

We have read this dissertation and recommend its acceptance:

Dr. Frank van Manen, Dr. Mark Knot, Dr. Mike Huston, Dr. Lou Gross, Dr. Arthur Echternacht

Accepted for the Council:

Carolyn R. Hodges

Vice Provost and Dean of the Graduate School

(Original signatures are on file with official student records.)

To the Graduate Council:

I am submitting herewith a dissertation written by Donald Alfonso Martorello entitled "Relationships between spatial environmental variability and black bear occurrence in the continental United States of America." I have examined the final paper copy of this dissertation for form and content and recommend that it be accepted in partial fulfillment of the requirements for the degree of Doctor of Philosophy, with a major in Ecology and Evolutionary Biology.

Michael R. Pelton, Major Professor

Christine R. B. Boake, Department Head

We have read this dissertation and recommend its acceptance.

Accepted for the Council:

Vice Provost and Dean of Graduate Studies

RELATIONSHIPS BETWEEN SPATIAL ENVIRONMENTAL VARIABILITY AND BLACK BEAR OCCURRENCE IN THE CONTINENTAL UNITED STATES OF AMERICA

A Dissertation

Presented for the

Doctor of Philosophy

Degree

The University of Tennessee, Knoxville

Donald Alfonso Martorello

May 2004

DEDICATION

I dedicate this dissertation to Dr. Michael R. Pelton for his lifetime contribution to black bear research and science. During his 33 years of bear research at the University of Tennessee, Dr. Pelton directed 56 graduate students who investigated nearly every aspect of black bear ecology. Through his work and his students, Dr. Pelton has made countless contributions to our knowledge of black bear biology and ecology. Dr. Pelton is, without question, a true pioneer of black bear research and management.

ACKNOWLEDGMENTS

Completing this dissertation has been a long, hard road and I would like to thank several people for their help along the way. First, I would like to thank my major professor, Dr. Michael R. Pelton, for giving me the opportunity to pursue a Ph.D. degree and further my education and experience with black bears; I am truly indebted to him for the opportunities he has given me. I also thank my committee members: Dr. Frank van Manen, Dr. Mark Kot, Dr. Mike Huston, Dr. Lou Gross, and Dr. Arthur Echternacht for their support and advice, particularly in the final stages of this dissertation. I thank Kurt Riitters for developing the custom forest fragmentation grid for this study and Dr. Bill Hargrove for assistance with the soil nitrogen grid. I thank Holli Martorello for reviewing an earlier draft of this dissertation. I owe many thanks to several people who "nudged" me over the past 3 years to complete this dissertation, those include my wife, Holli Martorello, and co-workers Dave Ware and Dave Brittell.

There are many students and university personnel who I would like to thank for their advice, help, support, and friendship: Thomas Eason, Rich Beausoleil, Jay Clark, Daron Barnes, Meghan Carr, Jamie McNutt, Marty Stratman, David Brandenburg, Shyamala Ratnayeke, Rick Eastridge, Bob Inman, Jun Yoshizaki, Jennifer Murrow, Steve Dobey, Mike Janis, Mark Boersen, Andy Edwards, Brandon Wear, Carrie Schumacher, Dr. Joe Clark, and Dr. George Hopper.

Finally, I would like to thank my family for their love, support, and financial help. Most of all, I would like to thank my wife, Holli, for putting up with me. After 12 years of marriage, we can finally enter a phase of our lives where I don't have a degree to wrap-up.

Funding for this project was provided by McIntire Stennis project 55 of the Agriculture Experiment Station through the Department of Forestry, Wildlife and Fisheries at the University of Tennessee and Oak Ridge National Laboratory.

ABSTRACT

The American black bear (*Ursus americanus*) historically occurred throughout the forested regions of the continental United States of America (USA), and was absent only in central Nevada and portions of southern California and Arizona. Today, black bears only occur in a fraction of their former range, particularly in the Southeast where bear populations are highly fragmented and isolated.

Past research efforts have investigated the habitat preferences of black bears in several regions of the continental USA, but these studies were either limited to relatively small geographic areas or focused on selection preferences of individual bears. As a result, there is a general lack of knowledge about the composition of environmental conditions that demarcate suitable bear range or how bears respond to environmental variability at the macro-scale. To that end, I investigated the relationship between spatial environmental variability and black bear occurrence in the continental USA. The objectives of this study were to: (1) determine if spatial environmental variability influences the distribution of black bears, (2) identify spatial environmental variables correlated with black bear distribution, and (3) develop a model to predict the spatial distribution of suitable bear habitat and potential relocation areas.

I used logistic regression to assess the correlation between spatial environmental variability and bear occurrence, and to develop a model predicting the spatial occurrence of bears. I divided the continental USA into two areas; bottomland hardwood areas of the Southeastern coastal plain, termed lowland environments, and the remainder of the continental USA, termed upland environments. I found that bear presence was correlated with 10 landscape-scale variables in upland and lowland environments of the continental

USA. In upland environments, bear presence was positively correlated with all macrohabitat types (except grassland–shrubland mosaic), lands actively managed as wild lands, snowfall >122 cm, and increasing levels of spring-summer normalized difference vegetation index (NDVI). In contrast, bear presence was negatively correlated with forest fragmentation, road density index, human densities >10 persons/km^2, greater distances from streams, and increasing levels of wetness.

In lowland environments, bear presence was positively correlated with deciduous and evergreen forests, grassland–shrubland mosaic, perforated through edge levels of forest fragmentation, lands actively managed as wild lands, human density <43 persons/km^2, increasing soil nitrogen levels, and increasing levels of spring NDVI. In contrast, bear presence was negatively correlated with herbaceous–woodland wetland, sparsely vegetated areas, increasing road density index, and increasing levels of wetness.

The relative probability of bear occurrence models indicated that there is about 2.8 million square kilometers of suitable bear habitat in the continental USA, distributed in about 1,400 distinct patches. However, only 306 of the suitable habitat patches are ≥200 km^2, corresponding to 2,721,803 km^2 of suitable habitat. The models identified 981,061 km^2 of vacant suitable bear habitat in the continental USA. These habitats are distributed in 394 patches, of which 155 (743,558 km^2) are adjacent to occupied bear range and 239 (237,503 km^2) are isolated from occupied range. The probability of occurrence models identified 34 habitat patches as priority (≥5,000 km^2) reintroduction areas.

This study describes bear-habitat use patterns across a broad spatial extent and identified landscape variables that may influence bear occurrence. In so doing, the study

provides a new interactive model that can be adapted and used to predict the relative probability of bear occurrence due to changing spatial conditions and identify potential reintroduction areas. In addition, the results of this study may contribute to future research efforts on corridor analyses or metapopulation dynamics.

TABLE OF CONTENTS

Chapter Page

LIST OF TABLES

Table		Page

LIST OF FIGURES

Figure Page

Figure Page

CHAPTER I

INTRODUCTION

There are 8 species of bears (Ursidae) in the world. They live in more than 65 countries or autonomous regions and occur on all continents except Australia, Antarctica, and Africa (Servheen et al. 1999). While globally their distribution is widespread, the abundance and range of most bear species are declining because of habitat loss, habitat fragmentation, and human-induced mortality (Servheen et al. 1999). Their long-term outlook is further jeopardized because of the general lack of knowledge on critical bear-habitat relationships. Bears at the greatest risk include the giant panda (*Ailuropoda melanoleuca*), Asiatic black bear (*Ursus thibetanus*), sun bear (*Helarctos malayanus*), sloth bear (*Melursus ursinus*), and Andean bear (*Tremarctos ornatus*) (Servheen et al. 1999).

The American black bear (*Ursus americanus*), one of the 3 bear species found in North America, seems to be the most resilient of all the bear species to anthropogenic influences. Indeed, more than 500,000 black bears occur throughout their range and many populations are stable to increasing (Pelton et al. 1999). Despite their resiliency, many black bear populations are in jeopardy and considered endangered or threatened (Pelton et al. 1999). Within the United States of America (USA), black bears in Louisiana, eastern Texas, and southern Mississippi are federally listed as a threatened subspecies under the Endangered Species Act of 1973. In 7 other states black bears are classified as rare, threatened, or endangered (Pelton et al. 1999). Black bears in Mexico also are listed as endangered (Pelton et al. 1999).

With individual black bear populations ranging from thriving to endangered, opinions also range from considering them a pest to an important resource. In many areas black bears raid campgrounds, damage agricultural crops, destroy apiaries and are considered a nuisance (Warburton and Maddrey 1994). However, in all Canadian Provinces and 28 states in the USA bears are a valued game species and are legally hunted, with about 40,000 bears harvested annually (Pelton et al. 1999). In some areas black bears even are considered an indicator species (USDA 1994).

While information on status, distribution, and threats is more complete for black bears compared with bear species on other continents, many black bear populations are isolated and dependent on careful management, particularly in the southeastern and southwestern USA. As a result, many black bear management programs include restrictions on poisons, regulated harvests, and limited access to habitat reserves. Like other bear species, however, habitat loss and habitat fragmentation are considered the greatest threats to black bear populations. Yet, only a few black bear management programs include habitat components. In Canada, Alberta is the only province currently managing habitat for black bears (Pelton et al. 1999). Their management program consists of habitat inventory, protection, retention, and enhancement. The only habitat management in Mexico is by private ranchers, who frequently provide bears with food and water. In the USA, only 10 of 41 states with bears manage habitat for black bears (Pelton et al. 1999). Management techniques range in scale from protection of mature den trees, to land acquisition, to cooperative management between state, federal, and private organizations. Even in these few programs, no guidelines exist that address habitat loss and habitat fragmentation specifically.

Habitat loss and fragmentation likely will continue to impact black bears across a broad spatial extent as human populations continue to increase and expand into the rural landscape. As a result, many bear populations may retract, whereas others in more secure habitats may expand. To successfully manage black bears and their habitats it's crucial for wildlife managers to understand how bears respond to landscape features and habitat changes. Indeed, many black bear studies have investigated bear-habitat relationships, but inferences from most of these studies are limited to specific bear populations, habitat conditions, or management situations because the studies focused on individual animals or local environmental conditions (Clark et al. 1993, Rudis and Tansey 1995, van Manen and Pelton 1997, Jones et al. 1998, Bull et al. 2001). Consequently, there is a paucity of information on landscape-level patterns of bear-habitat relationships.

Ecological Framework

Central to the study of animal ecology is the usage an animal makes of its environment and one of the most important and widely used terms in ecology is "niche" (Whittaker et al. 1973). The term niche was first described in the early 1900s and generally referred to the habits, food, and mode of life of a species (Grinnell 1917; Elton 1927; Hutchinson 1957, 1978). However, the concept has received considerable attention, both in terms of defining exactly how niche should be defined and its usefulness in ecological theory (Whittaker et al. 1973). Among the early definitions, Hutchinson (1957, 1978) proposed that a given niche could be demarcated by n number of environmental variables that are suitable for the species to exist. Hutchinson termed the resulting area where the species can exist as an n-dimensional hypervolume. That type of niche is termed the fundamental or physiological niche. In cases where

competition or other interactions exclude a species from portions of its fundamental niche, the remaining usable area of the hypervolume is termed the realized or ecological niche. Hutchinson (1957) further suggested that the probability of occurrence at all points in the niche may not be equal. This concept of optimal and suboptimal regions in niche hyperspace thereby suggests that environmental variability also may affect survival and other population response variables as well as species presence (Whittaker 1967, Whittaker et al. 1973). Despite Hutchinson's early definition of a niche, ecologists have broadened the term by applying the word niche to several different concepts (Whittaker et al. 1973). The primary source of the confusion stems from the lack of differentiation between niche and habitat (Udvardy 1959, Whittaker et al. 1973). Whittaker et al. (1973) clarified some of the confusion by defining niche as the intracommunity role of a species and habitat as aspects of the physical and chemical environment. Whittaker et al. (1973) further defined ecotope as niche and habitat combined to represent both intra- and intercommunity variables. Thus, an ecotope represents the relationship of a species to the full range of environmental and biotic variables affecting it (Whittaker et al. 1973; Fig. 1.1).

Numerous studies have investigated various components of the niche, habitat, and ecotope of a species (Tilman 1977, Sabo 1980, Nudds 1983, Seagle and McCracken 1986, Austin et al. 1990, Westman 1991). However, due to the complexity of many natural systems, many niche studies have been limited to theoretical concepts, lab experiments, simple mathematical models, and site-specific investigations. Consequently, few studies have linked niche-theory to extensive empirical data sets encompassing large geographical areas. However, with the advancement of geographical

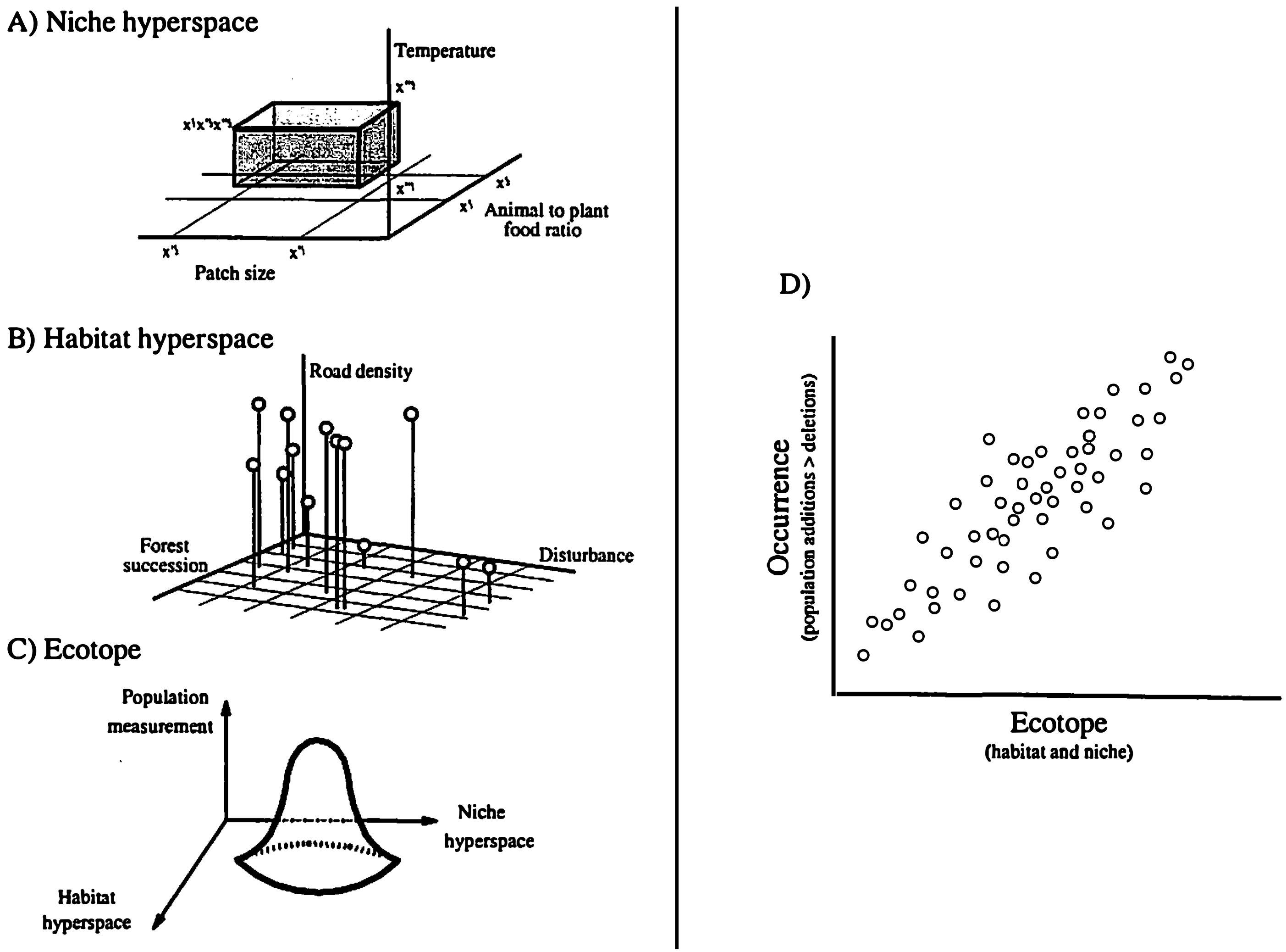


Fig. 1.1. Graphical representation of ecological concepts including niche (A), habitat (B), ecotope (C), and species occurrence (D) (Modified from Whittaker et al. [1973] and Hutchinson [1978]).

information systems (GIS) and multivariate statistical analysis techniques, methods are now available to investigate complex assemblages of environmental factors that describe the niche of a species, and demarcate current and potential distributions.

Study Goal and Objectives

The goal of my study was to identify landscape-level patterns of bear-habitat relationships. To accomplish this I quantified and described the ecotope of the American black bear by investigating the relationships between spatial environmental variability and the distribution of black bears. I determined whether available spatial data can be used to describe the distribution of black bears in the continental USA and I developed a predictive spatial model to delineate current and potential bear range. I tested the following null hypotheses:

Objective 1. Determine if spatial variability influences the distribution of American black bears.

1. H_0: The distribution of black bears is not correlated with spatial variability.

Objective 2. If spatial variability influences the distribution of American black bears, identify which environmental factors are correlated with black bear distribution.

2. H_0: Anthropogenic influences (e.g., habitat fragmentation, human density, road density, land management practices) are not negatively correlated with the distribution of black bears.

Objective 3. If spatial variability influences the distribution of American black bears, develop a model to predict the spatial distribution of suitable bear habitat (i.e., potential range).

3. H_0: All suitable black bear habitat currently is occupied by bears.

CHAPTER II

GEOGRAPHIC EXTENT

General

Black bears historically were found throughout the forested regions of North America (Hall 1981; Fig. 2.1). However, the most recent documentation of known bear range indicates that bears only occur in a fraction of their historic range, particularly in the continental USA (Pelton and van Manen 1994; Fig. 2.2). For my study the ideal geographic extent (see Appendix A for glossary of terms) was the entire historic range of black bears. However, the availability of spatial data was limited for many Canadian Provinces and Mexico. Therefore, I limited my investigations to the continental USA. The most recent black bear distribution map provided by Pelton and van Manen (1994) was based on a 1993 survey and indicated that black bears occur in 41 of the 48 states in the continental USA. Based on their map, black bears occur in approximately 60 discrete populations with a total range of about 2,000,000 km^2.

The continental USA is located in North America, bordered by Canada to the north, the Pacific ocean to the west, Mexico to the south, and the north Atlantic ocean to the east (Fig. 2.3). The continental USA is divided into 48 administrative states, plus the District of Columbia. Each state is subdivided into administrative counties. The total land area of the continental USA is approximately 9,200,000 km^2.

Topography and Climate

Elevations in the continental USA range from -86 to 6,194 m. There are two major mountain ranges in the USA, the Continental Divide in the west and the

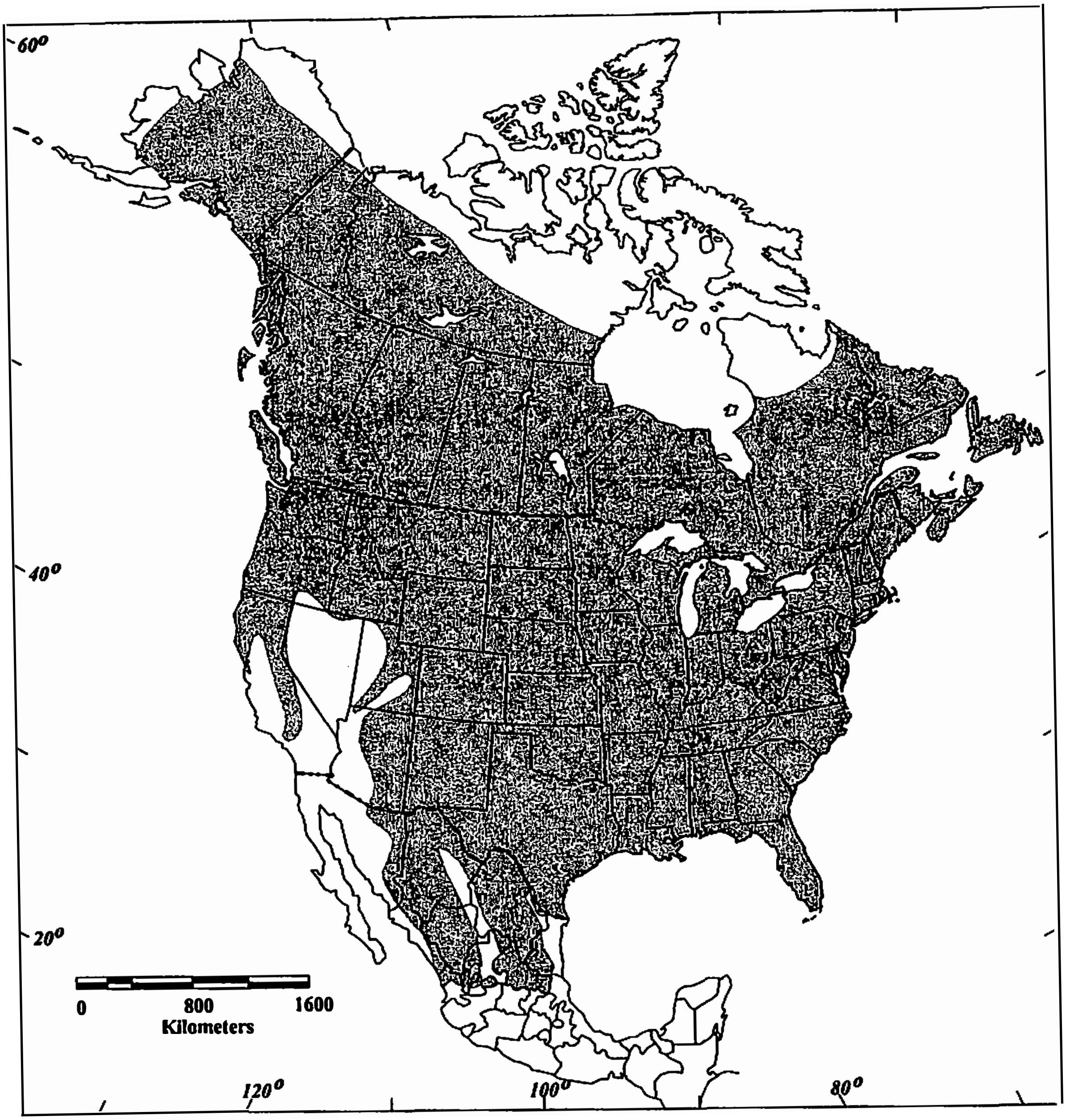


Figure 2.1. Historic distribution of American black bears in North America (Hall 1981).

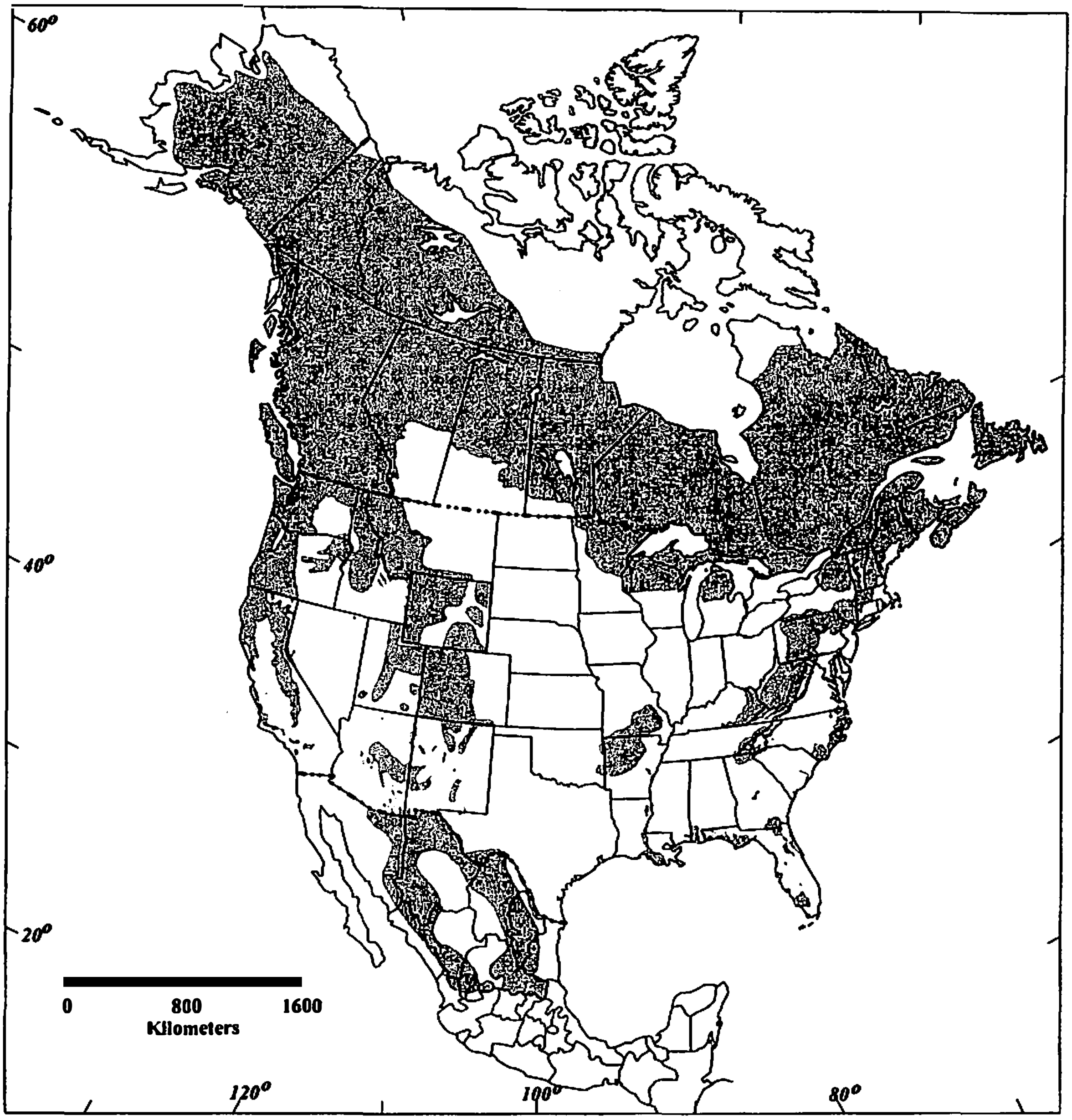


Figure 2.2. Distribution of American black bears in North America in 1993 (Pelton and van Manen 1994).

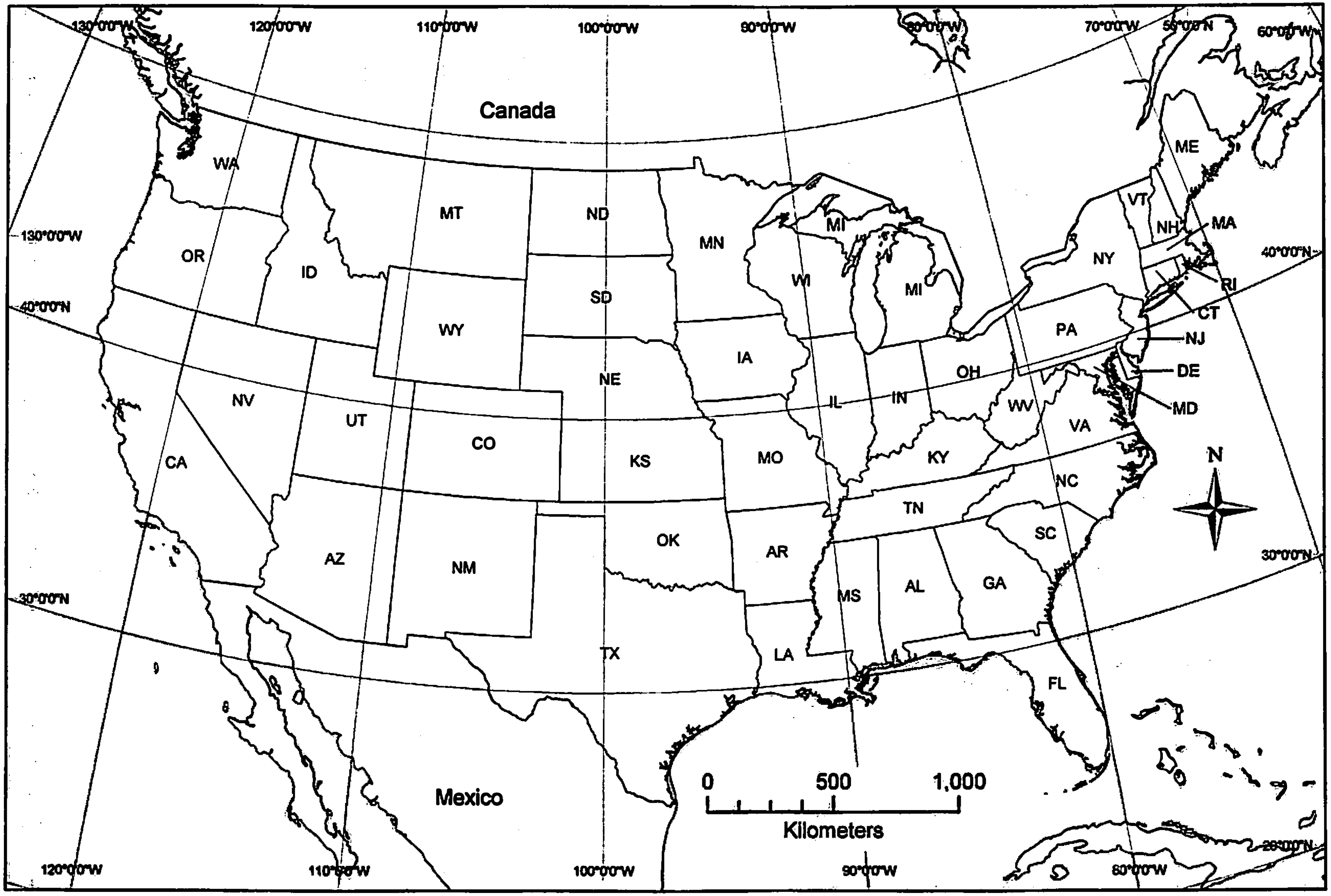


Figure 2.3. States of the continental USA (see Appendix B for definition of state abbreviations).

Appalachian Mountains in the east (Fig. 2.4). Both ranges are characterized by high, rugged mountains and steep slopes. Elevations along the Continental Divide range from 200–6,194 m, whereas elevations in the Appalachians range from 200–2,024 m. The central USA is characterized by vast plains and rolling hills. Much of the southern USA is low coastal plains or high plateaus and desert.

The climate in most of the continental USA is temperate, except for the semiarid Great Plains west of the Mississippi River, arid regions in the Great Basin of the southwest, and subtropical areas in south Florida. Average annual precipitation ranges from about 16.5 cm in the southwestern USA to 165 cm in the Pacific Northwest, and seasonal extremes range from <0.65 cm/month to 18 cm/month (National Oceanic and Atmospheric Administration, National Climate Data Center, Asheville, North Carolina, USA). Average snowfall ranges from 0–260 cm annually, and typically is associated with the elevations >500 m. Average annual temperatures range from 5.5–22.7°C, with average winter temperatures ranging -10.0–16.1°C and average summer temperatures ranging 18.3–27.8°C.

Macrohabitat

Within the continental USA, forested regions made up 40% of the land area, whereas open grass/shrubland and tundra/snow each comprised 22%, and cultivated cropland/pasture areas made up 15% (Fig. 2.5, Table 2.1). Macrohabitat types included evergreen needleleaf, deciduous broadleaf, mixed forest, closed shrubland, open shrubland, woody savanna, savanna, grassland, permanent wetland, cropland, and cropland/natural vegetation mosaic.

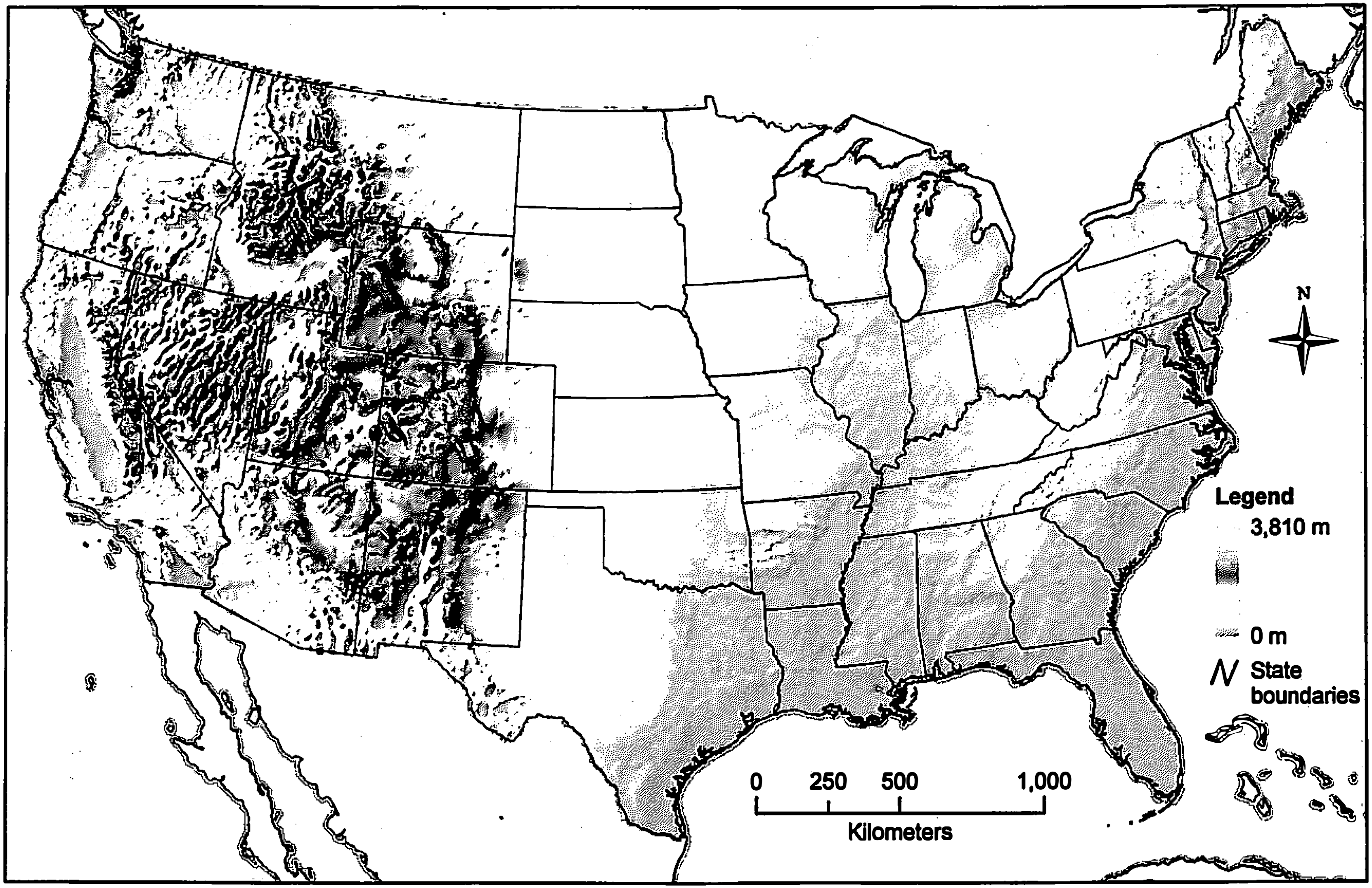


Figure 2.4. Elevation in the continental USA (USGS, Sioux Falls, South Dakota, USA).

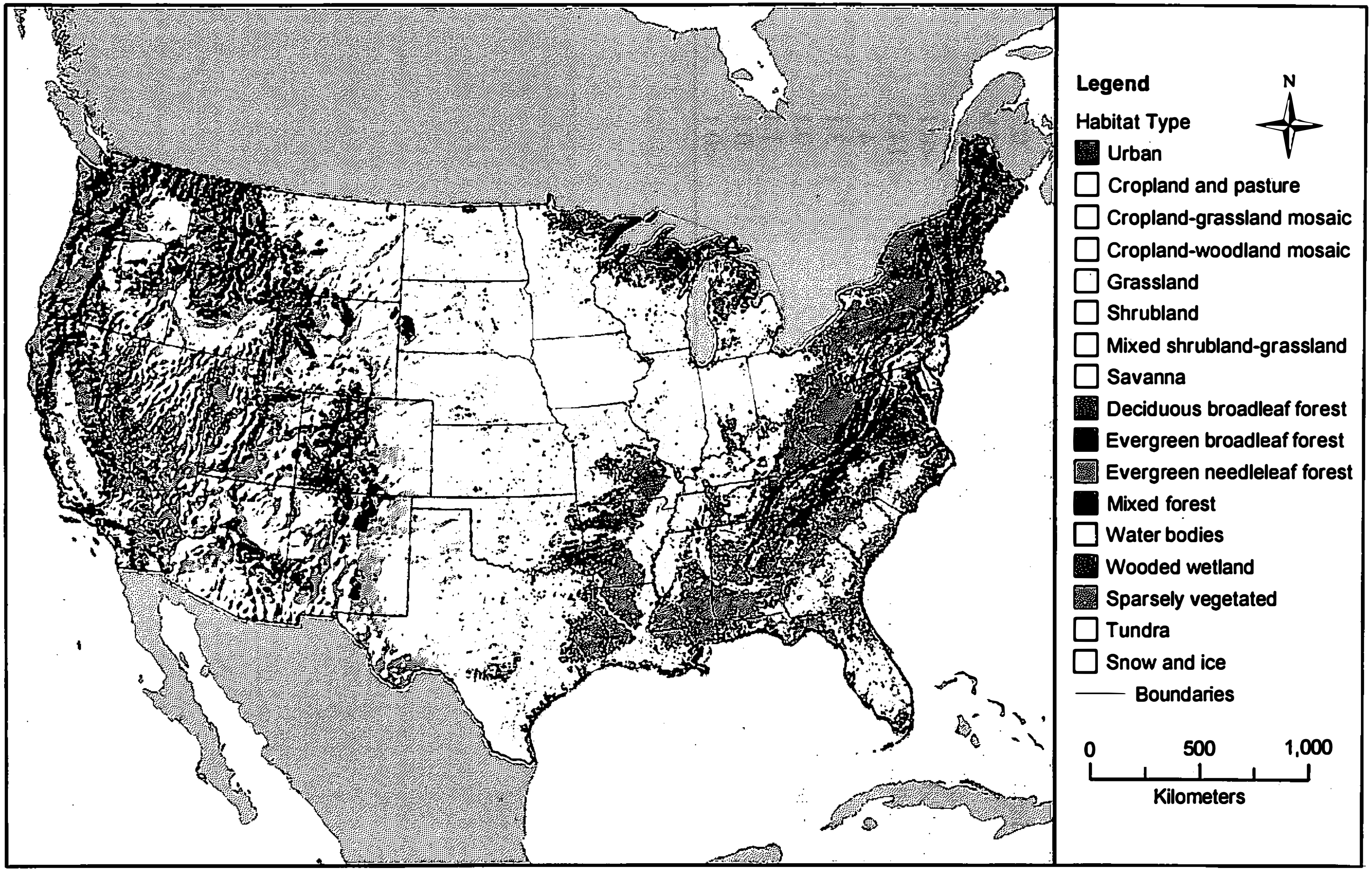


Figure 2.5. Macrohabitat types in the continental USA (AVHRR 1992-93; USGS, Sioux Falls, South Dakota, USA).

Table 2.1. Occurrence and proportion of each macrohabitat type in the continental USA (1992-1993 advanced-very-high-resolution-radiometry and thermatic mapper data, U.S. Geological Survey).

Macrohabitat type	km^2	% of USA
Urban	78,867	1.0
Cropland and pasture	1,153,828	14.5
Cropland-grassland mosaic	794,607	10.0
Cropland-woodland mosaic	454,829	5.7
Grassland	1,240,937	15.6
Shrubland	1,370,849	17.2
Mixed grassland-shrubland	14,607	0.2
Savanna	232,963	2.9
Deciduous broadleaf forest	775,624	9.7
Evergreen broadleaf forest	342	<0.1
Evergreen needleleaf forest	1,138,656	14.3
Mixed forest	371,729	4.7
Water bodies	243,217	3.1
Wooded wetland	6,635	0.1
Sparsely vegetated	85,739	1.1
Tundra	5,611	0.1
Snow and ice	369	<0.1

Anthropogenic Statistics

In 1993, approximately 280 million people lived in the USA, of which 80% lived in metropolitan areas and 239 cities had ≥100,000 people (Central Intelligence Agency 2002). Approximately 6.3 million km of roads occurred throughout the USA, of which 1% were high-speed interstate roads, 89% were other paved roads, and 10% were unpaved roads (Central Intelligence Agency 2002).

CHAPTER III

METHODS

Black Bear Distribution

I investigated the relationship between black bear occurrence and spatial environmental variability to identify factors that are associated with bear presence and predict the spatial distribution of suitable bear habitat in the continental USA. I used the black bear distribution map generated by Pelton and van Manen (1994) as a measure of occupied range (Fig. 3.1). During 1993, state biologists were asked to delineate regions of a statewide county map that corresponded to occupied black bear range. In many cases, the returned maps contained primary and secondary ranges or with different density zones. For the purpose of this study, primary and secondary ranges and different density zones were considered occupied black bear range. Using the original maps from Pelton and van Manen's (1994) survey, I digitized the occupied range for black bears in the continental USA. The grain of the original range maps approximated a sub-county level and represented the known bear distribution in 1993.

Grain Size

The selection of an appropriate spatial grain size is crucial for the usefulness of a species occurrence model (Maurer 2002). An appropriate grain size depends, in part, on whether the study seeks to describe process or pattern, home range sizes, and the grain size of spatial data (Maurer 2002, Trani 2002). Generally, a fine-grain size ($\leq$25% of home range size) is used for studies that describe processes between species demographics and the environment, whereas a coarse-grain size (relative to home range

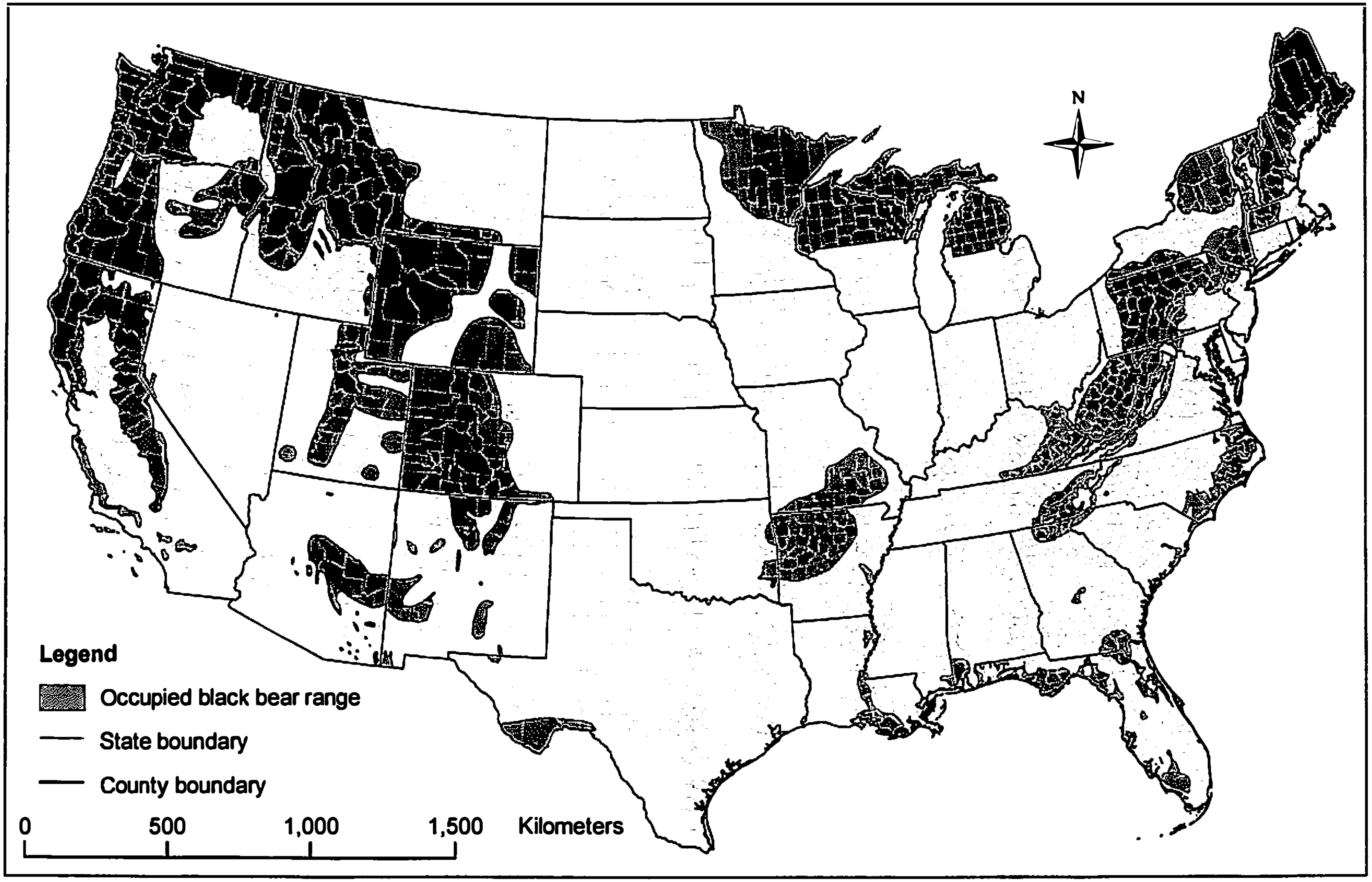


Figure 3.1. Occupied range of the American black bear in the continental USA, 1993 (from Pelton and van Manen 1994).

size and habitats) is used for studies that predict species occurrence and describe patterns (Schulz and Joyce 1992, Trani 2002). Fittingly, Johnson (1980) suggested that home range size provides an appropriate biological scale for modeling species occurrence within an animals entire geographic range.

My study describes patterns between spatial environmental variability and bear occurrence. The grain size of the original spatial environmental variables I used (see *Spatial Environmental Variables*) was 1 km^2, so grain sizes $\geq$1 km^2 (1×1 km, 2×2 km, 3×3 km, etc.) could be calculated. I used home range size as a basis for selecting a grain size. In a review of black bear home range sizes in the continental USA by van Manen (1994), the average home range size for black bears was approximately 49 km^2 (excluding 1 outlier; Table 3.1). A grain size of 49 km^2 also corresponded to the approximate midpoint in the range of grain sizes identified by Murrow (2001), where grain sizes of 20 km^2 and 75 km^2 were appropriate for black bear occupancy models. Therefore, I selected a grain size of 49 km^2 for my study.

Spatial Environmental Variables

To identify spatial environmental variables that are correlated with bear occurrence and suitable black bear habitat, I investigated the relationship between known bear occurrence and 20 landscape variables (Table 3.2). I limited my investigation to spatial environmental variability because temporal data was limited, particularly in a GIS format. The existence of a population can be defined as a situation where animal additions $\geq$ deletions (Caughley 1977). Therefore, I selected spatial variables that, from a biological standpoint, had the potential to influence bear reproduction or mortality. I did not include variables that may influence immigration or emigration per se, because my

Table 3.1. Estimated home range sizes for black bears in the continental USA (adopted from van Manen [1994]).

Location	Home range size (km^2) Females	Males	Study
Arkansas	34.7	89.7	Clark (1991)
Arkansas	1.0	128.0	Smith (1985)
California	17.1	22.4	Novick and Stewart (1982)
Idaho	48.9	112.4	Amstrup and Beecham (1976)
Maine	43.0	1,721.0[a]	Hugie (1982)
Massachusetts	28.0	318.0	Elowe (1984)
North Carolina	16.9	61.0	Warburton (1984)
North Carolina	14.8	61.4	Beringer (1986)
North Carolina	12.0	39.0	Seibert (1989)
North Carolina	9.1	---	Reagan (1991)
Tennessee	7.0	21.0	Beeman (1975)
Tennessee	8.4	21.2	Garshelis (1978)
Tennessee	5.2	32.1	Quigley (1982)
Tennessee	13.0	119.0	Carr (1983)
Tennessee	12.3	32.4	Villarrubia (1982)
Tennessee	18.9	126.3	Garris (1983)
Tennessee	6.9	51.2	van Manen (1994)
Virginia	38.0	195.0	Garner (1986)
Virginia	27.0	111.7	Hellgren and Vaughan (1990)
Washington	5.3	51.6	Poelker and Hartwell (1973)
Washington	2.4	5.1	Lindzey and Meslow (1977)

[a] Treated as outlier observation and not included in average home range size calculation.

Table 3.2. Spatial environmental variables for analysis of black bear occurrence in the continental USA, 2004.

Code	Name	Variable type	Data type	Explanation/measurement unit
Y	Bear range	Dependent	Binomial	1 = bear presence 0 = bear absence
HT	Macrohabitat type	Independent	Nominal	1 = mixed forest 2 = deciduous forest 3 = evergreen needleleaf forest 4 = cropland-woodland mosaic 5 = grassland-shrubland mosaic 6 = sparsely-vegetated, snow, ice 7 = urban and built-up 8 = cropland, pasture, grassland 9 = herbaceous-wooded wetland
FF	Forest fragmentation	Independent	Ordinal	1 = forest 2 = perforated 3 = transitional 4 = edge 5 = patch 6 = non-forested
EL	Elevation	Independent	Continuous	Meters
FC	Percent forested cover	Independent	Continuous	Percent
PR	Precipitation	Independent	Continuous	Centimeters
HR	Habitat richness	Independent	Continuous	Habitat types within 49 km^2 square
ST	Proximity to stream	Independent	Continuous	Kilometers
SL	Slope	Independent	Continuous	Degrees
SN	Snowfall	Independent	Continuous	Centimeters
TE	Temperature	Independent	Continuous	Degrees Fahrenheit
NI	Soil nitrogen	Independent	Continuous	g/m^2
WE	Wetness index	Independent	Continuous	Index 0-11
GR	Grain crop area	Independent	Continuous	Hectares
HD	Human density	Independent	Continuous	$Persons/km^2$
RD	Road density index	Independent	Continuous	Ha/km^2
SP	Spring NDVI[a]	Independent	Continuous	Index 0-550
SU	Summer NDVI	Independent	Continuous	Index 0-550
FA	Fall NDVI	Independent	Continuous	Index 0-550
WI	Winter NDVI	Independent	Continuous	Index 0-550
ML	Managed lands	Independent	Nominal	1 = managed lands 0 = non-managed lands

[a] NDVI = Normalized Difference Vegetation Index

study was not spatially explicit. As potential factors that influence reproduction, I considered 6 variables related to plant growth (precipitation, temperature, soil nitrogen, wetness, snowfall, and normalized difference vegetation index [NDVI; for 4 seasons]) and 5 variables related to habitat structure (macrohabitat type, habitat richness, elevation, slope, and proximity to streams). I also included agricultural grain crops because of the prevalence of crops in the diet of bears in the eastern USA (Landers et al. 1979, Hellgren and Vaughan 1988, Maddrey 1995, Anderson 1997). I considered 5 variables that likely influence mortality, including human density, road density index, forest fragmentation, percent forested cover, and whether the landscape was actively managed as wild lands (e.g., National Forests, National Parks, National Recreation Areas). For each variable, I generated a grid using ARC/INFO® (ESRI, Redlands, California, USA) GIS.

Macrohabitat Type.—I included macrohabitat type as a variable because of the importance of specific forest types for providing forage (i.e., hard mast) and escape cover for bears (Pelton 1982). I obtained a macrohabitat type grid from U.S. Geological Survey's (USGS) Earth Resources Observation System (EROS) Data Center (Sioux Falls, South Dakota, USA). The grid was derived from 1-km^2 advanced-very-high-resolution-radiometry (AVHRR) data collected from April 1992 through March 1993 and core thermatic map data (Anderson et al. 1976; Sellers et al. 1986, 1996; Olson 1994a, 1994b; Belward 1996; Dickinson et al. 1986). Classification accuracy for the macrohabitat grid ranged from 59.4–90.2%, depending on the validation method used (Scepan 1999). To convert from 1-km^2 to 49-km^2 cell size, I assigned the most frequent macrohabitat type in a 49-km^2 square window to a new cell corresponding to the window size and location (Fig. 3.2). I repeated the process for the entire grid by sliding the 49-

(A)

1	3	3	1	3	3	2	2	2	2	2	3	3	1
4	3	3	1	3	3	2	2	2	2	1	2	3	2
1	6	3	1	2	2	4	4	2	2	3	4	4	4
2	4	3	5	4	3	4	4	4	3	5	4	3	4
2	3	3	5	4	2	2	2	1	3	2	6	3	4
2	3	3	3	4	4	1	1	2	2	3	4	4	4
2	3	3	3	3	4	3	3	3	3	3	3	4	4
2	3	3	3	3	4	4	4	3	3	1	3	2	2
4	3	3	1	3	4	4	4	4	3	3	3	2	2
6	6	3	1	2	2	4	4	4	3	3	2	2	2
6	6	6	5	4	3	4	2	4	3	3	4	3	1
6	6	6	6	4	2	2	2	3	3	2	2	1	1
6	6	6	6	6	4	1	2	2	2	2	2	1	1
3	3	6	6	6	6	3	2	2	2	2	1	1	1

(B)

3	2
6	2

Figure 3.2. Procedure for assigning the most common value in a square window with forty-nine 1-km^2 cells (A) to one 49-km^2 cell (B).

km^2 window throughout the grid. This resulted in a new grid of dominant macrohabitat types with a cell size of 49 km^2.

Percent Forested Cover and Habitat Richness.—I included percent forested cover as a variable because some proportion of forested area is considered a prerequisite for bears (Pelton 1982). I included habitat richness to represent forage diversity (Landers et al. 1979). I calculated percent forested cover and habitat richness from the 1-km^2 macrohabitat type grid. Percent forest cover equaled the proportion of forested cells in each 49-km^2 window. That value was assigned to a new grid with a cell size of 49 km^2. Similarly, I calculated habitat richness for each 49-km^2 window by summing the number of different macrohabitat types (1-km^2 cell size) and assigning that value to the new cell.

Forest Fragmentation.—I included forest fragmentation as a variable because of the negative association between high levels of fragmentation and bear population dynamics (Hellgren and Maehr 1993, Anderson 1997, Stratman et al. 2001b). For black bears, forest fragmentation occurs when a large forested area is transformed into smaller forested patches of a total smaller area that are surrounded by a matrix of different vegetation and landuses than the original unit (Wilcove et al. 1986, Saunders et al. 1991, Hellgren and Maehr 1993). Therefore, I calculated a forest fragmentation grid by applying a spatial algorithm to each forested cell of the 1-km^2 macrohabitat type grid (Riitters et al. 2000). I assigned one of six levels of fragmentation to each 1-km^2 cell based on the amount of forest (Pf) and its occurrence to adjacent forest cells (Pff) within a 49-km^2 window (Riitters et al. 2000). Using criteria established by Riitters et al. (2000) for values of Pf and Pff, I classified ordinal levels of forest fragmentation as: (1) forest, (2) perforated, (3) edge, (4) transitional, (5) patch, and (6) non-forested. I again used a

49-km^2 window to calculate the mean fragmentation level, and assigned that value to a new grid.

Elevation.—I included elevation as a variable because of its relationship to human disturbance sites (van Manen 1994), and vegetation gradients and climate conditions which influence the habitat structure and forage availability. I obtained a digital elevation model (DEM) grid from the USGS-EROS Data Center (Sioux Falls, South Dakota, USA). Elevations within the DEM occur at regularly spaced 30-arc seconds, which approximates a 1-km^2 grain. For the continental USA, vertical accuracy of the DEM was 30 m at the 90% confidence level. I used the 49-km^2 sliding window procedure described previously to assign mean elevation to each cell in a new grid (Fig. 2.4).

Slope, Wetness Index, and Streams.—I included slope and wetness index as variables because of their relationship to patterns of forage (i.e., soft mast) availability. I also included a proximity to streams variable because of the escape cover and forage availability associated with stream riparian areas (Anderson 1997, Stratman et al. 2001). I obtained grids for slope, wetness index, and streams (vector coverage) from USGS-EROS Data Center (Sioux Falls, South Dakota, USA). Each grid was generated from EROS's DEM and have corresponding accuracy assumptions. Slope was calculated as the maximum change in elevation between each cell and its neighboring eight cells. Measurements for slope range from 0 to 90 degrees, with 0 defined as flat topography. Wetness index, or compound topographic index, is a function of the upstream contributing area and slope of the landscape (Moore et al. 1991). Using flow

accumulation (FA) (i.e., area of upstream catchment) and slope grids, wetness is defined as:

$$Wetness = \ln\left[\frac{FA}{\tan(slope)}\right].$$

In areas of no slope, a wetness value was obtained by substituting a slope of 0.001. Measurements for wetness index are between 0.001 and 9.000, with 9.000 representing maximum wetness. The stream coverage is a function of FA and flow direction, where streams are defined as vectors generated from STREAMLINK and STREAMLINE functions in ARC/INFO (EROS, Sioux Falls, South Dakota, USA).

For slope and wetness grids, I calculated mean values using the sliding 49-km^2 window procedure, and assigned those values to a new grid with that cell size. I generated a distance-to-streams grid by calculating the distance from a cell to the nearest stream and assigning that value to the respective cell. I then used the sliding 49-km^2 window procedure to generate a new grid of mean distance-to-stream.

Road Density Index.—I included a measure of road density as a variable because of documented avoidance of bears to paved roads (Kasworm and Manely 1990, Wooding and Maddrey 1994). I obtained a vector coverage of class 1-4 paved roads from ESRI® U.S. Street Database (Redlands, California, USA). I was unable to calculate exact road density (where total road length is calculated for each cell) because of computer storage and computation limitations. As an alternative, I converted the road vector coverage into a grid with 30×30 m cells with values of 1 (road) and 0 (no road) (Wooding and Maddrey 1994). I then used the 49-km^2 sliding window procedure to calculate the proportion of cells that were classified as roads as an index to road density. To determine

if road density index was correlated with exact road density, I compared the two in Washington State using simple linear regression (I used the NOINT model option to force the regression response to pass through the origin; SAS Institute 1999). Road density index was correlated with exact road density ($t_{1,3926} = 171.9$; $r^2 = 0.63$; $n = 3{,}927$; $P \leq 0.001$).

Normalized Difference Vegetation Index.— Soft mast has been documented as a primary food item for bears (Inman and Pelton 2002); however, I did not have a direct measure of soft mast availability. Therefore, I included NDVI as a correlate to soft-mast availability. I obtained grids of monthly NDVI for 1993 from the USGS-EROS Data Center (Sioux Falls, South Dakota, USA). NDVI often is used to monitor plant growth and biomass production. NDVI is generated from two channels of AVHRR, one in the visible spectrum and one in the near infrared spectrum. The principle behind NDVI is that measurements in the visible spectrum represent a plant's reflectance due to plant chlorophyll, whereas measurements in the near infrared spectrum represent a plant's reflectance due to spongy mesophyll leaf structure (Tucker 1979, Jackson et al. 1983, Tucker et al. 1991). In the resulting ratio, high values are an index to vigorously growing plants and low values to non-vegetative features. Measurements of NDVI ranged from -1.0 to 1.0.

I generated spring, summer, fall, and winter NDVI grids by summing individual cell values from appropriate monthly NDVI grids. I defined spring as April through June, summer as July through September, fall as October through December, and winter as January through March (van Manen 1994). I used the sliding 49-km^2 window procedure to generate a mean NDVI grid from the 1-km^2 seasonal grids.

Agricultural Grain Crops.—I included agricultural grain crops as a variable because of their prevalence in the diet of bears, particularly in the Southeast (Maddrey 1995). I obtained a vector coverage of agricultural grain crops from ESRI® USA – Agricultural Product Inventory (Redlands, California, USA). The database was generated based on the 1987 U.S. Census of Agriculture and included acres of individual crops summarized by county. From these data, I generated a county-level vector coverage of total combined acres of corn, wheat, oats, and soybeans. I selected these grain crops because of their documented importance as major food items for black bears, particularly in the Southeastern coastal plain (Landers et al. 1979, Hellgren and Vaughan 1988, Maddrey 1995, Anderson 1997). I generated a grid with a cell size of 49-km^2 from the county-level summary information.

Human Density.—I included human density as a variable because of the avoidance of bears to human activity sites (van Manen and Pelton 1997, Jones et al. 1998) and the associated bear mortality factors (Wooding and Maddrey 1994). I obtained a grid of human density from the Center for International Earth Science Information Network (CIESIN) (Palisades, New York, USA). The grid was generated by the Bureau of Census in 1990 from the decennial census. The grid cell size was 13 km^2. I used the sliding 49-km^2 window procedure to generate a mean human density grid from the 13-km^2 grid.

Managed Lands.—I included managed lands as a variable because of the association between lands actively managed as wild lands and beneficial habitat for black bears (Rudis and Tansey 1995). I obtained a vector coverage of managed lands from University of California, Remote Sensing Research Unit (Santa Barbara, California,

USA; McGhie 1996). The coverage contained all types of managed areas ≥100 ha, including land held by federal, state, tribal, and private agencies and organizations. I used the sliding 49-km^2 window procedure to generate a grid of managed lands from the original vector coverage (Table 3.2).

Soil Nitrogen.—I included soil nitrogen as a variable because of its association to plant productivity and, thus, forage availability (Chapin et al. 1987). I obtained a soil nitrogen grid from Oak Ridge National Laboratory, Distributed Active Archive Center (Oak Ridge, Tennessee, USA; Global Soil Data Task Group 2000). The cell size of the soil nitrogen grid was 1 km^2. I used the sliding 49-km^2 window procedure to generate a mean soil nitrogen grid from the original grid.

Precipitation, Snowfall, and Temperature.—Similar to slope and wetness index, I included precipitation, snowfall, and temperature as variables because of their association with vegetative growth patterns (Chapin et al. 1987). I obtained vector coverages for mean total precipitation, mean total snowfall, and mean daily temperature from the National Oceanic and Atmospheric Administration's National Climate Data Center (Asheville, North Carolina, USA). The vector coverages were based on 30-year annual means from 1961–1990 climate data. I used the sliding 49-km^2 window procedure to generate mean total precipitation, mean total snowfall, and mean daily temperature grids from the original vector coverages.

Model Development

There is no single "best" model for predicting species occurrence from environmental factors (Austin 2002, Van Horne 2002). Indeed, a number of models have been used to accurately predict species occurrence (Scott et al. 2002). Jones et al. (2002)

recently reviewed 4 prominent journals (*Ecology*, *Ecological Applications*, *Ecological Monographs*, and *Conservation Biology*; 1995-1999) to determine the most commonly used models for predicting species occurrence and population response. They found the most commonly used models were multiple linear regression (43%), logistic regression (27%), other parametric techniques (e.g., Mahalanobis Distance, Principle Component Analysis) (34%), and classification and regression trees (2%). Even beyond these, there are several more models that recently have been develop that show promise for species prediction studies (e.g., GARP, autologistic regression; Klute et al. 2002, Scott et al. 2002, Stockwell and Peterson 2002). However, issues of accuracy, calibration, and biological interpretation have not been as thoroughly examined in these models compared to more commonly used modeling techniques (Austin 2002).

I selected logistic regression as the modeling technique in my study because: (1) the dependent variable is binary, making it ideal for presence/absence data, (2) the independent variables can have continuous, ordinal, or nominal structure, (3) the logistic distribution is, from a mathematical standpoint, an extremely flexible and easily used function, (4) the parameterization and associated odds ratio lends itself to biologically meaningful interpretation, and (5) issues of accuracy and calibration have been thoroughly examined in several species prediction applications (Scott et al. 2002).

I used logistic regression to identify variables correlated with bear occurrence and predict the distribution of black bears in the continental USA from the 20 spatial variables. Logistic regression is a technique that is based on the logistic distribution (Hosmer and Lemeshow 2000) and describes the relationship between a dependent variable (outcome) and a set of independent variables (predictors). The principles of

logistic regression are similar to those in linear regression except the dependent variable is binomial. Using logistic regression, the conditional mean of the outcome (relative probability of y) given the independent variables is estimated by:

$$\pi(x) = \frac{e^{\beta_0 + \beta_1 x_1 + \beta_2 x_2 + \ldots \beta_p x_p}}{1 + e^{\beta_0 + \beta_1 x_1 + \beta_2 x_2 + \ldots \beta_p x_p}}, \qquad \text{eq. 1}$$

where β_0 is the estimated model intercept and β_1 is the estimated parameter value of the independent variable x_1. Central to logistic regression is the odds ratio, $e^{g(x)}$, where $g(x)$ is the logit transformation, denoted as:

$$g(x) = \beta_0 + \beta_1 x_1 + \beta_2 x_2 + \ldots \beta_p x_p. \qquad \text{eq. 2}$$

The odds ratio is a useful measure of association, and for this study was interpreted as the relative increase or decrease in the likelihood of bear presence given one unit change in the independent variable. I estimated the variance of the logit as:

$$V\hat{a}r[\hat{g}(x)] = \sum_{j=0}^{p} x_j^2 V\hat{a}r\left(\hat{\beta}_j\right) + \sum_{j=0}^{p} \sum_{k=j+1}^{p} 2 x_j x_k C\hat{o}v\left(\hat{\beta}_j, \hat{\beta}_k\right) \qquad \text{eq. 3}$$

where p equals the number of parameter coefficients in the model and $C\hat{o}v$ equals the coefficient covariance estimates.

Developing a logistic regression model is a complex process and requires adequate understanding of the dependent and independent variables, and the mechanics of logistic regression. I used statistical software (SAS Institute 1999) to conduct a five step process (Hosmer and Lemeshow 2000) to aid in variable selection and model development; (1) smoothed scatter plots and variable screening, (2) best subset selection, (3) univariate to multivariate model comparison, (4) examination of linearity in the logit for continuous variables, and (5) inclusion of appropriate interaction terms.

Smoothed Scatter Plots and Variable Screening.—I fit each independent variable to a univariate logistic regression model (proc LOGISTIC; SAS Institute 1999) to examine its association with bear occurrence. For nominal variables, I examined likelihood ratio tests to determine if design variables should be pooled to increase model fit (the likelihood ratio test in a univariate logistic model is equivalent to the likelihood ratio chi-square test in a contingency table). I only considered independent variables with a *P*-value <0.25 from the univariate logistic regression model as candidates for best subset selection (Hosmer and Lemeshow 2000). I also generated a smoothed scatter plot for each continuous variable to visually examine the association with bear occurrence and to determine if variables should be reclassified to ordinal or nominal scales to increase model fit. I excluded variables that displayed a weak association in the smoothed scatter plots. I reduced multicollinearity by discarding variables that were highly correlated ($r \geq 0.70$) based on the Pearson product-moment correlation coefficient (Johnson et al. 2002, Tabalske 2002, Young and Hutto 2002). If two variables were highly correlated, I discarded the variable that displayed the weakest association to bear occurrence based on the univariate logistic regression analysis (Tabalske 2002). I also assessed multicollinearity in the final model by estimating dispersion. A dispersion value of 1 indicates there is no overdispersion (i.e., parameter variance underestimated) or underdispersion (i.e., parameter variance overestimated); values >1 indicate overdispersion, whereas values <1 indicate underdispersion (SAS Institute 1999).

Best Subset Selection.—The variable screening step produced a list of candidate variables for inclusion in the best subset selection process. I fit a multiple variable logistic regression model to all possible combinations of candidate variables. I then used

Akaike's information criterion (AIC) to select the best approximating model that described bear presence or absence from the full set of candidate models (Burnham and Anderson 1998). AIC is an information based approach that identifies the best approximating model by evaluating the trade-off between bias and variance or the trade-off between under- and over-fitting (Burnham and Anderson 1998).

AIC uses Kullback–Liebler information (distance) theory and the log-likelihood functions to compare the relative distance between the "true" model and the approximating models and selects the model that minimizes that distance while maximizing entropy (Burnham and Anderson 1998). AIC values are calculated as:

$$\text{AIC} = -2 \log (\text{L} (\hat{\theta} \mid y)) + 2\text{K}, \qquad \text{eq. 4}$$

where y equals the dependent variable, $\text{L} (\hat{\theta} \mid y)$ equals the likelihood estimate of the estimated parameter value ($\hat{\theta}$) with respect to y, and K equals the number of parameters (including the intercept $\hat{\theta}_0$). The selection process follows the principle of parsimony by decreasing the $-2 \log (\text{L} (\hat{\theta} \mid y))$ term as additional parameters are added and increasing the 2K term as parameters are added. I used SAS to calculate an AIC value for each candidate model and I selected the model with the lowest value as the best approximating model.

Univariate to Multiple Variable Model Comparison.—I verified the importance of each variable in the best subset model by examining the Wald statistic of each variable, and by comparing each estimated coefficient to the coefficient in the univariate logistic regression model. I also compared the Wald statistic for each variable to the Wald statistic of the global model (all variables) and discarded variables with a marked change.

Examination of Linearity in the Logit.—I assessed linearity of the logit by examining smoothed scatter plots for each continuous variable. I generated the plots by refitting the multiple variable model treating each continuous variable, one-by-one, as nominal where the design variables corresponded to the quartiles of the continuous variable. I then plotted the resulting predicted coefficients of the design variables against the midpoints of the original continuous variable (Hosmer and Lemeshow 2000). I also assessed linearity of the logit using a Box-Tidwell transformation, where transformed variables [$x_i \ln(x_i)$] are included for each continuous independent variable. Deviance from linearity is assumed when the parameter estimate of the transformed variable is significant.

Inclusion of Appropriate Interaction Terms.—I considered interaction terms for variable pairs where the effect of one variable likely was not constant for different levels of another variable. I assessed the presence of an interaction by examining scatter plots and the Wald chi-square statistic of the interaction term in the logistic regression model (Hosmer and Lemeshow 2000).

Assessment of Model Fit

Regression Diagnostics.—I used the LOGISTIC procedure in SAS to calculate four regression diagnostics (deviance $[\Delta D]$, change in chi-square goodness of fit statistic $[\Delta\chi^2]$, confidence interval displacement $[C]$, and diagonal elements of the hat matrix $[h]$) to identify outlier observations with a large influence and observations that fit the model poorly. I used a series of plots of the regression diagnostics to determine if

individual observations should be excluded from the final model to increase model fit (Hosmer and Lemeshow 2000).

Internal Validation.—I used the LOGISTIC procedure in SAS to calculate the Hosmer-Lemeshow goodness-of-fit statistic $(\hat{C})$, which assesses the fit or calibration of the model (Hosmer and Lemeshow 2000). The Hosmer-Lemeshow goodness-of-fit statistic is based on deciles of risk, where the sample units are divided into 10 groups corresponding to the percentiles of the estimated probabilities. The test statistic is then obtained by calculating the Pearson chi-square statistic from the 10×2 table of observed and estimated expected frequencies.

I also calculated 5 measures of model accuracy, including sensitivity, specificity, false positive rate, false negative rate, and correct classification rate (Hosmer and Lemeshow 2000). Sensitivity is a measure of accuracy of predicted events, that is the proportion of event observations that the model predicts to be events for a given probability (i.e., cut-off point). Specificity is a measure of accuracy for predicted nonevents and is the proportion of nonevent observations that the model predicts to be nonevents for a given cut-off point. Specificity also equals 1-sensitivity. False positive rate is the number of nonevent observations that the model incorrectly predicts as events for a given probability cut-off point, whereas false negative rate is the number of event observations that the model incorrectly predicts as nonevents. The correct classification rate is the number of event and nonevent observations that the model correctly predicts for a given probability cut-off point. Because the measures of model accuracy can vary substantially given the selected cut-off point, I selected a cut-off point where specificity

equaled sensitivity because this probability level best approximates known bear occurrence. Therefore, I only reported sensitivity, specificity, false positive rate, false negative rate, and correct classification rate at the cut-off point where specificity equaled sensitivity.

I used the receiver operating characteristic (ROC) curve to assess model discrimination ability (i.e., bear presence versus absence; Pearce et al. 2002). The ROC curve is a graphic display between sensitivity and 1-specificity, and represents a measure of predictive accuracy at all possible cut-off points. As such, the corresponding area under the curve (AUC) represents the models discrimination ability. Hosmer and Lemeshow (2000) provided the following general rule for interpreting the AUC:

- No discrimination if AUC = 0.5.
- Acceptable discrimination if $0.7 \leq$ AUC <0.8.
- Excellent discrimination if $0.8 \leq$ AUC <0.9.
- Outstanding discrimination if AUC ≥ 0.9.

I used a modified Mann–Whitney test in program AccuROC (Accumetric Corporation, Montreal, Quebec, Canada) to calculate 95% confidence intervals for AUC and the sample size needed for retrospective power = 0.95, where $\alpha = 0.05$ and $\beta = 0.05$ (DeLong et al. 1988, Steidl et al. 1997). I compared the model AUC to an AUC of 0.5 (no discrimination ability) to estimate sample size for retrospective power = 0.95.

External Validation.—The preferred validation method is to use independent data to test models (Capen et al. 1986). In my study, confirmation of bear presence could be obtained by sampling random sites for evidence of bears (e.g., scat, hair, tracks). However, the large geographic extent of this project makes ground truthing an unrealistic

task (Scott et al. 1993). Therefore, I used the ROC curve (Hosmer and Lemeshow 2000) with a 10-fold re-sampling procedure (Verbyla and Litvaitis 1989) to assess the performance of the model based on independent data. I selected the ROC rather than the Hosmer-Lemeshow goodness-of-fit statistic as a measure of validation because vacant suitable bear habitat likely exists in the continental USA (Rudis and Tansey 1995; Murrow 2001; Bowman et al., unpublished data), thus validation of discrimination ability was more appropriate than model calibration, respectively (Pearce et al. 2002, Zimmermann and Breitenmoser 2002) (see *Discussion–Model Validation*). I divided all sample units into 10 random subsamples. I developed the logistic regression model with 9 subsamples (training group) and tested it with the remaining subsample (test group). I repeated this procedure 10 times, excluding a different subsample from the training group each time. I then calculated the area under the ROC curve and 95% confidence interval for the 10 training and test groups. I used a modified Mann–Whitney test in program AccuROC to determine if differences existed in model discrimination ability between the training and test groups (DeLong et al. 1988). Based on the same 10 test groups, I also calculated mean sensitivity, specificity, false positive rate, false negative rate, and correct classification rate to assess model accuracy.

Upland and Lowland Environments.—During the model development phase, the first attempt to fit a preliminary final model to the entire continental USA resulted in a model with poor calibration ($\hat{C} = 346.9$, 8 df, $P < 0.001$) and relatively low discrimination ability (AUC = 0.71). Graphically, the inconsistencies between predicted and observed bear occurrence was most prominent in bottomland hardwood regions of the Southeast. This suggests that perhaps a different suite of spatial variables influence

bears in the Southeast compared to the remainder of the continental USA. Indeed, numerous studies have documented that bear habitat use and population dynamics in bottomland hardwoods differ from bear populations in other habitats (Hellgren and Vaughan 1989, Brandenburg 1996, Jones 1996, Anderson 1997, Beausoleil 1999). Based on this biological evidence, I divided the continental USA into two geographic areas, the Southeastern coastal and Mississippi alluvial plains (hereafter referred to as "lowland environments") and the remainder of the continental USA (hereafter referred to as "upland environments"). I used the "division" hierarchical level of Bailey's ecoregions to spatially define lowland and upland environments (Bailey 1995). I developed a separate logistic regression model for each environment (Fig. 3.3).

Mapping Suitable Habitat Areas

I defined suitable bear habitat as predicted probabilities $\geq$ the cut-off point, where specificity equaled sensitivity. I then defined individual habitat patches based on contiguous areas (cells with common boundaries) of suitable habitat. I calculated the relative quality of each patch by averaging the probability of bear occurrence for the entire patch. I used the occupied bear range map (Pelton and van Manen 1994) and the predicted probability of bear occurrence to define vacant habitat patches (i.e., patches not in occupied range, but with a predicted probability of occurrence $\geq$ the cut-off points). I identified unoccupied habitat $\geq$200 km^2 (van Manen 1991) as potential reintroduction areas and patches $\geq$5,000 km^2 as priority reintroduction areas.

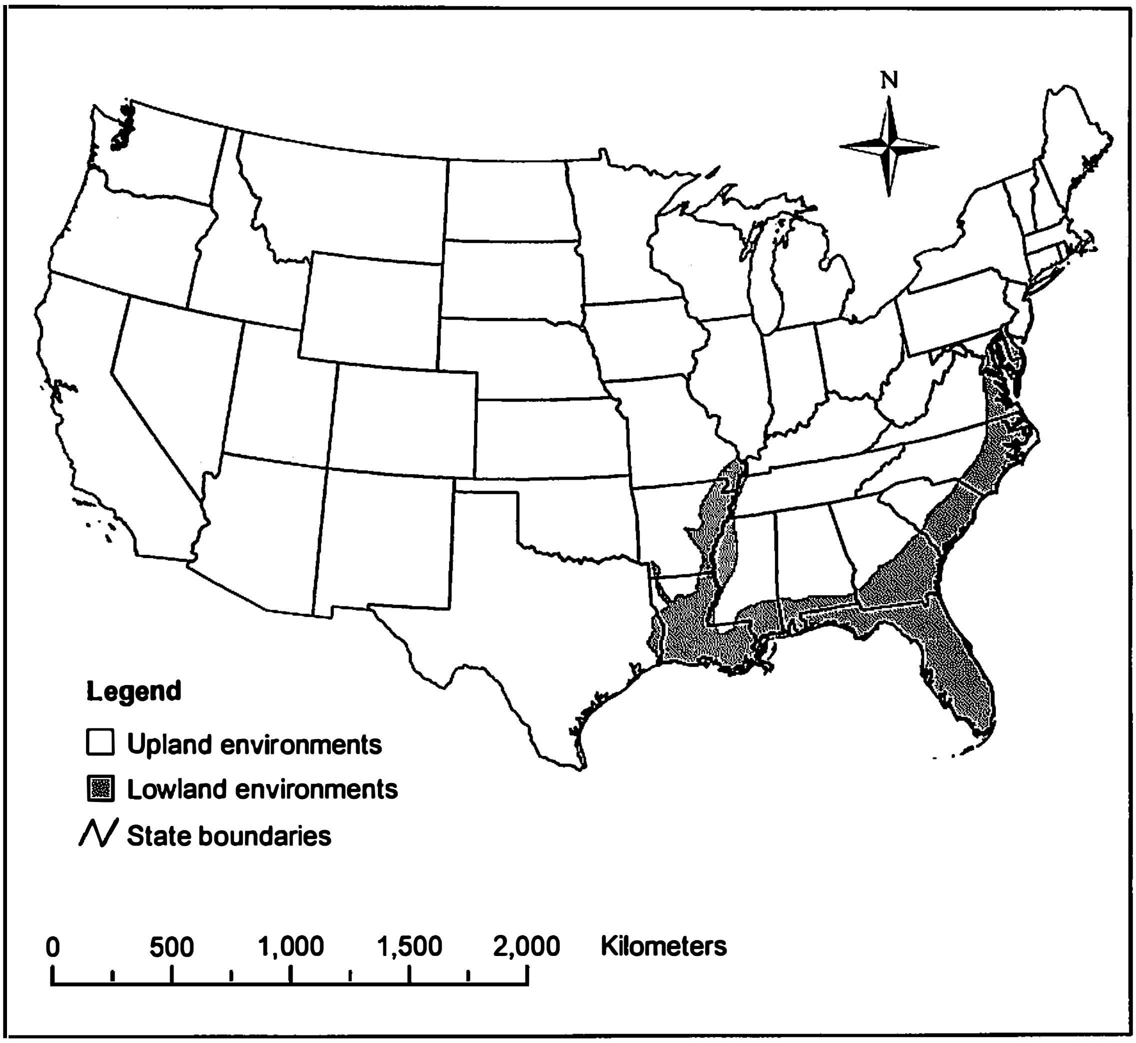
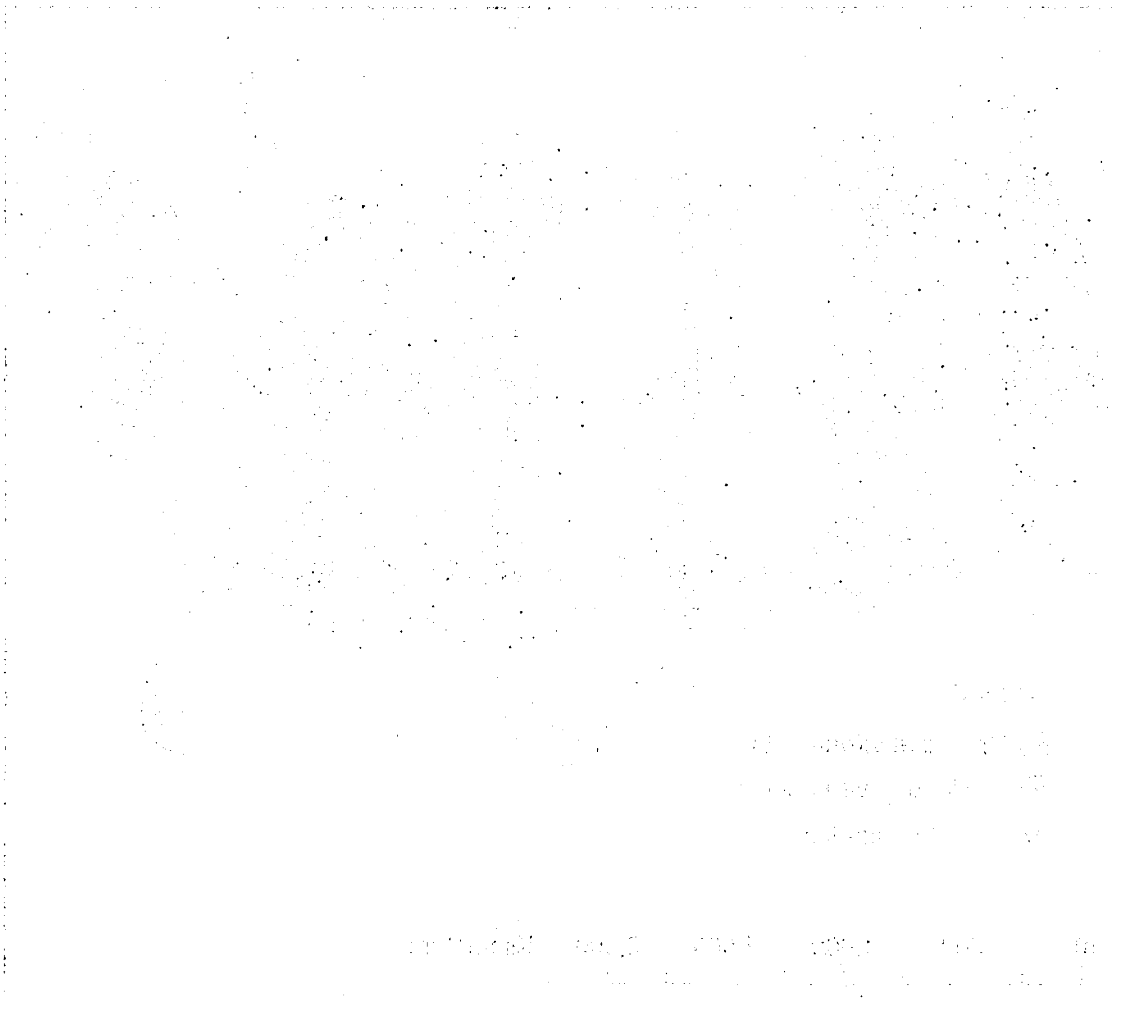


Figure 3.3. Upland and lowland environments used for a logistic regression analysis of black bear range in the continental USA, 2004.



CHAPTER IV

RESULTS

Upland Environments

I excluded habitat richness, soil nitrogen, grain crops, fall NDVI, and winter NDVI from the analysis because the smoothed scatter plot for each variable suggested a weak relationship with bear occurrence (Appendix C). The remaining independent variables displayed a strong association with bear occurrence, both in terms of inspection of the scatter plots and screening of each variable with univariate logistic regression (Table 4.1). I also excluded percent forest, temperature, slope, and precipitation from the analysis because of high correlation coefficients with other independent variables (Appendix D). Spring and summer NDVIs displayed similar scatter plots and were highly correlated, therefore I combined them into one variable by summing the grids.

I included the remaining 10 variables (macrohabitat type, elevation, forest fragmentation, human density, managed lands, proximity to stream, road density index, wetness index, snowfall, and spring-summer NDVI) in the best subset selection step. Of the resulting 1,024 models, the model with all 10 independent variables generated the lowest AIC value (Table 4.2). I did not exclude any variables from the best subset model based on comparison of individual variable Wald statistics between the best subset model and the univariate logistic model. I reclassified human density from a continuous variable to a nominal variable (Table 4.3) because of a lack of linearity in the logit. I also reclassified snowfall from a continuous variable to a dichotomous variable because of a lack of linearity in the logit.

Table 4.1. Univariate logistic regression analysis of black bear occurrence in upland environments of the continental USA, 2004.

Independent variable	Parameter estimate	Standard error	Wald chi-square	*P*-value
Macrohabitat type[a]				
Mixed forest	3.7892	0.0358	11,205.4	<0.0001
Deciduous forest	2.8009	0.0300	8,734.3	<0.0001
Evergreen needleleaf forest	3.6328	0.0299	14,787.9	<0.0001
Cropland-woodland mosaic	2.2856	0.0401	3,250.7	<0.0001
Grassland-shrubland mosaic	1.3591	0.0289	2,208.9	<0.0001
Sparsely vegetated, snow, ice	2.2742	0.0580	1,536.1	<0.0001
Urban and built-up	0.2508	0.1763	2.0	0.1549
Percent forest[b]	2.5600	0.0150	28,934.7	<0.0001
Elevation	0.000840	8.136E-6	10,659.5	<0.0001
Slope[b]	0.4925	0.00347	20,171.6	<0.0001
Fragmentation	-0.5830	0.00358	26,585.7	<0.0001
Human density	-0.00351	0.000128	755.6	<0.0001
Managed lands	1.6526	0.0142	13,614.9	<0.0001
Proximity to streams	-0.0529	0.00149	1,260.5	<0.0001
Road density index	-0.00059	0.000012	2,302.0	<0.0001
Wetness	-0.4869	0.00321	22,951.5	<0.0001
Precipitation[b]	0.2688	0.00369	5,309.8	<0.0001
Temperature[b]	-0.6675	0.00472	20,022.4	<0.0001
Snowfall	0.6366	0.00390	26,648.0	<0.0001
Spring NDVI[c]	0.00757	0.000125	3,652.9	<0.0001
Summer NDVI[c]	0.00690	0.000102	4,564.6	<0.0001

[a] Cropland-pasture-grassland habitat type served as the reference design variable. Therefore, no parameter estimate was generated and the influence of the design variable was included in the intercept term.

[b] Variable excluded because of high correlation with other independent variables.

[c] Spring and summer NDVIs combined into one variable because of similar association with the dependent variable and high correlation with each other.

Table 4.2. Summary of Akaike's information criterion (AIC) values for all univariate logistic regression models and for each level of p (p = number of independent variables) with the lowest AIC value to predict black bear occurrence in upland environments of the continental USA, 2004.

No. of variables	No. of parameter estimates	AIC	Independent variables[a]									
1	7	135,939.5	HT									
1	1	133,635.1		SN								
1	1	144,633.9			WE							
1	1	142,416.3				FF						
1	1	172,298.0					ST					
1	1	172,542.7						HD				
1	1	162,558.3							EL			
1	1	159,843.3								ML		
1	1	171,200.9									RD	
1	1	168,715.9										SPSU
2	8	106,670.5	HT	SN								
3	9	101,998.2	HT	SN	WE							
4	10	99,724.9	HT	SN	WE	FF						
5	11	98,802.2	HT	SN	WE	FF	ST					
6	12	97,907.4	HT	SN	WE	FF	ST	HD				
7	13	97,541.5	HT	SN	WE	FF	ST	HD	EL			
8	14	97,427.0	HT	SN	WE	FF	ST	HD	EL	ML		
9	15	97,356.7	HT	SN	WE	FF	ST	HD	EL	ML	RD	
10	16	97,349.0†	HT	SN	WE	FF	ST	HD	EL	ML	RD	SPSU

[a] See table 3.1 for variable codes

† global minimum

Table 4.3. Results of multiple variable logistic regression analysis to predict black bear occurrence in upland environments of the continental USA, 2004.

Independent variable	Parameter estimate	Standard error	Wald chi-square	*P*-value	Standardized estimate
Intercept	0.2180	0.1469	2.2	0.1378	
Macrohabitat type[a]					
Mixed forest	1.5934	0.0473	1134.9	<0.0001	
Deciduous forest	0.9119	0.0435	438.8	<0.0001	
Evergreen needleleaf forest	1.0616	0.0421	635.2	<0.0001	
Cropland-woodland mosaic	2.3254	0.0442	2765.1	<0.0001	
Grassland-shrubland mosaic	0.0578	0.0365	2.5	0.1132	
Sparsely vegetated, snow, ice	1.6498	0.0854	372.9	<0.0001	
Urban and built-up	1.3359	0.1953	46.8	<0.0001	
Elevation	0.000618	0.000021	892.0	<0.0001	0.2466
Fragmentation	-0.3581	0.00863	1720.2	<0.0001	-0.3543
Human density[b]					
Human density (> 55 persons/km^2)	-0.6942	0.0349	395.7	<0.0001	
Human density (> 10 and ≤ 55 persons/km^2)	-0.3437	0.0216	254.0	<0.0001	
Managed lands	0.1606	0.0233	47.6	<0.0001	0.0348
Proximity to stream	-0.0789	0.00238	1103.4	<0.0001	-0.2238
Road density index	-0.00023	0.000021	124.8	<0.0001	-0.0731
Wetness	-0.2531	0.00522	2353.3	<0.0001	-0.3186
Snowfall[c]	1.7225	0.0195	7778.2	<0.0001	0.4019
Spring-Summer NDVI	0.00109	0.000131	69.4	<0.0001	0.0702

[a] Cropland-pasture-grassland habitat type served as the reference design variable. Therefore, no parameter estimate was generated and the influence of the design variable was included in the intercept term.

[b] Human density <10 served as the reference design variable. Therefore, no parameter estimate was generated and the influence of the design variable was included in the intercept term.

[c] Snowfall reclassified to 0 (≤122 cm) and 1 (>122 cm).

The final model included 10 independent variables: macrohabitat type, elevation, forest fragmentation, human density, managed lands, proximity to streams, road density index, wetness index, snowfall, and spring-summer NDVI. The model was based on a sample size of 144,217 cells, of which 41,881 (29%) were classified as bear presence and 102,336 (71%) as bear absence. The likelihood ratio chi-square test indicated a significant fit for the overall model ($\chi^2 = 75{,}030.9$, 17 df, $P < 0.0001$) and each independent variable was significant (except 1 macrohabitat type; Table 4.3). I generated a spatial model of the relative probability of black bear occurrence (Fig. 4.1) by calculating $\pi(x)$ (eq. 1) for every cell in a new grid from the parameter estimates, where:

$$g(x) = (0.2180 + (HT_1 \times 1.5934) + (HT_2 \times 0.9119) + (HT_3 \times 1.0616) + (HT_4 \times 2.3254) + (HT_5 \times 0.0578) + (HT_6 \times 1.6498) + (HT_7 \times 1.3359) + (EL \times 0.000618) + (FF \times -0.3581) + (HD_1 \times -0.6942) + (HD_2 \times -0.3437) + (ML \times 0.1606) + (ST \times -0.0789) + (RD \times -0.00023) + (WE \times -0.2531) + (SN \times 1.7225) + (SPSU \times 0.00109)).$$

I also calculated $g(x)$ for all values of each independent variable to represent the association between predicted occurrence and the variable (Figs. 4.2–4.4).

In terms of interpreting the model, the sign of the parameter estimate indicates whether the parameter was used more (+) or less (-) than expected, and the value of the parameter estimate represents the magnitude of the relationship. For each parameter, the Wald chi-square statistic and associated P-value indicates whether the parameter was correlated with bear occurrence and significantly different from zero. I used contrast statements in SAS to determine significance in bear use for class levels of nominal variables. For continuous variables, the odds ratio represents the mean change in predicted probability per unit change in the variable.

For macrohabitat type, mixed forest was associated more with bear occurrence than deciduous forest ($\chi^2 = 415.1962$, 1 df, $P < 0.0001$) and evergreen needleleaf forest

(χ^2 = 232.1988, 1 df, P < 0.0001) (Fig. 4.2). Evergreen needleleaf forest was associated more with bear occurrence than deciduous forest (χ^2 = 28.9217, 1 df, P < 0.0001). All three forest types (mixed, deciduous, evergreen needleleaf) were associated more with bear occurrence than non-forested types (grassland-shrubland mosaic, sparsely vegetated, snow, ice, urban, built-up) (χ^2 = 5.4474, 1 df, P = 0.0196). However, the cropland-woodland mosaic was associated more with bear occurrence than mixed forest (χ^2 = 212.7142, 1 df, P < 0.0001), deciduous forest (χ^2 = 907.2845, 1 df, P < 0.0001), and evergreen needleleaf forest (χ^2 = 731.8958, 1 df, P < 0.0001).

Areas with human density between 10 and 55 persons/km^2 were associated more with bear occurrence than human density >55 persons/km^2 (χ^2 = 112.6279, 1 df, P < 0.0001) (Fig. 4.2). Areas with human density <10 persons/km^2 were associated more with bear occurrence than areas with human density between 10 and 55 persons/km^2 or >55 persons/km^2 (Table 4.3).

The odds ratio for elevation was 1.1, indicating that the relative probability of bear presence increased by an average factor of 1.1 ($e^{100 \times 0.000618}$) for each 100-m increase in elevation. For each unit increase in fragmentation level, the relative probability of bear presence decreased by an average factor of 0.7. For managed lands, the odds ratio indicated that the probability of bear presence on managed lands was on average 1.2 times more likely than on non-managed lands. As distance to stream increased by 1 km, the relative probability of bear presence decreased on average by a factor of 0.9. As road density index increased by 10 units and wetness increased by 1 unit, the relative probability of bear presence decreased on average by a factor of 0.9 and 0.8, respectively.

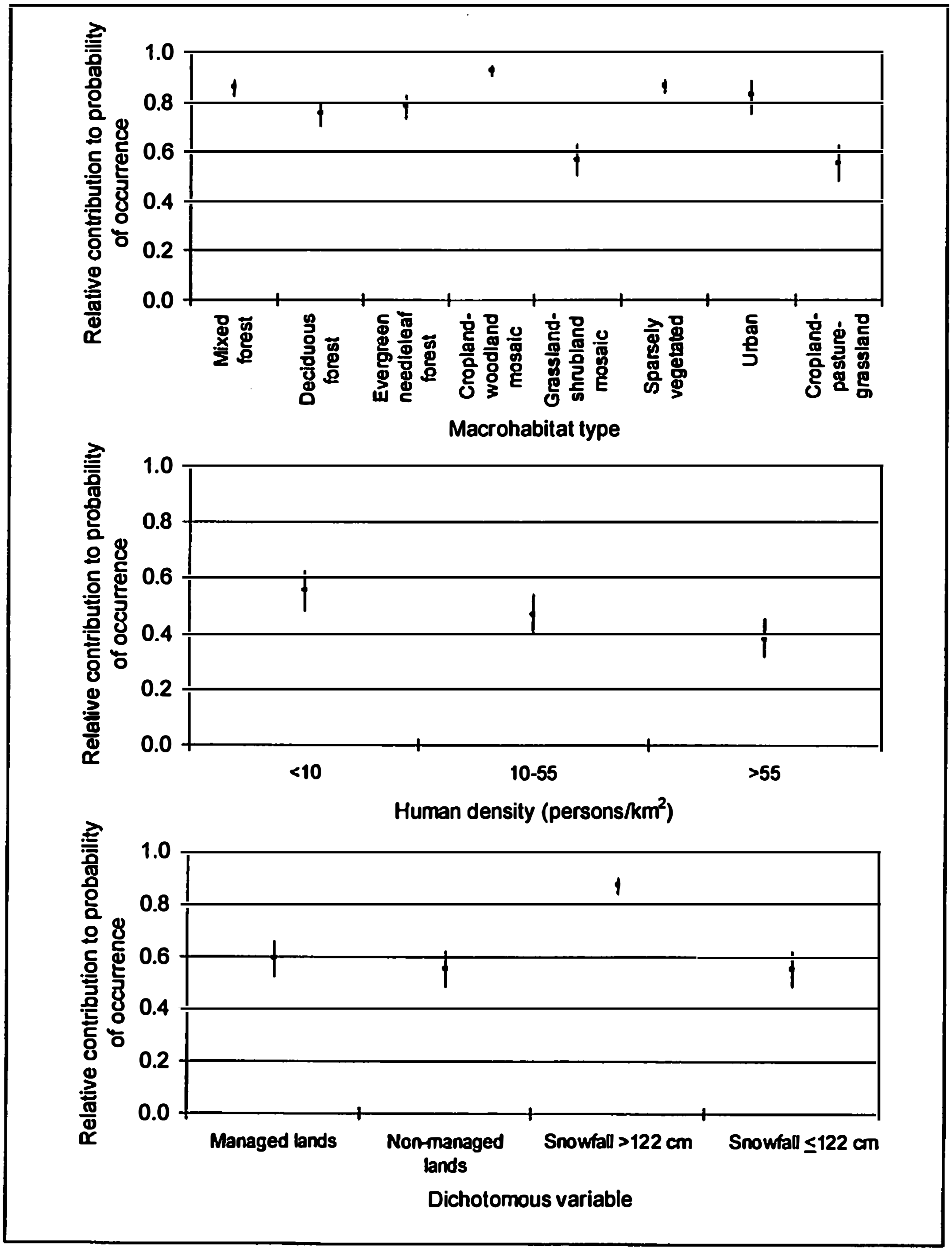


Figure 4.2. Relative contribution of macrohabitat type, human density, managed lands, and snowfall to relative probability of black bear occurrence, upland environments of the continental USA, 2004 (vertical bars represent 95% confidence interval).

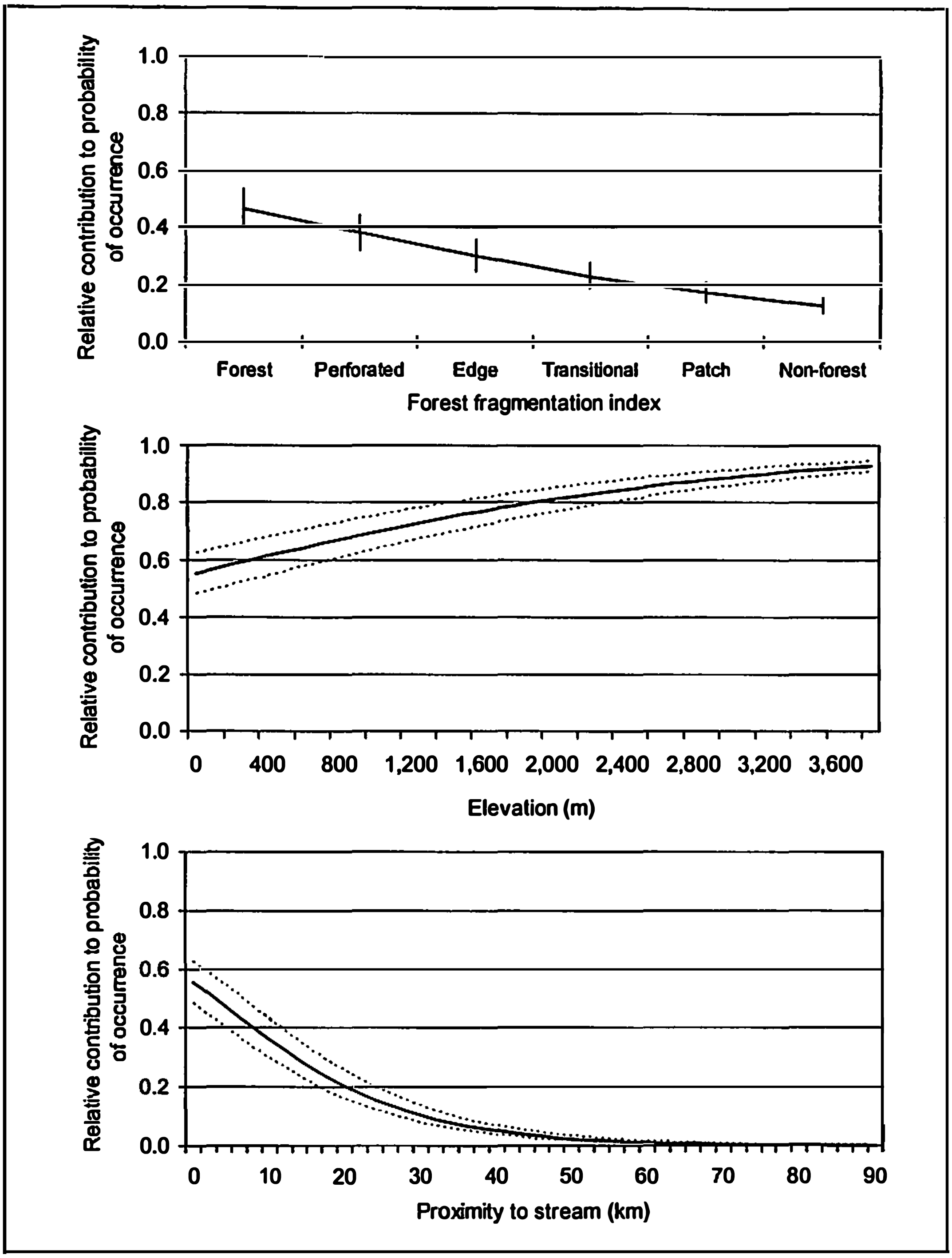


Figure 4.3. Relative contribution of forest fragmentation, elevation, and proximity to stream to relative probability of black bear occurrence, upland environments of the continental USA, 2004 (vertical bars and dashed lines represent 95% confidence interval).

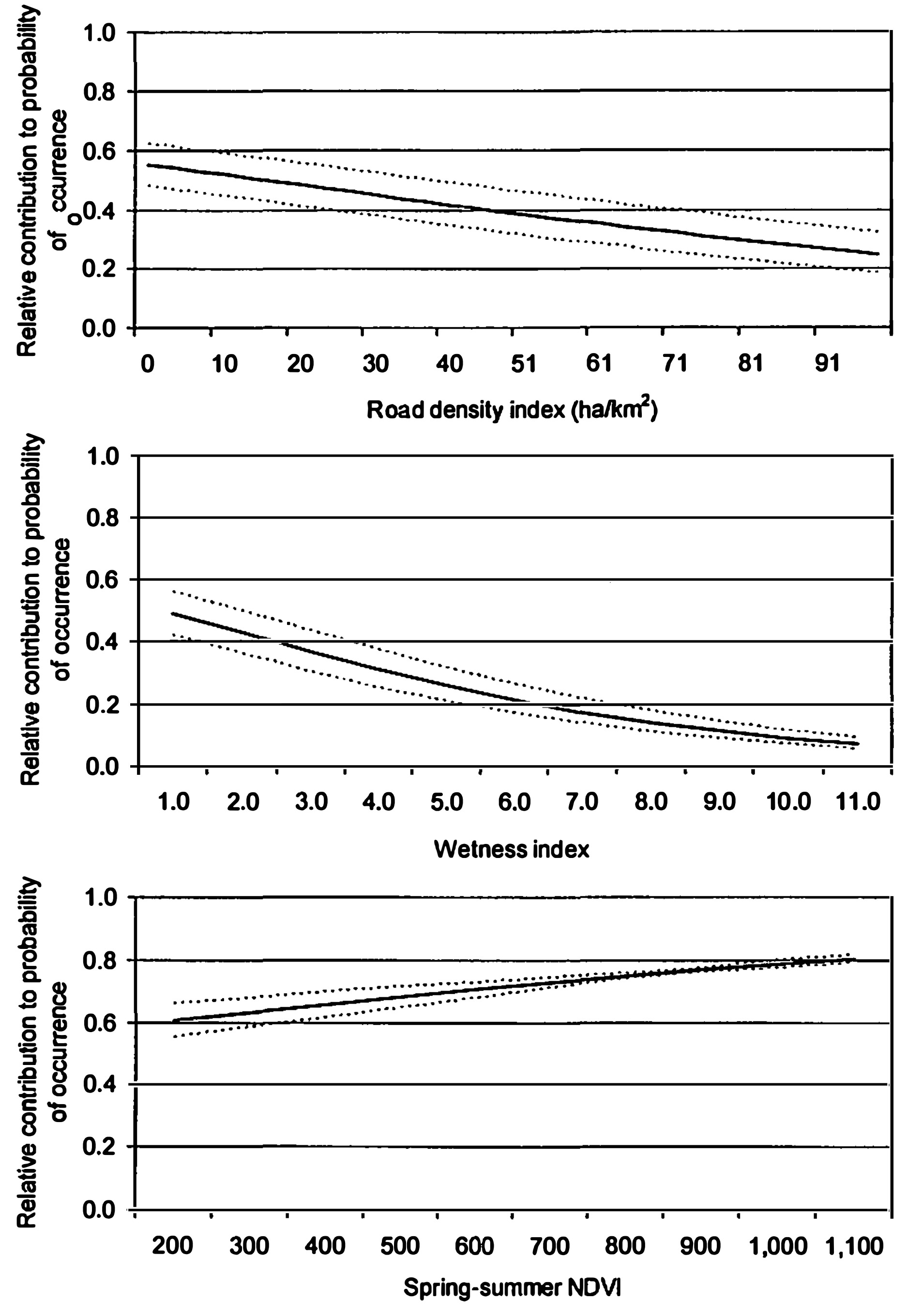


Figure 4.4. Relative contribution of road density index, wetness, and spring-summer NDVI to relative probability of black bear occurrence, upland environments of the continental USA, 2004 (dashed lines represent 95% confidence interval).

The odds ratio for snowfall indicated that the probability of bear presence for areas with more than 122 cm of mean snowfall was 5.6 times more likely than areas with less than 122 cm. Finally, as the NDVI for spring and summer increased by 10%, the relative probability of bear presence increased on average by a factor of 1.1.

Assessment of Model Fit.— The cut-off point were sensitivity equaled specificity was 0.25. At this cut-off point, sensitivity and specificity were approximately 82.7%, false positive rate was 34.1%, false negative rate was 7.9%, and correct classification rate was 82.6% (Fig. 4.5). Model dispersion was not different from 1 (dispersion = 1.0, P = 0.341), indicating no over- or under-dispersion. The ROC curve and AUC indicated that the model had outstanding discrimination (AUC = 0.905, 95% CI = 0.903-0.906) (Fig. 4.5). Model discrimination was significantly different from random (Z = 213.235, P < 0.001) and the sample size was sufficient for retrospective power = 0.95. The Hosmer and Lemeshow goodness-of-fit test indicated the model had poor calibration ($\hat{C}$ = 168.8, 8 df, P < 0.001); deletion of outliers identified by regression diagnostics did not improve the model fit. The model tended to overestimate bear presence at predicted probabilities <0.50.

The mean AUC for the trial (AUC = 0.906, n = 10, range = 0.905-0.906, 95% CI = 0.904-0.908) and test (AUC = 0.905, n = 10, range = 0.903-0.908, 95% CI = 0.900-0.911) groups were not significantly different (Z_{mean} = 0.469, P_{mean} = 0.653) using the 10-fold re-sampling validation procedure. Thus, model discrimination also was outstanding with independent data. At the 0.25 cut-off point, mean sensitivity was 82.6% (SD = 0.0025, n = 10, range = 82.3-83.1%) and mean specificity was 82.7% (SD = 0.0025, n = 10, range = 82.4-83.3%). Mean false positive and negative rates were 33.8% (SD =

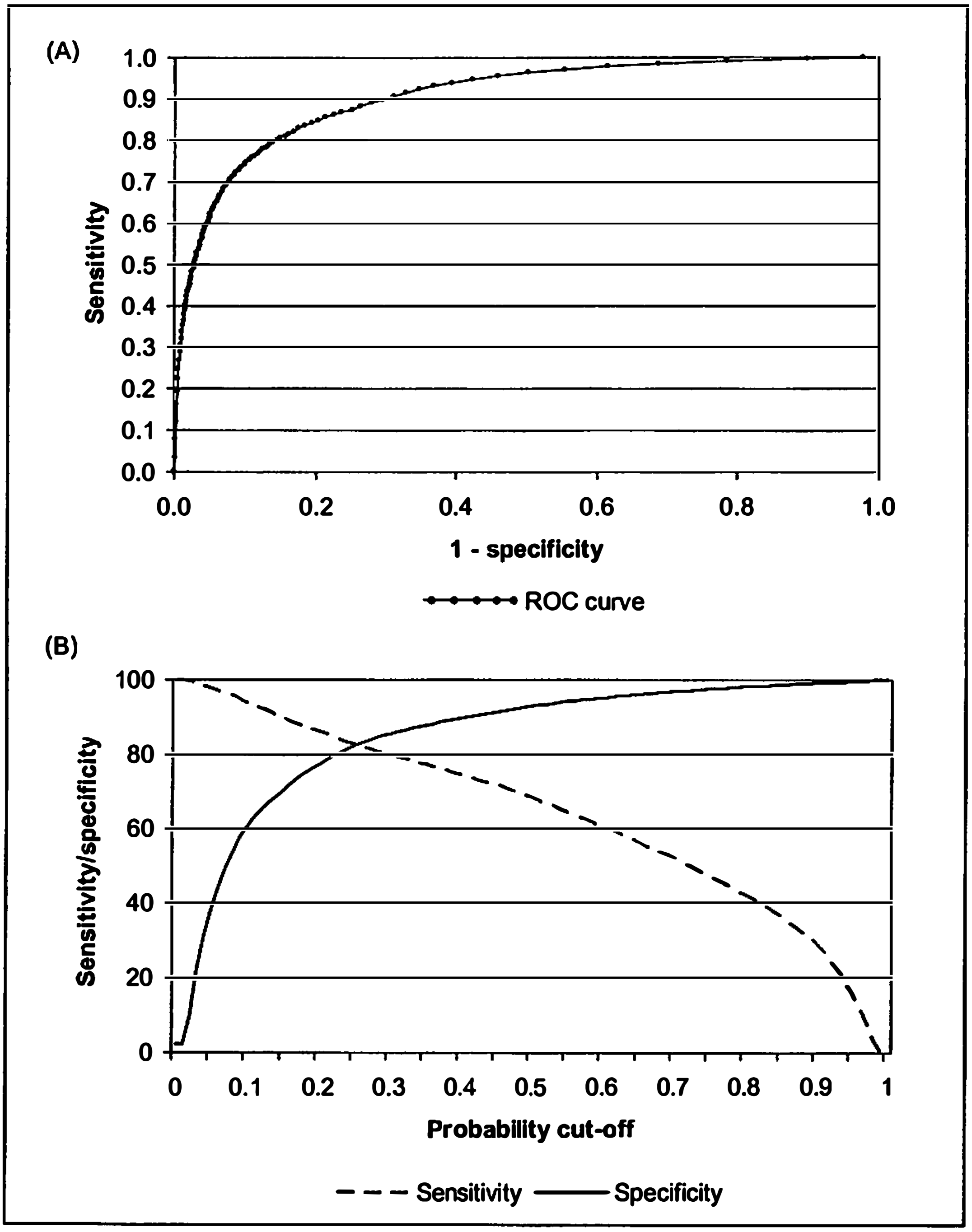


Figure 4.5. (A) Receiver operating characteristic (ROC) curve displaying high predictive accuracy (AUC = 0.905) and (B) plot of sensitivity and specificity for all possible probability cut-off points. Intersection of sensitivity and specificity best approximates known bear occurrence in upland environments of the continental USA, 2004.

0.0039, n = 10, range = 33.2-34.4%) and 7.9% (SD = 0.0015, n = 10, range = 7.6-8.1%), respectively. Mean correct classification rate was 82.7% (SD = 0.0023, n = 10, range = 82.4-83.2%).

Lowland Environments

I excluded precipitation, proximity to streams, slope, snowfall, temperature, grain crops, summer NDVI, fall NDVI, and winter NDVI from the analysis because the smoothed scatter plot for each variable suggested a weak relationship with bear occurrence. I reclassified habitat richness, soil nitrogen, forest fragmentation, and spring NDVI from continuous variables to nominal or ordinal variables based on the natural breaks observed in the scatter plots (Table 4.4). The remaining independent variables, and the reclassified variables, displayed a good fit based on inspections of the scatter plots and screening each variable with univariate logistic regression (Table 4.5). I did not exclude any variables because of correlations with other independent variables (Appendix D).

I included 11 variables in the best subset selection step. Of the resulting 2,048 models, the model with the lowest AIC value included all variables except habitat richness (Table 4.6). I did not exclude any variables from the best subset model based on comparison of individual variable Wald statistics between the best subset model and the univariate logistic models. I reclassified human density from a continuous variable to a nominal variable because of a lack of linearity in the logit (Table 4.7).

The final model included 10 independent variables; macrohabitat type, elevation, percent forest, forest fragmentation, soil nitrogen, human density, managed lands, road density index, wetness index, and spring NDVI. The model was based on a sample size

Table 4.4. Independent variables reclassified for logistic regression analysis of black bear range in lowland environments of the continental USA, 2004.

Variable code	Variable name	Data type: Original	Data type: Reclassified	Explanation
FF	Forest fragmentation	Ordinal	Nominal	1 = forest 2 = perforated 3 = transitional 4 = edge 5 = patch 6 = nonforested
HR	Habitat richness	Continuous	Nominal	1 = $\leq$8 habitat types within 49-km^2 square 0 = >8 habitat types within 49-km^2 square
NI	Soil nitrogen	Continuous	Ordinal	1 = $\leq$1,200 g/m^2 2 = >1,200 and $\leq$1,800 g/m^2 3 = >1,800 and $\leq$2,700 g/m^2 4 = >2,700 g/m^2
HD	Human density	Continuous	Nominal	1= $\leq$43 persons/km^2 0= >43 persons/km^2
SP	Spring NDVI	Continuous	Nominal	1 = $\geq$500 0 = <500

Table 4.5. Univariate logistic regression analysis of black bear occurrence in lowland environments of the continental USA, 2004.

Independent variable	Parameter estimate	Standard error	Wald chi-square	*P*-value
Elevation	-0.0320	0.00117	746.7	<0.0001
Fragmentation[a]				
Forest	1.0323	0.1459	50.1	<0.0001
Perforated	1.7370	0.1286	182.5	<0.0001
Transitional	1.6398	0.1050	243.9	<0.0001
Edge	1.7157	0.1248	189.1	<0.0001
Patch	0.7919	0.1010	61.5	<0.0001
Macrohabitat type[b]				
Mixed forest	1.2194	0.1340	82.8	<0.0001
Deciduous forest	1.3683	0.1163	138.5	<0.0001
Evergreen needleleaf forest	1.6035	0.0752	454.3	<0.0001
Cropland-woodland mosaic	0.7236	0.0936	59.7	<0.0001
Herbaceous-woodland wetland	0.3105	0.3248	0.9	0.3390
Grassland-shrubland mosaic	2.0949	0.2194	91.2	<0.0001
Sparsely vegetated, snow, ice	0.9061	0.1337	45.9	<0.0001
Urban and built-up	-0.8317	0.7224	1.3	0.2496
Human density	-0.00437	0.000506	74.6	<0.0001
Habitat richness	1.3211	0.7283	3.3	0.0697
Managed lands	1.0357	0.0813	162.2	<0.0001
Percent forested cover	1.3265	0.0638	432.5	<0.0001
Road density index	-0.00055	0.000045	150.9	<0.0001
Spring NDVI	1.6506	0.3109	28.2	<0.0001
Soil nitrogen	0.8353	0.0286	854.0	<0.0001
Wetness	0.3139	0.0298	111.3	<0.0001

[a] Non-forested served as the reference design variable. Therefore, no parameter estimate was generated and the influence of the design variable was included in the intercept term.

[b] Cropland-pasture-grassland habitat type served as the reference design variable. Therefore, no parameter estimate was generated and the influence of the design variable was included in the intercept term.

Table 4.6. Summary of Akaike's information criterion (AIC) values for all univariate logistic regression models and for each level of p (p = number of independent variables) with the lowest AIC value to predict black bear occurrence in lowland environments of the continental USA, 2004.

No. of variables	No. of parameter estimates	AIC	Independent variables [a]										
1	8	10,458.4	HT										
1	1	10,021.9		NI									
1	1	10,087.8			EL								
1	1	10,993.1				HD							
1	5	10,632.8					FF						
1	1	10,961.7						ML					
1	1	10,942.1							RD				
1	1	10,992.2								WE			
1	1	11,082.4									SP		
1	1	10,664.9										FC	
1	1	11,104.2											HR
2	9	9,287.5	HT	NI									
3	10	8,761.4	HT	NI	EL								
4	11	8,535.4	HT	NI	EL	HD							
5	16	8,464.8	HT	NI	EL	HD	FF						
6	17	8,416.8	HT	NI	EL	HD	FF	ML					
7	18	8,403.8	HT	NI	EL	HD	FF	ML	RD				
8	19	8,387.9	HT	NI	EL	HD	FF	ML	RD	WE			
9	20	8,379.8	HT	NI	EL	HD	FF	ML	RD	WE	SP		
10	21	8,377.4†	HT	NI	EL	HD	FF	ML	RD	WE	SP	FC	
11	22	8,379.3	HT	NI	EL	HD	FF	ML	RD	WE	SP	FC	HR

[a] See Table 3.2 for variable codes

† global minimum

Table 4.7. Results of multiple variable logistic regression analysis to predict black bear occurrence in lowland environments of the continental USA, 2004.

Independent variable	Parameter estimate	Standard error	Wald chi-square	*P*-value	Standardized estimate
Intercept	-1.8008	0.4514	15.9	<0.0001	
Elevation	-0.0347	0.00168	428.5	<0.0001	-0.5733
Fragmentation[a]					
Forest	0.2452	0.2239	1.2	0.2735	
Perforated	0.9161	0.1882	23.7	<0.0001	
Transitional	0.8818	0.1766	24.9	<0.0001	
Edge	1.1737	0.1691	48.2	<0.0001	
Patch	0.7742	0.1252	38.3	<0.0001	
Macrohabitat type[b]					
Mixed forest	0.3024	0.1751	3.0	0.0842	
Deciduous forest	1.1545	0.1465	62.1	<0.0001	
Evergreen needleleaf forest	1.0538	0.1183	79.4	<0.0001	
Cropland-woodland mosaic	0.3350	0.1019	10.8	0.0010	
Herbaceous-woodland wetland	-1.6315	0.3475	22.0	<0.0001	
Grassland-shrubland mosaic	0.6055	0.2574	5.5	0.0187	
Sparsely vegetated, snow, ice	-0.4520	0.1625	7.7	0.0054	
Urban and built-up	0.0773	0.7530	0.1	0.9182	
Human density	0.4516	0.0690	42.8	<0.0001	0.1065
Managed lands	0.7468	0.1016	54.0	<0.0001	0.0997
Percent forested cover	0.4214	0.1891	5.0	0.0258	0.0875
Road density index	-0.00033	0.000058	31.8	<0.0001	-0.1097
Spring NDVI	1.1699	0.3775	9.6	0.0019	0.0394
Soil nitrogen	0.5947	0.0371	256.7	<0.0001	0.2734
Wetness	-0.1497	0.0406	13.6	0.0002	-0.0720

[a] Non-forested served as the reference design variable. Therefore, no parameter estimate was generated and the influence of the design variable was included in the intercept term.

[b] Cropland-pasture-grassland habitat type served as the reference design variable. Therefore, no parameter estimate was generated and the influence of the design variable was included in the intercept term.

of 11,225 cells, with 2,134 cells (19%) classified as bear presence and 9,091 cells (81%) as bear absence. The likelihood ratio chi-square test indicated a significant fit for the overall model (χ^2 = 2,477.5533, 21 df, $P < 0.0001$) and each independent variable was significant (except 1 forest fragmentation level and 2 macrohabitat types; Table 4.7).

Similar to the model for upland environments, I generated a spatial model of the relative probability of black bear occurrence (Fig. 4.6) by calculating $\pi(x)$ (eq. 1) for every cell in a new grid from the parameter estimates, where:

$$g(x) = (-1.8008 + (EL \times -0.0347) + (FF_1 \times 0.2452) + (FF_2 \times 0.9161) + (FF_3 \times 0.8818) + (FF_4 \times 1.1737) + (FF_5 \times 0.7742) + (HT_1 \times 0.3024) + (HT_2 \times 1.1545) + (HT_3 \times 1.0538) + (HT_4 \times 0.3350) + (HT_5 \times 0.6055) + (HT_6 \times -0.4520) + (HT_7 \times 0.0773) + (HT_8 \times -1.6315) + (HD \times 0.4516) + (ML \times 0.7468) + (FC \times 0.4214) + (RD \times -0.00033) + (SP \times 1.1699) + (NI \times 0.5947) + (WE \times -0.1497)).$$

I also calculated *g(x)* for all values of each independent variable to represent the association between predicted occurrence and the variable (Figures 4.7–4.9).

For macrohabitat type, deciduous forest was associated more with bear occurrence than mixed forest (χ^2 = 24.9362, 1 df, $P < 0.0001$), but not evergreen needleleaf forest (χ^2 = 0.7580, 1 df, P = 7580) (Fig. 4.7). Evergreen needleleaf forest was associated more with bear occurrence than mixed forest (χ^2 = 30.8206, 1 df, $P <$ 0.0001). All three forest types (mixed, deciduous, evergreen needleleaf) were associated more with bear occurrence than non-forested types (grassland-shrubland mosaic, sparsely vegetated, snow, ice, urban, built-up) (χ^2 = 6.9102, 1 df, P = 0.0086). Unlike upland environments, cropland-woodland mosaic was associated less with bear occurrence than deciduous forest (χ^2 = 31.6947, 1 df, $P < 0.0001$) and evergreen needleleaf forest (χ^2 = 38.1486, 1 df, $P < 0.0001$), but not mixed forest (χ^2 = 0.0347, 1 df, P = 0.8521).

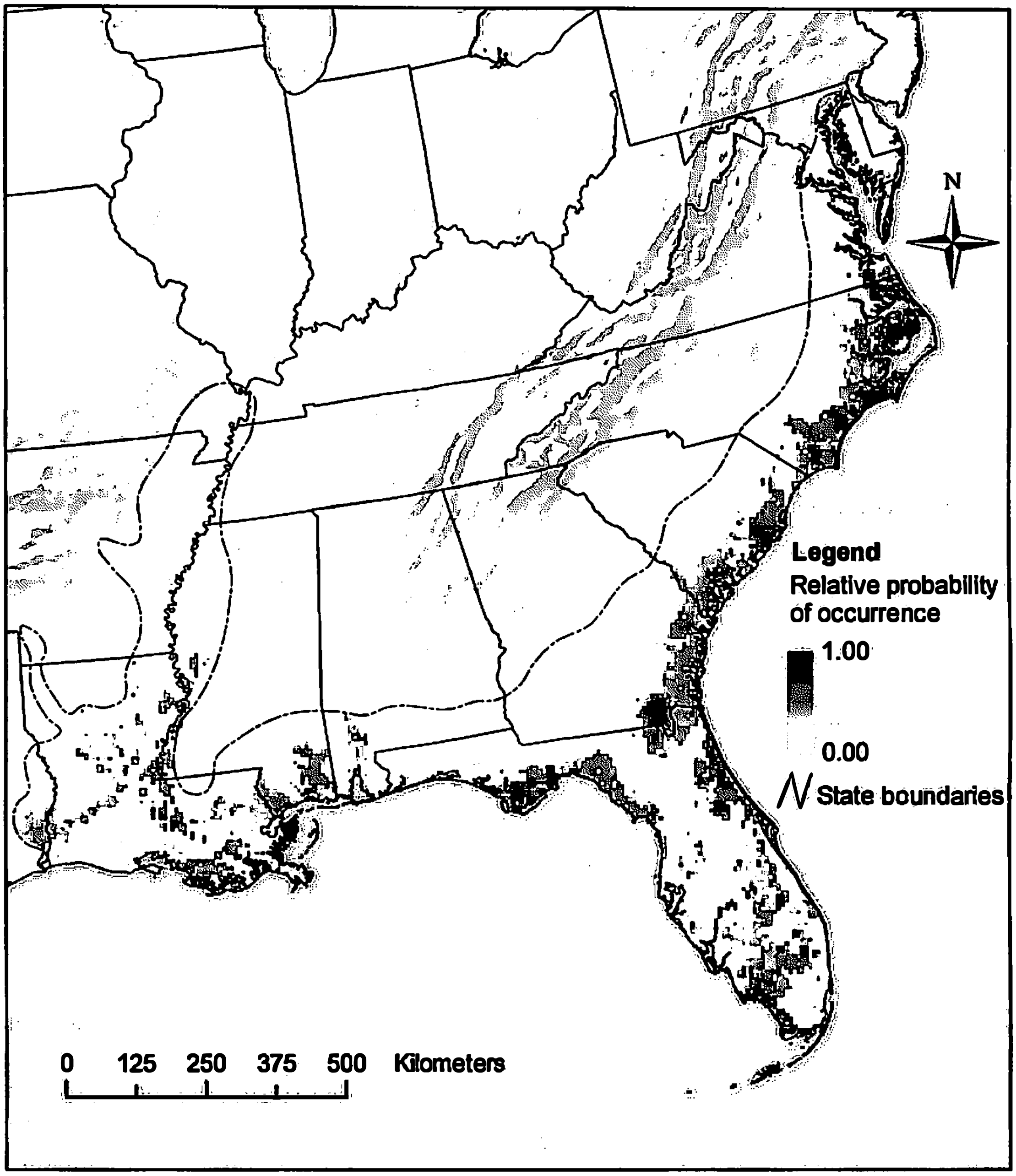


Figure 4.6. Relative probability of black bear occurrence in lowland environments of the continental USA, 2004.

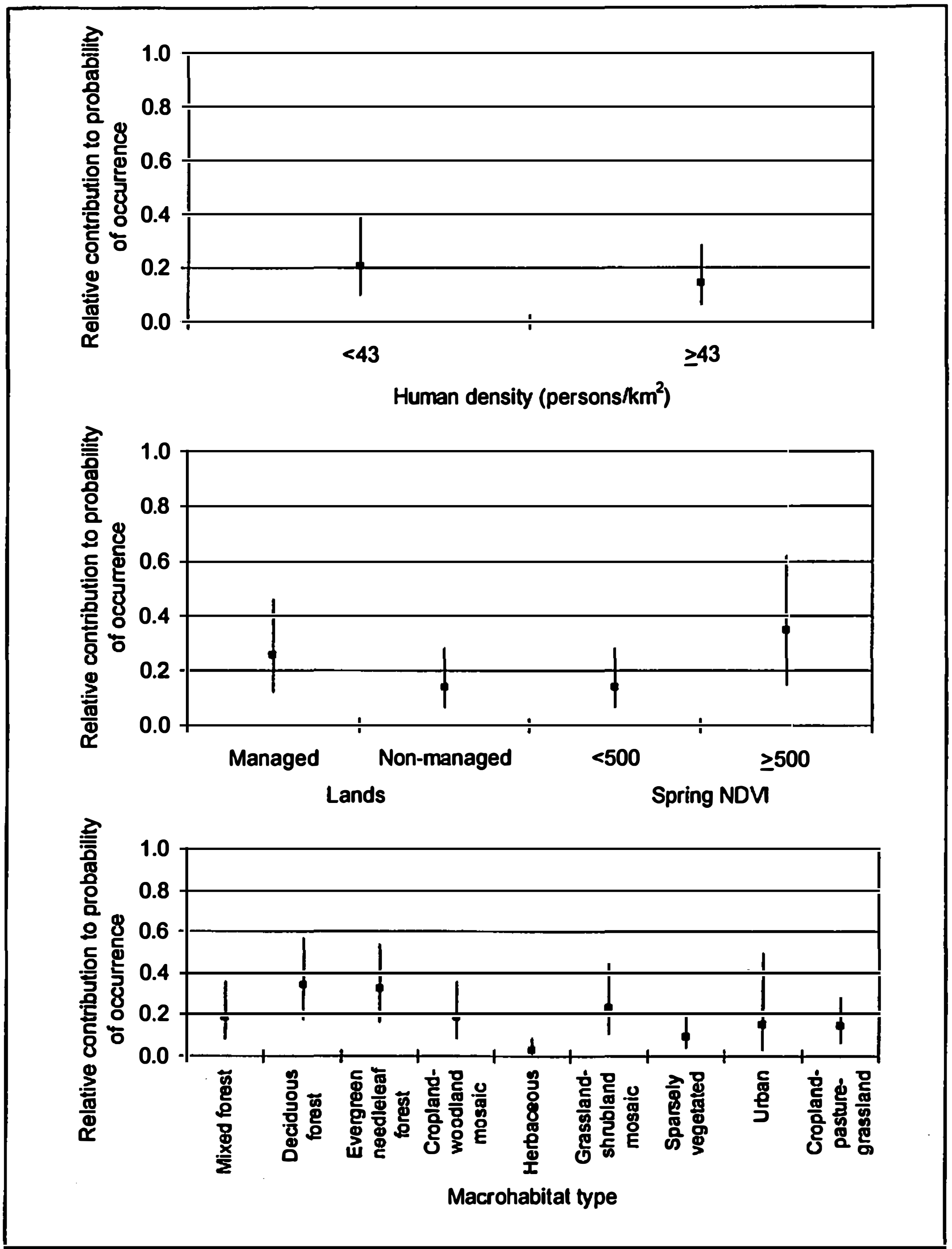


Figure 4.7. Relative contribution of human density, managed lands, spring NDVI, and macrohabitat type to relative probability of black bear occurrence, lowland environments of the continental USA, 2004 (vertical bars represent 95% confidence interval).

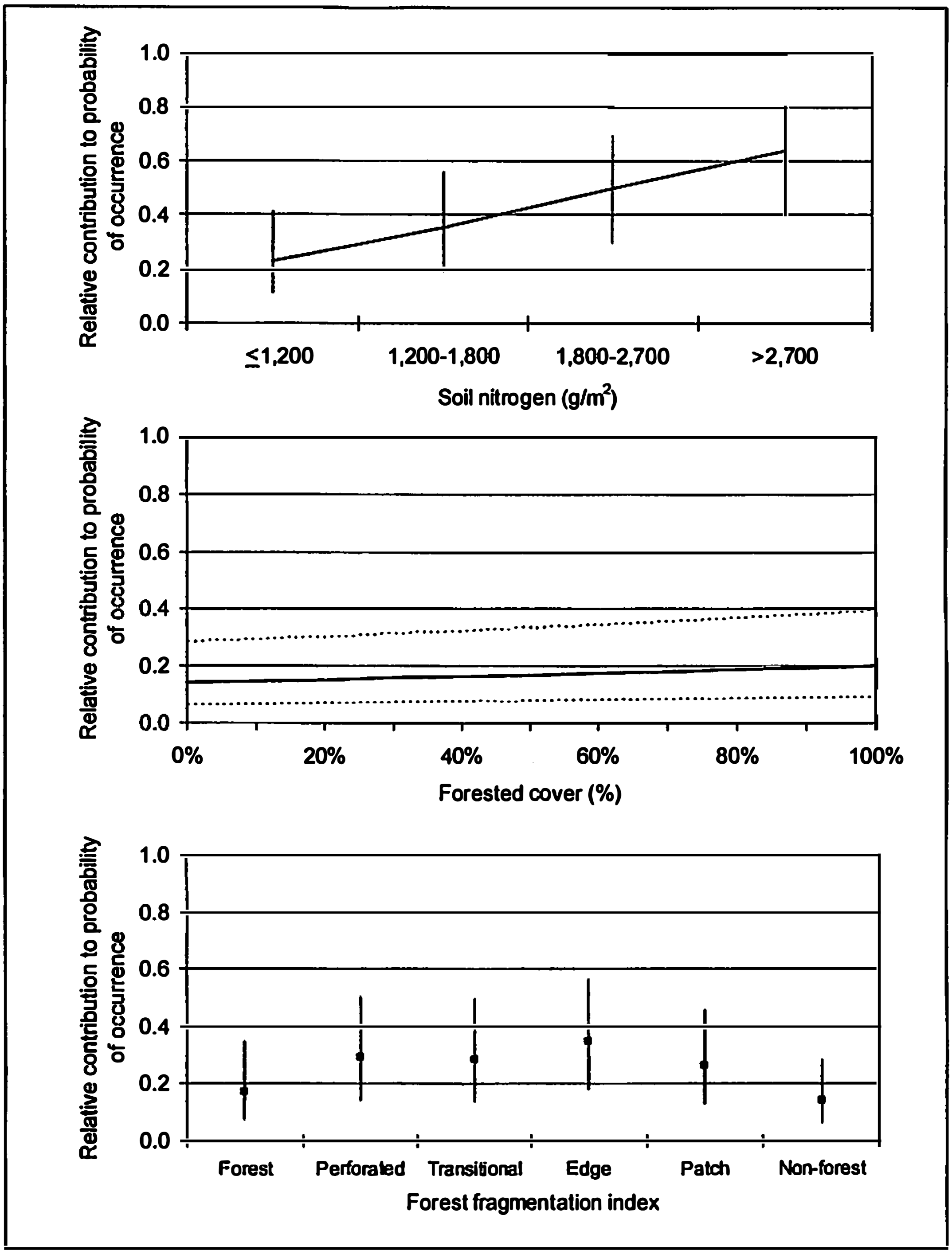


Figure 4.8. Relative contribution of soil nitrogen, forest cover, and forest fragmentation index to relative probability of black bear occurrence, lowland environments of the continental USA, 2004 (vertical bars and dashed lines represent 95% confidence interval).

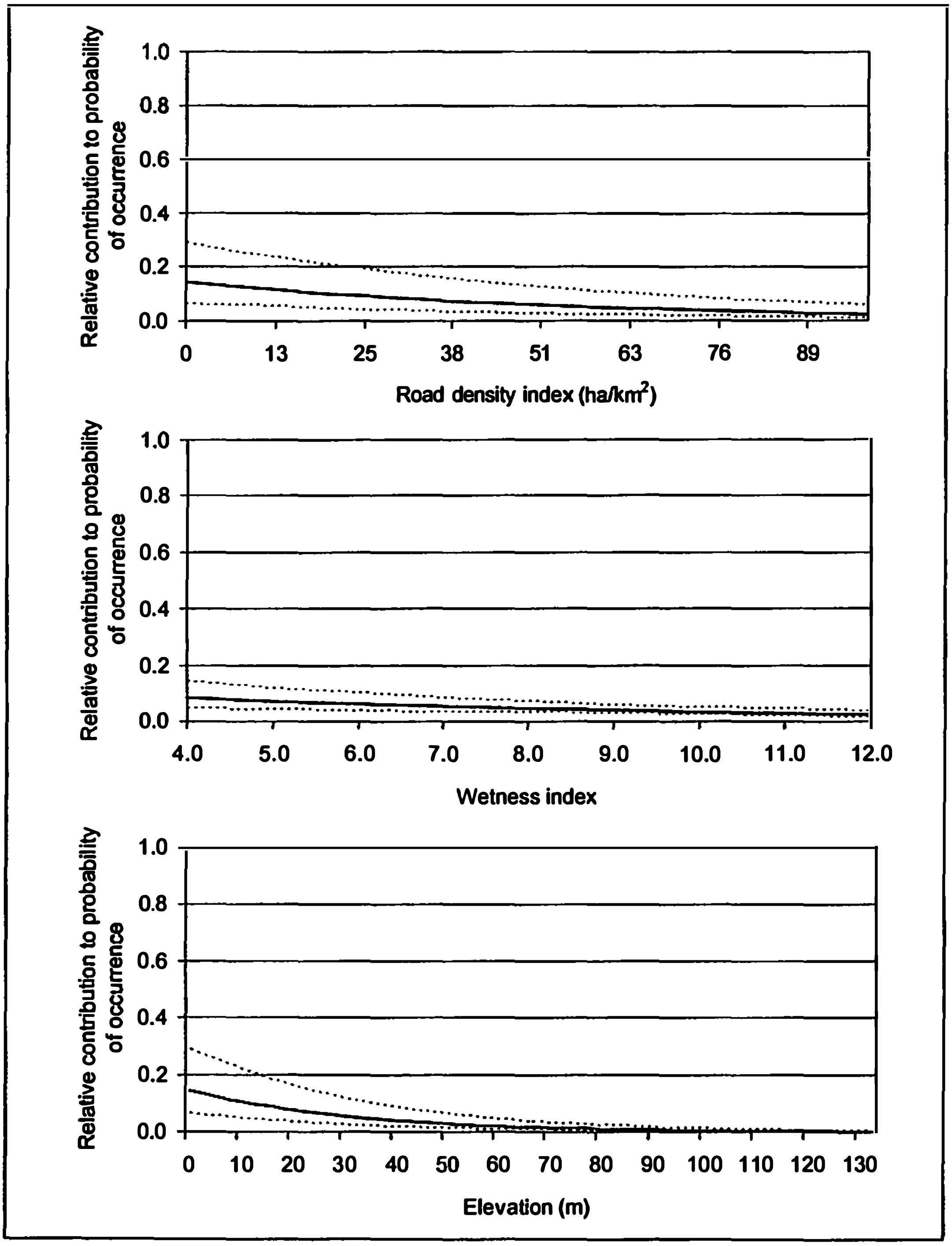


Figure 4.9. Relative contribution of road density index, wetness, and elevation to relative probability of black bear occurrence, lowland environments of the continental USA, 2004 (dashed lines represent 95% confidence interval).

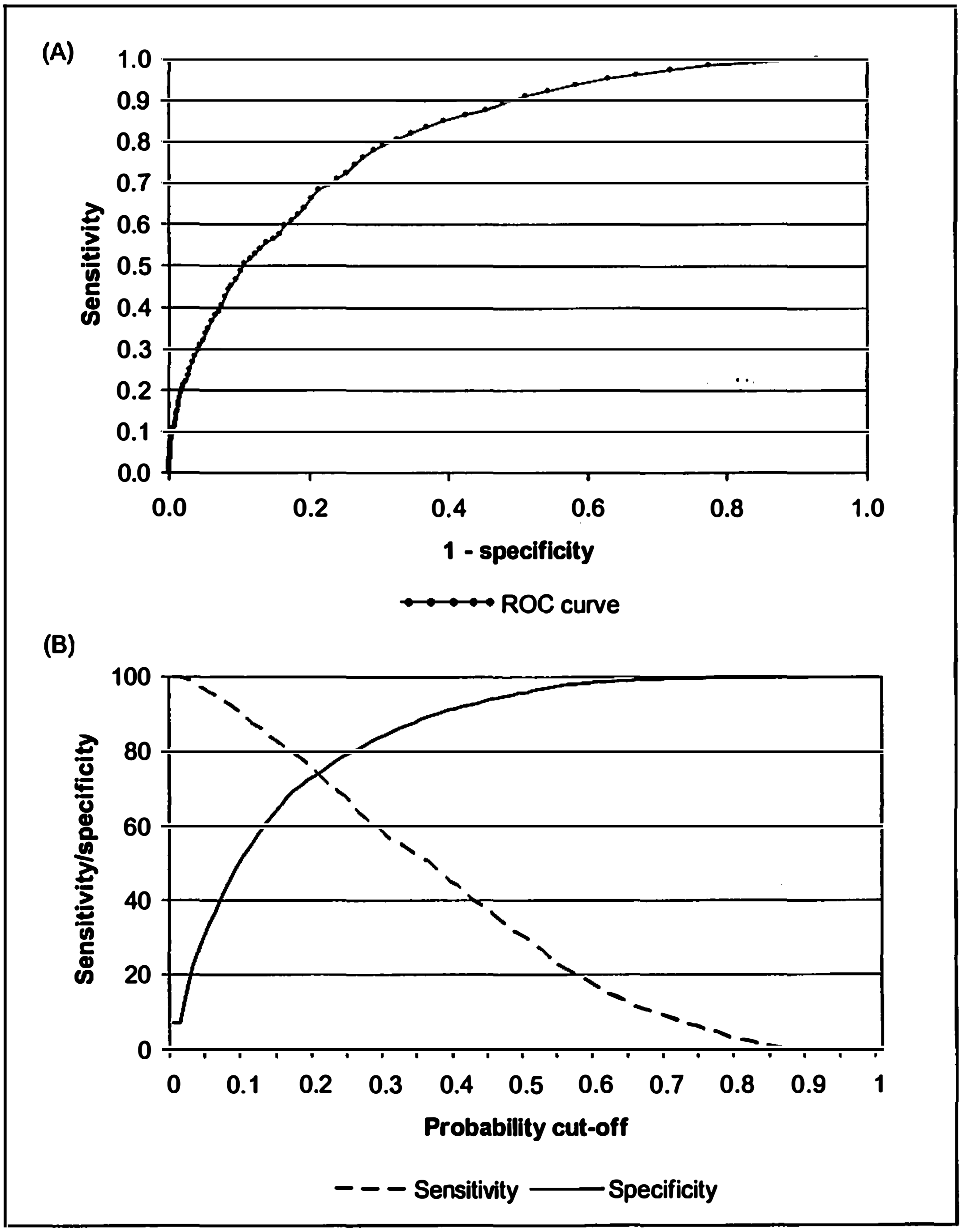


Figure 4.10. (A) Receiver operating characteristic (ROC) curve displaying high predictive accuracy (AUC = 0.818) and (B) plot of sensitivity and specificity for all possible probability cut-off points. Intersection of sensitivity and specificity best approximates known bear occurrence in lowland environments of the continental USA, 2004.

Assessment of Model Fit.— The cut-off point were sensitivity equaled specificity was 0.21. At this cut-off point, sensitivity and specificity were approximately 73.7%, false positive rate was 59.7%, false negative rate was 7.9%, and correct classification rate was 74.4% (Fig. 4.10). Model dispersion was not different from 1 (dispersion = 1.0, P = 0.125), indicating no over- or under-dispersion. The area under the ROC curve indicated that the model had excellent discrimination (AUC = 0.818, 95% CI = 0.809-0.828). Model discrimination was significantly different from random (Z = 45.851, P < 0.001) and the sample size was sufficient for retrospective power = 0.95. The Hosmer and Lemeshow goodness-of-fit test indicated the model fit the response data well ($\hat{C}$ = 4.5, 8 df, P = 0.8073) (Fig. 4.10).

The mean AUC for the trial (AUC = 0.819, n = 10, range = 0.817-0.820, 95% CI = 0.809-0.829) and test (AUC = 0.816, n = 10, range = 0.804-0.834, 95% CI = 0.783-0.847) groups were not significantly different (Z_{mean} = 0.672, P_{mean} = 0.521) using the 10-fold re-sampling validation procedure. Thus, model discrimination also was excellent with independent data. At the 0.21 cut-off point for test groups, mean sensitivity was 74.0% (SD = 0.010, n = 10, range = 72.6-75.8%) and mean specificity was 73.9% (SD = 0.012, n = 10, range = 72.6-76.1%). Mean false positive and negative rates were 60.1% (SD = 0.032, n = 10, range = 55.7-64.5%) and 7.7% (SD = 0.010, n = 10, range = 6.5-9.3%), respectively. Mean correct classification rate was 73.9% (SD = 0.012, n = 10, range = 72.7-76.0%).

Mapping Suitable Habitat Areas

Combining upland and lowland environments, suitable bear habitat was distributed in 1,414 patches and totaled 2,804,662 km^2 (Fig. 4.11). Mean patch size was

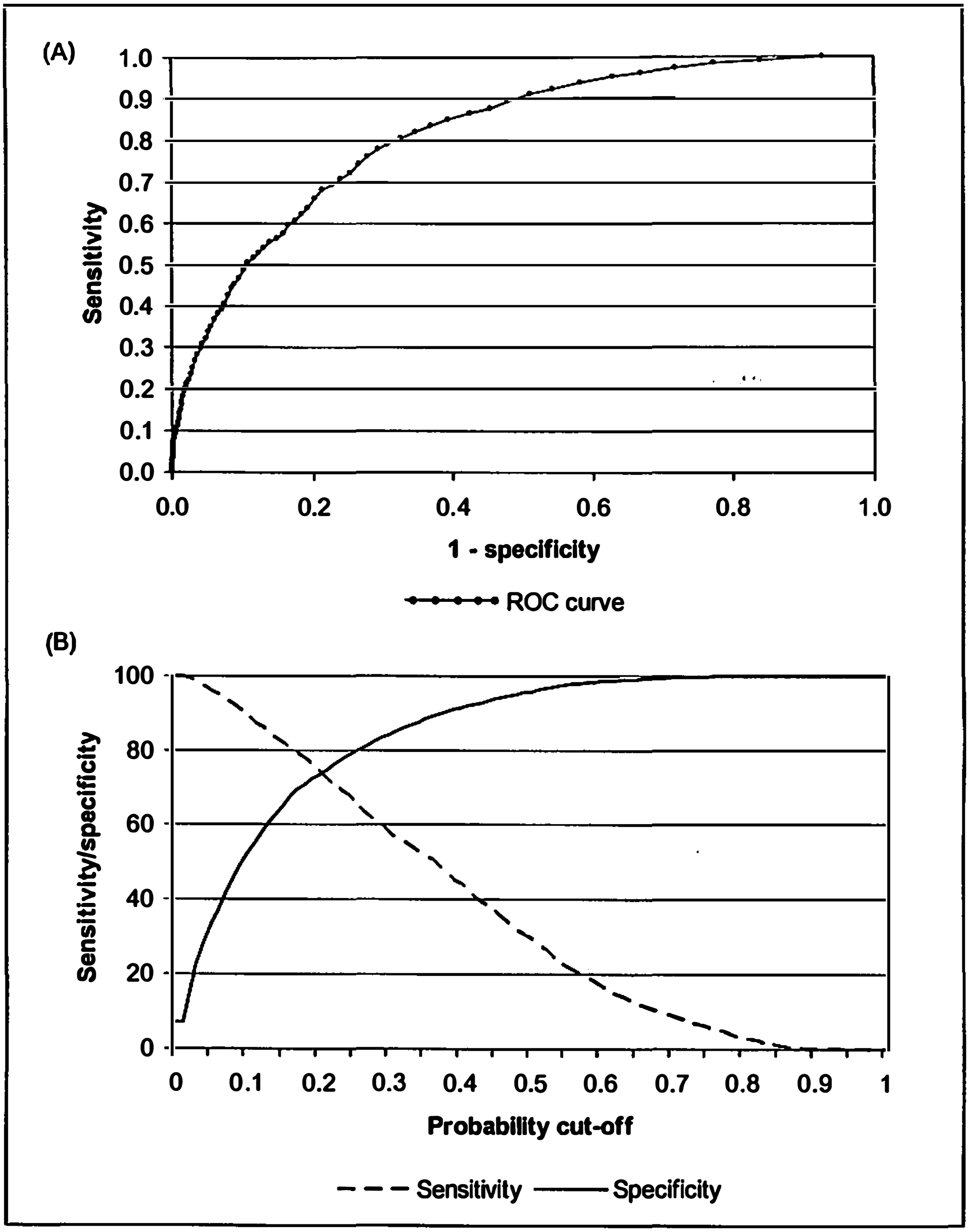


Figure 4.10. (A) Receiver operating characteristic (ROC) curve displaying high predictive accuracy (AUC = 0.818) and (B) plot of sensitivity and specificity for all possible probability cut-off points. Intersection of sensitivity and specificity best approximates known bear occurrence in lowland environments of the continental USA, 2004.

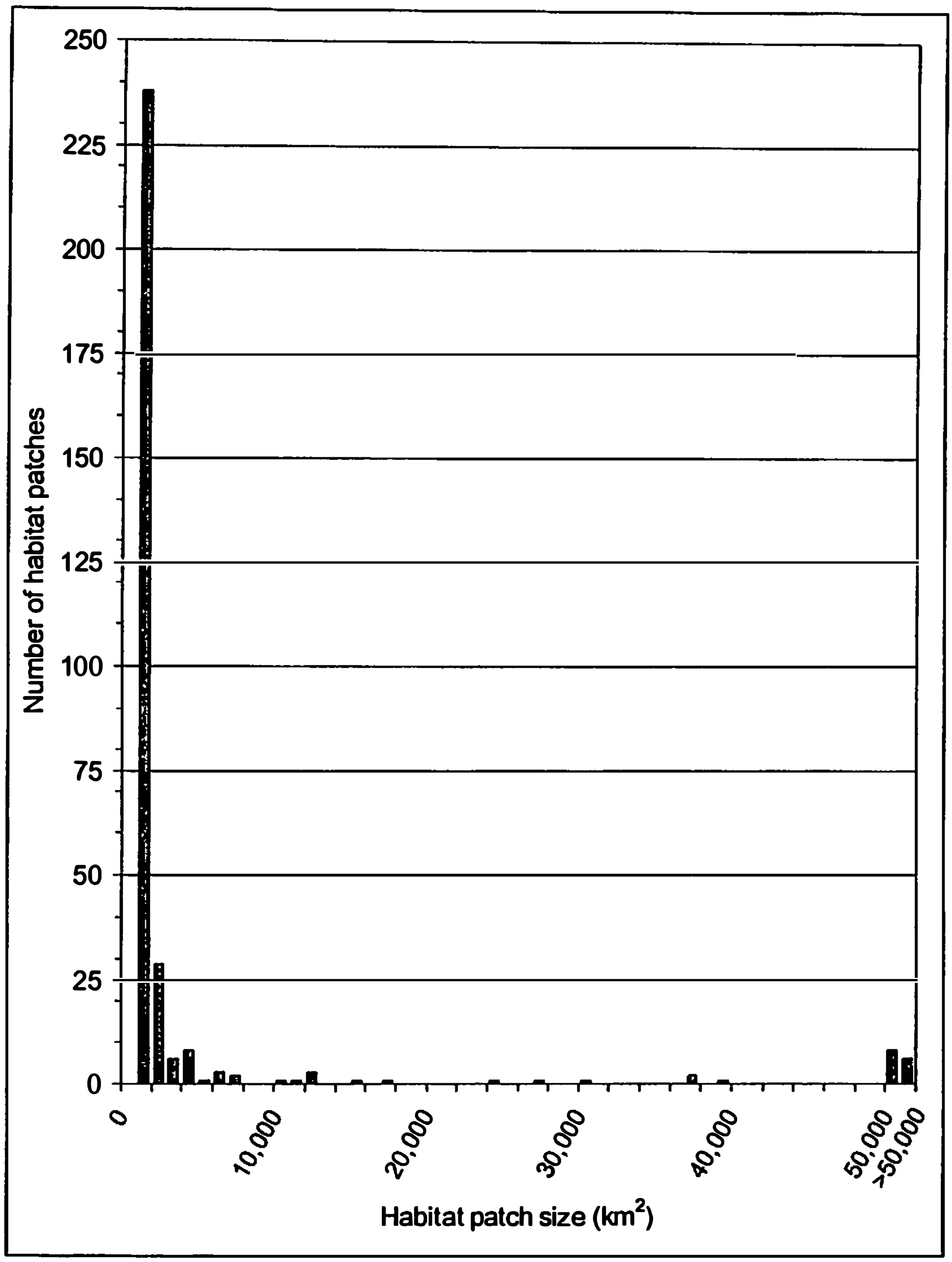


Figure 4.11. Frequency of black bear habitat patches by patch size (patch defined as contiguous areas with relative probability of black bear occurrence ≥ cut-off points) in the continental USA, 2004.

1,938 km^2 and mean probability of occurrence was 0.32; only 5 patches were >100,000 km^2 (Fig. 4.12). Excluding patches <200 km^2, the number of habitat patches declined to 306 patches and total habitat area declined to 2,721,803 km^2. Patches were distributed in all states except Kansas, although 6 states had <5,000 km^2 of bear habitat (Table 4.8, Fig. 4.13). Of the 41 states with $\geq$5,000 km^2 of bear habitat, 25 (61%) averaged $\geq$5,000 km^2 of bear habitat/patch. Eight states had >100,000 km^2 of bear habitat, including California, Colorado, Idaho, Montana, New York, Oregon, Washington, and Wyoming (Table 4.8, Fig. 4.13).

I identified 394 vacant habitat patches (exceeds 306 because occupied bear range only overlapped portions of some suitable habitat patches, thereby creating several "slivers" of suitable vacant habitat) with area $\geq$200 km^2, representing a total area of 981,061 km^2 with individual patch sizes ranging from 202 to 152,028 km^2. Of the 394 vacant patches, 155 (39.3%) were contiguous with occupied bear range, whereas 239 (60.7%) were non-contiguous to occupied range. For non-contiguous patches, vacant patch size ranged from 245 to 17,003 km^2, totaling 237,503 km^2 or 24.2% of total vacant habitat. Vacant habitats occurred in all states except Kansas. Thirty-four patches ($\geq$5,000 km^2) were identified as priority reintroduction areas (Fig. 4.14).

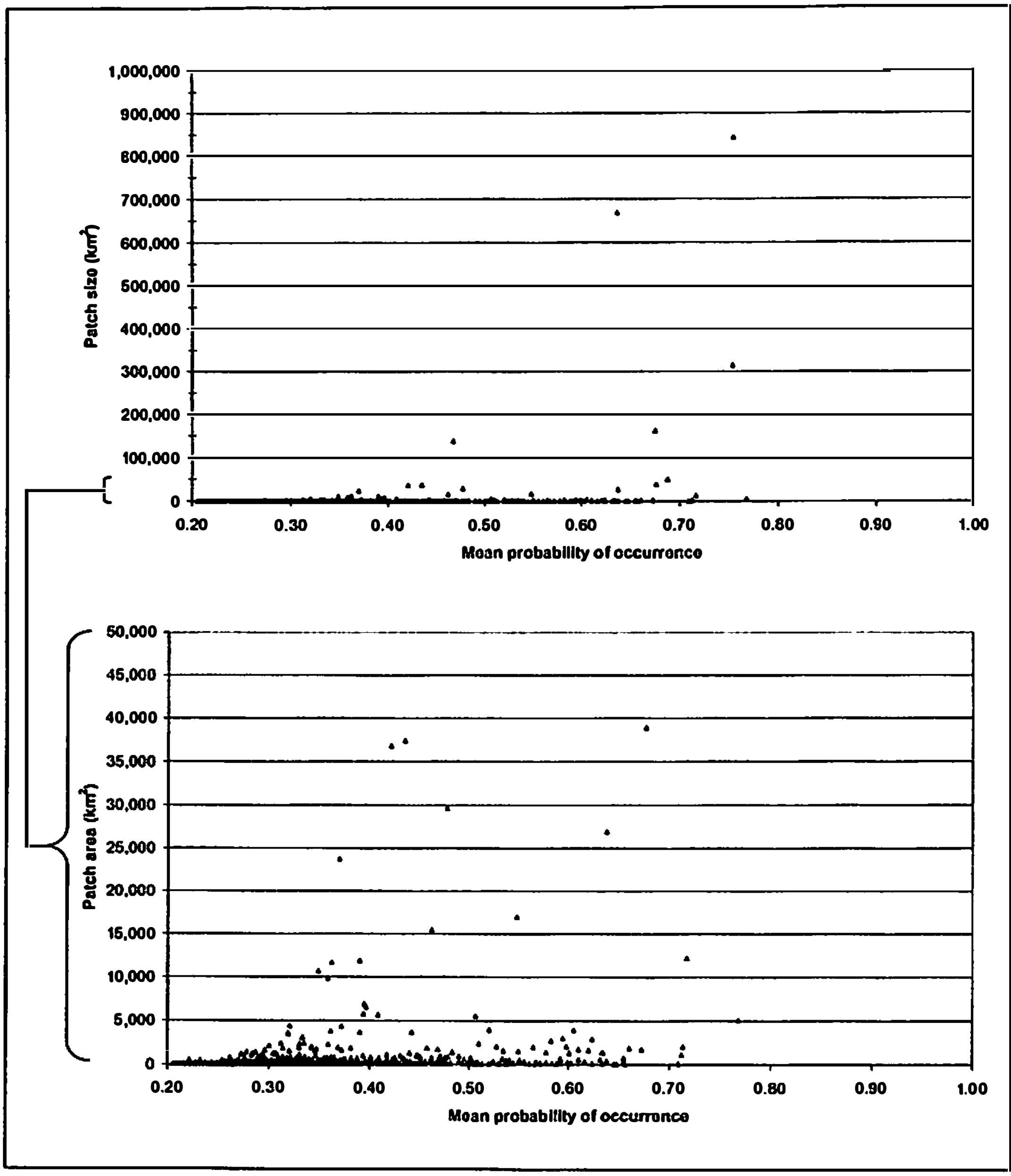


Figure 4.12. Relationship between patch area and mean probability of black bear occurrence for the continental USA, 2004.

Table 4.8. Area of suitable habitat (km^2) and quality of black bear habitat patches by state, USA, 2004.

	Area (km^2)		
State	Range map[a]	Suitable habitat[b]	Mean relative probability of occurrence (suitable habitat only)
Alabama	5,097	49,980	0.37
Arizona	43,814	61,985	0.63
Arkansas	60,044	53,998	0.46
California	151,989	149,450	0.73
Colorado	159,674	155,967	0.81
Connecticut	51	6,027	0.52
Delaware	0	980	0.26
Florida	36,533	65,856	0.42
Georgia	15,586	42,875	0.45
Idaho	99,412	146,559	0.81
Illinois	0	16,513	0.32
Indiana	0	12,544	0.33
Iowa	0	3,087	0.36
Kentucky	29,123	58,261	0.42
Louisiana	13,325	42,875	0.34
Maine	69,789	82,908	0.83
Maryland	4,634	7,448	0.42
Massachusetts	9,207	13,083	0.67
Michigan	78,026	86,730	0.70
Minnesota	102,051	91,532	0.59
Mississippi	4,780	38,171	0.36
Missouri	41,188	79,625	0.42
Montana	162,082	196,245	0.75
Nebraska	10	3,724	0.41
Nevada	3,191	86,093	0.55
New Hampshire	21,981	23,618	0.82
New Jersey	2,563	2,499	0.38
New Mexico	57,421	67,767	0.65
New York	69,991	111,818	0.74
North Carolina	36,813	69,384	0.54
North Dakota	0	2,499	0.34
Ohio	40	31,017	0.38
Oklahoma	6,586	17,689	0.49
Oregon	151,897	141,022	0.73
Pennsylvania	78,884	80,605	0.61
Rode Island	0	686	0.37
South Carolina	3,697	27,685	0.41
South Dakota	20	7,154	0.76
Tennessee	9,320	61,250	0.47
Texas	20,518	18,228	0.34
Utah	84,324	95,550	0.70
Vermont	14,686	24,108	0.85
Virginia	28,417	79,037	0.57
Washington	121,541	103,096	0.77
West Virginia	52,056	57,134	0.59
Wisconsin	73,310	50,666	0.63
Wyoming	186,529	178,703	0.67
TOTAL	2,110,200	2,803,731	

[a] From Pelton and van Manen 1994

[b] Based on the logistic regression models; patches $\geq$200 km^2 and a relative probability of occurrence $\geq$25% for upland environments or $\geq$21% for lowland environments.

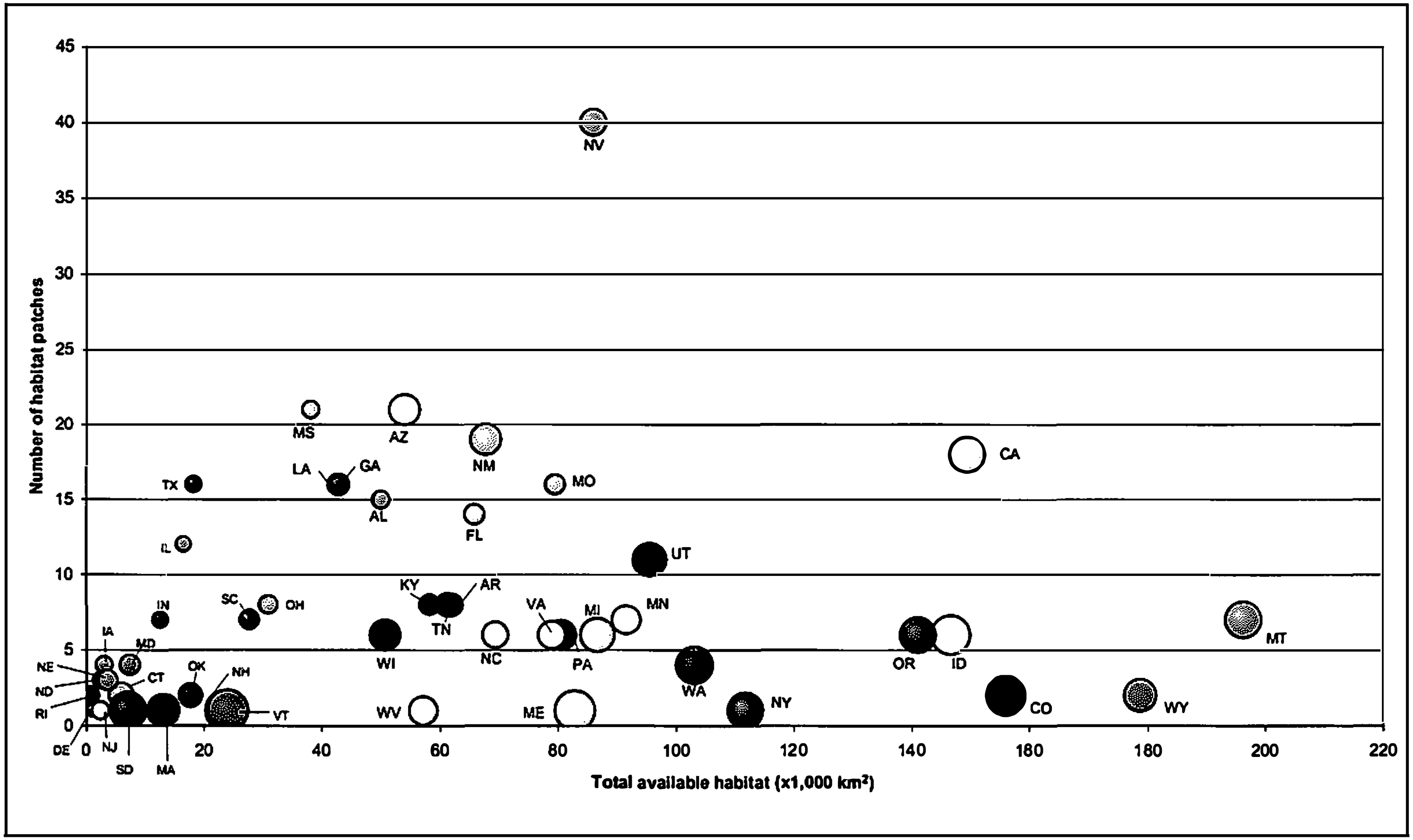


Figure 4.13. Number of habitat patches and total available habitat area by State, continental USA, 2004. Bubble sizes proportional to relative probability of black bear occurrence.

CHAPTER V

DISCUSSION

Issues of Accuracy and Scale

Grain Size.—Based on the objectives of my study, I selected a grain size of 49 km^2. This grain size corresponded well to the average home range size of black bears and grain sizes from other studies of black bear occurrence. However, 75% (15/20) of the spatial environmental variables I used had an original grain size of 1 km^2. Therefore, I re-scaled to 49 km^2 using the average, majority, or diversity of the original coverage. In so doing, I smoothed (i.e., reduced) the spatial variability for many variables. For example, in areas with rugged mountains, the slope for each 1-km^2 cell was averaged over 49 km^2. As a result, the range and variability of slope over 49 km^2 was eliminated. For several of the variables I used, there is little, if any, biological information that describes the "grain size" in which bears perceive and use particular resources. Therefore, it's unknown whether this type of data smoothing influenced my ability to predict bear occurrence.

Spatial Extent.—I found that a single model did not describe a correlation between bear occurrence and spatial environmental variability in the continental USA. The discrepancy between predicted and observed bear occurrence was most prominent along the Southeastern coastal plain. This suggests that perhaps: (1) a different suite of spatial variables influence bears in the Southeast compared to the remainder of the continental USA (Rudis and Tansey 1995), (2) spatial environmental conditions influence bear occurrence in different ways in the two areas, (3) I did not include the appropriate

variables in the model, or (4) bears respond to spatial environmental conditions at different grain sizes in the two areas.

From a habitat standpoint, the Southeastern coastal plain does have marked differences compared with other regions of the continental USA. Large contiguous blocks of forested land, which occur in many areas with bears, are for the most part absent from the Southeastern coastal plain (Hellgren and Maehr 1993). The coastal plain is better characterized as fragmented blocks of bottomland hardwood and pine forests interspersed with agriculture and human developments. Also, major differences exist in bear food items between the Southeastern coastal plain and upland areas, namely the use of agricultural grain crops in coastal environments. Indeed, some authors have suggested that grain crops are crucial for the presence and productivity of black bears in specific areas of the Southeastern coastal plain (Jones 1996, Anderson 1997, Beausoleil 1999). For example, in a large expanse of agricultural land in Louisiana, a bear population has been documented in a small network of isolated forested blocks no larger than 32 km^2 (Beausoleil 1999).

These differences between upland and lowland environments suggest that spatial environmental variability may influence bear presence differently in the two areas. The models from this study indicate that differences do exist between the two areas. The final models included different subsets of variables and some variables which were included in both models had different associations with bear occurrence.

I intentionally limited the candidate list of variables to those with an *a priori* relationship to bear ecology in order to provide a more biologically meaningful model (Hosmer and Lemeshow 2000, James and McCulloch 2002). As a result, most of the

parameter estimates for the independent variables were significant. However, a consequence of my model building strategy was that important variables may have been overlooked because of a lack of knowledge linking the variable to bear ecology. In my study, the likelihood of overlooking an important variable was probably low because the abundance and variety of black bear studies. I suspect that this situation is more likely to occur for species where basic life history information and species-habitat relationships are poorly documented.

An artifact of dividing the continental USA into two areas and developing a model for each is the boundary between the areas. In some cases the probability of occurrence for cells adjacent to the boundary may be debatable because the boundary was derived from ecoregions rather than bear-use patterns. However, even for cells adjacent to the boundary but from different models, the probability of occurrence values are, for the most part, consistent and relatively low (Figs. 4.1, 4.6, and 4.14).

Model Validation.—The Hosmer and Lemeshow goodness-of-fit test indicated the probability of occurrence model for upland environments fit the response data poorly. The poor fit may be related to two reasons that warrant discussion. First, the original range map generated by Pelton and van Manen (1994) had some scale and accuracy issues given the application in this study. The map was generated from statewide county maps and no other spatial references were used to increase the accuracy of the occupied range delineation. That likely resulted in a fairly crude estimate of occupied range given the smaller grain size used in this study. For example, when I digitized the individual state maps, I recognized polygons of occupied range that were the same size and shape as a corresponding island of forested land, but offset by as much as 100 km. I left the data

unchanged from its original form. However, if those types of anomalies were spatially aligned the fit may have improved.

Second, the most striking difference between the bear range map and the relative probability of bear occurrence for upland environments was the amount of suitable habitat that was unoccupied by bears. The spatial distribution of deviance values, which is a measure of fit for individual cells, suggests that the areas that fit the response data poorly were areas suitable for bears, but were unoccupied. Indeed, deviance values were significantly greater in suitable vacant habitats ($\bar{x} = 1.64$, SE = 0.010, n = 17,927, range = 0.58-10.03) compared to the remaining area ($\bar{x} = 0.55$, SE = 0.003, n = 126,290, range = 0.01-13.80) ($t = 120.9$, 14×10^4 df , $P < 0.001$). For this reason, the models ability to accurately discriminate between presence and absence may be a better reflection of model performance (Fielding 2002). The analysis of the ROC curves indicated that the model for upland environments had excellent discrimination ability.

Assumptions.—Logistic regression was an ideal modeling technique for this study because of the dichotomous classification of bear occurrence (presence versus absence), the mathematical flexibility of the function, and the ease of interpretation (Hosmer and Lemeshow 2000). There are, however, a number of assumptions associated with using logistic regression for species prediction exercises.

The basic assumptions are that the dependent variable was correctly classified and the classification does not change; thus areas classified as "absence" were not previously or later classified as "presence" (Morrison et al. 1992). Failure to meet this assumption may result in spurious results, or under- or over-estimation of the outcome, depending on

the nature of the misclassification (Hosmer and Lemeshow 2000). For example, in this study the dependent variable was generated from the range maps provided by biologists from each state. When shading in areas of occupied bear range, most of the biologists provided a coarse depiction of bear occurrence. Therefore, occupied range sometimes overlapped with major cities. When digitizing the range maps, I choose not to alter the original version provided by the biologists. The result of the final logistic regression model was a biased measurement of bear occurrence near major cities. This source of bias likely explains the unexpected importance of urban macrohabitat in upland environments.

The second assumption is that predictor variables are independent, thereby minimizing multicollinearity in the model (Hosmer and Lemeshow 2000). I used 3 strategies to reduce multicollinearity. I excluded correlated candidate variables from the best subset selection process (Hosmer and Lemeshow 2000). By calculating an AIC value for every possible combination of variables, I also discarded variables that did not provide additional explanatory information. Finally, I assessed multicollinearity in the final models by testing for over- and under-dispersion.

The third assumption typically included in habitat selection analyses is that observations of the dependent variable are collected randomly (Morrison et al. 1992). However, this assumption applies primarily to studies where the analysis is carried out on a subset of the total population, such as radio telemetry studies. In contrast, my study included all grid cells in the continental USA, so random selection of dependent observations was less pertinent.

The fourth assumption is that bears had the opportunity to use any of the landscape variables deemed available (Johnson 1980). Given the mobility (Stratman et al. 2001a) and wide distribution of bears, it seems reasonable to assume bears had the opportunity to occupy any area of the continental USA.

Causal Versus Correlation.—The relationship between the independent variables and bear occurrence is not necessarily causal. Rather, some predictor variables may be correlates to the "true" causal agent. For example, the negative relationship between bear presence in lowland environments and increasing elevation likely is not a biologically driven cause-and-effect relationship. Lower elevations probably served as a surrogate to the true landscape variable, perhaps related to flooding zones, plant composition, or some other characteristic. When there is no *a priori* information linking the predictor to the outcome, caution should be used when interpreting the importance of the variable. In some cases, there may not be a biological interpretation at all, because the correlation between the predictor variable and outcome is merely random.

Black Bear Ecotope and Model Interpretation

Many researchers have investigated resource selection of black bears (Clark 1991, Hellgren et al. 1991, van Manen 1994, van Manen and Pelton 1997, Jones 1996, Bull et al. 2001, Stratman et al. 2001b, Lyons et al. 2003). In these studies "used" habitats often were compared with "available" habitats within a defined geographical area and then ranked according to selection preferences. However, habitat selection by an animal or population is not necessarily limited to a particular scale (Krausman 1999). Rather, selection can occur at various scales, ranging from micro- to macro-habitat levels. Recognizing this, Johnson (1980) classified habitat selection studies into four categories.

First-order selection is the selection of the physical or geographical range of a species, *second-order selection* is the selection of a home range of an individual or social group within their geographical range, *third-order selection* relates to how resources within the home range are used (i.e., areas used for foraging), and *fourth-order selection* relates to how components of a habitat are used (e.g., if third-order selection determines a foraging site, fourth-order selection would reflect the actual procurement of food items from those available at that site).

My study involved first-order selection by black bears. I used the presence of bears as a measure of resources "used" and the entire continental USA as a measure of resources that were "available." Within first-order selection, I included resources related to habitat and niche. In so doing, my study provides a quantitative description of the ecotope of the American black bear.

Spatial Variables that Describe Ecotope.—Bear presence in upland environments was correlated with ten landscape variables, including three related to plant growth (spring-summer NDVI, wetness, and snowfall), three related to habitat structure (macrohabitat type, elevation, proximity to streams), and four related to potential mortality forces (human density, road density index, forest fragmentation, and managed lands). The probability of bear presence was positively correlated with all macrohabitat types (except grassland-shrubland mosaic), elevation, lands actively managed as wild lands, snowfall >122 cm, and increasing levels of spring-summer NDVI. In contrast, the probability of bear presence was negatively correlated with increasing levels of forest fragmentation, human densities >55 persons/km^2, increasing distances from streams, increasing road densities, and increasing levels of wetness. Five of the ten variables

contributed to the relative probability of bear presence >0.50 (i.e., lower 95% confidence interval of adjusted odds ratio >1.0); these included non-fragmented forests at elevations ≥200 meters, lands actively managed as wild lands, areas with >122 cm of snowfall, and areas with spring-summer NDVI >200.

Bear occurrence in lowland environments also was correlated with ten landscape variables, including three related to plant growth (spring NDVI, wetness, and soil nitrogen), two related to habitat structure (macrohabitat type, elevation), and five related to mortality forces (human density, road density index, forest fragmentation, percent forest cover, and managed lands). The probability of bear presence was positively correlated with deciduous and evergreen forests, grassland-shrubland mosaic, perforated through edge levels of forest fragmentation, lands actively managed as wild lands, increasing levels of percent forested cover, high levels of spring NDVI, and increasing soil nitrogen levels. In contrast, the probability of bear presence was negatively correlated with elevation, herbaceous-woodland wetlands, sparsely vegetated areas, human density, road density index, and increasing levels of wetness. None of the variables contributed to the relative probability of bear presence >0.50 (i.e., lower 95% confidence interval of adjusted odds ratio >1.0).

I found that the occurrence of black bears was correlated with a slightly different set of spatial variables when comparing upland to lowland regions of the continental USA. The models for upland and lowland environments had 8 variables in common (macrohabitat type, forest fragmentation, elevation, human density, road density index, managed lands, NDVI, and wetness). Variables unique to upland environments were proximity to streams and snowfall, whereas percent forest cover and soil nitrogen were

unique to lowland environments. Forest fragmentation was negatively associated with bear presence in upland environments, whereas moderate levels of fragmentation were positively associated with bear presence in lowland environments. The relationship between bear presence and human density and road density were similar for upland and lowland environments, except that the negative correlations were magnified in lowland environments. These differences suggest that negative impacts of human and road densities on bears are greater in the fragmented environments of the Southeastern coastal plain. Another key difference between upland and lowland environments was the importance of high soil nitrogen in lowland environments. Soil nitrogen strongly influences vegetation composition and growth (Rockwell 1998), particularly in the Southeast. Where soil nitrogen is high, the vegetative growth potential has attracted commercial agricultural and forestry industries (Johnson 1990, Thompson 1990), whom as an artifact of their businesses provide increased cover and forage for black bears.

Relationship to Empirical Data

The variables that I found to be associated with bear occurrence corresponded well to those identified in other studies. Overall, 7 of the 12 variables (macrohabitat type, percent forested cover, managed lands, road density, human density, elevation, and proximity to streams) identified in my models also were associated with bear occurrence in other studies in the continental USA (Clark et al. 1993, van Manen 1994, Rudis and Tansey 1995, van Manen and Pelton 1997, Jones et al. 1998, Murrow 2001). Interestingly, these variables also were identified at various grain sizes, ranging from 0.81 ha (van Manen 1994) to county level (Rudis and Tansey 1995, Jones et al. 1998).

My study was the first to quantitatively link forest fragmentation, wetness, snowfall, NDVI, and soil nitrogen to bear occurrence patterns.

Percent Forest and Macrohabitat Type.— Probably the most common variables associated with bear occurrence are percent forested cover and macrohabitat type (Pelton 1982). In addition to my models, forested macrohabitat types were found to be correlated with bear occurrence in the southern Appalachian Mountains (van Manen 1994, van Manen and Pelton 1997, Murrow 2001), southeastern USA (Rudis and Tansey 1995), eastern North Carolina (Jones et al. 1998), and Arkansas (Clark et al. 1993).

The tie between bears and a forested landscape probably is related to, at a minimum, escape cover and food availability (Stirling and Derocher 1989). The use of a forested environment is closely tied to the evolution of black bears (Herrero 1978, Stirling and Derocher 1989). Black bears evolved in a forested environment and, as such, have developed phenotypic adaptations that are conducive to living in a forest. Most prominent are the rounded claws, muscular anterior appendages, and relatively small body size of black bears, all of which are ideally suited for climbing trees (Gordon 1986, Stirling and Derocher 1989, McLellan and Reiner 1994). Not surprisingly, studies in Maine (Allen 1984), Wisconsin (Massopust and Anderson 1984), and New England and Utah (Elowe 1990) found that bears climb trees about 30% of the time when pursued by dogs. Forested environments also provide escape cover by acting as a visual obstruction and impeding travel of people or other animals. Based on studies in North Carolina (Lombardo 1993, Brandenburg 1996), Florida (Stratman 1998) and Louisiana (Anderson 1997) it is evident that forested environments act as escape cover for concealing bear

movements and foraging (Massopust and Anderson 1984) and as a barrier while denning (Martorello and Pelton 2003) or on day beds (Johnson and Pelton 1983, Mollohan 1986).

The role of forested environments also is closely tied to bear food items provided directly from trees. Bear studies in several regions of the continental USA have documented tree fruits and nuts (hard mast) in the diet of bears (Graber and White 1980, Hellgren and Vaughan 1988, Noyce and Coy 1990, Maddrey 1995, Inman and Pelton 2002, Costello et al. 2003), and hard mast is considered a major driving force in bear population dynamics (Pelton 1982). In New Mexico, temporal changes in hard mast availability were found to be related to bear survival and cub production (Costello et al. 2003). This has important biological implications to bear presence because in some areas hard mast may account for as much as 74% of available forage for bears (Inman and Pelton 2002).

Forest Fragmentation.— Hellgren and Maehr (1993) suggested that fragmentation can negatively influence genetic diversity, demographics, dispersal, home range size, movement patterns, population density, and population viability of black bears. My results are consistent with their assessment, where I found the probability of bear presence was negatively correlated to increasing levels of forest fragmentation. Empirical studies specifically investigating the impacts of fragmentation found that forest fragmentation negatively impacted bears by limiting movements within a metapopulation, limiting dispersal (and perhaps genetic diversity), and increasing resource competition by increasing home range overlap in high bear density areas (Marchinton 1995, Anderson 1997, Beausoleil 1999). Increased fragmentation also has been directly linked to increased mortality and low recruitment (Mollohan and LeCount

1989). Interestingly, Laurance (1991) suggested that a species response to fragmentation would include increased exploitation of edge environments. This corresponds well to the results of this study, where bear occurrence had a strong association with edge environments in fragmented landscapes (i.e., lowland environments).

Elevation.— Habitat use studies in the Great Smoky Mountains (van Manen 1994, van Manen and Pelton 1997) and the Ozark-Ouachita mountains of Arkansas (Clark 1991) found that elevation was significantly correlated with habitat use probability. I observed a marked contrast between elevation and bear presence in lowland versus upland environments. Elevation was positively correlated with bear presence in upland environments and negatively correlated with bear presence in lowland environments (Figs. 4.3 and 4.9). Both van Manen (1994) and Clark (1991) suggested that selection of different elevations by bears was probably related to food availability during different times of the year and land use history. Their findings suggest that the correlation between elevation and bear presence likely reflect that elevation may be a surrogate to plant growth and species composition, and thus food availability.

In Great Smoky Mountains, van Manen (1994) found that the correlation between elevation and bear habitat use also was related to forested lands that were historically cut, because cuts typically occurred at lower elevations where human access was greater. A similar pattern may be occurring at the macro-scale; bear presence may be positively correlated with increasing elevation because historically those areas were least settled by humans and now may serve as refugia.

The negative correlation between elevation and bear presence in lowland environments can be explained by a similar rationale. Along the Southeastern coastal

plain, periodic flooding of low elevation areas likely limit human access (Rudis and Tansey 1995, White et al. 2001). As a result, these areas typically are associated with the most productive forest type (bottomland hardwood forest), which is further enhanced by favorable climate and soil conditions for vigorous plant growth. Consequently, a sizable portion of the low elevation areas of the Southeastern coastal plain are managed for timber, which in turn, further strengthens the negative correlation between elevation and bear presence in the region.

Streams.—I found that the probability of bear presence in upland environments was negatively correlated with proximity to streams. Clark (1991) and van Manen and Pelton (1997) found similar results in their multivariate habitat use analyses in Arkansas and Tennessee, respectively. Of course, the relationship does not imply the actual use of streams, but more likely the habitat features commonly associated with stream corridors and riparian areas. van Manen and Pelton (1996) speculated that bears may use the thick understory habitats typical of stream areas as escape cover and possibly as thermal cover. On Eglin Air Force Base in Florida, Stratman (1998) found that bear use was almost exclusively tied to stream habitats; the stream riparian areas provided forage, escape cover, and movement corridors. These empirical data suggest that the relationship between bear use and proximity to streams likely operates at the micro-scale. However, the same general patterns may also be occurring at the macro-scale, where bears are responding to the spatial conditions typical of areas within 6 km of streams, such as forested corridors (Stratman et al. 2001b), escape cover (Anderson 1997), thermal cover (van Manen 1994), and factors that contribute to plant productivity and diversity.

Road Density Index.— The negative correlation that I found between bear presence and road density index is consistent with findings from several black bear studies. Investigations conducted by Clark et al. (1993) in Arkansas and van Manen (1994) in Great Smoky Mountains found that habitat use probability also was negatively correlated with distance to roads. Black bears also avoided habitats within 274 m of open roads in the Cabinet Mountains of northwest Montana (Kasworm and Manely 1990). Brandenburg (1996) and Martorello (1998) found similar results in eastern North Carolina, were bears avoided areas within 100–200 m and 258 m of roads, respectively. Brody and Pelton (1989) also found that bears avoided roads in Pisgah National Forest, North Carolina and attributed the avoidance to different levels of traffic volume. The actual avoidance of roads is probably related to the increased human disturbance level near roads (Hellgren and Maehr 1993, Warburton et al. 1993, Wooding and Maddrey 1994, Martorello 1998) and this response seems to be evident at multiple scales.

Human Density.—I found that the relative probability of bear presence was negatively correlated with human density. Jones et al. (1998) found the same negative correlation between bear presence and human density in eastern North Carolina. Their analysis also was carried out at the macro-scale, where counties were used as sample units. However, in micro-scale studies where the sample unit of "use" was actual bear locations, bear use was both positively and negatively correlated with proximity to human activity centers, depending on the season and sex (van Manen 1994, van Manen and Pelton 1997). van Manen speculated that the correlations likely were related to the close proximity of high-quality forage sites and human activity centers, coupled with the social avoidance interaction between male and female bears.

This finding suggests that the relationship between bear use and human density (or activity centers) may differ at different levels of selection. In studies of third-order selection, such as those done by van Manen (1994) and van Manen and Pelton (1997), bears have already established a home range within the plausible geographical range of the population, and therefore have already had an opportunity to select areas with low human densities. From the perspective of first-order selection, my models suggest that bear use decreases with increasing levels of human density. I hypothesize that this relationship is a result of increased disturbance and mortality near human activity centers. At human densities <10 persons/km^2 the disturbance and mortality factors may be within suitable limits given favorable conditions from other factors like food, escape cover, fragmentation, and road density.

Managed Lands.—I found that the probability of bear presence was correlated with lands actively managed as wild lands. Rudis and Tansey (1995) also found that bear occurrence was correlated with wild lands in the Southeast, and suggested the correlation was related to the low human disturbance in remote timberlands. Forested wild lands likely provide more secure bear habitat, with lower human densities, lower road traffic volumes, and lower levels of forest fragmentation compared to non-wild lands. As a result, forested wild lands probably correspond to fewer mortality factors for bears or more regulated mortality factors (i.e., regulated hunting).

Normalized Difference Vegetation Index, Wetness Index, Snowfall, and Soil Nitrogen.— I found the bear presence was correlated with spring-summer NDVI, spring NDVI, wetness index, snowfall, and soil nitrogen. I am not aware of any empirical data that evaluated the relationships between bear use and these variables per se. However,

several micro-scale studies have documented the importance of plants as forage items, such as grasses, forbs, and various soft mast producing species (Beeman and Pelton 1977, Graber and White 1980, Noyce and Coy 1990, Maddrey 1995). I suspect that these variables probably acted as a surrogate to plant composition and productivity, and thus the association between bear occurrence and forage availability.

Ecological Interpretation

The logistic regression models explain the relative probability of bear occurrence from a statistical perspective, and most of the parameters are consistent with information gained from other studies or at least appear realistic. To describe the probability of bear occurrence in an ecological context, I will use the gradient of "most preferred" to "least preferred" spatial conditions as a logical order for interpretation. For discussion purposes, I classified landscape preferences into 5 ordinal classes;

- optimal when probability of bear occurrence >0.80,
- suboptimal when probability of bear occurrence >0.60 and ≤0.80,
- satisfactory when probability of bear occurrence >0.40 and ≤0.60,
- marginal when probability of bear occurrence >0.20 and ≤0.40, and
- unsuitable when probability of bear occurrence ≤0.20.

Given the objectives of my study, I will highlight the anthropogenic differences between each ordinal class.

Optimal landscape conditions for black bears are probably best described by four key characteristics. First, the models in this study suggest that optimal conditions include large blocks of contiguous forest. In upland and lowland environments with a probability of occurrence >0.80, over 70% of the area had fragmentation levels between interior

forest and transitional (Appendix E.9). In addition, over 95% of the same area was comprised of mixed, deciduous, and evergreen forest types. Second, optimal conditions probably include low human and road densities. Upland and lowland areas with optimal conditions also had the greatest proportion of low human density areas and a mean road density index $\leq$10.7 ha/km^2 (Appendix E.8 and E.9). Third, in upland and lowland environments with a probability of occurrence >0.80, about 62% and 45% were actively managed as wild lands, respectively (Appendix E.10). Fourth, areas with optimal conditions had relatively high NDVI values and in lowland environments high soil nitrogen levels. Given the relationship between these variables and plant productivity, optimal conditions may also include a substantial understory component that provides spring and summer food sources (Inman and Pelton 2002) (e.g., *Conopholis americana*, *Gaylussacia* spp., *Vaccinium* spp., *Rubus* spp., *Phytolacca americana*), and escape (Anderson 1997, Stratman et al. 2001b) and thermal cover (van Manen 1994). Today, landscapes that best approximate optimal conditions for black bears are national parks with sizable areas of forested land. Indeed, the mean probability of bear occurrence was 0.83 for forested national parks in the continental USA.

Suboptimal landscape conditions for bears probably fit into two major scenarios. First, in some cases climate or other physiographical conditions simply are not conducive for the overstory and understory vegetation types that result in optimal conditions for bears. Landscapes that make up the fringe of bear range may represent these conditions, particularly in the western USA where the gradation between optimal and unsuitable conditions occur over a relatively short distance and is related to macrohabitat type rather than anthropogenic influences (Fig. 4.1) (Mollohan and LeCount 1989). Second, my

results indicate that suboptimal conditions are correlated with human densities up to 10 persons/km^2 and road densities up to 14 ha/km^2 (Figs. 4.2 and 4.7, Appendix E.9). Even these moderate levels of disturbance may result in some unusable habitats because of avoidance, fragmentation and increased human-related mortality (Hellgren and Maehr 1993, Wooding and Maddrey 1994, Martorello 1998). With increasing anthropogenic disturbances, escape cover becomes more important to offset mortality forces associated with increased hunter access and bear-vehicle collisions (Brandenburg 1996, Wooding and Maddrey 1994). Landscapes that reflect suboptimal conditions may be areas like national forests, national recreation areas, or other forested lands with low to moderate human disturbance.

Satisfactory conditions likely result when suboptimal landscapes become fragmented, perhaps at the point where approximately 50% of the area is comprised of edge to non-forested levels of fragmentation (Appendix E.9). Satisfactory conditions are associated with road density indices <15.2 ha/km^2 in non-fragmented forests, and much less in fragmented landscapes. Likewise, satisfactory conditions were correlated with human densities <16.0 persons/km^2 in non-fragmented environments, and far less in fragmented areas. These relationships are complex and influenced by the composition of overstory and understory vegetation (Jones 1996), escape cover (Brandenburg 1996), and food availability (van Manen 1994). These disturbances also may reduce available forage by changing vegetative composition, or may influence the distribution of forage by changing the juxtaposition and interspersion of vegetation types (Jones 1996). Consequently, the temporal and spatial reliability of food sources probably becomes essential, to the extreme where atypical food sources like agricultural grains may be the

variable driving bear presence (Maddrey 1995). In these environments, factors that reduce or manage human related mortality may be important, such as thick understory escape cover, bear sanctuaries (Martorello 1998), and the occurrence of relatively larger blocks of higher quality bear habitats strategically located to enhance metapopulation dynamics (Murrow 2001). Small parcels of privately owned forested land connected with remnant bottomland hardwood forests provide examples of suitable landscape conditions for black bears.

The landscape may be considered marginal for black bears when the level of forest fragmentation appears as islands of forested land in a background of non-forested land (Beausoleil 1999, Riitters et al. 2000). My study suggests that marginal conditions are associated with human densities up to 24 persons/km^2 and a road density index up to 16.9 ha/km^2. For bear populations to persist in these environments, escape cover is crucial and agricultural food sources probably are necessary (Anderson 1997, Jones 1996). In these conditions, bear populations may actually exist as either subpopulations within a larger metapopulation, or as a sink population on the fringe of higher quality habitats that serve as a source population (Murrow 2001). In either case, the local demographics are influenced by the effects of immigration. In these environments, the behavioral plasticity of black bears becomes increasingly evident; more tolerance for human activity, diets dominated by agricultural food sources (Maddrey 1995), unusually high bear densities per unit area of forested land (Beausoleil 1999), and use of atypical den structures (Weaver and Pelton 1994). Isolated patches of forested habitat <900 km^2 (van Manen 1991) with surrounding agricultural food sources are probably examples of marginal landscape conditions for black bears.

In marginal landscapes, increased human or road densities, or the absence of any key habitat component likely will result in unsuitable conditions for black bears to persist. This could range from moderately sized forested blocks with low food abundance (e.g., forest monocultures) to small isolated woodlots, where the absence of sufficient escape cover could potentially limit bear presence (Marchinton 1995, Brandenburg 1996). Non-forested landscapes generally are considered unsuitable for black bears. However, black bears have been documented in the non-forested landscape of Big Bend National Park in southern Texas (Taylor and Garner 1994) and barren grounds of northern Canada (Jonkel and Miller 1970), illustrating the adaptability of black bears to various combinations of spatial factors.

Identifying Potential Reintroduction Areas

By comparing occupied to unoccupied bear range, I identified landscape conditions that were correlated with bear presence. In so doing, I also identified areas of unoccupied range that could potentially support bears. The relative probability of bear occurrence models indicated that nearly 1 million square kilometers of vacant suitable bear habitat exists in the continental USA. About one-quarter of this habitat is isolated from occupied bear range.

The bear occurrence models identified 34 priority ($\geq$5,000 km^2) reintroduction areas, including some in central Nevada. Interestingly, the areas in Nevada are not considered historic range for black bears (Hall 1981). Identifying these areas for reintroduction could be a result of the poor fit for the upland environment model, or perhaps historically bears never colonized these areas because of the degree of isolation.

Only a few independent habitat assessments have been done to identify areas for possible reintroductions. Using a habitat suitability index (HSI), van Manen (1991) indicated that the Big South Fork area of Tennessee and Kentucky was suitable for black bears. The Big South Fork area is the northern portion of the Cumberland Plateau and is connected to the south by a network of national recreation areas, state wildlife areas, state parks, and privately owned forests, which, based on my study and assessments by Rudis and Tansey (1995) and Murrow (2001) seem to be suitable for bears. Following van Manen's assessment, Eastridge and Clark (2001) released 14 bears in the Big South Fork during an experiment to assess release techniques. If these founding bears establish a viable population, bears may eventually inhabit the southern areas of the Cumberland Plateau through natural colonization.

Bears are absent from most of Mississippi and, based on the range map from Pelton and van Manen (1994), exist only in portions of the extreme southwestern counties. To determine if suitable habitat exists elsewhere in the state, Shropshire (1996) and J. L. Bowman, F. J. Vilella, B. D. Leopold, and H. A. Jacobson (unpublished data) modified the HSI models developed for the Great Lakes region by Rogers and Allen (1987) and for the Big South Fork area (van Manen 1991). Their assessment indicated that Delta, DeSoto, and Holly Springs National Forests were suitable for black bears. The relative probability of bear occurrence models for this study also identified these areas as suitable bear habitat.

The methods I used to identify reintroduction areas were based solely on an evaluation at the macro-scale. An assessment of the micro-scale habitat is necessary for a more complete evaluation of potential reintroduction sites, particularly for parameters

associated with food availability and human conflict zones (van Manen 1991, Rudis and Tansey 1995, Clark et al. 2002). I would consider the results of my study as a coarse-scale filter for identifying bear reintroduction areas.

Research and Management Implications

One of the main values of the relative probability of bear occurrence models from this study is the increased understanding about the relationship between spatial environmental variability and bear presence; this makes the models useful to managers in a variety of ways. Managers throughout the continental USA now have a predictive tool to assess the potential impacts of landscape changes on black bear occurrence. For example, if a manager wants to assess the impacts of population growth and human sprawl 20 years from now on black bear distributions, the parameters in the model can be modified to reflect population densities for various regions in 20 years to generate a new predicted distribution of suitable bear habitat. In the same fashion, managers can assess the impacts of major land use changes, such as timber harvest or road building, prior to actually implementing the changes. Of course, the models also can be used to design landscape changes to discourage the presence of bears. For example, managers may be interested in landscape changes that limit bear distribution in areas prone to human-bear conflicts.

Managers also can use the models for the spatial management of bear populations, by identifying areas that likely serve as source or sink environments (Clark 1999). Caution should be used when applying the models for this purpose, because the models make no direct tie between landscape conditions and bear dynamics per se. However, managers may be able to better use source and sink concepts for meeting their

management goals given ancillary data on mortality factors and the ability to identify areas with a relatively high probability of occurrence.

For bear conservation, the models may be especially useful as a macro-scale filter to identify potential reintroduction areas, particularly in the southeastern USA, where bear habitat tends to be more fragmented. Managers also can use the model output as a "cost" surface for identifying corridors between isolated populations or to identify landscape modifications to build or enhance corridors (Mietz 1994, Sandstrom 1996). Moreover, such applications could serve as stepping stones to a comprehensive metapopulation analysis of entire regions of the continental USA (Hanski 1999).

The models also may have some utility for other bear species in the world, particular those where identifying potential reintroduction sites is critical for the future of the species (Servheen et al. 1999). That type of application would probably require some form of modification to the models because the models were not designed for species other than the American black bear in the continental USA. Therefore, cross-species applications may be more appropriate for bear species that fill a fundamental niche similar to the American black bear.

Finally, managers may find the information from this study useful for areas where habitat assessments have not been done and only macro-scale information is needed. In these cases, the use of the models likely equate to substantial savings in time and cost, and the models can be easily adapted for local needs.

CHAPTER VI

SUMMARY

1. This study was the first investigation of first order selection for black bears in their entire historic range in the continental USA.
2. The presence of black bears was correlated with spatial patterns of environmental variability.
3. The presence of black bears in the Southeastern coastal plain (lowland environment) was correlated with a different set of environmental factors compared to bears in the remaining continental USA (upland environment).
4. Patterns of bear presence in upland environments were explained by a logistic regression model with 10 variables. The model included macrohabitat type, elevation, forest fragmentation, human density, road density index, managed lands, proximity to streams, relative wetness, snowfall, and spring-summer NDVI.
5. In upland environments, bear presence was positively correlated with all macrohabitat types (except grassland–shrubland mosaic), lands actively managed as wild lands, snowfall >122 cm, and increasing levels of spring–summer NDVI. In contrast, bear presence was negatively correlated with forest fragmentation, road density index, human densities >10 persons/km^2, greater distances from streams, and increasing levels of wetness.
6. In upland environments, the probability of bear presence $\geq$0.50 was correlated with non-fragmented forests at elevations $\geq$200 meters, lands actively managed as

wild lands, areas with >122 cm of snowfall, and areas with spring-summer NDVI >200.

7. Patterns of bear presence in lowland environments were explained by a logistic regression model with 10 variables. The model included macrohabitat type, elevation, percent forested cover, forest fragmentation, human density, road density index, managed lands, relative wetness, soil nitrogen, and spring NDVI.
8. For lowland environments, bear presence was positively correlated with deciduous and evergreen forests, grassland–shrubland mosaic, perforated through edge levels of forest fragmentation, lands actively managed as wildlands, human density <43 persons/km^2, increasing soil nitrogen, and increasing levels of spring NDVI. In contrast, bear presence was negatively correlated with herbaceous–woodland wetland, sparsely vegetated areas, increasing road density index, and increasing levels of wetness.
9. In lowland environments, none of variables contributed to the relative probability of bear presence >0.50.
10. Seven of the eleven environmental variables identified as correlates with bear presence were consistent with findings from similar black bear studies done at the micro-scale, and appeared to be linked to the biological and ecological processes of black bears. The remaining four variables (managed land, wetness index, soil nitrogen, and NDVI) have not been considered as correlates to bear use patterns in prior studies.
11. The relative probability of bear occurrence models indicated that there were 2,804,662 km^2 of suitable bear habitat in the continental USA. Total suitable

habitat was distributed in 1,414 distinct patches, of which only 306 were ≥200 km^2.

12. Defining suitable macro-habitat as areas ≥200 km^2 and the probability of occurrence ≥0.25 in upland environments and ≥0.21 in lowland environments, the models identified 981,061 km^2 of vacant suitable bear habitat in the continental USA. These habitats were distributed in 394 patches, of which 155 (743,558 km^2) were adjacent to occupied bear range and 239 (237,503 km^2) were isolated from occupied range.
13. The probability of occurrence models identified 34 vacant habitat patches as priority areas (≥5,00 km^2) for relocating bears.
14. The management implications of this study include; (1) a new interactive model that can be adapted and used to predict the relative probability of bear occurrence due to changing environmental conditions, (2) increased information for the spatial management of population source and sink areas, (3) course scale filter for identifying potential black bear reintroduction areas, and (4) application to other bear species to identify suitable or vacant macro-habitats.
15. Future efforts should be made to validate the models developed in this study. Validation methods range from intensive and broad-scale ground truthing to a simple survey of wildlife management institutions similar to the survey conducted by Pelton and van Manen (1994).
16. The results of this study may contribute to future research efforts on corridor analyses and metapopulation dynamics. The models could be used to develop

"cost" estimates for travel corridors or to identify potential populations in a regional metapopulation analysis.

17. The models in this study could be used (or modified) to identify suitable habitats for other bear species, particular those species with a fundamental niche similar to the American black bear.

LITERATURE CITED

Allen, R. B. 1984. Experimental pursuit of black bears with trained bear dogs. Eastern Workshop on Black Bear Research and Management 7:54-58.

Amstrup, S. C., and J. J. Beecham. 1976. Activity patterns of radio-collared black bears in Idaho. Journal of Wildlife Management 40:340-348.

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.

Anderson, J. R., E. E. Hardy, J. T. Roach, and R. E. Witmer. 1976. A land use and land cover classification system for use with remote sensor data. U.S. Geological Survey Professional Paper 964.

Austin, M. P., A. O. Nicholls, and C. R. Margules. 1990. Measurement of the realized qualitative niche: environmental niches of five Eucalyptus species. Ecological Monographs 60:161-177.

Austin, P. A. 2002. Case studies of the use of environmental gradients in vegetation and fauna modeling: theory and practice in Australia and New Zealand. Pages 73-82 *in* J. M. Scott, P. J. Heglund, and M. L. Morrison, eds. Predicting species occurrences: issues of accuracy and scale. Island Press, Washington D. C., USA.

Bailey, R. G. 1995. Description of the ecoregions of the United States. 2nd ed., U.S. Forest Service Publication number 1391, Washington D.C., 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.

Beeman, L. E. 1975. Population characteristics, movements, and activities of the black bear (*Ursus americanus*) in the Great Smoky Mountains National Park. Dissertation, University of Tennessee, Knoxville, Tennessee, USA.

______, and M. R. Pelton. 1977. Seasonal foods and feeding ecology of black bears in the Smoky Mountains. International Conference on Bear Research and Management 4:414-147.

Belward, A.S. 1996. The IGBP-DIS global 1 km land cover data set (DISCover)-proposal and implementation plans: IGBP-DIS Working Paper No. 13, Toulouse, France.

Beringer, J. J. 1986. Habitat use and response to roads by black bears in Harmon Den, Pisgah National Forest, North Carolina. Thesis, University of Tennessee, Knoxville, Tennessee, USA.

Brandenburg, D. M. 1996. Effects of roads on behavior and survival of black bears in coastal North Carolina. Thesis, University of Tennessee, Knoxville, Tennessee, USA.

Brody, A. J., and M. R. Pelton. 1989. Effects of roads on black bear movements in western North Carolina. Wildlife Society Bulletin 17:5-10.

Bull, E. L., T. W. Heater, T. L. Wertz. 2001. Black bear habitat use in northeastern Oregon. Western Workshop on Black Bear Research and Management 7:82-91.

Burnham, K. P., and D. R. Anderson. 1998. Model selection and inference: a practical information-theoretical approach. Springer-Verlag New York Inc., New York, New York, USA.

Capen, D. E., J. W. Fenwick, D. B. Inkley, and A. C. Boynton. 1986. Multivariate models of songbird habitat in New England forests. Pages 171-175 *in* J. Verner, M. L. Morrison, and C. J. Ralph, eds., Wildlife 2000: modeling habitat relationships of terrestrial vertebrates. University of Wisconsin Press, Madison, Wisconsin, USA.

Carr, P. C. 1983. Habitat utilization and seasonal movements of black bears in Great Smoky Mountains National Park. Thesis, University of Tennessee, Knoxville, Tennessee, USA.

Caughley, G. 1977. Analysis of vertebrate populations. John Wiley and Sons Publishers, New York, New York, USA.

Central Intelligence Agency. 2002. World Fact Book 2002. Central Intelligence Agency, Washington D.C., USA.

Chapin, F. S. III, A. J. Bloom, C. B. Field, and R. H. Waring. 1987. Plant response to multiple environmental factors. Bioscience 37:49-57.

Clark, J. D. 1991. Ecology of two black bear populations (*Ursus americanus*) in the Interior Highlands of Arkansas. Dissertation, University of Arkansas., Fayetteville, Arkansas, USA.

______. 1999. Black bear population dynamics in the Southeast: some new perspectives on some old problems. Eastern Workshop on Black Bear Research and Management 15:97-115.

______, J. E. Dunn, and K. G. Smith. 1993. A multivariate model of female black bear habitat use for a geographical information system. Journal of wildlife Management 57:519-526.

______, D. Huber, and C. Servheen. 2002. Bear reintroductions: lessons and challenges. Ursus 13:335-345.

Costello, C. M., D. E. Jones, R. M. Inman, K. H. Inman, B. C. Thompson, and H. B. Quigley. 2003. Relationships of variable mast production to American black bear reproductive parameters in New Mexico. Ursus 14:1-16.

DeLong, E. R., D. M. DeLong, and D. L. Clarke-Pearson. 1988. Comparing the areas under two or more correlated receiver operating characteristic curves: a nonparametric approach. Biometrics 44:837-845.

Dickinson, R.E., A. Henderson-Sellers, P. J. Kennedy, and M. F. Wilson. 1986. Biosphere-atmosphere transfer scheme (BATS) for the NCAR community climate model: NCAR Technical Note NCAR/TN275+STR, Boulder, Colorado, USA.

Eastridge, R., and J. D. Clark. 2001. Evaluation of 2 soft-release techniques to reintroduce black bears. Wildlife Society Bulletin 29:1163-1174.

Elowe, K. D. 1984. Home range, movements, and habitat preferences of black bears (*Ursus americanus*) in western Massachusetts. Thesis, University of Massachusetts, Amherst, USA.

______. 1990. Bear hunting with hounds: techniques and effects on bears and the public. Eastern Workshop on Black Bear Research and Management 10:101-109.

Elton, C. 1927. Animal ecology. MacMillan Company, New York, New York, USA.

Fielding, A. H. 2002. What are the appropriate characteristics of an accuracy measure? Pages 271-280 *in* J. M. Scott, P. J. Heglund, and M. L. Morrison, eds. Predicting species occurrences: issues of accuracy and scale. Island Press, Washington D.C., USA.

Garner, N. P. 1986. Seasonal movements, habitat selection, and food habits of black bears (*Ursus americanus*) in Shenandoah National Park, Virginia. Thesis, Virginia Polytech Institute and State University, Blacksburg, Virginia, USA.

Garris, R. S. 1983. Habitat utilization and movement ecology of black bears in Cherokee National Forest. Thesis, University of Tennessee, Knoxville, Tennessee, USA.

Garshelis, D. L. 1978. Movement ecology and activity behavior of black bears in the Great Smoky Mountains National Park. Thesis, University of Tennessee, Knoxville, Tennessee, USA.

Gordon, K. R. 1986. Insular evolutionary body size trends in *Ursus*. Journal of Mammalogy 67:395-399.

Graber, D. M, and M. White. 1980. Black bear food habits in Yosemite National Park. International Conference on Bear Research and Management 5:1-10.

Grinnell, J. 1917. The niche-relationships of the California Thrasher. Auk 34:427-433.

Hall, E. R. 1981. The mammals of North America. Vol. 2. 2nd ed. John Wiley and Sons, New York, New York, USA.

Hanski, I. 1999. Metapopulation ecology. Oxford University Press, New York, New York, USA.

Hellgren, E. C., and D. S. Maehr. 1993. Habitat fragmentation and black bears in the eastern United States. Eastern Workshop on Black Bear Research and Management 11:154-165.

______, and M. R. Vaughan. 1988. Seasonal food habits of black bears in Great Dismal Swamp, Virginia-North Carolina. Proceedings of the Annual Conference of the Southeastern Association of Fish and Wildlife Agencies 42:295-305.

______, and ______. 1989. Demographic analysis of a black bear population in the Great Dismal Swamp. Journal of Wildlife Management 53:969-977.

______, and ______. 1990. Range dynamics of black bears in Great Dismal Swamp, Virginia-North Carolina. Proceedings of the Annual Conference of the Southeastern Association of Fish and Wildlife Agencies 44:268-278.

______, ______, and D. F. Stauffer. 1991. Macrohabitat use by black bears in a southeastern wetland. Journal of Wildlife Management 55:442-448.

Herrero, S. M. 1978. A comparison of some features of the evolution, ecology, and behavior of black bear and grizzly/brown bears. Carnivore 1:7-17.

Holdridge, L. R. 1947. Determination of world plant formations from simple climatic data. Science 105:367-368.

Hosmer, D. W., Jr. and S. Lemeshow. 2000. Applied logistic regression. 2nd ed. John Wiley and Sons, New York, New York, USA.

Hugie, R. D. 1982. Black bear ecology and management in the northern conifer-deciduous forests of Maine. Dissertation, University of Montana, Missoula, USA.

Hutchinson, G. E. 1957. Concluding remarks. Cold Spring Harbor Symposium on Quantitative Biology 22:415-427.

______. 1978. An introduction to population ecology. The Murray Printing Company, Westford, Massachusetts, USA.

Inman, R. M., and M. R. Pelton. 2002. Energetic production by soft and hard mast foods of American black bears in the Smoky Mountains. Ursus 13:57-68.

Jackson, R. D., P. N. Slater, and P. J. Pinter. 1983. Discrimination of growth and water stress in wheat by various vegetation indices through clear and turbid atmospheres. Remote Sensing of the Environment 15:187-208.

James, F. C., and C. E. McCulloch. 2002. Predicting species presence and abundance. Pages 461-465 *in* J. M. Scott, P. J. Heglund, and M. L. Morrison, eds. Predicting species occurrences: issues of accuracy and scale. Island Press, Washington D.C., USA.

Johnson, C. M., L. B. Johnson, C. Richards, and V. Beasley. 2002. Predicting the occurrence of amphibians: an assessment of multiple-scale models. Pages 157-170 *in* J. M. Scott, P. J. Heglund, and M. L. Morrison, eds. Predicting species occurrences: issues of accuracy and scale. Island Press, Washington D.C., USA.

Johnson, D. H. 1980. The comparison of usage and availability measurements for evaluating resource preference. Ecology 61:65-71.

Johnson, K. G., and M. R. Pelton. 1983. Bedding behavior of black bears in Tennessee. Proceedings of the Annual Conference of the Southeastern Association of Fish and Wildlife Agencies 37:237-243.

Johnson, T. G. 1990. Forest statistics for the southern coastal plain of North Carolina. Resource Bulletin SE-111. U.S. Forest Service, Southeastern Forest Experiment Station, Ashville, North Carolina, USA.

Jones, M. D. 1996. Black bear use of forest and agricultural environments in coastal North Carolina. Thesis, University of Tennessee, Knoxville, Tennessee, USA.

______, G. S. Warburton, and M. R. Pelton. 1998. Models for predicting occupied black bear habitat in coastal North Carolina. Ursus 10:203-207.

Jones, M. T., G. J. Niemi, J. M. Hanowski, and R. R. Regal. 2002. Poisson regression: a better approach to modeling abundance data? Pages 411-418 *in* J. M. Scott, P. J. Heglund, and M. L. Morrison, eds. Predicting species occurrences: issues of accuracy and scale. Island Press, Washington D. C., USA.

Jonkel, C., and F. L. Miller. 1970. Recent records of black bears (*Ursus americanus*) on the barren grounds of Canada. Journal of Mammalogy 51:826-828.

Kasworm, W. F., and T. L. Manley. 1990. Road and trail influences on grizzly bears and black bears in northwest Montana. International Conference on Bear Research and Management 8:79-84.

Klute, D. S., M. J. Lovallo, and W. M. Tzilkowski. 2002. Autologistic regression modeling of American woodcock habitat use with spatial dependent data. Pages 335-343 *in* J. M. Scott, P. J. Heglund, and M. L. Morrison, eds. Predicting species occurrences: issues of accuracy and scale. Island Press, Washington D.C., USA.

Krausman, P. R. 1999. Some basic principles of habitat use. Idaho Forest, Wildlife, and Range Experiment Station Bulletin Number 70.

Landers, J. L., R. J. Hamilton, A. S. Johnson, and R. L. Marchinton. 1979. Foods and habitat of black bears in southeastern North Carolina. Journal of Wildlife Management 43:143-153.

Laurance, W. F. 1991. Ecological correlates of extinction proneness in Australian tropical rain forest mammals. Conservation Biology 5:79-89.

Lindzey, F. G., and E. C. Meslow. 1977. Home range and habitat use by bears in southwestern Washington. Journal of Wildlife Management 41:413-425.

Lombardo, C. A. 1993. The population ecology of black bears on Camp LeJeune, North Carolina. Thesis, University of Tennessee, Knoxville, Tennessee, USA.

Lyons, A. L., W. L. Gaines, and C. Servheen. 2003. Black bear resource selection in the northeast Cascades, Washington. Biological Conservation 113:55-62.

Maddrey, R. C. 1995. Morphology, reproduction, food habits, crop depredation, and mortality of black bears on the Neuse-Pamilico peninsula, North Carolina. Thesis, University of Tennessee, Knoxville, Tennessee.

Marchinton, F. B. 1995. Movement ecology of black bears in a fragmented bottomland hardwood habitat in Louisiana. Thesis, University of Tennessee, Knoxville, Tennessee, USA.

Martorello, D. A. 1998. Ecology of black bears in coastal North Carolina. Thesis, University of Tennessee, Knoxville, Tennessee, USA.

______, and M. R. Pelton. 2003. Microhabitat characteristics of American black bear nest dens. Ursus 14:21-26.

Massopust, J. L., and R. K. Anderson. 1984. The response of black bears to being chased by hunting dogs. Eastern Workshop on Black Bear Research and Management 7:59-65.

Maurer, B. A. 2002. Predicting distribution and abundance: thinking within and between scales. Pages 125-132 *in* J. M. Scott, P. J. Heglund, and M. L. Morrison, eds. Predicting species occurrences: issues of accuracy and scale. Island Press, Washington D. C., USA.

McGhie, R. G. 1996. Creation of a comprehensive managed areas spatial database for the conterminous United States. Technical report 96-4, NASA-NAGW-1743. University of California, Santa Barbara, California, USA.

McLellan, B., and D. C. Reiner. 1994. A review of bear evolution. International Conference on Bear Research and Management 9:85-96.

Mietz, S. N. 1994. Linkage zone identification and evaluation of management options for grizzly bears in the Evaro Hill area. Thesis, University of Montana, Missoula, Montana, USA.

Mollohan, C. M. 1986. Characteristics of adult female black bear daybeds in northern Arizona. International Conference on Bear Research and Management 7:145-149.

______, and A. L. LeCount. 1989. Problems of maintaining a viable black bear population in a fragmented forest. Pages 149-159 *in* A, Tecle, W. W. Covington, and R. H. Hamre, Technical Correspondence. Multiresource management of ponderosa pine forests. U.S. Forest Service, General Technical Report RM-185, Fort Collins, Colorado, USA.

Moore, I. D., R. B. Grayson, and A. R. Ladson. 1991. Digital terrain modeling: a review of hydrological, geomorphological and biological applications. Hydrological Processes and International Journal, January–March:3-30.

Morrison, M. L., and L. S. Hall. 2002. Standard terminology: toward a common language to advance ecological understanding and application. Pages 43-52 *in* J. M. Scott, P. J. Heglund, and M. L. Morrison, eds. Predicting species occurrences: issues of accuracy and scale. Island Press, Washington D. C., USA.

______, B. G. Marcot, and R. W. Mannan. 1992. Wildlife-habitat relationships: concepts and applications. University of Wisconsin Press, Madison, Wisconsin, USA.

Murrow, J. L. 2001. A black bear metapopulation analysis for the southern Appalachians. Thesis, University of Tennessee, Knoxville, Tennessee, USA.

Novick, H. J., and G. R. Stewart. 1982. Home range and habitat preference of black bears in the San Bernardino Mountains of southern California. California Fish and Game Journal 67:21-35.

Noyce, K. V., and P. L. Coy. 1990. Abundance and production of bear food species in different forest types of northcentral Minnesota. International Conference on Bear Research and Management 8:169-181.

Nudds, T. D. 1983. Niche dynamics and organization of waterfowl guilds in variable environments. Ecological Monographs Number 2.

Olson, J. S. 1994*a*. Global ecosystem framework-definitions. USGS EROS Data Center Internal Report, Sioux Falls, South Dakota, USA.

______. 1994*b*. Global ecosystem framework-translation strategy. USGS EROS Data Center Internal Report, Sioux Falls, South Dakota, USA.

Pearce, J. L., L. A. Venier, S. Ferrier, and D. W. McKenney. 2002. Measuring prediction uncertainty in models of species distribution. Pages 383-390 *in* J. M. Scott, P. J. Heglund, and M. L. Morrison, eds. Predicting species occurrences: issues of accuracy and scale. Island Press, Washington D. C., USA.

Pelton, M. R. 1982. Black bear. Pages 504-514 *in* J. A. Chapman and G. A. Feldhamer, editors. Wild mammals of North America: biology, management, and economics. John Hopkins University Press, Baltimore, Maryland, USA.

______, and F. T. van Manen. 1994. Distribution of black bears in North America. Eastern Workshop on Black Bear Research and Management 12:133-138.

______, A. B. Coley, T. H. Eason, D. L. 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, compilers. Bears: Status survey and conservation action plan. 1999. IUCN/SSC bear and polar bear specialist groups. IUCN, Gland, Switzerland and Cambridge, United Kingdom.

Poelker, R. J., and H. D. Hartwell. 1973. The black bear of Washington. Biological Bulletin 14. Washington State Game Department, Olympia, Washington, USA.

Quigley, H. B. 1982. Activity patterns, movement ecology, and habitat utilization of black bears in the Great Smoky Mountains National Park. Thesis, University of Tennessee, Knoxville, Tennessee, USA.

Reagan, S. R. 1991. Habitat use by female black bears in a southern Appalachian bear sanctuary. Thesis, University of Tennessee, Knoxville, Tennessee, USA.

Riitters, K., J. Wickham, R. O'Neill, B. Jones, and E. Smith. 2000. Global-scale patterns of forest fragmentation. Conservation Ecology 4(2): 3. [online] URL: http://www.consecol.org/vol4/iss2/art3.

Rockwell, D. 1998. The nature of North America: a handbook to the continent. The Berkley Publishing Group, New York, New York, USA.

Rogers, L. L., and A. W. Allen. 1987. Habitat suitability index models: black bear, Upper Great Lakes Region. U.S. Fish and Wildlife Service Biological Report 82 (10.144).

Rudis, V. A., and J. B. Tansey. 1995. Regional assessment of remote forests and black bear habitat from forest resource surveys. Journal of Wildlife Management 59:170-180.

Sabo, S. R. 1980. Niche and habitat relations in subalpine bird communities of the White Mountains of New Hampshire. Ecological Monographs Number 2.

Sandstrom, P. L. 1996. Identification of potential linkage zones for grizzly bears in the Swan-Clearwater valley using GIS. Thesis, University of Montana, Missoula, Montana, USA.

SAS Institute, Inc. 1999. SAS User's guide, version 8.2. SAS Institute Inc., Cary, North Carolina, USA.

Saunders., D. A., R. J. Hobbs, and C. R. Margules. 1991. Biological consequences of ecosystem fragmentation: a review. Conservation Biology 5:18-32.

Scepan, J. 1999. Thematic validation of high-resolution global land-cover data sets. Photogrammetric Engineering and Remote Sensing 65:1051-1060.

Schulz, T. T., and L. A. Joyce. 1992. A spatial application of a marten habitat model. Wildlife Society Bulletin 20:74-83.

Scott, J. M., F. Davis, B. Csuti, R. Noss, B. Butterfield, C. Groves, H. Anderson, S. Caicco, F. D'Erchia, T. C. Edwards, J. Ulliman Jr., and R. G. Wright. 1993. GAP analysis: a geographic approach to protection of biological diversity. Wildlife Monograph 123.

______, P. J. Heglund, and M. L. Morrison, editors. 2002. Predicting species occurrence: issues of accuracy and scale. Island Press, Washington D.C., USA.

Seagle, S. W., and G. F. McCracken. 1986. Species abundance, niche position, and niche breadth for five terrestrial animal assemblages. Ecology 67:816-818.

Seibert, S. G. 1989. Black bear habitat use and response to roads on Pisgah National Forest, North Carolina. Thesis, University of Tennessee, Knoxville, Tennessee, USA.

Sellers, P. J., Y. Mintz, Y. C. Sud, and A. Dalcher. 1986. A simple biosphere model (SiB) for use within general circulation models. Journal of Atmospheric Science 43:505-531.

Servheen, C., S. Herrero, and B. Peyton. 1999. Bears: Status survey and conservation action plan. IUCN/SSC bear and polar bear specialist groups. IUCN, Gland, Switzerland and Cambridge, United Kingdom.

Shropshire, C. C. 1996. History, status and habitat components of black bears in Mississippi. Dissertation, Mississippi State University, Mississippi State, Mississippi, USA.

Smith, T. R. 1985. Ecology of black bears in the bottomland hardwood forest in Arkansas. Dissertation, University of Tennessee, Knoxville, Tennessee, USA.

Steidl, R. J., J. P. Hayes, and E. Schauber. 1997. Statistical power analysis in wildlife research. Journal of Wildlife Management 61:270-279.

Stirling, I. and A. E. Derocher. 1989. Factors affecting the evolution and behavioral ecology of the modern bears. International Conference on Bear Research and Management 8:189-204.

Stockwell, D. R. B, and A. T. Peterson. 2002. Controlling bias in biodiversity data. Pages 537-546 *in* J. M. Scott, P. J. Heglund, and M. L. Morrison, eds. Predicting species occurrences: issues of accuracy and scale. Island Press, Washington D.C., USA.

Stratman, M. R. 1998. Habitat use and effects of prescribed fire on black bears in northwestern Florida. Thesis, University of Tennessee, Knoxville, Tennessee, USA.

______, C. D. Alden, M. R. Pelton, and M. E. Sunquist. 2001a. Long distance movement of a Florida black bear in the Southeastern Coastal Plain. Ursus 12:55-58.

______, C. D. Alden, M. R. Pelton, and M. E. Sunquist. 2001b. Habitat use by American black bears in the Sandhills of Florida. Ursus 12:109-114.

Taylor, R. B., and N. P. Garner. 1994. Texas status report. Eastern Workshop on Black Bear Research and Management 12:65-66.

Thompson, M. T. 1990. Forest statistics for the southern coastal plain of North Carolina. Resource Bulletin SE-113. U.S. Forest Service, Southeastern Forest Experiment Station, Ashville, North Carolina, USA.

Tilman, D. 1977. Resource competition between planktonic algae: an experimental and theoretical approach. Ecology 58:338-348.

Tobalske, C. 2002. Effects of spatial scale on the predictive ability of habitat models for the green woodpecker in Switzerland. Pages 197-204 *in* J. M. Scott, P. J. Heglund, and M. L. Morrison, eds. Predicting species occurrences: issues of accuracy and scale. Island Press, Washington D. C., USA.

Trani, M. K. 2002. The influence of spatial scale on landscape pattern description and wildlife habitat assessment. Pages 141-155 *in* J. M. Scott, P. J. Heglund, and M. L. Morrison, eds. Predicting species occurrences: issues of accuracy and scale. Island Press, Washington D. C., USA.

Tucker, C. J. 1979. Red and photographic infrared linear combinations for monitoring vegetation. Remote Sensing of the Environment 8:127-150.

Tucker, C. J., W. W. Newcomb, S. O. Los, and S. D. Prince. 1991. Mean and inter-year variation of growing-season normalized difference vegetation index for the Sahel 1981-1989. International Journal of Remote Sensing 12:1113-1115.

Udvardy, M. F. D. 1959. Notes on the ecological concepts of habitat, biotope, and niche. Ecology 40:725-728.

USDA Forest Service. 1994. Final Supplement to the final Environmental Impact Statement, Land and Resource Management Plan, Nantahala and Pisgah National Forests. Forest Service Southern Region. Volume I and II.

Van Horne, B. 2002. Approaches to habitat modeling: the tension between pattern and process and between specificity and generality. Pages 63-72 *in* J. M. Scott, P. J. Heglund, and M. L. Morrison, eds. Predicting species occurrences: issues of accuracy and scale. Island Press, Washington D. C., USA.

van Manen, F. T. 1991. A feasibility study for the potential reintroduction of black bears into the Big South Fork Area of Kentucky and Tennessee. Tennessee Wildlife Resources Agency, Technical Report Number 91-3, Nashville, Tennessee, USA.

______. 1994. Black bear habitat use in Great Smoky Mountains National Park. Dissertation, University of Tennessee, Knoxville, Tennessee, USA.

______, and M. R. Pelton. 1996. Habitat use by black bears on Cherokee National Forest, Tennessee. Tennessee Wildlife Resources Agency, Technical Report Number 96-8, Nashville, Tennessee, USA.

______, and _____. 1997. A GIS model to predict black bear habitat use. Journal of Forestry 95:6-12.

Verbyla, D. L., and J. A. Litvaitis. 1989. Resampling methods for evaluating classification accuracy of wildlife habitat models. Environmental Management 13:783-787.

Villarrubia, C. R. 1982. Movement ecology and habitat utilization of black bears in Cherokee National Forest, Tennessee. Thesis, University of Tennessee, Knoxville, Tennessee, USA.

Warburton, G. S. 1984. An analysis of a black bear sanctuary in western North Carolina. Thesis, North Carolina State University, Raleigh, North Carolina, USA.

Warburton, G. S., and R. C. Maddrey. 1994. Survey of nuisance bear programs in eastern North America. Eastern Workshop on Black Bear Research and Management 12:115-123.

______, ______, D. W. Rowe. 1993. Characteristics of black bear mortality on the coastal plain of North Carolina. Proceedings from the Annual Conference of the Southeastern Association of Fish and Wildlife Agencies 47:276-286.

Weaver, K. M., and M. R. Pelton. 1994. Denning ecology of black bears in the Tensas river basin of Louisiana. International Conference on Bear Research and Management 9:427–433

Westman, W. E. 1991. Measuring realized niche spaces: climatic response of chaparral and coastal sage scrub. Ecology 72:1678-1684.

White, H. T., J. L. Bowman, H. A. Jacobson, B. D. Leopold, and W. P. Smith. 2001. Forest management and female black bear denning. Journal of Wildlife Management 65:34–40.

Whittaker, R. H. 1967. Gradient analysis of vegetation. Biol. Rev. 42:229.

______, S. A. Levins, and R. B. Root. 1973. Niche, habitat, and ecotope. American Naturalist 107:321-338.

Wilcove, D. S., C. H. McLellan, and A. P. Dobson. 1986. Habitat fragmentation in the temperate zone. Pages 256-273 *in* M. E. Soule, editor. Conservation Biology. The science of scarcity and diversity. Sinauer Associates, Sunderland, Massachusetts, USA.

Wooding, J. B., and R. C. Maddrey. 1994. Impacts of roads on black bears. Eastern Workshop on Black Bear Research and Management 12:124-129.

Young, J. S., and R. L. Hutto. 2002. Use of regional-scale exploratory studies to determine bird-habitat relationships. Pages 107-119 *in* J. M. Scott, P. J. Heglund, and M. L. Morrison, eds. Predicting species occurrences: issues of accuracy and scale. Island Press, Washington D. C., USA.

Zimmermann, F., and U. Breitenmoser. 2002. A distribution model for the Eurasian lynx (*Lynx lynx*) in the Jura Mountains, Switzerland. Pages 653-659 *in* J. M. Scott, P. J. Heglund, and M. L. Morrison, eds. Predicting species occurrences: issues of accuracy and scale. Island Press, Washington D. C., USA.

APPENDICES

Appendix A. Glossary of Terms

Appendix A.1. Glossary of terms (modified from Morrison and Hall 2002).

Distribution – the spread or scatter of an entity within its range.

Extent – the area over which observations are made.

Grain – the spatial resolution of observations.

Habitat – the physical space within which an animal lives, and the abiotic and biotic entities in that space.

Habitat availability – the accessibility and procurability of physical and biological components in a habitat.

Habitat preference – used to describe the relative use of locations (habitats) by an individual or population.

Habitat quality – the ability of the area to provide conditions appropriate for individual and population persistence.

Habitat selection – a hierarchical process involving a series of innate and learned behavioral decisions made by an animal about what habitat it would use at different scales of the environment.

Habitat use – the way an animal uses (or consumes) a collection of physical and biological entities in a habitat.

Landscape – a spatially heterogeneous area used to describe features of interest.

Landscape scale or level – level of organization revealed by observation at the spatial extent of whole kilometers.

Macrohabitat – measures of habitat at relatively large grain sizes; includes characteristics of overstory cover types.

Appendix A.1. Continued.

Microhabitat – measures of habitat at relatively small grain sizes; includes characteristics of understory cover types.

Model – a formal representation of the world.

Niche – intracommunity role of a species.

Appendix B. State Abbreviations

Table B.1. State abbreviations, continental USA.

State	Abbreviation
Alabama	AL
Arizona	AZ
Arkansas	AR
California	CA
Colorado	CO
Connecticut	CT
Delaware	DE
Florida	FL
Georgia	GA
Idaho	ID
Illinois	IL
Indiana	IN
Iowa	IA
Kansas	KS
Kentucky	KY
Louisiana	LA
Maine	ME
Maryland	MD
Massachusetts	MA
Michigan	MI
Minnesota	MN
Mississippi	MS
Missouri	MO
Montana	MT
Nebraska	NE
Nevada	NV
New Hampshire	NH
New Jersey	NJ
New Mexico	NM
New York	NY
North Carolina	NC
North Dakota	ND
Ohio	OH
Oklahoma	OK
Oregon	OR
Pennsylvania	PA
Rhode Island	RI
South Carolina	SC
South Dakota	SD
Tennessee	TN
Texas	TX
Utah	UT
Vermont	VT
Virginia	VA
Washington	WA
West Virginia	WV
Wisconsin	WI
Wyoming	WY

Appendix C. Example Scatter Plot

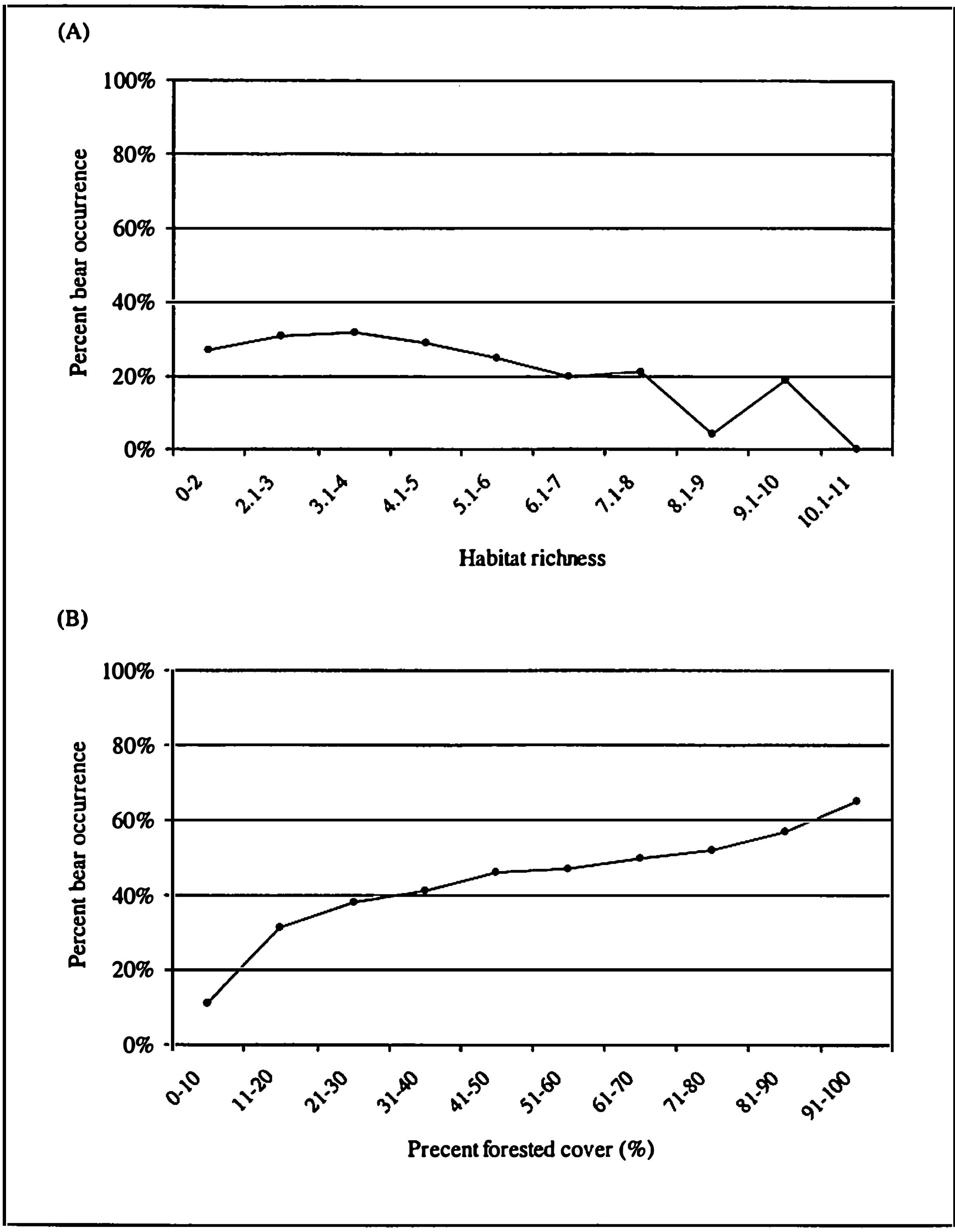


Figure C.1. Scatter plot of percent bear occurrence by habitat richness (A) and percent forested cover (B) classes, upland environments of the continental USA, 2004.

Appendix D. Correlation Coefficients of Independent Variables

Table D.1. Correlation coefficients for independent variables in upland environments of the continental USA, 2004.

	Variable														
Variable	EL	HT	FF	HD	ML	ST	RD	SP	SU	SN	WE	FC	SL	TE	PR
EL	1.00														
HT	0.16	1.00													
FF	0.12	-0.68	1.00												
HD	-0.12	-0.05	-0.01	1.00											
ML	0.45	0.34	-0.20	-0.05	1.00										
RI	0.13	0.00	0.12	-0.00	0.12	1.00									
RD	-0.42	-0.03	-0.15	0.37	-0.28	-0.10	1.00								
SP	-0.46	0.20	-0.54	0.04	-0.13	-0.24	0.34	1.00							
SU	-0.45	0.06	-0.50	0.04	-0.13	-0.26	0.27	0.85	1.00						
SN	0.46	0.15	-0.19	-0.05	0.24	-0.11	-0.26	-0.05	0.19	1.00					
WE	-0.54	-0.43	0.32	0.05	-0.45	-0.10	0.24	0.04	0.12	-0.32	1.00				
FC	-0.08	-0.77	-0.93	-0.20	0.24	-0.12	0.13	0.56	0.51	0.21	-0.34	1.00			
SL	0.55	-0.29	-0.28	0.12	0.56	0.07	-0.30	-0.07	-0.08	0.36	-0.80	0.32	1.00		
TE	-0.44	0.09	0.09	-0.21	-0.19	0.10	0.31	0.13	-0.14	-0.89	0.24	-0.11	-0.27	1.00	
PR	-0.48	-0.36	-0.66	-0.39	-0.03	-0.22	0.35	0.69	0.71	-0.01	0.03	0.66	0.02	0.11	1.00

Table D.2. Correlation coefficients for independent variables in lowland environments of the continental USA, 2004.

	Variable										
Variable	EL	FF	HT	HD	ML	FC	RD	SP	NI	HR	WE
EL	1.00										
FF	-0.05	1.00									
HT	0.09	0.54	1.00								
HD	-0.14	0.14	0.06	1.00							
ML	-0.03	-0.17	-0.12	-0.01	1.00						
FC	0.03	-0.64	-0.67	-0.13	0.16	1.00					
RD	0.02	0.04	0.05	0.31	-0.12	-0.02	1.00				
SP	0.00	-0.10	-0.05	-0.02	0.00	0.09	-0.04	1.00			
NI	-0.46	0.06	-0.04	0.10	0.09	-0.06	-0.23	0.01	1.00		
RI	-0.07	-0.02	-0.01	-0.02	0.01	0.03	0.03	0.00	-0.01	1.00	
WE	-0.46	0.23	0.12	-0.02	-0.02	-0.23	-0.17	-0.05	0.26	-0.03	1.00

Appendix E. Descriptive Statistics for Independent Variables

Table E.1. Descriptive statistics for continuous independent variables in upland environments of the continental USA, 2004. Statistics are summarized by five probability of occurrence levels.

Independent variable	Probability range	Mean	*n*	Standard error	95% Confidence Interval Lower	95% Confidence Interval Upper	Minimum	Maximum
Elevation (m)	0.00-0.20	695.07	85,186	1.85	691.44	698.70	-73.51	3,087.45
	0.21-0.40	709.15	17,426	5.53	698.30	720.00	-27.06	2,739.90
	0.41-0.60	832.60	11,354	6.78	819.32	845.88	12.35	2,901.06
	0.61-0.80	993.10	10,693	7.58	978.25	1,007.95	12.49	3,298.78
	0.81-1.00	1,561.51	19,596	6.54	1,548.70	1,574.33	27.05	3,810.65
Forest fragmentation index	0.00-0.20	5.56	85,169	0.00	5.56	5.57	1.00	6.00
	0.21-0.40	3.86	17,426	0.01	3.83	3.88	1.00	6.00
	0.41-0.60	3.27	11,354	0.02	3.23	3.31	1.00	6.00
	0.61-0.80	3.31	10,693	0.02	3.27	3.34	1.00	6.00
	0.81-1.00	2.42	19,596	0.01	2.40	2.44	1.00	6.00
Proximity to stream (km)	0.00-0.20	5.32	85,186	0.02	5.27	5.36	0.00	89.81
	0.21-0.40	3.87	17,426	0.02	3.82	3.92	0.16	42.48
	0.41-0.60	3.92	11,354	0.03	3.85	3.98	0.44	42.11
	0.61-0.80	3.95	10,693	0.03	3.89	4.01	0.47	33.99
	0.81-1.00	3.87	19,596	0.02	3.83	3.91	0.42	31.43
Road density index (ha/km^2)	0.00-0.20	16.17	85,186	0.04	16.10	16.24	0.00	99.46
	0.21-0.40	16.71	17,426	0.07	16.58	16.84	0.00	91.28
	0.41-0.60	16.26	11,354	0.07	16.12	16.40	0.00	85.32
	0.61-0.80	14.75	10,693	0.07	14.60	14.89	0.00	66.87
	0.81-1.00	10.70	19,596	0.05	10.60	10.81	0.00	46.57
Spring-summer NDVI	0.00-0.20	808.56	85,186	0.40	807.78	809.35	200.69	997.82
	0.21-0.40	866.41	17,426	0.90	864.64	868.18	206.22	1,014.71
	0.41-0.60	874.75	11,354	1.09	872.61	876.88	210.31	1,023.94
	0.61-0.80	881.49	10,693	0.97	879.58	883.40	267.88	1,029.96
	0.81-1.00	883.60	19,596	0.55	882.52	884.68	296.59	1,019.39
Wetness index	0.00-0.20	7.36	85,186	0.01	7.35	7.38	1.43	10.98
	0.21-0.40	6.22	17,426	0.02	6.19	6.25	1.49	10.98
	0.41-0.60	5.53	11,354	0.02	5.50	5.56	1.43	10.98
	0.61-0.80	5.00	10,693	0.02	4.96	5.04	1.53	10.98
	0.81-1.00	3.65	19,596	0.01	3.63	3.67	1.14	10.78

Table E.2. Descriptive statistics for macrohabitat types in upland environments of the continental USA, 2004. Statistics are summarized by five probability of occurrence levels.

Macrohabitat type	Probability range	*n*	Area	Percent
Mixed forest	0.00-0.20	299	14,651	3.75
	0.21-0.40	682	33,418	8.55
	0.41-0.60	1,481	72,569	18.56
	0.61-0.80	2,498	122,402	31.31
	0.81-1.00	3,018	147,882	37.83
Deciduous forest	0.00-0.20	5,334	261,366	26.24
	0.21-0.40	5,059	247,891	24.89
	0.41-0.60	3,700	181,300	18.20
	0.61-0.80	2,095	102,655	10.31
	0.81-1.00	4,138	202,762	20.36
Evergreen needleleaf forest	0.00-0.20	3,514	172,186	15.41
	0.21-0.40	3,526	172,774	15.46
	0.41-0.60	1,981	97,069	8.69
	0.61-0.80	2,132	104,468	9.35
	0.81-1.00	11,654	571,046	51.10
Cropland-woodland mosaic	0.00-0.20	1,497	73,353	29.91
	0.21-0.40	2,323	113,827	46.41
	0.41-0.60	299	14,651	5.97
	0.61-0.80	789	38,661	15.76
	0.81-1.00	97	4,753	1.94
Grassland-shrubland mosaic	0.00-0.20	41,950	2,055,550	77.74
	0.21-0.40	5,038	246,862	9.34
	0.41-0.60	3,526	172,774	6.53
	0.61-0.80	2,983	146,167	5.53
	0.81-1.00	468	22,932	0.87
Sparsely vegetated, snow, or ice	0.00-0.20	828	40,572	48.42
	0.21-0.40	376	18,424	21.99
	0.41-0.60	167	8,183	9.77
	0.61-0.80	130	6,370	7.60
	0.81-1.00	209	10,241	12.22
Urban or built-up	0.00-0.20	554	27,146	94.54
	0.21-0.40	26	1,274	4.44
	0.41-0.60	5	245	0.85
	0.61-0.80	1	49	0.17
	0.81-1.00	0	0	0.00
Cropland, pasture, or grassland	0.00-0.20	31,189	1,528,261	97.90
	0.21-0.40	396	19,404	1.24
	0.41-0.60	195	9,555	0.61
	0.61-0.80	65	3,185	0.20
	0.81-1.00	12	588	0.04

Table E.3. Descriptive statistics for human density, managed lands, and snowfall in upland environments of the continental USA, 2004. Statistics are summarized by five probability of occurrence levels.

Independent variable	Probability range	*n*	Area	Percent
Human Density				
≤10 persons/km^2	0.00-0.20	53,892	2,640,708	59.17
	0.21-0.40	9,043	443,107	9.93
	0.41-0.60	6,640	325,360	7.29
	0.61-0.80	6,619	324,331	7.27
	0.81-1.00	14,879	729,071	16.34
>10 and ≤55 persons/km^2	0.00-0.20	21,521	1,054,529	54.48
	0.21-0.40	6,605	323,645	16.72
	0.41-0.60	3,878	190,022	9.82
	0.61-0.80	3,325	162,925	8.42
	0.81-1.00	4,177	204,673	10.57
>55 persons/km^2	0.00-0.20	9,773	478,877	71.46
	0.21-0.40	1,778	87,122	13.00
	0.41-0.60	836	40,964	6.11
	0.61-0.80	749	36,701	5.48
	0.81-1.00	540	26,460	3.95
Managed Lands				
Managed lands	0.00-0.20	7,057	345,793	25.61
	0.21-0.40	2,923	143,227	10.61
	0.41-0.60	1,853	90,797	6.72
	0.61-0.80	3,265	159,985	11.85
	0.81-1.00	12,458	610,442	45.21
Non-managed lands	0.00-0.20	78,129	3,828,321	66.95
	0.21-0.40	14,503	710,647	12.43
	0.41-0.60	9,501	465,549	8.14
	0.61-0.80	7,428	363,972	6.37
	0.81-1.00	7,138	349,762	6.12
Snowfall				
≤122 cm	0.00-0.20	84,391	4,135,159	76.34
	0.21-0.40	15,348	752,052	13.88
	0.41-0.60	6,415	314,335	5.80
	0.61-0.80	3,464	169,736	3.13
	0.81-1.00	925	45,325	0.84
>122 cm	0.00-0.20	795	38,955	2.36
	0.21-0.40	2,078	101,822	6.16
	0.41-0.60	4,939	242,011	14.65
	0.61-0.80	7,229	354,221	21.44
	0.81-1.00	18,671	914,879	55.38

Table E.4. Descriptive statistics for continuous independent variables in lowland environments of the continental USA, 2004. Statistics are summarized by five probability of occurrence levels.

Independent variable	Probability range	Mean	*n*	Standard error	95% Confidence Interval Lower	95% Confidence Interval Upper	Minimum	Maximum
Elevation (m)	0.00-0.20	47.57	7,437	0.36	46.88	48.27	-0.10	129.18
	0.21-0.40	18.96	2,283	0.31	18.35	19.56	-0.02	81.08
	0.41-0.60	13.07	1,219	0.30	12.48	13.66	0.00	60.86
	0.61-0.80	10.48	424	0.52	9.46	11.50	0.00	47.55
	0.81-1.00	8.15	69	1.30	5.55	10.76	0.00	36.86
Percent forest	0.00-0.20	0.30	7,437	0.00	0.29	0.31	0.00	1.00
	0.21-0.40	0.50	2,283	0.01	0.49	0.51	0.00	1.00
	0.41-0.60	0.65	1,219	0.01	0.64	0.67	0.00	1.00
	0.61-0.80	0.71	424	0.01	0.68	0.74	0.00	1.00
	0.81-1.00	0.80	69	0.02	0.75	0.84	0.03	1.00
Road density index (ha/km^2)	0.00-0.20	23.27	7,437	0.13	23.02	23.52	0.00	93.69
	0.21-0.40	19.43	2,283	0.18	19.06	19.79	0.00	66.94
	0.41-0.60	19.05	1,219	0.22	18.62	19.48	0.00	45.82
	0.61-0.80	15.85	424	0.40	15.07	16.63	0.00	33.90
	0.81-1.00	10.29	69	0.80	8.69	11.88	0.00	29.38
Wetness index	0.00-0.20	8.98	7,437	0.01	8.96	9.00	4.82	10.98
	0.21-0.40	9.28	2,283	0.02	9.25	9.31	5.86	10.98
	0.41-0.60	9.40	1,219	0.02	9.36	9.43	5.92	10.96
	0.61-0.80	9.46	424	0.03	9.39	9.52	6.00	10.98
	0.81-1.00	9.30	69	0.06	9.19	9.41	8.59	10.45

Table E.5. Descriptive statistics for human density, managed lands, and soil nitrogen in lowland environments of the continental USA, 2004. Statistics are summarized by five probability of occurrence levels.

Independent variable	Probability range	*n*	Area	Percent
Human Density				
≤43 persons/km^2	0.00-0.20	5,506	269,794	63.85
	0.21-0.40	1,714	83,986	19.87
	0.41-0.60	968	47,432	11.22
	0.61-0.80	372	18,228	4.31
	0.81-1.00	64	3,136	0.74
>43 persons/km^2	0.00-0.20	1,931	94,619	68.77
	0.21-0.40	569	27,881	20.26
	0.41-0.60	251	12,299	8.94
	0.61-0.80	52	2,548	1.85
	0.81-1.00	5	245	0.18
Managed Lands				
Managed lands	0.00-0.20	256	12,544	35.96
	0.21-0.40	137	6,713	19.24
	0.41-0.60	139	6,811	19.52
	0.61-0.80	149	7,301	20.93
	0.81-1.00	31	1,519	4.35
Non-managed lands	0.00-0.20	7,181	351,869	66.99
	0.21-0.40	2,146	105,154	20.02
	0.41-0.60	1,080	52,920	10.07
	0.61-0.80	275	13,475	2.57
	0.81-1.00	38	1,862	0.35
Soil nitrogen				
≤1,200 g	0.00-0.20	4,513	221,137	89.94
	0.21-0.40	472	23,128	9.41
	0.41-0.60	31	1,519	0.62
	0.61-0.80	2	98	0.04
	0.81-1.00	0	0	0.00
>1,200 and ≤1,800 g	0.00-0.20	2,253	110,397	54.05
	0.21-0.40	1,169	57,281	28.05
	0.41-0.60	656	32,144	15.74
	0.61-0.80	86	4,214	2.06
	0.81-1.00	4	196	0.10
>1,800 and ≤2,700 g	0.00-0.20	418	20,482	8.33
	0.21-0.40	539	26,411	10.74
	0.41-0.60	420	20,580	8.37
	0.61-0.80	219	10,731	4.36
	0.81-1.00	11	539	0.22
>2,700 g	0.00-0.20	52	2,548	1.25
	0.21-0.40	103	5,047	2.47
	0.41-0.60	112	5,488	2.69
	0.61-0.80	117	5,733	2.81
	0.81-1.00	54	2,646	1.30

Table E.6. Descriptive statistics for forest fragmentation and spring NDVI categories in lowland environments of the continental USA, 2004. Statistics are summarized by five probability of occurrence levels.

Independent variable	Probability range	*n*	Area	Percent
Forest fragmentation				
Forest	0.00-0.20	360	17,640	67.92
	0.21-0.40	100	4,900	18.87
	0.41-0.60	38	1,862	7.17
	0.61-0.80	27	1,323	5.09
	0.81-1.00	5	245	0.94
Perforated	0.00-0.20	243	11,907	40.37
	0.21-0.40	166	8,134	27.57
	0.41-0.60	106	5,194	17.61
	0.61-0.80	72	3,528	11.96
	0.81-1.00	15	735	2.49
Transitional	0.00-0.20	960	47,040	43.34
	0.21-0.40	568	27,832	25.64
	0.41-0.60	503	24,647	22.71
	0.61-0.80	152	7,448	6.86
	0.81-1.00	32	1,568	1.44
Edge	0.00-0.20	263	12,887	37.90
	0.21-0.40	208	10,192	29.97
	0.41-0.60	141	6,909	20.32
	0.61-0.80	71	3,479	10.23
	0.81-1.00	11	539	1.59
Patch	0.00-0.20	4,147	203,203	71.85
	0.21-0.40	1,112	54,488	19.27
	0.41-0.60	406	19,894	7.03
	0.61-0.80	101	4,949	1.75
	0.81-1.00	6	294	0.10
Non-forested	0.00-0.20	1,459	71,491	90.40
	0.21-0.40	129	6,321	7.99
	0.41-0.60	25	1,225	1.55
	0.61-0.80	1	49	0.06
	0.81-1.00	0	0	0.00
Spring NDVI				
<500	0.00-0.20	7,430	364,070	65.23
	0.21-0.40	2,275	111,475	19.97
	0.41-0.60	1,216	59,584	10.68
	0.61-0.80	409	20,041	3.59
	0.81-1.00	60	2,940	0.53
≥500	0.00-0.20	7	343	16.67
	0.21-0.40	8	392	19.05
	0.41-0.60	3	147	7.14
	0.61-0.80	15	735	35.71
	0.81-1.00	9	441	21.43

Table E.7. Descriptive statistics for macrohabitat types in lowland environments of the continental USA, 2004. Statistics are summarized by five probability of occurrence levels.

Macrohabitat type	Probability range	*n*	Area	Percent
Mixed forest	0.00-0.20	267	13,083	60.27
	0.21-0.40	136	6,664	30.70
	0.41-0.60	18	882	4.06
	0.61-0.80	17	833	3.84
	0.81-1.00	5	245	1.13
Deciduous forest	0.00-0.20	311	15,239	50.90
	0.21-0.40	169	8,281	27.66
	0.41-0.60	109	5,341	17.84
	0.61-0.80	17	833	2.78
	0.81-1.00	5	245	0.82
Evergreen needleleaf forest	0.00-0.20	1,986	97,314	44.64
	0.21-0.40	1,138	55,762	25.58
	0.41-0.60	911	44,639	20.48
	0.61-0.80	355	17,395	7.98
	0.81-1.00	59	2,891	1.33
Cropland-woodland mosaic	0.00-0.20	1,445	70,805	74.37
	0.21-0.40	410	20,090	21.10
	0.41-0.60	80	3,920	4.12
	0.61-0.80	8	392	0.41
	0.81-1.00	0	0	0.00
Herbaceous-wooded wetland	0.00-0.20	103	5,047	92.79
	0.21-0.40	8	392	7.21
	0.41-0.60	0	0	0.00
	0.61-0.80	0	0	0.00
	0.81-1.00	0	0	0.00
Grassland-shrubland mosaic	0.00-0.20	25	1,225	26.04
	0.21-0.40	24	1,176	25.00
	0.41-0.60	27	1,323	28.13
	0.61-0.80	20	980	20.83
	0.81-1.00	0	0	0.00
Sparsely vegetated, snow, or ice	0.00-0.20	388	19,012	71.72
	0.21-0.40	134	6,566	24.77
	0.41-0.60	19	931	3.51
	0.61-0.80	0	0	0.00
	0.81-1.00	0	0	0.00
Urban or built-up	0.00-0.20	59	2,891	100.00
	0.21-0.40	0	0	0.00
	0.41-0.60	0	0	0.00
	0.61-0.80	0	0	0.00
	0.81-1.00	0	0	0.00
Cropland, pasture, or grassland	0.00-0.20	2,850	139,650	89.74
	0.21-0.40	264	12,936	8.31
	0.41-0.60	55	2,695	1.73
	0.61-0.80	7	343	0.22
	0.81-1.00	0	0	0.00

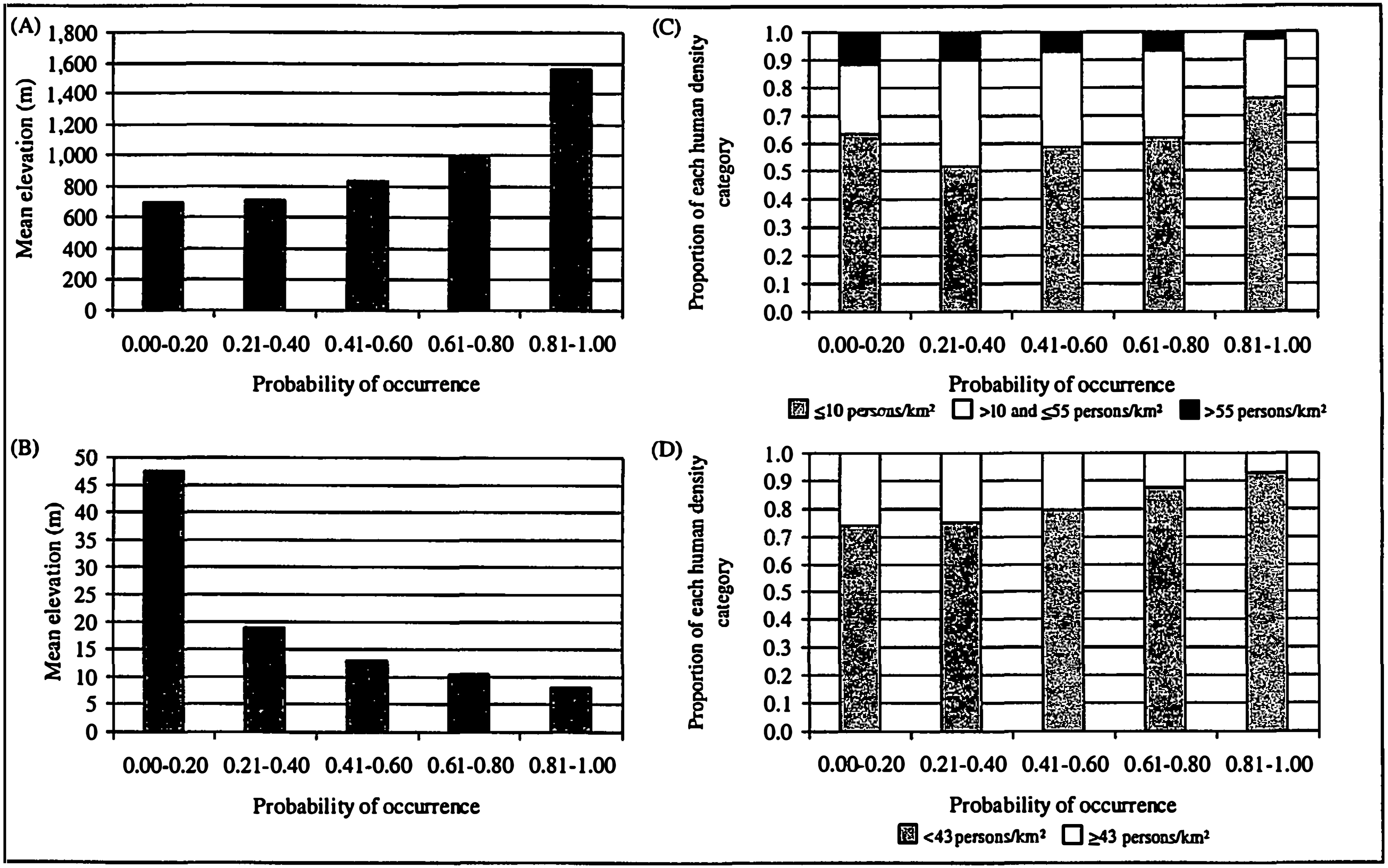


Figure E.8. Mean elevation in upland (A) and lowland (B) environments, and proportion of each human density category in upland (C) and lowland (D) environments, continental USA, 2004. Statistics are summarized by five probability of occurrence levels.

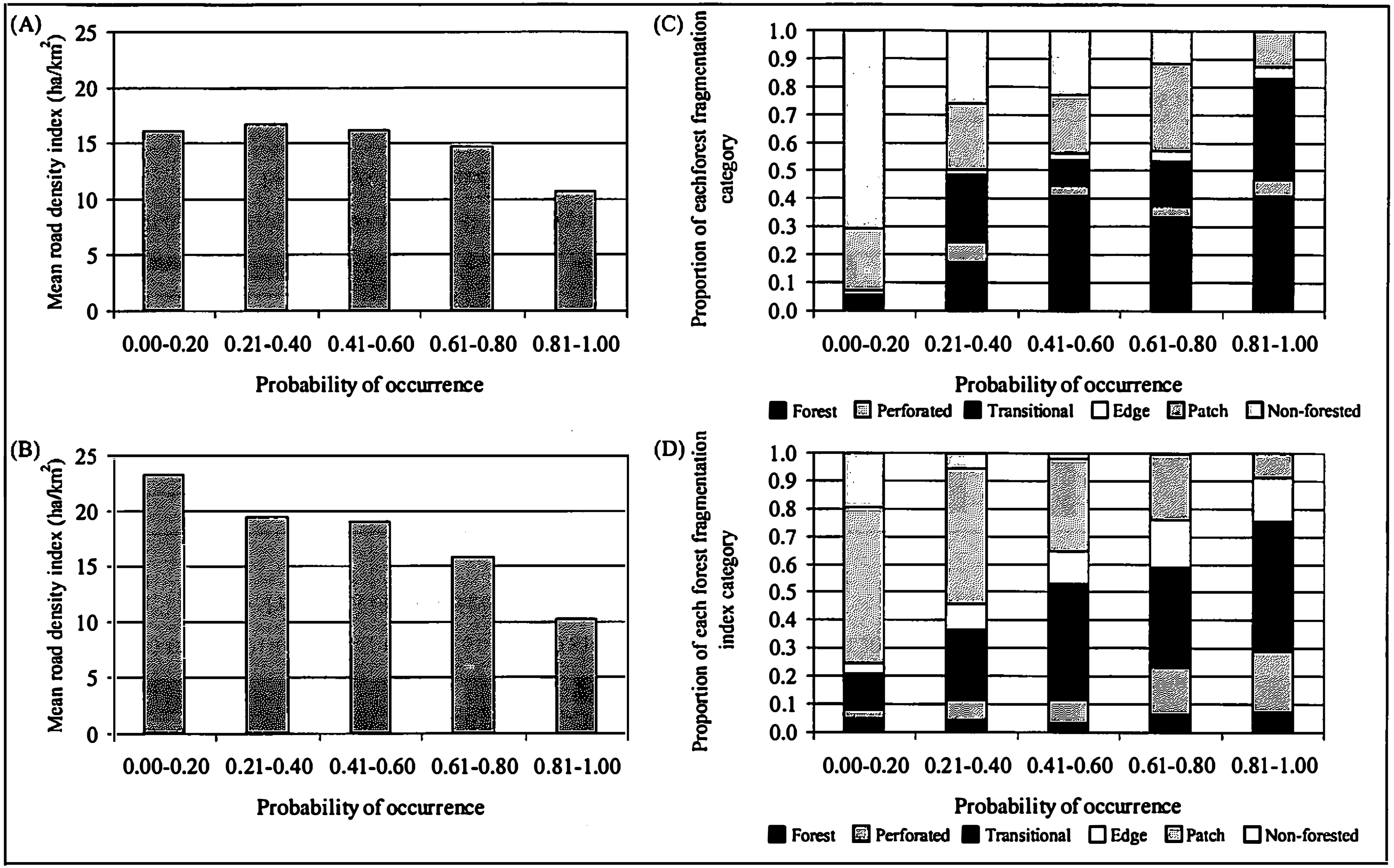


Figure E.9. Mean road density index in upland (A) and lowland (B) environments, and proportion of each forest fragmentation category in upland (C) and lowland (D) environments, continental USA, 2004. Statistics are summarized by five probability of occurrence levels.

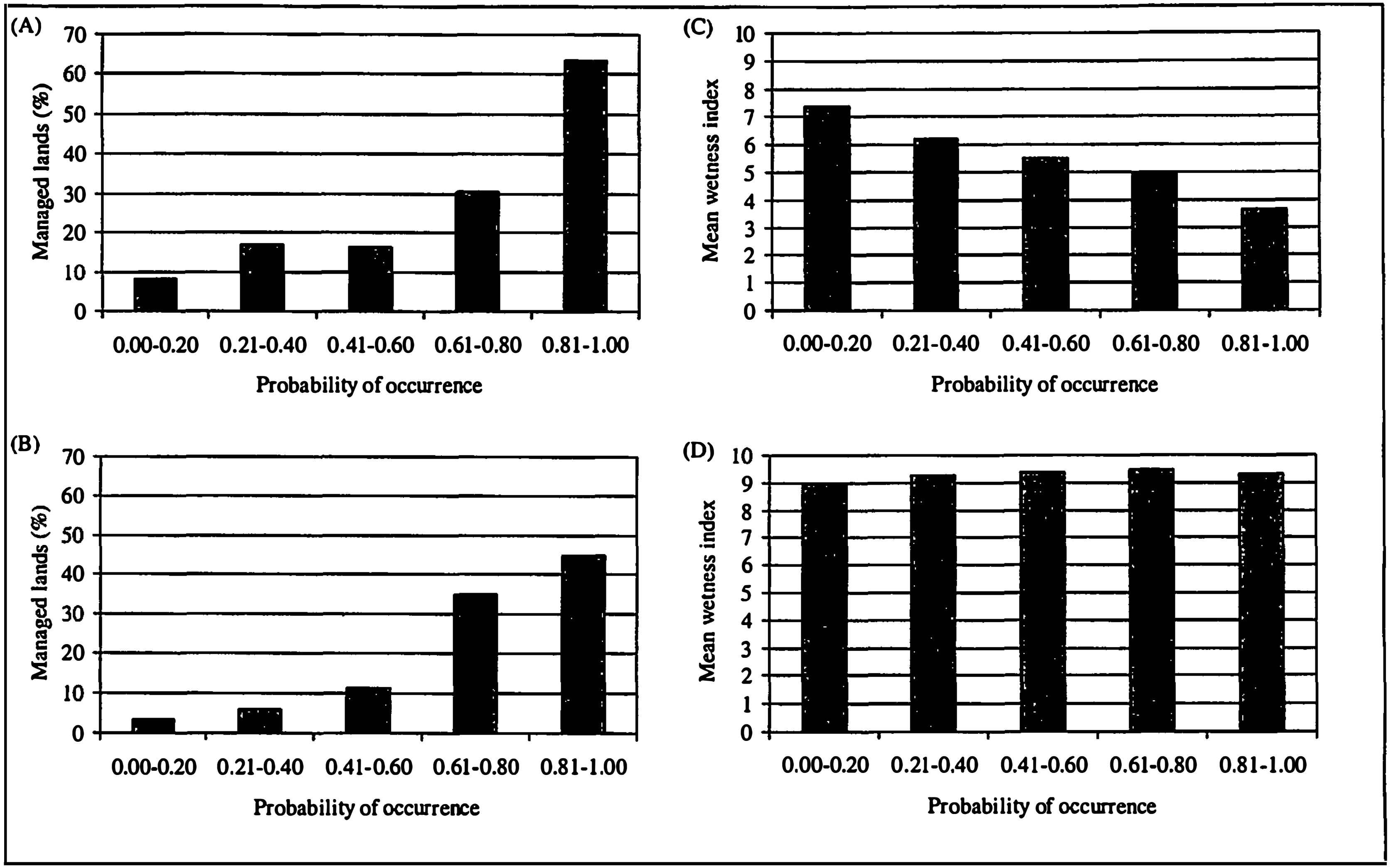


Figure E.10. Proportion of managed lands in upland (A) and lowland (B) environments, and mean wetness index in upland (C) and lowland (D) environments, continental USA, 2004. Statistics are summarized by five probability of occurrence levels.

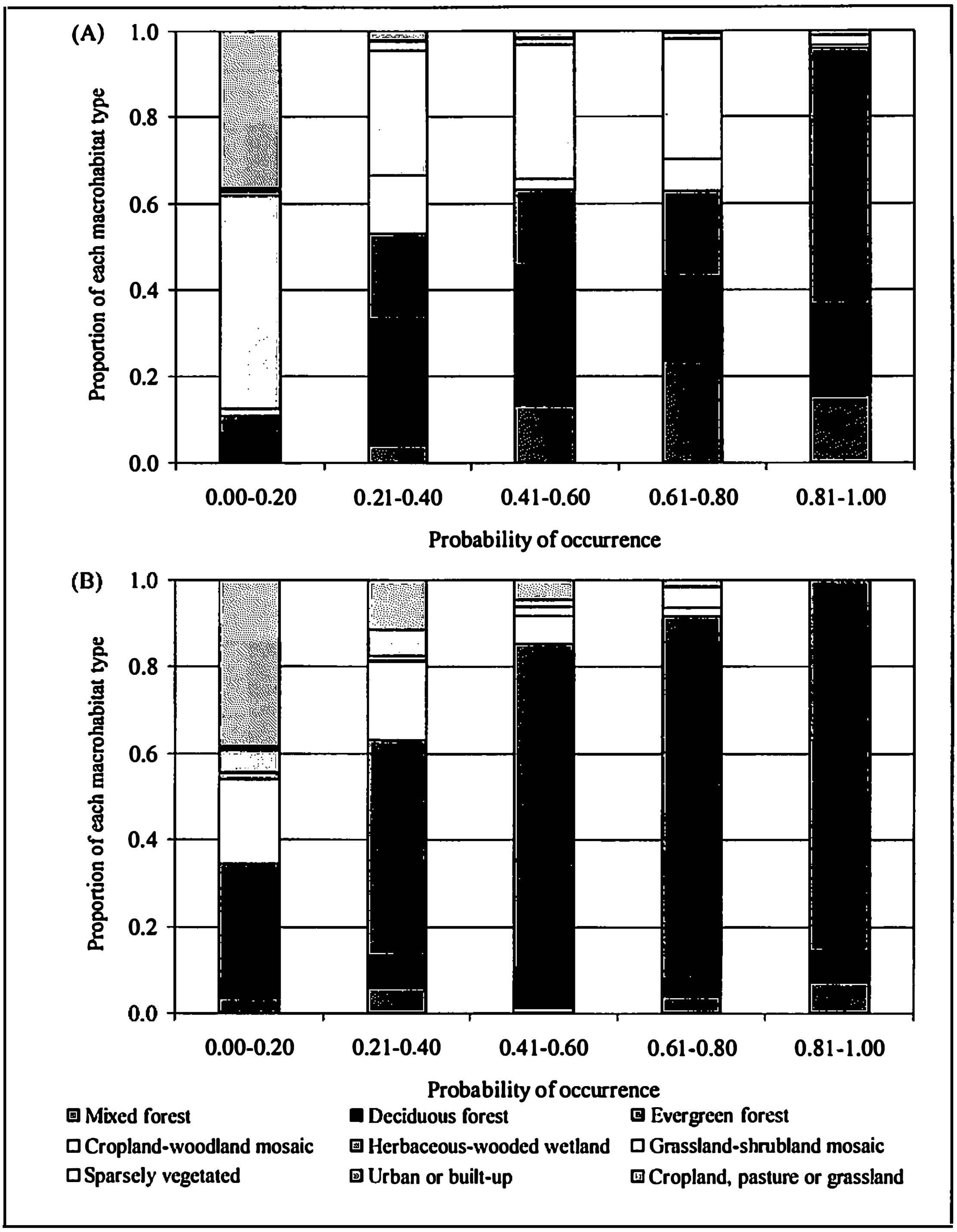


Figure E.11. Proportion of each macrohabitat type in upland (A) and lowland (B) environments of the continental USA, 2004. Statistics are summarized by five probability of occurrence levels.

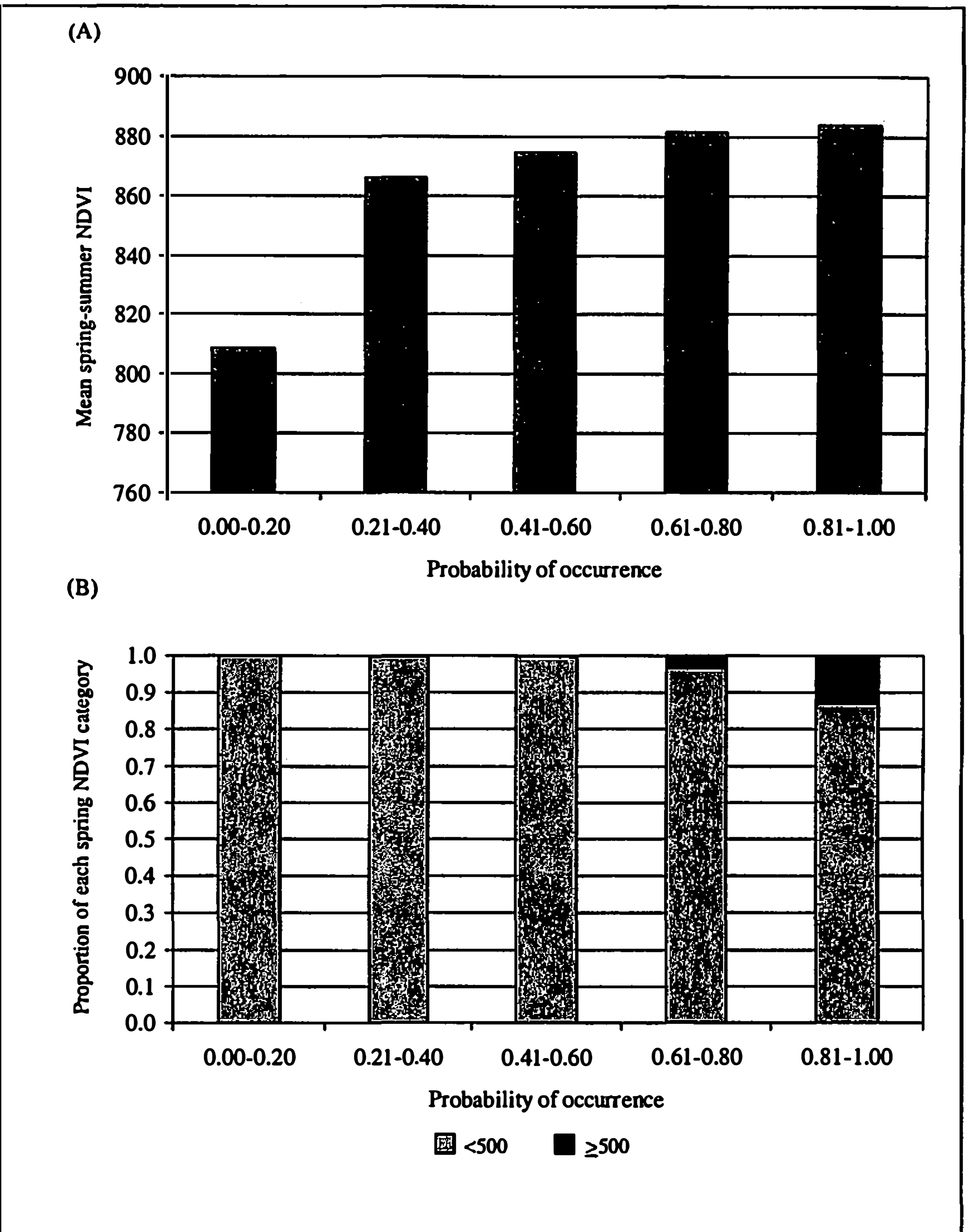


Figure E.12. Mean spring-summer NDVI in upland environments (A) and proportion of each spring NDVI category in lowland environments (B), continental USA, 2004. Statistics are summarized by five probability of occurrence levels.

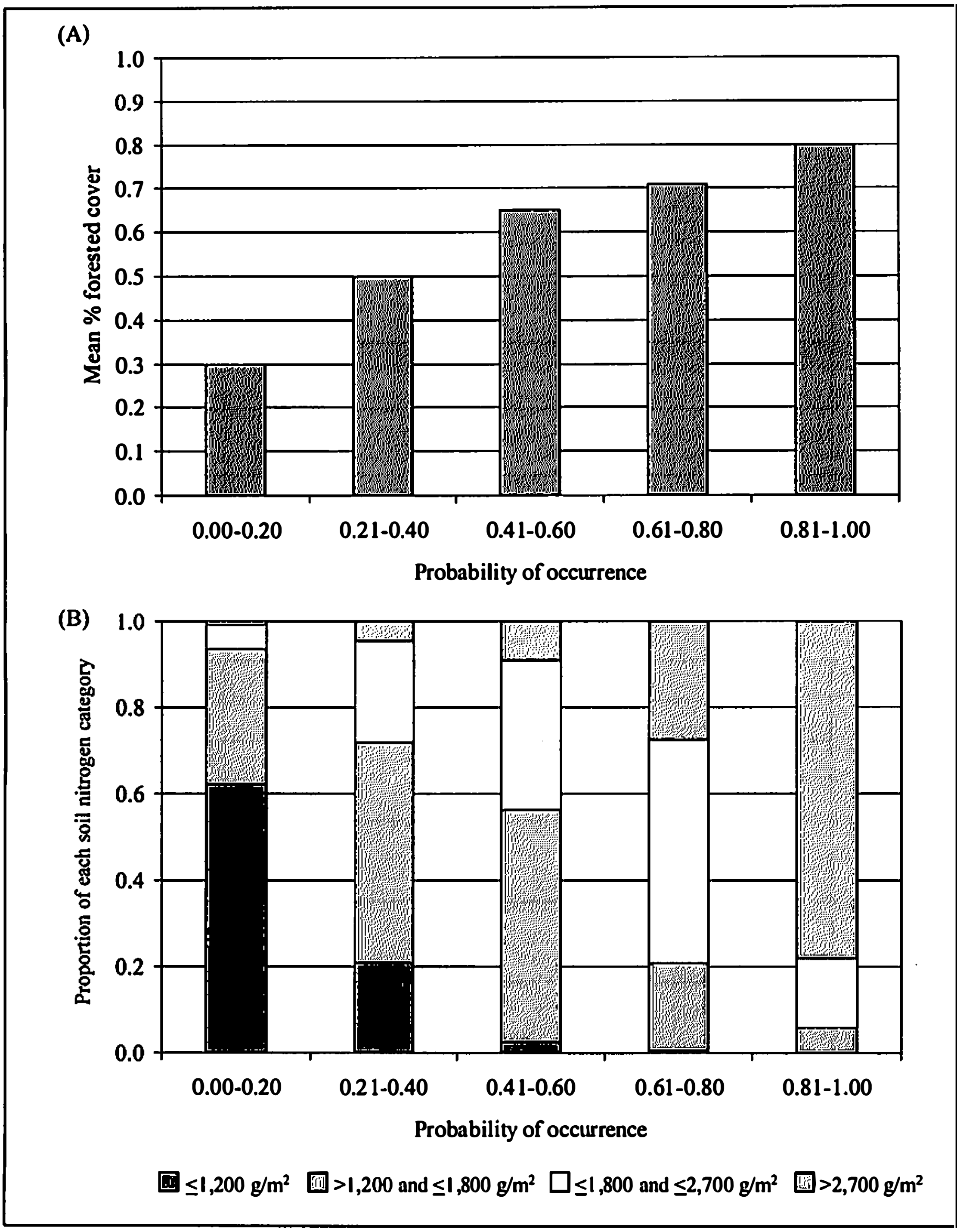


Figure E.13. Mean percent forested cover (A) and proportion of each soil nitrogen category (B) in lowland environments of the continental USA, 2004. Statistics are summarized by five probability of occurrence levels.

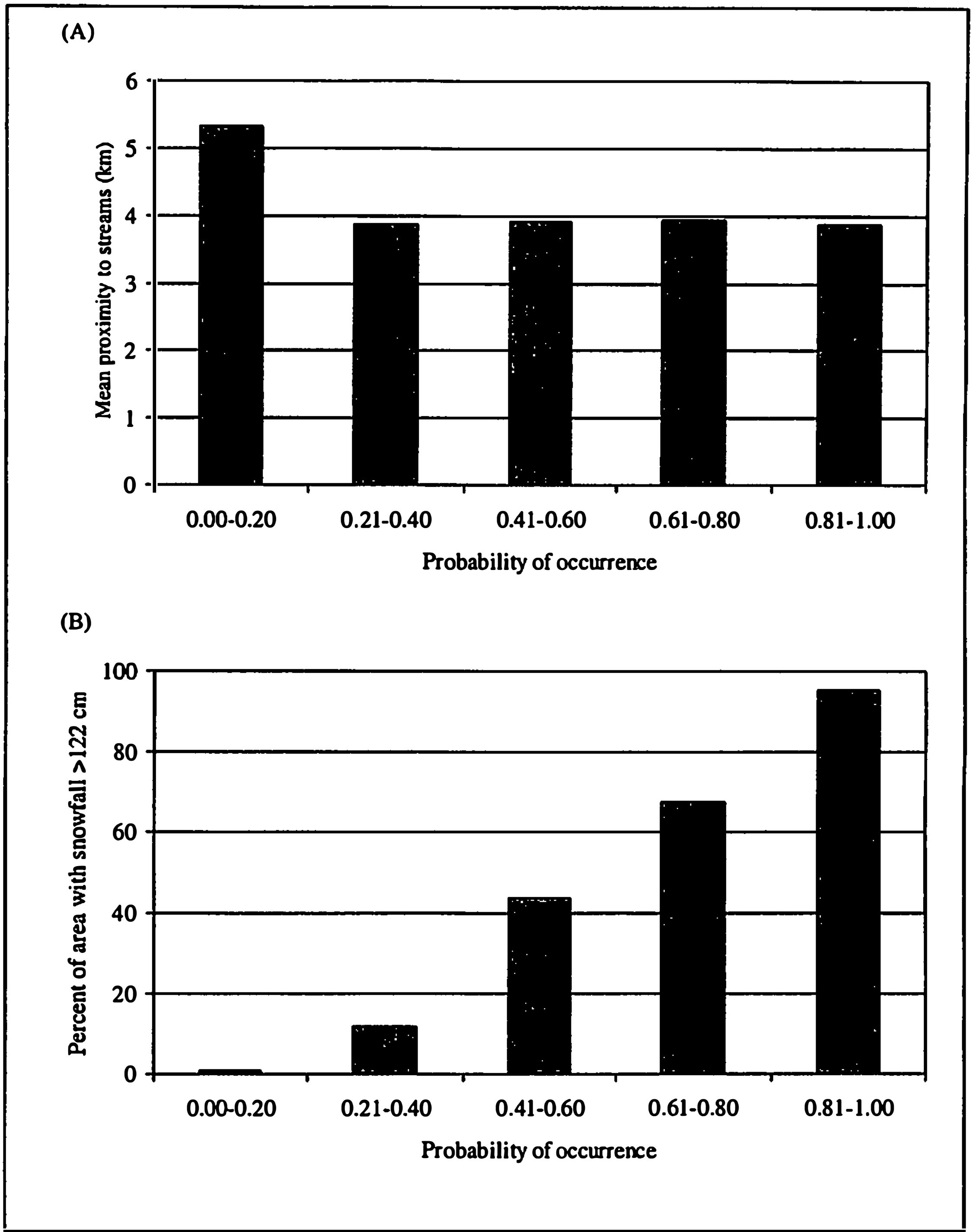


Figure E.14. Mean proximity to streams (A) and percent of area with snowfall >122 cm (B) in upland environments of the continental USA, 2004. Statistics are summarized by five probability of occurrence levels.

VITA

Donald Alfonso Martorello was born on December 4, 1968 in Los Gatos, California. He graduated from Meridian High School in Meridian Idaho in 1987. He attended Boise State University from January 1988 to May 1992 as a biology student. While at Boise State University, Donny decided to pursue a degree in wildlife and transferred to the University of Idaho in May 1992, where he received a Bachelor of Science degree in Wildlife Resources in May 1994. Also in May 1994, Donny began his master's research on black bears at the University of Tennessee, Knoxville, in the Department of Forestry, Wildlife and Fisheries. He received his Master of Science degree in Wildlife and Fisheries Science in May 1998. Donny started his doctoral research in the Department of Ecology and Evolutionary Biology at the University of Tennessee in 1998, and received his Ph.D. degree in May 2004. Donny is married to Holli Elizabeth Martorello and they reside in Tenino, Washington.