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I am submitting herewith a dissertation written by Frank Teunissen van Manen entitled "Black bear habitat use in Great Smoky Mountains National Park". I have examined the final 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.

Michael R. Pelton, Major Professor

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and Dean of the Graduate School

BLACK BEAR HABITAT USE IN GREAT SMOKY MOUNTAINS NATIONAL PARK

A Dissertation

Presented for the

Doctor of Philosophy

Degree

The University of Tennessee, Knoxville

Frank Teunissen van Manen

May 1994

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DEDICATION

I dedicate this dissertation to the people who had the incredible foresight to establish Great Smoky Mountains National Park and to all wild creatures that still put man in its place.....

Just say a word and the boys will be right there,
With claws at your back to send a chill through the night air.
Is it so frightening to have me at your shoulder?
Thunder and lightning couldn't be bolder.
I'll write on your tombstone,
"I thank you for dinner":
This game that we animals play is a winner.

Excerpt from "Bungle in the Jungle"
by Ian Anderson, Jethro Tull

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ABSTRACT

I used telemetry locations of American black bears (*Ursus americanus*), collected in Great Smoky Mountains National Park (GSMNP) from 1976 to 1982, to evaluate home ranges, movements, and habitat use. Annual home range estimates averaged 7.6 km^2 (SD = 7.1) for females and 48.5 km^2 (SD = 21.1) for males. For both sexes, fall ranges were larger than summer ranges and shifts occurred between summer and fall centers of activity. Annual and seasonal changes in spatial use of black bears are largely explained by changing activity and movement patterns in response to variation in distribution, abundance, and nutritive value of foods. Extensive home range overlap was common for both sexes and use of overlapping areas generally was unrelated to the presence of other bears of the same sex. There were some temporal intraspecific effects, however, because distances between locations of females and males collected simultaneously were greater than expected.

I analyzed habitat use of black bears based on 10 variables in a geographic information system (GIS) database using logistic regression of bear locations compared with random sites. I used Akaike's information criterion (AIC) and information-theoretic measure of complexity (ICOMP) to select the best predicting subset of habitat variables. Although the habitat use models fit the data, external validation of the overall model of female habitat use indicated that the model may be more appropriate for hindcasting than forecasting.

Female bear habitat use was best described by 4 micro- and 5 macro-scale

variables whereas 6 macro-scale variables best explained male habitat use. Female use of habitat types was mostly restricted to areas of secondary importance for seasonal foraging. I hypothesize that female habitat use is partly a result of social interactions with males who may prevent females from using productive or otherwise important habitats. Future research should use an experimental approach to test this hypothesis of sex and reproductive class habitat segregation in black bears.

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CHAPTER I

INTRODUCTION

General Problem Statement

Throughout the world, bears face an uncertain future (Schoen 1990). All species of bears, except the American black bear and the brown bear (*Ursus arctos*), are listed as endangered or vulnerable by the International Union for the Conservation of Nature (IUCN) and all are listed under the Convention on International Trade in Endangered Species (CITES), which regulates or restricts export and import of species vulnerable to trade. Bears are large-bodied, long-lived, intelligent, individualistic, wide-ranging, and opportunistic mammals; these traits have allowed bears to exploit a wide variety of habitats (Schoen 1990). All bears, except the polar bear, are predominantly herbivorous. However, their inefficient carnivore digestive system forces bears to exploit high quality and abundant food sources, often resulting in conflicts with humans using the same productive lands (Schoen 1990). Such conflicts will continue to increase as human populations expand and wild lands are developed. Bears have low reproductive rates (Bunnell and Tait 1981), which, in combination with the earlier mentioned traits, makes them especially vulnerable to human-induced mortality (Schoen 1990).

Although the black bear is the most numerous bear species in the world (Servheen 1990), its present distribution in several regions of the United States is

fragmented and resembles only a small fraction of the historical distribution (Hall 1981, Pelton 1982, Maehr 1984) (Figs. 1 and 2). The fragmented distribution in the southeastern United States (Fig. 3) is mostly due to intensive development, high density of human populations, and historically unregulated exploitation (Pelton 1982). The long-term survival of the black bear in the Southeast largely depends upon the ability of managers to maintain the integrity of black bear habitat on a landscape scale, especially in light of increasing demands on forest habitat for recreation, development, and timber resources. Effective management and conservation of bear populations depends mainly upon our ability to understand and predict bear-habitat relationships (Schoen 1990, Clark *et al.* 1993).

Long-term data are necessary to effectively study bear-habitat relationships. The southern Appalachians provided an excellent case study because of the availability of long-term ecological baseline data on the relatively unexploited black bear population of Great Smoky Mountains National Park (GSMNP) and harvested populations on national forest land surrounding the national park.

Theoretical Framework

Habitat Studies. Systematic studies of animal-habitat relationships started around 1930, partly due to an increasingly scientific approach to management of wildlife and their environment (Morrison *et al.* 1992). With a rapidly increasing human population in North America and elsewhere, increased exploitation of natural resources has resulted in dramatic impacts on natural environments and associated



Fig. 1. Historical distribution of the American black bear. Modified from Hall (1981).

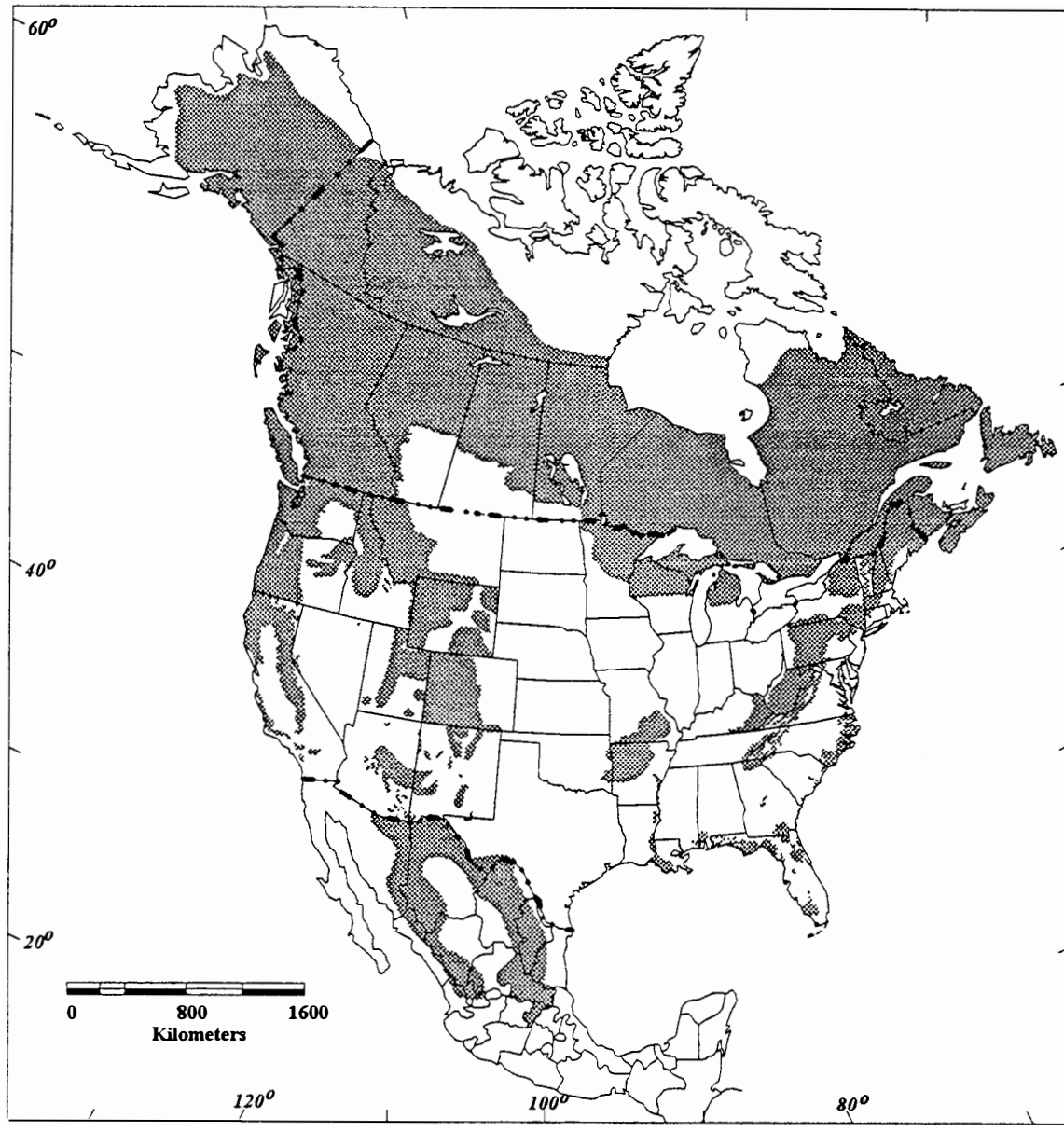


Fig. 2. Present distribution of the American black bear. Distribution is based on 1993 survey responses from provinces and states and additional information from Maehr (1984), Leopold (1959), and research projects in Mexico (D. Doan, pers. commun.).

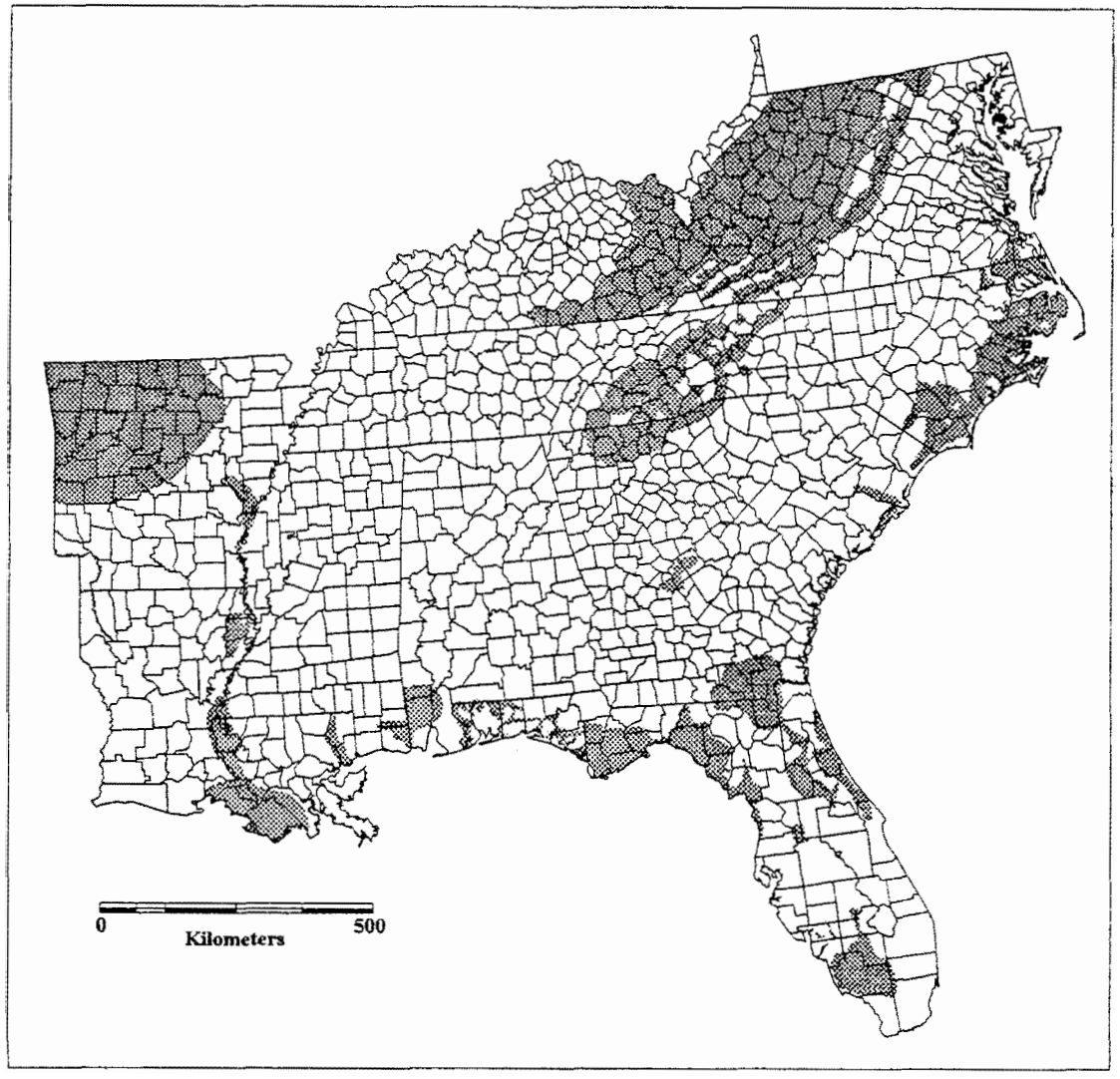


Fig. 3. Present distribution of the American black bear in the southeastern United States. Distribution is based on 1993 survey responses.

wildlife (Morrison *et al.* 1992). In the U.S., concern about the extent of those impacts led to legislation designed to reduce environmental disturbance; the National Environmental Policy Act (1969), the Endangered Species Conservation Act (1973), the Federal Land Policy and Management Act (1976), and the National Forest Management Act (1976) especially stimulated research on animal-habitat relationships (Morrison *et al.* 1992). In response to these legislative mandates, researchers started to study habitat requirements of both game and nongame animals and developed models to predict, rather than only describe, the effects of environmental changes on animal populations (Verner *et al.* 1986). Morrison *et al.* (1992) discussed a third factor that plays a role in studies of animal-habitat relationships: ecological ethics. Although there are several, sometimes opposing, ethical views of wildlife and nature, the ecological ethic focuses on the moral obligation of humans to maintain our human and social integrity and the integrity of the biotic community (Leopold 1949, Morrison *et al.* 1992). The main justification for this study should be seen within the context of the ecological ethic.

The concepts of habitat and niche have been defined in various ways. Hutchinson (1957) first combined several existing concepts of niche and defined a niche as an *n*-dimensional hypervolume, representing the range of *n* independent environmental variables to which a species responds. Habitat has generally been defined as the area where an organism lives (Odum 1971). A second concept of habitat, however, relates more to the place occupied by an entire community (Odum 1971, Harris and Kangas 1988). Unfortunately, this second concept of habitat often

is erroneously used to refer to a particular vegetation type (Harris and Kangas 1988). Harris and Kangas (1988) criticized the use of the habitat concepts because they are not equally applicable to all species, do not explicitly include area requirements to support viable populations, and do not consider metapopulation concepts. Whittaker *et al.* (1973), however, recognized some of these difficulties and were some of the first researchers to describe the concepts of niche, habitat, and ecotope; they defined habitat as the distributional response of a species to intercommunity environmental factors, niche as the position or role of a species within a community, and ecotope as the full range of adaptations to external factors of both niche and habitat. Moreover, Whittaker *et al.* (1973) recognized the significance of a population response to niche and habitat factors in terms of relative success of populations (e.g., density, fitness, frequency of resource use) (Fig. 4), thereby linking the concepts of Hutchinson's (1957) 'realized niche' with Elton's (1927) 'functional niche'. Thus, habitat is specific to a species or population and refers to the suite of available resources and environmental conditions that allows individuals of a certain species or population to survive and reproduce (Morrison *et al.* 1992). Environmental conditions may include interactions with conspecifics or other species (including humans), climatic conditions, and the physical environment (e.g., elevation, aspect, slope). Following the definitions of Whittaker *et al.* (1973), Van Horne (1983), and Morrison *et al.* (1992), the quality of habitat is related to the ability of individuals of a species or population to survive and reproduce, to the survival of their offspring, and to the temporal stability of habitat.

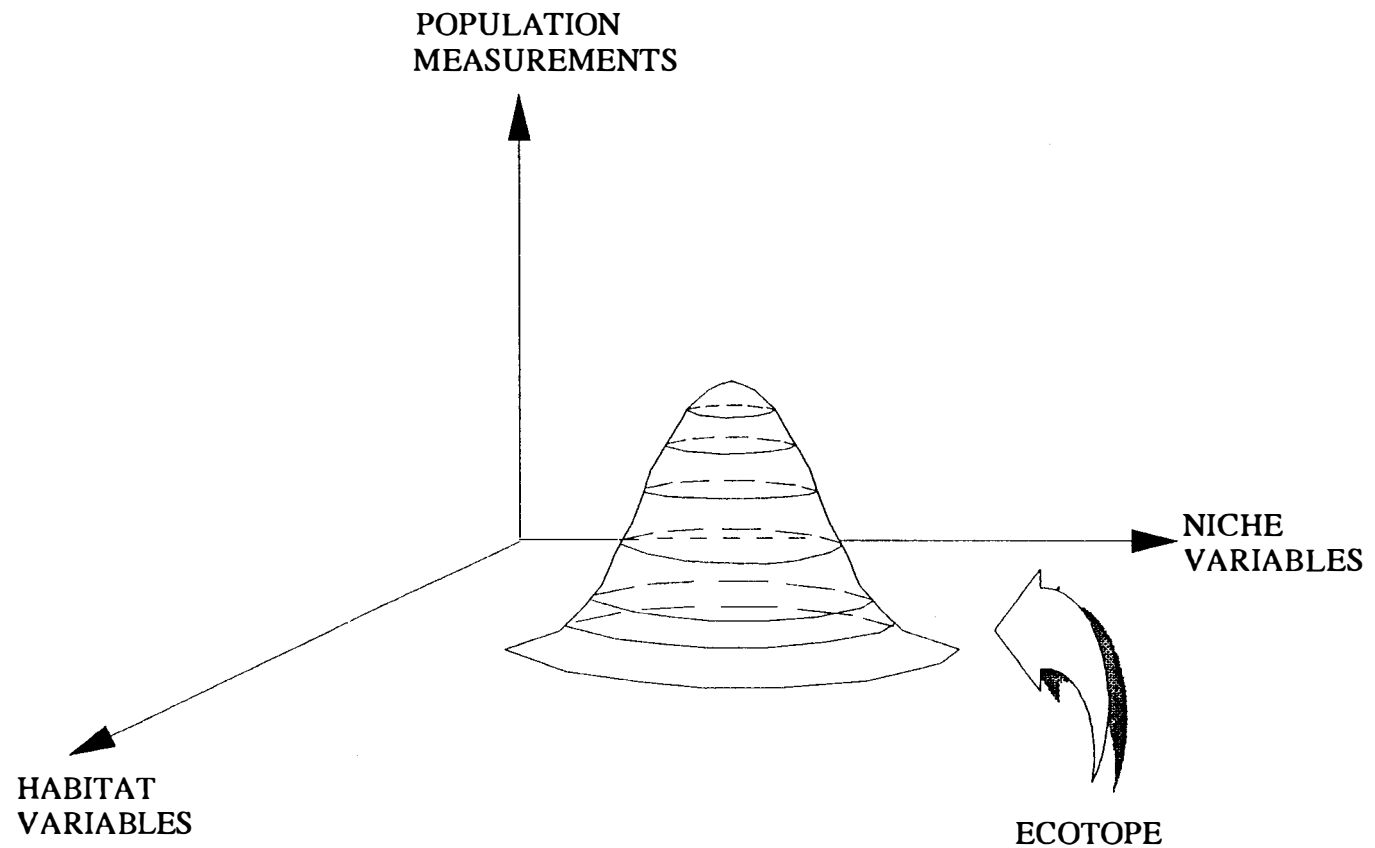


Fig 4. Graphical presentation of niche, habitat, and ecotope concepts. Modified from Whittaker *et al.* (1973).

The use of the appropriate spatial and temporal scales is important in the studyof animal-habitat relationships. Even after defining the general scope of a study (i.e., niche, habitat, ecotope) how does one determine the appropriate scales? Do appropriate scales even exist? To answer these questions one needs to know how an organism perceives its habitat. Obviously, it is difficult, if not impossible, to identify an organism's perception of habitat, especially because it most likely is dynamic. One solution may be to study animals at several different spatial and temporal scales. Johnson (1980) discussed the concept of order in habitat selection, which is directly related to the niche, habitat, and ecotope concepts of Whittaker *et al.* (1973). First-order selection is the selection of a physical or geographical range of a species; second-order selection refers to the home range of an individual or social group; third-order selection relates to the use of habitat components within the home range; and fourth-order selection pertains to selection within a third-order selected habitat component (e.g., individual food items, den site) (Johnson 1980). One aspect of this ordering is that habitat use is not absolute (Johnson 1980). If consumption of an abundant food item by an animal is less than expected, this may not necessarily imply avoidance. A particular area may have been selected by that animal because of the abundance of that food item (Johnson 1980). Within the context of scale and hierarchical structure of habitat use, studying relative use within a geographical range, home range, or habitat component is principally the same. Because the processes at each level are dependent, results from studies at one level may not be fully interpretable until other levels have been studied.

For many animal species, the home range is the most common scale at which habitat use is evaluated. A home range can be defined as the area where an animal normally lives for food gathering, mating, and caring for the young, excluding occasional excursions outside the area (Burt 1943). Occasional wanderings outside the area, however, likely have a function (Brown 1966) and probably deserve special attention. Another approach is to use individual locations within a home range to study habitat use; the advantage of such an approach is that habitat allocation within a home range can be calculated, providing high resolution but retaining dynamics at the scale of home range.

Several authors have argued against the use of the terms "selection" and "avoidance" because they imply active choice decisions by an animal (Hutto 1985, Rosenzweig 1990). Choice is difficult to prove and separate from responses to environmental stimuli without elaborate experimental designs (Rosenzweig 1990). Therefore, I will use the term 'habitat use' except when I refer to specific studies where other terms were used.

Modelling. A considerable amount of research has been conducted on developing and testing models of animal-habitat relationships (see Verner *et al.* [1986] and Morrison *et al.* [1992] for overviews, discussions, and examples of habitat models). Habitat models can be grouped into 3 categories: (1) single-species models, (2) multiple-species or community models, and (3) habitat-analysis models (Berry 1986). Common single-species models are habitat capability (HC) models, pattern recognition (PATREC) models, habitat suitability index (HSI) models, and cumulative effects

models. Habitat models can be statistical models, although models often are not based on statistical procedures (e.g., many HSI models). Because of the multidimensional nature of niche, habitat, and ecotope, multivariate statistical techniques are especially applicable to model habitat use and have gained popularity during the last 2 decades due to the availability of statistical computer software. Multivariate statistical models of species-habitat relationships often use principal components analysis, canonical correlation analysis, multiple linear or nonlinear regression, discriminant function analysis, or logistic regression (Morrison *et al.* 1992). The ultimate goal of statistical models often is to predict the survival, abundance, and distribution of a species (Berry 1986). Such predictive models are useful to develop and test research hypotheses and provide knowledge, which can ultimately be used in management. Predictive models of wildlife habitat use may be effective tools in land acquisitions, mitigation procedures, and habitat management. Cumulative impact models, for example, estimate and predict the incremental effects of past, present, and reasonably foreseeable future actions on wildlife populations (Johnston *et al.* 1988), which may include negative and positive impacts. Cumulative impact assessment was introduced by the U.S. Council on Environmental Quality in 1978 in their suggestions for implementing the National Environmental Policy Act and has been given high priority (Williamson *et al.* 1986).

The recent development of geographic information system (GIS) technology may provide a powerful tool to develop, test, and apply multivariate statistical models; GIS is especially applicable to species with generalized habitat requirements

that use habitat at a landscape scale (Clark *et al.* 1993, Clark and van Manen 1993). GIS can be defined as the management, analysis, and manipulation of spatially-referenced information in a problem-solving synthesis (Fisher and Lindenberg 1989). GIS provides a means for conducting multiple impact assessments because of the ability of those systems to compile, process, and evaluate data collected over a long time period for a large geographic area. Habitat modelling is still in its infancy and GIS may be to habitat analysis what the high-speed computer has been to statistical analysis (Clark and van Manen 1993).

Habitat models for bears that incorporate GIS include a geographic analysis of grizzly bear sightings (Agee *et al.* 1989) and habitat use (Gaines *et al.* 1994) in the northern Cascades. Also, Williamson and Whelan (1983) developed a computer-based habitat map (an early form of GIS) for black bears in Shenandoah National Park. The developed model used proximity to poaching source, distance to campground, distance to road or development, and forest type preference as variables. Using GIS in a biometric approach, Clark *et al.* (1993) developed a multivariate statistical model to predict black bear habitat use in the Interior Highlands of Arkansas.

Justification and Scope of Study

Effective management of black bear populations (and large carnivores in general) is important to ensure long-term survival and depends largely upon our ability to understand and predict bear-habitat relationships (Clark *et al.* 1993).

Besides the underlying justification based on an ecological ethic, the main justifications for this study were: (1) the need to develop and test research hypotheses of bear habitat use, and (2) the need to better understand black bear habitat use through the development of predictive models.

The black bear is a wide-ranging species that uses habitat on a landscape scale (Schoen 1990). Past research has focused on describing black bear habitat with some emphasis on niche relationships. However, population responses to niche or habitat relationships rarely have been quantitatively studied whereas the black bear ecotope has been ignored altogether, mostly for logistical reasons. If conservation of large carnivores is to be effective, the niche, habitat, and ecotope concepts need to be addressed.

Modelling the multi-dimensional nature of bear habitat can involve multivariate calculations on a landscape scale; GIS technology provides the analytical tools for such analyses (Clark *et al.* 1993). GISs are especially effective at the landscape level and can provide a means by which statistical procedures, which were previously too cumbersome to be calculated on a landscape scale, can be employed to develop data-based habitat models (Clark *et al.* 1993). Ultimately, GIS may also provide the technology to include the ecotope concept.

In this study, I evaluated black bear habitat relationships in GSMNP. Because the black bear population in GSMNP is relatively unexploited and habitats relatively undisturbed, this study may provide an ecological basis for comparisons (Noss 1991) with other black bear populations in the southern Appalachian region. I evaluated

habitat use in all seasons except the winter season; winter denning habitat in the southern Appalachians has been described in detail by Johnson (1978) and Wathen (1983).

I used individual bear locations rather than the home range as the habitat sampling unit; this approach allowed detection of habitat use at a relatively high resolution while retaining the capability of evaluating patterns at larger scales. Moreover, with this approach, locations could be classified by a suite of habitat variables which better reflects the multidimensional concept of habitat use. My use of telemetry locations as the sampling unit also allowed inclusion of locations of bears for which home ranges could not be constructed due to small sample sizes.

I selected habitat variables for this study based on results from previous black bear studies in the southern Appalachians (Garshelis 1978, Quigley 1982, Villarrubia 1982, Carr 1983, Garris 1983, Brody 1984, Beringer 1986, Clevenger 1986, Seibert 1989, Reagan 1991). These studies described various aspects of bear habitat use and the importance of biological (overstory and understory vegetation type, vegetation structure, diversity, and disturbances), physical (elevation, aspect, slope), and cultural (trails, roads, and areas of human activity) variables.

I used analyses of home ranges and movements to evaluate long-term dynamics of spatial use and to confirm results from previous studies. Although habitat use of black bears in the southern Appalachians has been evaluated with single habitat variables, I would classify much of habitat modelling as exploratory research because of the multivariate approach.

The objectives of this study were to

(1) determine home range configurations and movement patterns of black bears in GSMNP,

(2) characterize biological, physical, and cultural habitat components associated with black bear locations in GSMNP,

(3) develop and test biometric models that quantify and predict habitat use by black bears,

(4) determine how habitat use of black bears relates to home range configurations and indices of habitat quality,

(5) determine the effectiveness of black bear bait-station surveys as an index of black bear habitat use, and

(6) test the effectiveness of simulations of selected biological and cultural habitat alterations on habitat use of black bears.

CHAPTER II

STUDY AREA

General

GSMNP is a 208,000-ha area on the Tennessee and North Carolina border, located at N 35°37', W 83°31'. GSMNP was authorized in 1926 by an act of Congress and, unlike many other national parks, was purchased from private owners often unwilling to give up their land (Campbell 1960). Land purchase began in 1926 by the North Carolina Park Commission in North Carolina and the Great Smoky Mountains Conservation Association in Tennessee. Starting in 1934, the states of North Carolina and Tennessee gradually purchased land with Federal assistance and a contribution by John D. Rockefeller, Jr. GSMNP was dedicated in 1940 after all major land purchases had been made.

The National Park area includes portions of Blount, Sevier, and Cocke counties in Tennessee and Haywood and Swain counties in North Carolina. GSMNP is surrounded by 3 national forests (Fig. 5): the Cherokee National Forest in Tennessee and the Nantahala and Pisgah national forests in North Carolina. The Cherokee Indian Reservation borders GSMNP on the Southeast. The Tennessee portion of GSMNP has the greatest visitation rates and is, in large part, bordered by private land, which continues to be developed for vacation homes and tourist facilities with accompanying infrastructure.

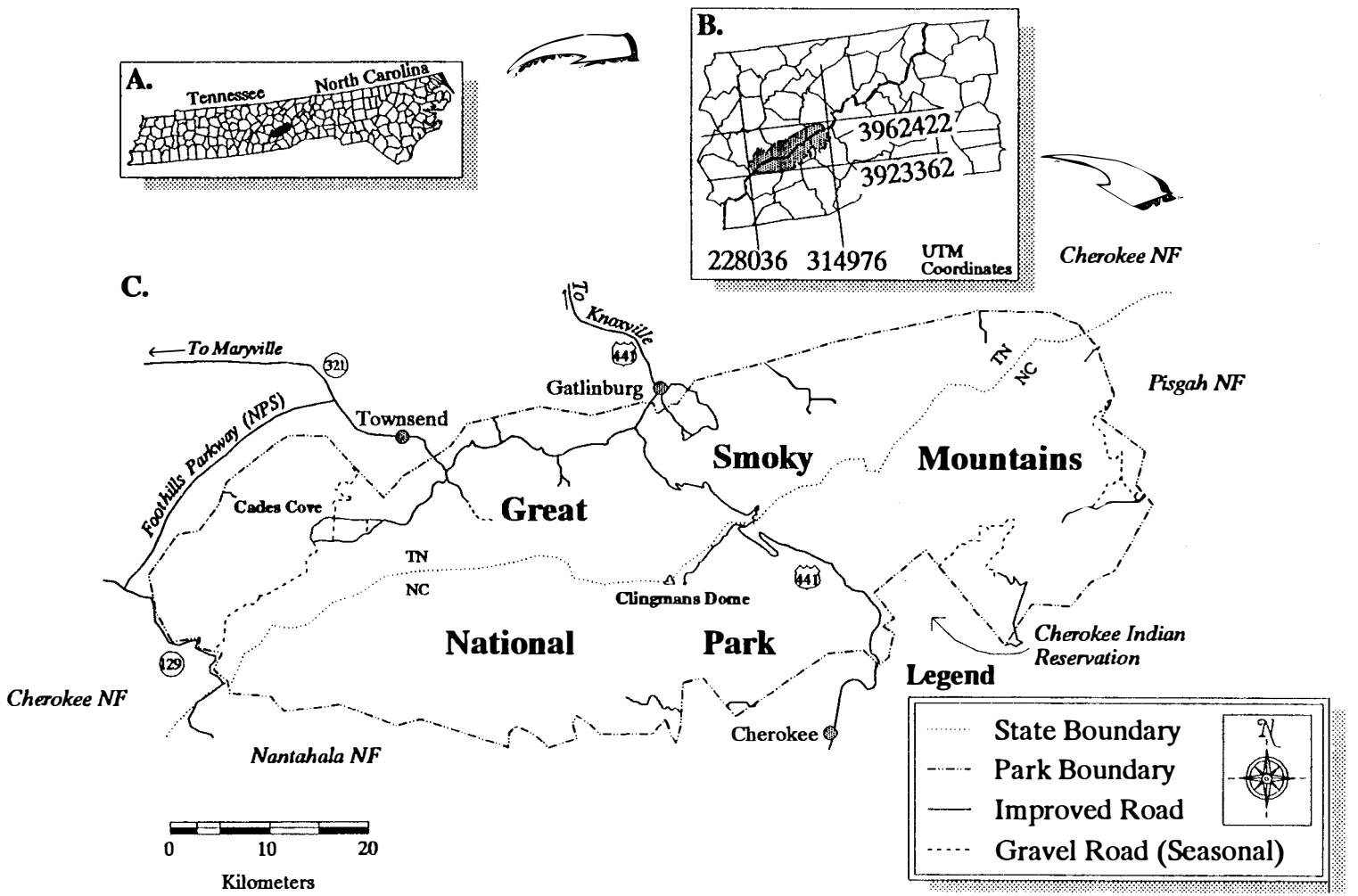


Fig. 5. Great Smoky Mountains National Park. A. General location. B. Detail of general location with Universal Transverse Mercator coordinates of boundaries of geographic information system data. C. Detail of national park.

The northwestern quadrant of GSMNP has been the focus area for studies on many different aspects of black bear ecology for the past 25 years (Pelton 1993). Within this general area, I defined separate study areas for females and males for habitat use analysis (see Methods). The female study area was 204.9 km^2, of which 4.7 km^2 was outside the boundary of GSMNP. The male study area was 1,738.6 km^2, of which 659.7 km^2 was outside GSMNP boundaries (Figs. 6 and 7).

Topography, Physiography, Geology, and Soils

The Great Smoky Mountains are part of the Unaka Mountain Range of the Blue Ridge Province in the southern division of the Appalachian Highlands (Fenneman 1938). The area is characterized by mountainous terrain with steep ridges extending outward from the main ridge and separated by narrow valleys and coves cut by fast-flowing streams (King and Stupka 1950) (Fig. 8). The main ridge is oriented northeast to southwest and connects the highest peaks within GSMNP for 113 km (Golden 1974). Elevations range from 270 m where Abrams Creek flows into the Little Tennessee river to 2,024 m at Clingman's Dome. Only 10.2% of GSMNP has slopes $\leq 5^\circ$ whereas 44.5% has slopes $> 15^\circ$ and 20.9% has slopes $> 20^\circ$.

The geology of the area is characterized by sandstones of the Ocoee series dating from the Precambrian Era (King *et al.* 1968). The rocks of the Ocoee series were disrupted by crustal movements during the late Paleozoic era, about 200 million years ago, forming mountain ranges (King and Stupka 1950). These mountains have been continuously eroded by streams and have become physiographically subdued to shape

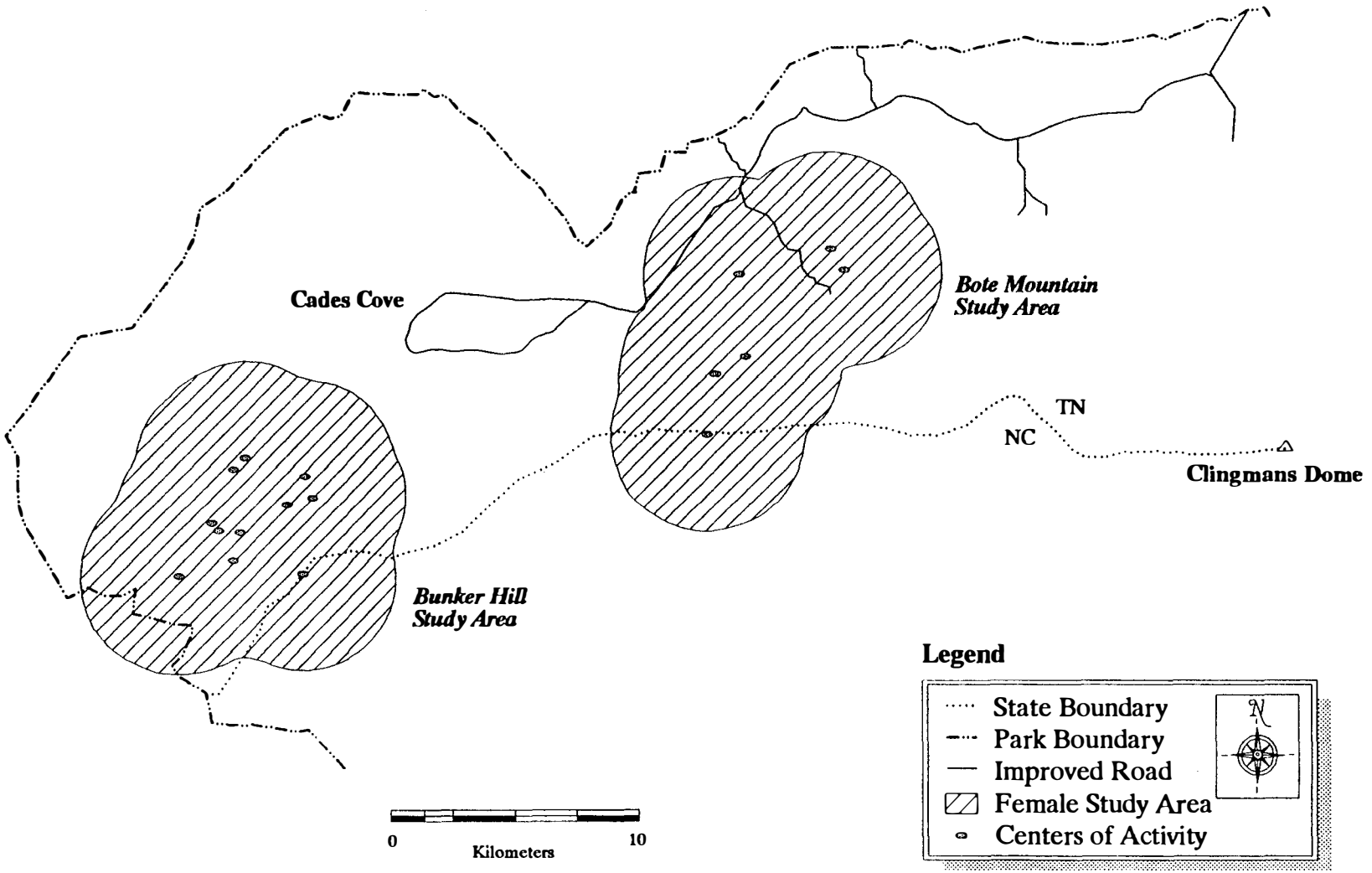


Fig. 6. Female black bear study area, Great Smoky Mountains National Park, 1976-1982.

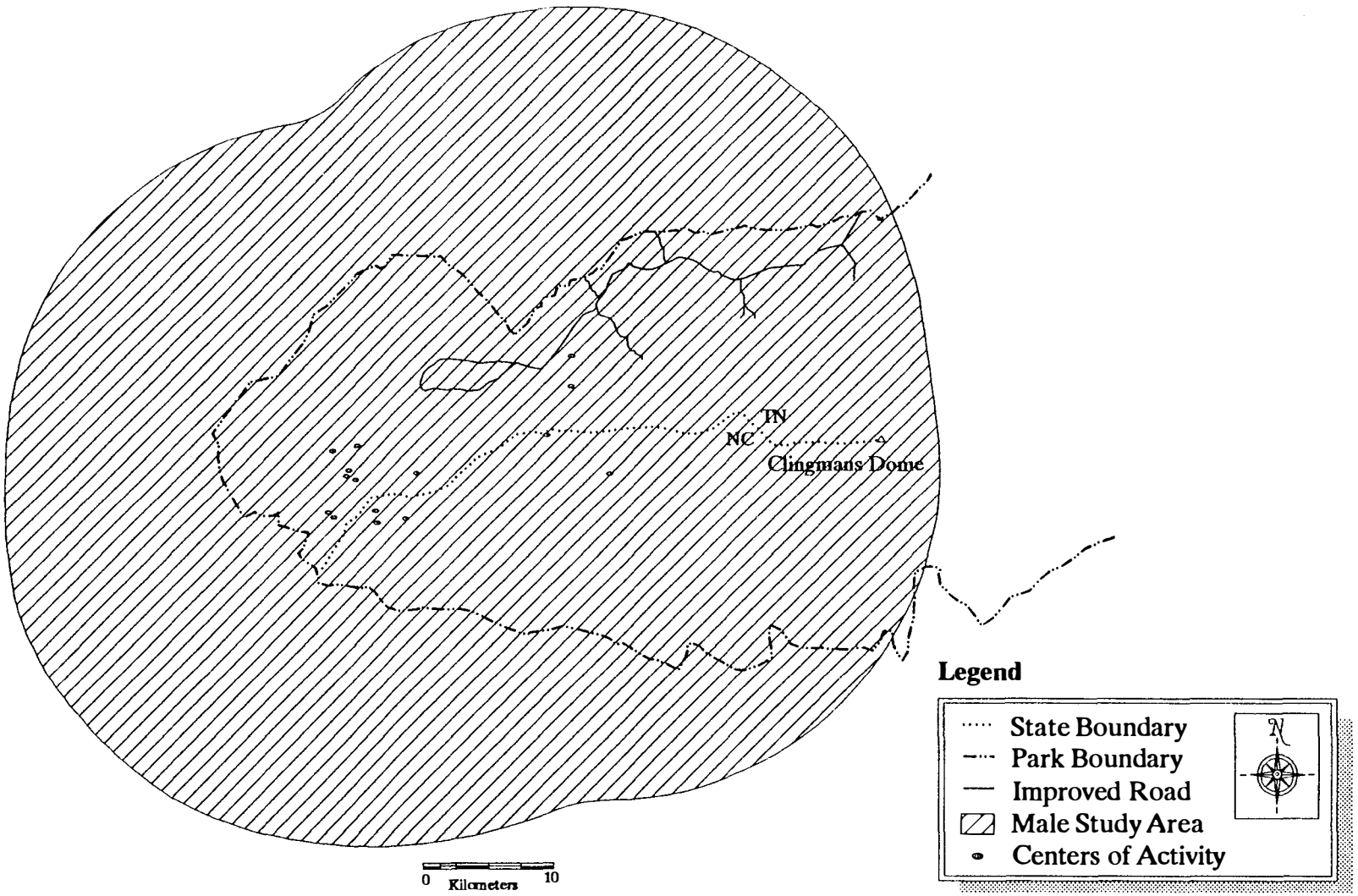


Fig. 7. Male black bear study area, Great Smoky Mountains National Park, 1976-1982.

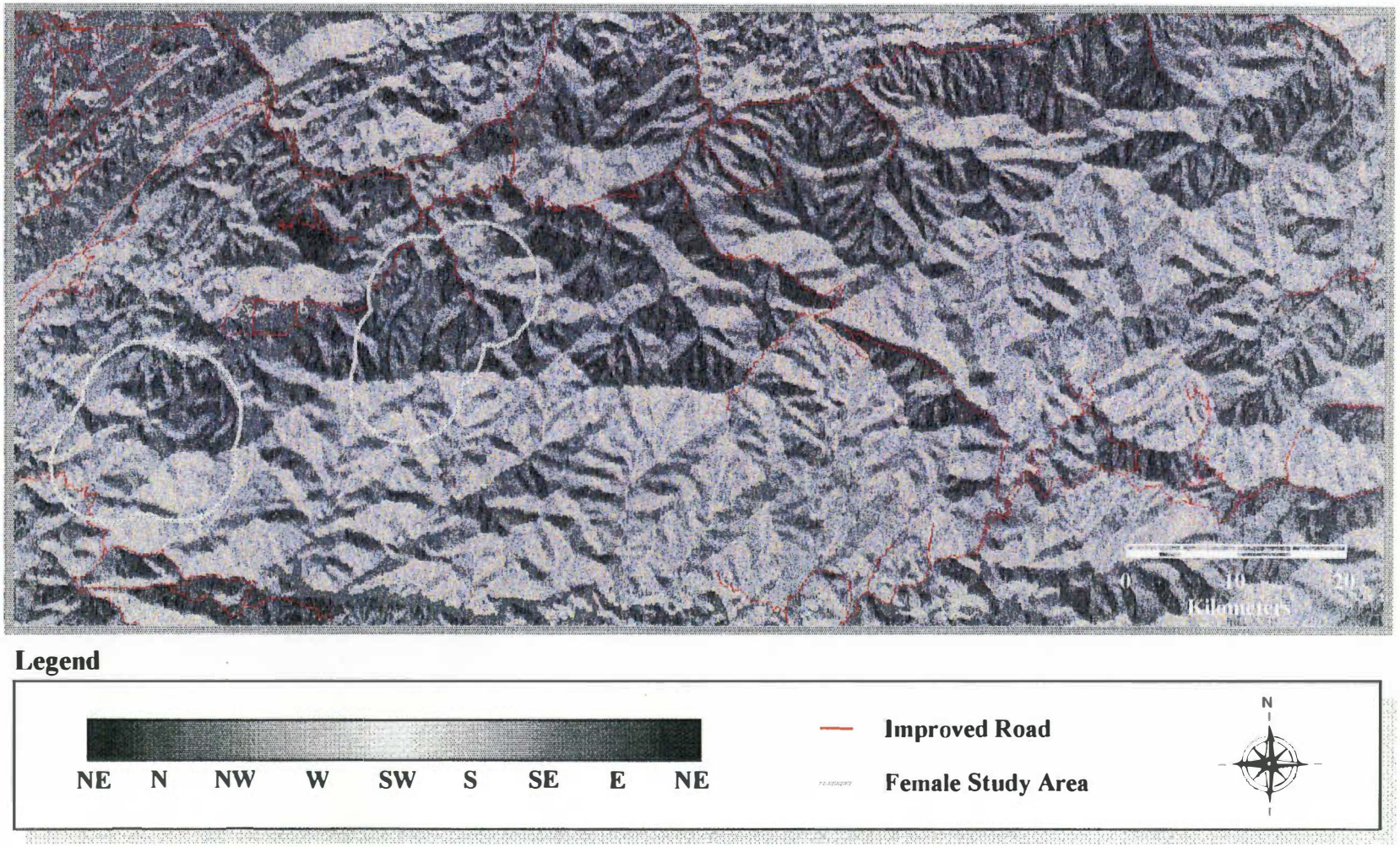


Fig. 8. Slope aspects in Great Smoky Mountains National Park (developed by Parker and Pipes [1990]).

the Smoky Mountains as we know them today (Fenneman 1938, King *et al.* 1968). Although glaciers never reached the Smokies during the Pleistocene, there may have been a timberline above 1,500 m elevation (King and Stupka 1950). Frost action at those upper elevations created boulder deposits commonly seen along stream valleys of the central Smokies (King and Stupka 1950).

Soils are of the Ramsey Association, characterized by medium to high acidity, low water storage capacity, and moderate fertility (Soil Survey 1953). Colluvial soils are most common in small narrow coves and ravines where they occur as rocks covering a buried soil; they are also common on gentle lower slopes and immediately below steep slopes (Golden 1974). Residual soils are mostly found on ridges and middle to upper slopes and may be > 50 cm deep except on narrow ridges and steep slopes (Golden 1974).

Climate

Microclimatic conditions vary substantially due to the large amount of variation in elevation, aspect, and slope (Shanks 1954, Stephens 1969). Thornthwaite (1948) classified the general climate of this area as mesothermal per-humid (warm-temperate rain forest) with annual precipitation ranging from approximately 140 cm at lower elevations to about 230 cm at higher elevations (Stephens 1969). Daily and seasonal variation in weather patterns are caused by alternating cold air systems from Canada and warm moist air from the Gulf of Mexico. Precipitation maxima usually occur in July, primarily as a result of thunderstorm activity, and in February, whereas

minimum precipitation usually occurs in September or October (Stephens 1969). Precipitation exceeds evapotranspiration in most years, except during rare drought years (Shanks 1954). The mean annual number of days with snowfall ranges from approximately 7 at lower elevations to almost 26 at the highest elevations (Shanks 1954); mean annual snowfall is approximately 63 cm, $< 3\%$ of annual rainfall. Annual temperatures range from 14°C at lower elevations to 8°C at higher elevations; the temperature gradient is 4°C per 1000 m change in elevation (Shanks 1954). Monthly mean temperatures range from 4.4°C to 22.0°C at lower and -1.8°C to 13.5°C at the highest elevations (Stephens 1969). Lowest monthly temperatures usually are recorded in February and the highest in July.

Vegetation

The great amount of variation in topography and climate provides the conditions for high richness of flora and vegetation types. The eastern forests of North America show the greatest diversity in the Great Smoky Mountains (Whittaker 1956). Because GSMNP is one of the richest temperate forest regions in the world, it is recognized as an International Biosphere Reserve (Herrmann and Bratton 1977). More than 1,300 flowering plants have been identified, including over 130 species of trees. Over 2,000 fungi, 330 mosses, 230 lichens, and 32 fern species have been identified (King and Stupka 1950, Stupka 1960). The vegetation of the Great Smoky Mountains has been studied and categorized by Cain (1935), Shanks (1954), Whittaker (1956), Golden (1974), and MacKenzie (1991, 1993). In this study I used the overstory

vegetation classification of MacKenzie (1991, 1993) (Tables 1 and A.1-A.3, Fig. 9). Cove hardwood, pine, xeric oak, and mixed mesic hardwood are the most common overstory vegetation types in GSMNP (Table 2); rhododendron (*Rhododendron maxima*) and mountain laurel (*Kalmia latifolia*) often form a dense understory throughout much of the study area. Forest habitat for the female and male study areas were representative of GSMNP as a whole (Table 2).

Fauna

Linzey and Linzey (1971) described 59 species of mammals occurring in GSMNP. Of 6 extirpated mammal species in GSMNP, 2 have recently been reintroduced: the river otter (*Lutra canadensis*) and the red wolf (*Canis rufus*). Over 200 species of birds, 30 species of reptiles, 39 species of amphibians, 80 species of fish, and a great variety of insects and other invertebrate species have been found in GSMNP (King and Stupka 1950). Hunting is not allowed within the national park. Although policies of the National Park Service System do not prohibit management of native wildlife populations and their habitat (U. S. National Park Service 1988), active management at the national park level, including GSMNP, usually is limited (Wagner *et al.* 1993).

The black bear population probably was only marginally affected by settlements during the early 1800's. In the late 1800's and early 1900's, however, the black bear population declined dramatically due to excessive logging, hunting, and trapping and became mostly restricted to higher elevations and inaccessible areas (LaFollette 1974).

Table 1. Dominant tree species of overstory forest types, Great Smoky Mountains National Park. From MacKenzie (1991, 1993).

Forest Type	Dominant Species[a]
Spruce-fir	*Betula lutea* (Yellow birch) *Picea rubens* (Red spruce) *Acer rubrum* (Red maple)
Northern hardwood	*Betula lutea* *Fagus grandifolia* (Beech) *Betula lenta* (Sweet birch) *Tsuga canadensis* (Eastern hemlock) *Acer rubrum* *Quercus rubra* (Northern red oak) *Picea rubens*
Cove hardwood	*Tsuga canadensis* *Betula lenta* *Acer rubrum* *Halesia carolina* (Carolina silverbell) *Liriodendron tulipifera* (Tulip poplar) *Quercus rubra* *Tilia heterophylla* (Basswood) *Betula lutea*
Mesic oak	*Quercus rubra* *Acer rubrum* *Quercus prinus* (Chestnut oak)
Mixed mesic hardwood	*Liriodendron tulipifera* *Acer rubrum* *Tsuga canadensis* *Quercus prinus*
Tulip poplar	*Liriodendron tulipifera* *Acer rubrum* *Halesia carolina*
Xeric oak	*Quercus prinus* *Acer rubrum* *Liriodendron tulipifera* *Oxydendrum arboreum* (Sourwood) *Quercus coccinea* (Scarlet oak)

Table 1. (Cont.).

Forest Type	Dominant Species[a]
Pine-oak	*Quercus coccinea* *Pinus pungens* (Table mountain pine) *Nyssa sylvatica* *Acer rubrum* *Quercus prinus*
Pine	*Pinus pungens* *Pinus rigida* (Pitch pine) *Pinus virginiana* (Virginia pine) *Quercus coccinea*

[a]Dominance based on a mean of species basal area > 2.0 m^2/ha, from MacKenzie (1991, 1993). Species within each forest classification are ordered according to dominance.

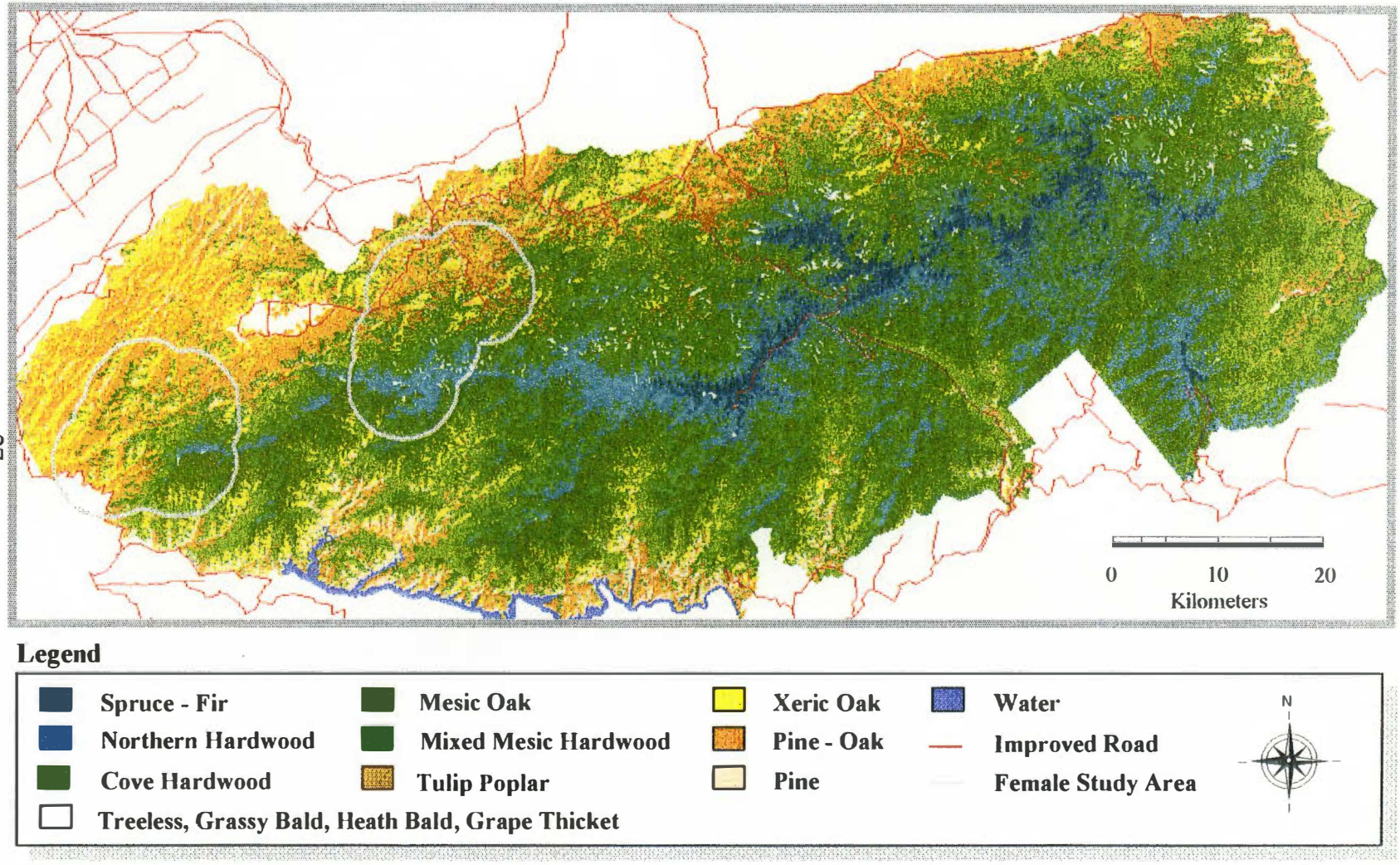


Fig. 9. Overstory vegetation types in Great Smoky Mountains National Park (developed by MacKenzie [1991, 1993]).

Table 2. Occurrence of forest types in Great Smoky Mountains National Park and black bear study areas. From MacKenzie (1991, 1993).

Forest Type	% in GSMNP	% in Female Study Area	% in Male Study Area
Spruce-Fir	2.3	0.0	0.7
Northern hardwood	9.4	7.0	6.1
Cove hardwood	33.4	22.1	24.1
Mesic oak	10.3	8.0	10.4
Mixed mesic hardwood	16.0	15.7	16.1
Tulip poplar	2.7	6.7	3.0
Xeric oak	10.0	17.3	16.5
Pine-oak	2.4	1.7	3.8
Pine	11.2	20.5	16.0
Nonforest	2.3	1.0	3.3

Under national park protection, the bear population seemed to increase. During the 1940's, however, loss of the American chestnut (*Castanea dentata*), due to the chestnut blight (caused by the fungus *Endothia parasitica*), along with several hard mast failures may have caused another population decline (LaFollette 1974). During the last 2 decades, the black bear population has gradually increased with a mean intrinsic rate of growth of 2% (McLean 1991).

History of Land Use

Before the first European settlers arrived in the middle of the 17th century, Cherokee indians inhabited the southern Appalachians and adjoining lowlands in semipermanent villages (Kephart 1936). Frontiersman and, later, the new United States government forced the Cherokees to abandon their land; in 1838, most were moved to Oklahoma (Kephart 1936). Commercial logging started around 1880 at relatively small scales and had a fairly small impact on the forests (Lambert 1960). Starting in the early 1900's, cable logging, by use of steam engine technology, altered logging practices. Several commercial timber companies, most notably the Little River Timber Company in Townsend, Tennessee, conducted large-scale logging, often in previously inaccessible areas (Lambert 1960). About 63% of GSMNP (60% of the female and 77% of the male study area) was logged, settled, or disturbed by humans before National Park Service protection began in 1934 (Pyle 1988) (Fig. 10).

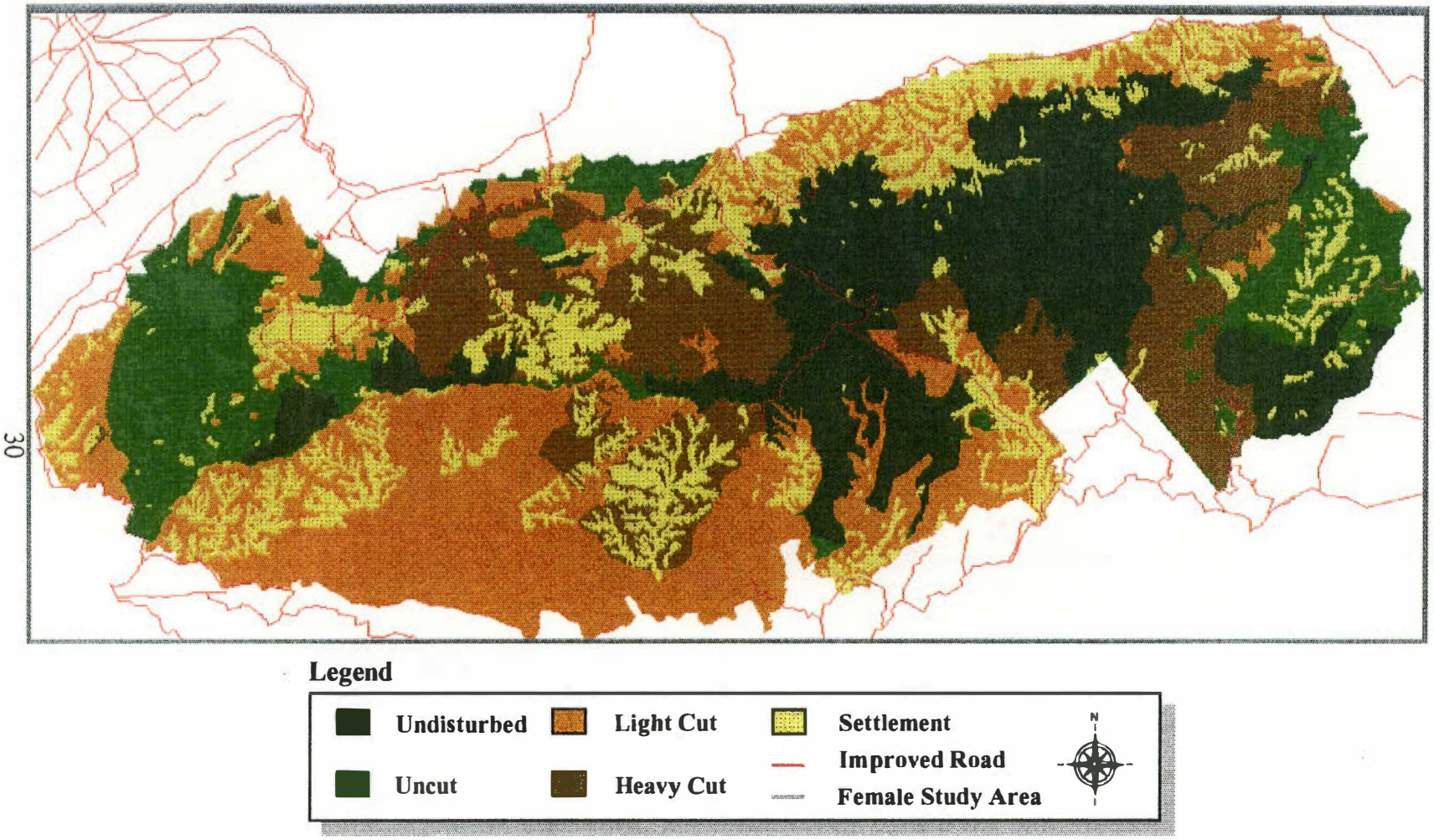


Fig. 10. Vegetation disturbance history in Great Smoky Mountains National Park (developed from Pyle [1988]).

Sociology and Economy

The female and male study areas are within Blount and Sevier Counties in Tennessee and within Swain County in North Carolina. These counties encompass 4,334 km^2 and contain most of GSMNP except for the extreme eastern part. The 1980 U. S. Census counted 129,471 or 29.9 persons/km^2 for these counties, a 28.4% increase from 1970 (United States Bureau of the Census [USBC] 1983). Around 77% of the human population in these counties lived in rural areas (USBC 1983).

In 1980, most of the labor force was employed in manufacturing (26%), followed by trade (20%), government services (20%), professional and related services (17%), and construction, entertainment, and public utilities (9%) (USBC 1983). Eight percent of the labor force was self-employed (USBC 1983). More than 15% of the families in the 3 counties were living below poverty level, 39.4% of persons 25 years and older had not finished high school, and unemployment for persons older than 16 years was 10.4% (USBC 1983).

Recreation

Approximately two-thirds of the human population in the United States live within a 17-hour driving distance from GSMNP. GSMNP is the most visited national park in the United States with 8-10 million visits per year. Hiking, camping, horseback riding, bicycling, kayaking, tubing, and wildlife viewing are popular activities. High human visitation and a high-density black bear population regularly result in human-bear incidents (LaFolette 1974, Stiver 1991).

CHAPTER III

METHODS

Location Data

I compiled 4,556 location estimates of 43 radio-collared black bears (22 females and 21 males) in GSMNP collected during 3 consecutive studies from 1976 to 1982 (Garshelis 1978, Quigley 1982, Carr 1983). In each study, black bears were captured with Aldrich, spring-activated, foot snares (Aldrich Animal Trap Co., Clallam Bay, WA), immobilized with intramuscular injections of etorphine (M-99) (D-M Pharmaceuticals, Rockville, MD) or phencyclidine hydrochloride (Sernylan) (BioCeutic Laboratories, St. Joseph, MO.), and tagged, measured, and weighed according to standardized procedures during annual summer trapping efforts (Johnson and Pelton 1980). Selected bears were equipped with motion-sensitive radio transmitters (Telonics, Mesa, AZ and Wildlife Materials, Inc., Carbondale, IL). Locations of radio-collared bears were estimated with receivers (Telonics, Mesa, AZ and Wildlife Materials, Inc., Carbondale, IL) with 8-element antennas (Hy-Gain Electronic, Lincoln, NE) mounted on 5-, 9-, or 12-m masts, 4 element hand-held antennas (Wildlife Materials, Inc., Carbondale, IL), or 2-element "H" antenna (Telonics, Mesa, AZ), and by aerial location from a Cessna 140, 170, or 172 (Garshelis and Pelton 1981, Quigley 1982, Carr 1983). Radio locations were rejected if the error polygon formed by the intersection of 3 or more radio bearings did not fit

within a circle with a radius of 150 m (Garshelis and Pelton 1981, Quigley 1982, Carr 1983). Most bears were located at least twice a week during the period from den emergence to den entrance (Garshelis and Pelton 1981, Quigley 1982, Carr 1983). Hourly locations for periods of 24-48 hours (diel locations) usually were collected for each bear during each season. All locations were coded to the nearest 100-m grid intersection on a Universal Transverse Mercator (UTM) coordinate system (Strahler 1969).

I used 4 criteria to select locations for the home range and habitat use analyses. First, for each locational record all of the following had to be available: bear-ID, day, month, year, and X and Y coordinates. Second, trap, denning, and diel locations were excluded from home range and habitat analyses except for the first location estimate of each diel collection period. Third, independence of locations was tested with Schoener's ratio t^2/r^2, where t^2 is the mean squared distance between successive locations and r^2 is the mean squared distance from the center of activity (Swihart and Slade 1985). For each bear I tested the null hypothesis that locations were independent ($t^2/r^2 \geq 2$) with an α-level of 0.25 to reduce type II error (Swihart and Slade 1986). Based on Schoener's ratio, location estimates for home range analyses were autocorrelated for all bears. Garshelis (1978) determined that a bear usually could move between any 2 points in a home range within approximately 6 hours. Based on that finding, I used only locations taken 6 or more hours apart for home range analysis.

The last selection criterion was related to the minimum number of locations. For

the habitat analysis, a minimum of 30 locations was used for each bear for the estimation of centers of activity, which were used to calculate study area boundaries. To estimate the minimum number of locations needed for home range estimation, I estimated home range sizes at increments of 10 locations for each bear. I tested the 50%, 75%, and 95% home range contours of the convex polygon and harmonic mean methods (see Home Range Estimates). When home range size is regressed against number of locations, the curve should become asymptotic, representing adequate sample sizes for home range estimation (Bekoff and Mech 1984). I also calculated the percentage change in home range size at increments of 10 locations. According to Messier and Barette (1982), a home range estimate may be adequate when the area estimate increases $< 10\%$ with 20 additional locations. For most convex polygon and harmonic mean home range contours, home range sizes peaked at < 50 locations (Figs. B.1 and B.2). The percentage change in home range size for each 10 additional locations was high at < 40 locations but declined at > 40 locations (Figs. B.3 and B.4). The second increase at > 80 locations was due to small sample sizes. Thus, estimates of home range size stabilized at a minimum of 40-50 locations. Based on these results, I used a minimum of 45 location estimates for all home range analyses. I compiled age and reproductive information for all females ($n = 12$) and males ($n = 11$) with ≥ 45 locations (Fig. 11).

I used 2,661 bear locations for habitat use analysis, 1,517 ($n = 17$) for females and 1,144 ($n = 15$) for males (Fig. 12). An equivalent number of random location sites was used for each sex to assess habitat availability (Fig. 13). Location types

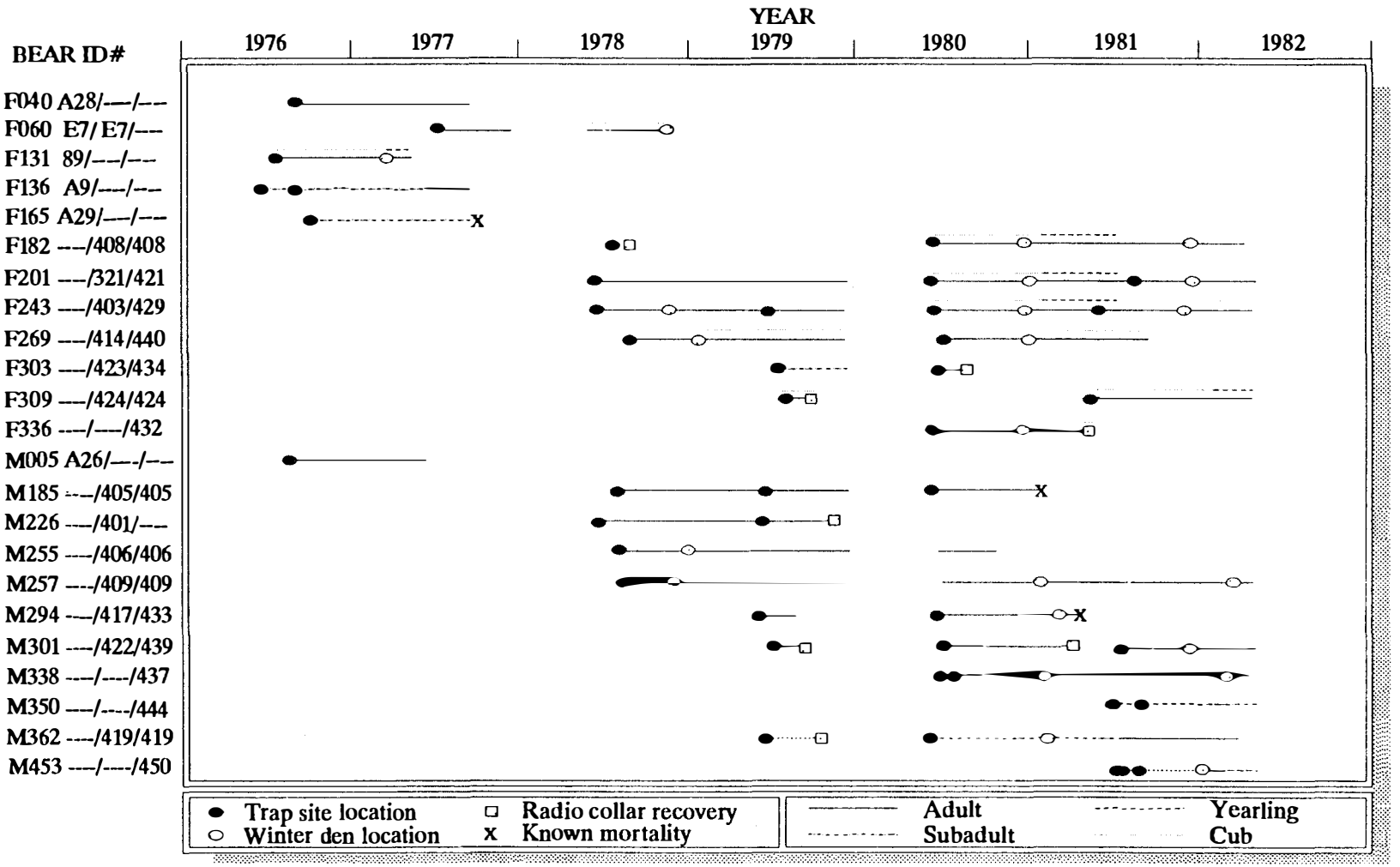


Fig. 11. Tracking history of black bears used in this study. Bear IDs from left to right are from this study, Garshelis (1978), Quigley (1982), and Carr (1983), respectively. Double lines for females indicate presence of cubs or yearlings.

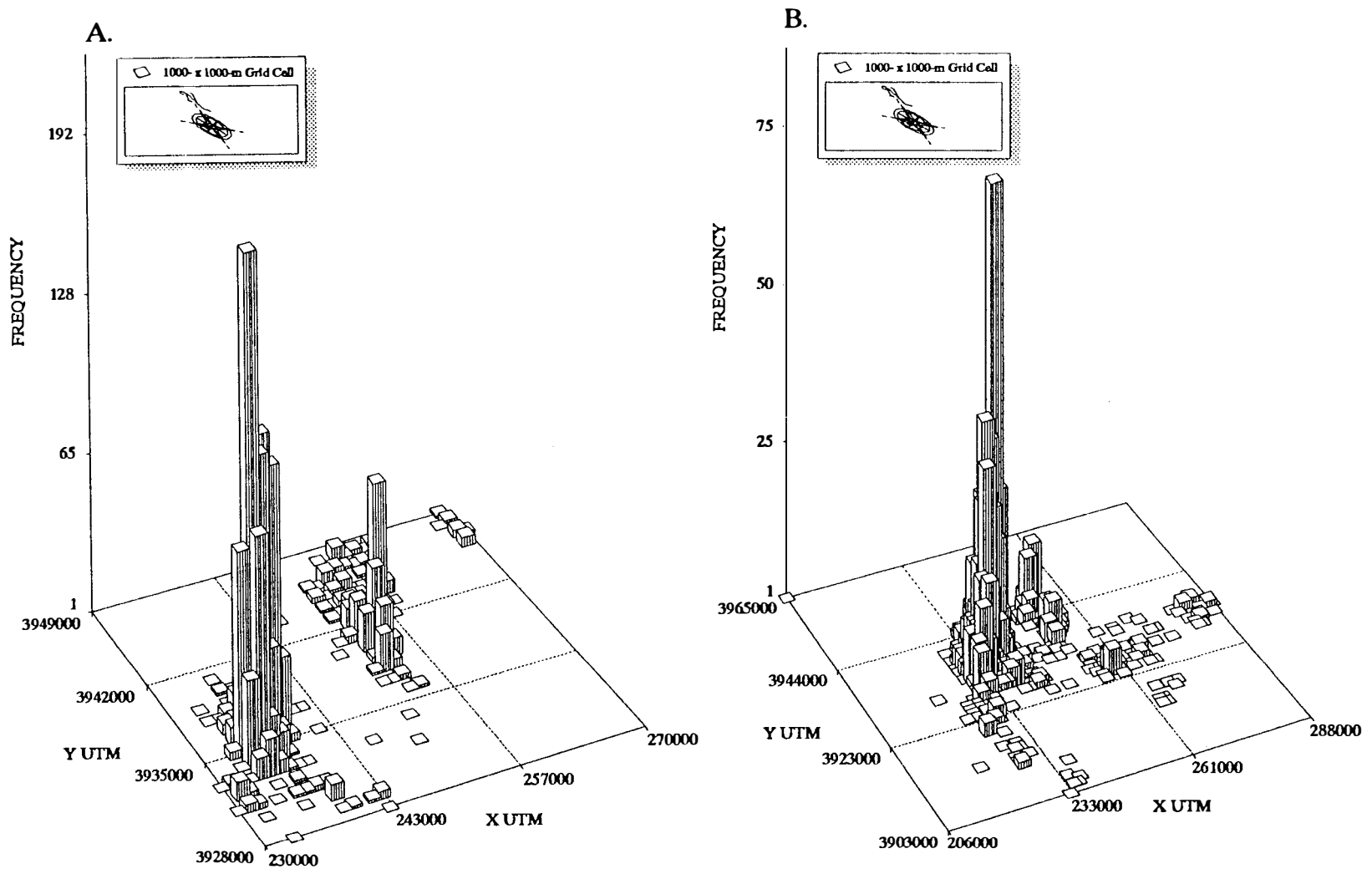


Fig. 12. Distribution of black bear locations in Great Smoky Mountains National Park, 1976-1982. A. Females. B. Males.

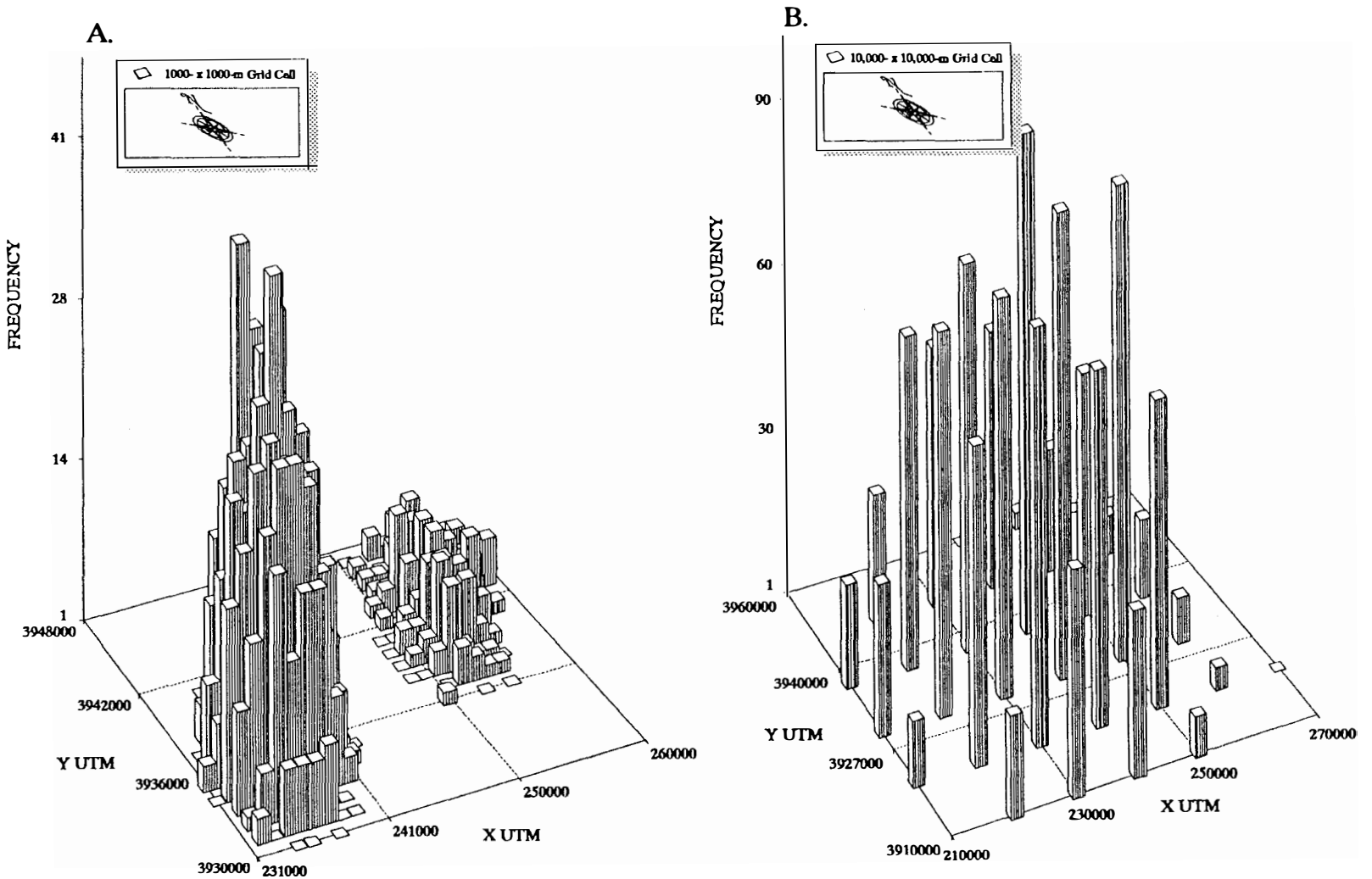


Fig. 13. Distribution of random locations in available habitat areas of black bears, Great Smoky Mountains National Park, 1976-1982. A. Females. B. Males.

were recorded for 1,393 locations: ground locations were most common (52%), followed by aerial (33%), first diel (10%), trap (3%), and visual or collar (2%) locations.

I calculated the frequencies of locations of bears within yearly age classes to determine whether the sampled bears and their locations were representative of the population. For comparison, I used 1976-1982 age-structure information determined with a back-dating technique (i.e., bears captured in GSMNP known to be alive) (A. Coley, Univ. Tenn., pers. commun.). I compared the shape of the 2 distributions with the asymptotic Kolmogorov-Smirnov test (Kiefer 1959). The frequency of locations was not entirely representative of the age-class structure of the trapped population for both females (asymptotic Kolmogorov-Smirnov statistic = 1.57, P = 0.0147) and males (asymptotic Kolmogorov-Smirnov statistic = 1.62, P = 0.0102). Subadult females and old adult males were underrepresented.

For seasonal analyses, locations were classified into 3 periods to represent marked changes in the diet and activity of black bears. These season definitions were based on a combination of food habit studies conducted in GSMNP (Beeman and Pelton 1980, Eagle and Pelton 1983) and activity studies in the southern Appalachians (Garshelis 1978, Quigley 1982, Villarrubia 1982, Carr 1983, Garris 1983). I defined spring as the period from 1 April through 15 June, summer as the period from 16 June through 15 September, and fall as the period from 16 September through 15 December.

Study Area Definition

To estimate available habitat, I used the following procedure to determine study area boundaries. I separately determined the study area for males and females due to substantial differences in home range size estimates. I calculated the harmonic mean center of activity for each bear by use of the software program HOME RANGE (Ackerman *et al.* 1990). I used the median of the distances of the furthest location estimate of each animal to its center of activity as the radii around each center of activity to estimate available habitat for each bears. This value was 3.4 km for females and 21.7 for males. To prevent large bias in the estimate of this distance, I restricted the habitat analysis to individuals for which 30 or more locations were recorded that met the location selection criteria. For the habitat use analysis, I created random locations within these defined areas of available habitat for each individual bear. The random locations were equal in number to the telemetry locations of each bear. I used the areas of available habitat for all bears combined to determine the female and male study areas (Figs. 6 and 7).

Home Range Estimates

I used the minimum and percent convex polygon (Hayne 1949, Michener 1979, Odum and Kuenzler 1955), harmonic mean measure of activity models (Dixon and Chapman 1980), and the adaptive kernel method (Worton 1989) to estimate home ranges and utilization distributions. A utilization distribution is a probabilistic definition of home range. It is based on the bivariate probability density function that

gives the probability of finding an animal at a particular position in the plane (Anderson 1982). I did not consider any home range estimation methods that require bivariate normal utilization distributions because this assumption could not be met for most bears.

The minimum convex polygon model is not statistical and is not restricted by assumptions of distribution and independence of observations. The peripheral animal locations are connected so that internal angles of the generated polygon do not exceed 180° (Ackerman *et al.* 1990). The convex polygon method has many disadvantages because it is sensitive to sample size, may not be asymptotic, has a convex shape of the home range (Anderson 1982), and the presence of outliers may result in substantial overestimation of home range size (MacDonald *et al.* 1980, Mykytka and Pelton 1988). The percent convex polygon method is the same as the minimum convex polygon but includes only a specified, innermost, percentage of the observations and provides some information on frequency of use within a home range (Ackerman *et al.* 1990). Because the minimum and percent convex polygon methods have frequently been used in black bear research, I included these methods mainly for comparative purposes.

The harmonic mean method is nonparametric and describes the intensity of use of a home range at grid points that are systematically located throughout the home range (Dixon and Chapman 1980). This method uses the harmonic mean distances of the grid points to all observations to calculate a utilization distribution (Dixon and Chapman 1980). Although the harmonic mean method has been found to have little

bias, it is not a precise method (Boulanger and White 1990).

The adaptive kernel method is another nonparametric method that requires no assumptions about underlying distributions (Worton 1989). This method uses a kernel estimator, a scaled-down probability density function, which is placed over each data point to construct the estimator (Worton 1989). Where location points are concentrated, the kernel estimate has a higher density than where there are fewer points (Worton 1989). I choose this method because it is robust, reliable, and flexible (Worton 1987, 1989) and used it for some of the spatial applications of home range configurations in the habitat analysis.

For both the harmonic mean and adaptive kernel method, the effect of outliers is small. Because underlying distributions need to be calculated from the observations, the harmonic mean and adaptive kernel methods both require relatively large sample sizes. Ackerman *et al.* (1990) recommended a sample size of 50 or greater for the harmonic mean method whereas Worton (1987) recommended 30-100 observations for nonparametric methods in general.

Harmonic mean and convex polygon home ranges were estimated with TELEM88 (Coleman and Jones 1988) and HOME RANGE (Ackerman *et al.* 1990) software programs, respectively. I used a beta test version of the software program CALHOME (U.S. Forest Service and California Department of Fish and Game) to calculate adaptive kernel home ranges and revise harmonic mean estimates. A home range estimate cannot capture the dynamics of spatial use by animals and is only a relative and general measure (Boulanger and White 1990). To determine some of

these dynamics, I estimated 100%, 95%, 75%, and 50% home range contours for all 3 methods. I used the 50% home range estimates to represent core areas (Anderson 1982). I estimated overall (all locations), annual (all locations within a year), and seasonal (all locations within a season) home range sizes for all bears with the minimum number of required locations. I combined seasonal locations from different years to reach adequate sample sizes; thus, the seasonal ranges incorporated annual variation.

After testing for normality, I compared estimates of home range size between males and females with Student's *t*-tests and differences among overall, annual, or seasonal home ranges with paired-difference *t*-tests (Snedecor and Cochran 1980). I used the nonparametric Wilcoxon rank sum test for statistical comparisons of 2 groups and Wilcoxon's signed-rank test for paired comparisons (Siegel 1956) when the distributions of home range sizes were not normal and could not be normalized. I used linear regression to test for relationships between annual home range size and age of bears (Snedecor and Cochran 1980); I only tested adaptive kernel estimates and individuals with more than 1 annual estimate were only used once.

I calculated harmonic mean centers of activity (Dixon and Chapman 1980) for each individual for all locations and by season and year. Unlike arithmetic centers of activity, harmonic mean estimators are robust to the underlying distribution and are always inside the home range, but not necessarily in the center, and more than one activity center may exist (Dixon and Chapman 1980, Lair 1987, Ackerman *et al.* 1990). I used distances among seasonal, annual, or overall centers of activity to

measure home range shifts. I determined the significance of seasonal shifts in home ranges by comparing distances between summer and fall centers of activity with distances between annual activity centers (Brody 1984). For each bear, I calculated the mean annual home range shift based on the mean distance between annual activity centers of all 2-year combinations. I used Student's *t*-tests to compare differences in distances between activity centers (Snedecor and Cochran 1980).

Travel rates were calculated from diel collection periods. These travel rates were compared between females and males with Student's *t*-tests or the Wilcoxon rank sum test and among seasons and years with paired-difference *t*-tests or the Wilcoxon signed-rank test (Siegel 1956, Snedecor and Cochran 1980). For comparison of travel rates during different hours or 3-hour periods of the day, travel rates were calculated from consecutive locations rather than entire diels. The maximum time difference allowed for consecutive diel locations was arbitrarily set at 4 hours. Travel rates among 3-hour periods were compared with repeated measures analysis of variance (Ott 1988).

For bears with home ranges that had > 50% overlap, I calculated and compared mean distances of paired simultaneous locations with pairs of randomized locations by use of techniques described by Clark (1991). I compared these distances among females and males separately, and between females and males. Davies (1978) argued that territoriality exists if individuals are spaced out more than would be expected from random use of suitable habitat. Thus, if bears with overlapping home ranges move completely independent of each other, the distance between simultaneous

locations should not be different from the distances between randomized location pairs. However, if simultaneous movements of bears are somehow influenced, one would expect the mean distance between paired simultaneous locations to be different from random sets of locations. For locations to be considered simultaneous, I used the same criterion as Clark (1991) who used a maximum of 8 hours difference between paired locations. Although this period seems fairly long for locations to be considered simultaneous, shorter periods would have the disadvantage of a potential bias in favor of animals that were close together due to the logistics of radio tracking (Clark 1991). Because I could not normalize all the data, I used the nonparametric Wilcoxon rank sum test to test for differences between mean paired and random distances (Siegel 1956). Mean distances were based on at least 6 location pairs. I also compared mean distances between simultaneous locations of females and males and among seasons for each sex separately with Student's *t*-tests and paired-difference *t*-tests or Wilcoxon's signed-rank tests, respectively (Siegel 1956, Snedecor and Cochran 1980).

Habitat Data

Digitized habitat information pertaining to a set of potentially important habitat variables was available or generated for GSMNP in IBM PC version 7.4 of the Earth Resources Data Analysis System (ERDAS, Inc., Atlanta, GA) (ERDAS, Inc. 1990) GIS of the Cooperative Park Studies Unit (CPSU) at the Department of Forestry, Wildlife and Fisheries, University of Tennessee. ERDAS is a raster-based GIS with

spatial features depicted by grid cells (Clark and van Manen 1993). Based on previous studies of black bear habitat use in the southern Appalachians, I selected 10 habitat variables for modelling (Table 3). The overstory vegetation type, elevation, slope, aspect, and vegetation disturbance history coverages were used without alterations.

The overstory vegetation coverage was developed by MacKenzie (1991, 1993) from Landsat-5 thematic mapper (TM) satellite imagery through image processing in ERDAS. The overstory vegetation types were described and validated based on field plots (MacKenzie 1991, 1993). Overall classification accuracy was 83%, ranging from 49.6% for pine-oak to 100% for spruce-fir and heathbalds (MacKenzie 1993). MacKenzie (1993) considered this classification accuracy to be satisfactory.

Vegetation patterns in GSMNP are complex and often represent continuums (Whittaker 1956), complicating the classification of digital satellite data (MacKenzie 1993). Moreover, in topographically complex regions, spectral reflectance of a certain vegetation type may vary due to the effects of shading (MacKenzie 1993). Topography also limits the ability to georectify the digital data to a coordinate system MacKenzie (1993). MacKenzie (1993) used field plots within the Thunderhead Mountain, 7.5', U. S. Geological Survey (USGS) topographic quadrangle for interpretation of the reflectance values of the satellite imagery. The black bear study areas were partly within this quadrangle. The overall accuracy assessment, however, was based on field plots mostly outside the black bear study areas. I combined grassy

Table 3. Geographic information system (GIS) variables for analysis of black bear habitat use, Great Smoky Mountains National Park, 1976-1982.

Variable Code	Variable Name	Variable Type	Data Type	Explanation
Y	Y	Dependent	Binomial	1 = Bear Location 0 = Random Location
VE	Overstory Vegetation Type	Independent	Nominal	2 = Northern Hardwood 3 = Cove Hardwood 4 = Mesic Oak 5 = Mixed Mesic Hrdw. 6 = Tulip Poplar 7 = Xeric Oak 8 = Pine-Oak 9 = Pine 10 = Nonforest
VR	Overstory Vegetation Richness	Independent	Continuous	Overstory Vegetation Types within 270 m Radius
ST	Proximity to Streams	Independent	Continuous	Meters
SL	Slope	Independent	Continuous	Degrees
EL	Elevation	Independent	Continuous	Meters
AS	Aspect	Independent	Nominal	1 = North 2 = Northeast 3 = East 4 = Southeast 5 = South 6 = Southwest 7 = West 8 = Northwest 9 = Flat
DH	History of Vegetation Disturbance	Independent	Nominal	1 = Uncut 2 = Light Cut 3 = Heavy Cut 4 = Undisturbed 5 = Settlement
TR	Proximity to Trails	Independent	Continuous	Meters
RO	Proximity to Improved Roads	Independent	Continuous	Meters
HA	Proximity to Human Activity Sites[a]	Independent	Continuous	Meters

[a]Developed campgrounds, other heavily used visitor areas, and residential areas.

bald, heath bald, grape thicket, and treeless vegetation categories into one "nonforest" class. Although MacKenzie (1991, 1993) did not describe the frequency of understory species, I interpreted their composition through comparisons with Whittaker (1956) and Golden (1974).

The topographic coverages (elevation, slope, and aspect) were derived from USGS digital elevation models (DEM) (Parker and Pipes 1990). Based on historical records, the vegetation disturbance history was mapped by Pyle (1988); areas were classified as uncut (diffused disturbances but no logging), light cut (small-scale logging and other diffuse disturbances), heavy cut (corporate logging), and settlement. Areas for which no records of disturbances existed were classified as undisturbed (high in virgin forest attributes); because of missing or unavailable records, this classification may have been incorrect in some areas. Vegetation disturbance history mostly represented physiognomic differences in the vegetation.

The coverage for overstory vegetation richness was developed through a filtering operation (SCAN in ERDAS) by moving a circular window with a radius of 3 pixels over the overstory vegetation coverage (Clark and van Manen 1993). The center cell of the window received the number of different overstory vegetation types within the entire matrix (Agee *et al.* 1989, Clark and van Manen 1993). By doing so for all pixels in the vegetation coverage, a coverage of vegetation richness was created. The radius of 3 was chosen so that potentially all vegetation types could be present in the window and to provide a high degree of spatial resolution. Larger window sizes captured the same range (e.g., 1-6 vs 3-8) of vegetation richness but the spatial

resolution of the resulting coverage was substantially smaller. Moreover, because I determined bear habitat use on a local scale (i.e., within 90- x 90-m pixels), I decided to use vegetation richness as a local measure rather than a landscape-scale measure.

The stream coverage was developed by Parker and Pipes (1990) for a watershed analysis of GSMNP. I created a trail coverage by selecting closed or unsurfaced roads, historic railroad beds, abandoned trails, and existing trails from an existing trail and road coverage developed by the National Park Service, GSMNP. The trail coverage was used to represent potential travel routes and small, open forest habitat. I digitized improved roads and human activity sites, within and outside GSMNP, into the GIS system. These 2 variables were used to represent potential human disturbance factors. The proximity coverages (e.g., proximity to streams, proximity to improved roads) were created from the original coverages through a buffer operation (SEARCH in ERDAS), which defines distances to nearest selected features (Clark and van Manen 1993).

To extract the habitat data for the bear locations from the GIS coverages, a GIS coverage of all the radio-telemetry and random locations was created in ERDAS. I used a procedure in ERDAS (GRDPOL), which assigned the UTM coordinates of the bear locations to a grid of 90- x 90-m pixels. Subsequently, the bear location coverage was superimposed on the 10 habitat variable coverages with an overlay procedure (OVERLAY in ERDAS) so that each location was linked to the habitat data (Clark and van Manen 1993). Because several GIS layers covered GSMNP only, locations outside GSMNP had missing data points and were not considered in the

analysis.

The resolution of the original data that was used to create the GIS coverages was not the same for each coverage. The overstory vegetation coverage, for example, was developed from Landsat-5 satellite imagery with a 30- x 30-m pixel resolution and mapped with a resolution of 90- x 90-m due to the complexity of the vegetation patterns. Because the vegetation coverage for GSMNP was the basis for much of the GIS database, the GIS database was developed with a 90-m resolution. Because of high mobility and large ranges of black bears, the 90-m resolution provided an appropriate unit for the purpose of this study, especially because the resolution of the telemetry locations was similar (100 m).

Habitat Use Analysis

General. All data associated with telemetry and random locations were compiled into one habitat database. For each location, the following data were recorded: observation number, bear-ID number, location type, X UTM, Y UTM, day, month, year, hour, minute, year of birth, age, reproductive status (females only), number of cubs or yearlings (females only), overstory vegetation type, overstory vegetation richness, proximity to streams, slope, elevation, aspect, vegetation disturbance history, proximity to trails, proximity to improved roads, and proximity to human activity sites.

Logistic Regression. To determine the joint relationships of the habitat variables and bear use, I used multivariate techniques. Rextad *et al.* (1988) criticized the use

of several multivariate wildlife analysis techniques (principal component analysis, canonical correlation analysis, and discriminant function analysis) arguing that statistical and biological significance are not necessarily related and that biological interpretation of coefficients often is arbitrary and not well founded in statistical theory. In a survey of 7 ecological journals, James and McCulloch (1990) found numerous misapplications and misinterpretations of 12 commonly used multivariate techniques. All multivariate statistical methods are descriptive but only a few methods can also be confirmatory, given appropriate sampling. Conclusions about causes from statistical tests based on descriptive models is one of the common misuses of multivariate methods (James and McCulloch 1990) and relates directly to Romesburg's (1981) criticisms of use of scientific methods and lack of experimentation in wildlife science.

I used logistic regression to describe black bear habitat use (Hosmer and Lemeshow 1989). A logistic regression model describes the relationship between a dependent (outcome) variable and a set of independent (predictor) variables based on the same general principles as linear regression. In logistic regression, however, the outcome variable is binomial, usually describing presence or absence, and its analysis is based on the logistic distribution (Hosmer and Lemeshow 1989). Logistic regression is a flexible technique and lends itself to biologically meaningful interpretation (Hosmer and Lemeshow 1989). Linear discriminant function analysis is similar to logistic regression but performs best with multivariate normal data when variances and covariances are the same for each group (Press and Wilson 1978, James

and McCulloch 1990). Use of categorical variables rules out multivariate normality and variances and covariances become poor summary statistics (Press and Wilson 1978, James and McCulloch 1990). Analysis of habitat use often involves data sets with mixtures of continuous and categorical variables (Capen *et al* 1986); in such instances, logistic regression is an appropriate alternative to linear discriminant function analysis because it does not require multivariate normality or equal variance-covariance matrices (Press and Wilson 1978, James and McCulloch 1990). Logistic regression can be used as a descriptive and confirmatory multivariate technique (James and McCulloch 1990).

In my study, the outcome variable described bear locations versus randomly generated locations within the study area. Although the bear locations represented presence, the random locations did not necessarily represent absence because the area may have been used by bears before or may be used by bears in the future. The random locations simply provided a measure of habitat availability. The logistic regression analysis provided a conservative measure of habitat allocation (if random and telemetry locations differ in habitat characteristics, even if random locations were sometimes used by bears, actual differences were equal to or greater than the differences I measured). The assumptions with this approach were similar to those discussed by Neu *et al.* (1974): (1) bears had an opportunity to use any of the habitats deemed available, and (2) the observations of habitat use were collected in a random, unbiased manner. The first assumption likely was not violated; the areas of available habitat (the study areas) were calculated based on the bear locations.

Although the radio-telemetry locations were not free of error, the locations usually were reliable relative to the habitat sampling unit. Tracking success (the ability to locate a bear at a desired time) for all 3 studies was high, which was partly due to the use of mast antennas and many aerial searches (Garshelis 1978, Quigley 1982, Carr 1983). Furthermore, I determined the effects of telemetry error in the habitat analysis. Thus, the second assumption also seemed to be satisfied.

Smoothed scatter plots of the continuous variables revealed that elevation should be treated as a categorical variable for females; proportional use was low at low and high elevations ($<$ 600 m and $>$ 1,000 m) but high at middle elevations (600-1,000 m). Similarly, proximity to the nearest improved road was categorized into 2 classes: $<$ 2,500 m and $\geq$ 2,500 m. Proximity to nearest human activity site also was categorized into 2 classes: $<$ 5,750 m and $\geq$ 5,750 m. Categories of several nominal variables were pooled to increase the fit of the model. For the overstory vegetation variable, the cove hardwood and pine-oak categories showed no statistical difference in bear use ($\chi^2 = 0.21$, 1 df, $P = 0.6430$). Although these vegetation types are ecologically different, I pooled them because they were the only types used in proportion to availability. For the aspect variable, northeastern, southeastern, southern, southwestern, and western aspects were pooled because no statistical differences were detected in bear use ($\chi^2 = 0.865$, 4 df, $P = 0.9290$). Light cut and undisturbed areas also were pooled because the small number of locations in undisturbed areas and the relative ecological similarity of the 2 classes. Although uncut and heavily cut areas received similar use, they were not pooled due to their

potential ecological differences.

Based on smoothed scatter plots of the male black bear data, I classified slope, elevation, proximity to human improved roads, and proximity to human activity sites as categorical variables. For overstory vegetation type, I pooled northern hardwood and mesic oak and mesic mixed hardwood, tulip poplar, and xeric oak because proportional use was not significantly different ($\chi^2 = 0.216$, 1 df, $P = 0.642$; $\chi^2 = 0.227$, 2 df, $P = 0.893$, respectively). Based on chi-square tests, western, northwestern, and northern aspects were pooled ($\chi^2 = 1.956$, 2 df, $P = 0.376$), and northeastern, eastern and southwestern aspects, and flat areas ($\chi^2 = 0.653$, 3 df, $P = 0.884$), and southeastern and southern aspects ($\chi^2 = 0.123$, 1 df, $P = 0.726$). For vegetation disturbance history, the classes heavy cut and settlement were pooled ($\chi^2 = 0.001$, 1 df, $P = 0.970$); light cut and undisturbed were pooled due to the ecological similarity of these 2 classes.

Subset Selection. Rextad *et al.* (1988) criticized the use of habitat variables in multivariate analysis without any *a priori* knowledge of their relation to habitat use. Therefore, I used a model selection procedure to select the best subset of habitat variables. I first screened all 10 variables with univariate logistic regression, comparison of means, and smoothed scatter plots for continuous variables and likelihood ratio chi-square tests for categorical variables (Hosmer and Lemeshow 1989). All variables that showed a significant relationship with an α-level of 0.25 (Mickey and Greenland 1989) were considered for best subset selection. Univariate analysis of the 10 habitat variables showed differences between bear and random

locations for 9 variables. I excluded proximity to nearest stream from the multivariate analysis because there were no differences between bear and random locations (females: $Z = 0.14$, $P = 0.89$; males: $Z = 0.96$, $P = 0.34$).

In multivariate methods, stepwise procedures are commonly used to select the 'best' subset of variables. However, stepwise procedures are highly unreliable and may not select the best fitting model because they are not intended to rank variables by their importance and they may eliminate variables that are important or include variables that are unimportant (James and McCulloch 1990).

To select the variable subset(s) that best described species absence or presence, I used Akaike's information criterion (AIC) (Akaike 1973, Bozdogan 1987) and information-theoretic measure of complexity (ICOMP) (Bozdogan 1990, 1994). AIC and ICOMP are information-based or entropic measures used for identifying an optimal statistical model. An optimal model is supported by the data and has enough parameters to provide a trade-off between bias and precision and adheres to the principle of parsimony (Burnham and Anderson 1992). AIC and ICOMP are calculated for each competing model and the model with the smallest AIC or ICOMP value is the model best supported by the data.

$$AIC = -2LogL(\underset{\sim}{\hat{\beta}}) + 2(k+1), \tag{1}$$

where

$$LogL(\underset{\sim}{\hat{\beta}}) = \sum \{\log \binom{n_i}{y_i} + y_i \log p_i + (n_i - y_i) \log (1-p_i)\}, \tag{2}$$

and

$$p_i = \frac{e^{(\beta_0+\beta_1 X_{1i}+\ldots\beta_K X_{Ki})}}{1+e^{(\beta_0+\beta_1 X_{1i}+\ldots\beta_K x_{Ki})}}, \tag{3}$$

and $k+1$ is the number of parameter estimates, including one for β_0, and y_i is the observed value of the response. The first term is a measure of the lack of fit between the model and data when using maximum likelihood estimators of the model. As the number of parameters increase, the fit between the model and the data will increase, resulting in a decrease of the -2*LogL* term. The 2*k* term penalizes against unnecessary increases in model size, emphasizing the principle of parsimony; as the number of parameters in the model increases, the penalty term increases.

ICOMP is based on the same principles as AIC but the penalty term (second term) is different:

$$ICOMP(\hat{F}^{-1}) = -2LogL(\underset{\sim}{\beta}) + 2C_1(\hat{F}^{-1}), \tag{4}$$

where

$$C_1(\hat{F}^{-1}) = \frac{dim\hat{F}^{-1}}{2}\log\left[\frac{tr\hat{F}^{-1}}{dim\hat{F}^{-1}}\right] - \frac{1}{2}\log|\hat{F}^{-1}|, \tag{5}$$

and

$$\hat{F}^{-1} = \begin{vmatrix} \hat{\sigma}^2 (X'WX)^{-1} & \underset{\sim}{0} \\ \underset{\sim}{0}' & \frac{2\hat{\sigma}^4}{N} \end{vmatrix}, \tag{6}$$

and

$$cov(\underline{\hat{\beta}}) = \hat{\sigma}^2 (X'WX)^{-1}, \quad (7)$$

and the loglikelihood term and p_i are the same as in equations (1) and (2), respectively. For logistic regression, the loglikelihood term and $\sigma^2 = 1$ for equations (6) and (7) are as given by Bozdogan (1990, 1994). Equation (5) is the second term and describes the complexity of the accuracy of the parameter estimates and penalizes for an increasing degree of interdependency among the variables. When interdependency is large, the complexity term is large. The second term uses the inverse of the Fisher information matrix described in equation (6).

AIC and ICOMP were calculated for all different subsets of variables ($n = 512$). The optimal model was the one with the smallest AIC or ICOMP value. The model selection criteria have only one real condition, which is that the 'true' model must be among the models that are considered (Burnham and Anderson 1992). Model selection criteria, however, seem to perform well as long as the main factors influencing the data are included in the global model (Burnham and Anderson 1992). Moreover, 'true' models for real data are probably nonexistent (Burnham and Anderson 1992).

The loglikelihood term for each model was derived with the CATMOD procedure in Statistical Analysis System (SAS Institute, Inc., Cary, NC) software (SAS Institute, Inc. 1990). I used CATMOD because one or more independent variables in the model were nominal (e.g., vegetation type). I tested whether SAS uses the same loglikelihood term as in equation (2). The loglikelihood was the same for SAS as for my calculations and I continued the analyses with SAS. To calculate the number of

parameters (k) in AIC, I used the number of parameter estimates provided by SAS. For categorical variables, SAS provides parameter estimates for q-1 class levels (there are q-1 independent parameter estimates). When, for example, 3 continuous and 1 categorical variable with 5 class levels were in the model, k was determined to be 3 + (5-1) = 7. To calculate the complexity term of ICOMP, I used the covariance matrix of the parameter estimates provided by the CATMOD procedure in SAS. This matrix was used in the software program MATLAB (The Mathworks, Inc., Natick, MA) (MATLAB, Inc. 1992) to build the inverse Fisher information matrix and calculate the complexity for each of the subsets. Due to the sparsity of the observations in some levels of the categorical variables, the inverse Fisher information matrix sometimes contained all zeros in some rows or columns. I used the singular value decomposition function in MATLAB (MATLAB, Inc. 1992) to calculate the inverse Fisher information matrix.

After I identified the best fitting model, I verified the assumption of linearity in the logit for continuous variables (Hosmer and Lemeshow 1989). I categorized several continuous variables that did not meet this assumption. I also pooled classes of some categorical variables to improve the fit of the model. I used χ^2 goodness-of-fit tests to verify that pooled classes were not different with respect to bear use (Snedecor and Cochran 1980). I developed the seasonal habitat use models for females based on the variables in the overall female habitat use model.

Regression Diagnostics. I used the LOGISTIC procedure in SAS (SAS Institute, Inc. 1990) to calculate several regression diagnostics (confidence interval

displacement [C], standardized Pearson residual, change in deviance, and diagonal elements of hat matrix [h]) to identify observations that fit the model poorly (standardized Pearson residual $\geq$ 2) and had high leverage ($h > 0.008$) as outlier observations.

Assessment of Fit - Internal Validation. Based on the a prior probability of group membership of 0.5, I calculated the sensitivity, specificity, overall correct classification, false positive rate, and false negative rate. These types of classification, however, may provide an unreliable evaluation of the model's performance because of the artificial cut-off point of 0.5 (Hosmer and Lemeshow 1989). A predicted probability of 0.48, for example, is not much different from 0.52 but would still be classified differently with this method. Therefore, I also used deciles of risk (Hosmer and Lemeshow 1989) as the basis for internal validation. This method assigns the data to 10 groups ranked and separated according to the estimated probabilities (e.g., group 1 has all observations with estimated probability $\leq$ 0.1, group 2 has all observations with estimated probability from 0.1 to 0.2, etc.) (Hosmer and Lemeshow 1989). For each of the 10 groups, the estimated expected frequencies of the bear and random locations can be calculated based on the sum of the estimated probabilities of all observations in the group. If the model fits the data well, observed and estimated expected frequencies in each group should not be different (Hosmer and Lemeshow 1989). Based on the differences between observed and estimated expected frequencies for each of the groups, the Hosmer-Lemeshow goodness-of-fit statistic, $\hat{C}$, can be calculated. This statistic follows a chi-square

distribution with 8 df (Hosmer and Lemeshow 1989). A large *P*-value for this test indicates small differences between predicted and observed outcomes whereas a small *P*-value indicates large differences and a poor fit of the model to the data. I used a mainframe version of BMDP (BMDP Statistical Software, Inc., Los Angeles, CA.) (BMDP Statistical Software, Inc. 1992) to calculate the Hosmer-Lemeshow goodness-of-fit statistics.

Assessment of Fit - External Validation. The best validation method is to use independent data to test models (Capen *et al.* 1986). However, collection of additional telemetry locations was too costly and time-consuming and exclusion of observations from analysis specifically for validation would decrease sample sizes. Therefore, I used deciles of risk (Hosmer and Lemeshow 1989) in a modified 10-fold validation procedure (Verbyla and Litvaitis 1989) to assess the performance of the model based on independent data. I divided all locations into 10 random subsamples and developed the model with 9 of those subsamples and tested it with the remaining subsample. I repeated this 10 times to exclude all subsamples once from model development. I subsequently calculated and averaged the Hosmer-Lemeshow goodness-of-fit statistics ($\hat{C}$) for each of the 10 trials to determine whether differences existed between actual and predicted outcomes. Based on the same 10 trials, I also calculated the mean sensitivity, specificity, false positive rate, and false negative rate.

Telemetry Error. Every radio-telemetry location exhibits some error. The location may not be exact because of a moving animal, reading and calculation errors, or signal disturbance due to uncontrollable factors such as topography. Generally,

telemetry error is not accounted for when testing for habitat use (Nams 1989). White and Garrot (1986) found that statistical power to detect habitat selection decreases with decreasing telemetry accuracy, increasing habitat complexity, and decreasing sample sizes. Telemetry accuracy was determined by Garshelis (1978) and Quigley (1982) through the placement of collars at known locations. Both authors concluded that the telemetry location estimates could be placed within a circle with a 300-m diameter. Carr (1983) verified these findings by locating test collars, and through recovery of dropped collars and visual observations on bears.

I tested the effect of telemetry error on the habitat analyses by incorporating telemetry error into a simulated set of locations (Clark et al. 1994). To represent the telemetry error reported by Garshelis (1978), Quigley (1982), and Carr (1983), I used a 150 m radius around female locations within which I created uniform random locations. I recorded the habitat characteristics for this set of simulated error locations for comparison with the habitat characteristics of the original telemetry locations. I used chi-square statistics to compare categorical variables and Wilcoxon rank sum tests for comparison of means of continuous variables (Snedecor and Cochran 1980). I also developed a black bear habitat use model based on the simulated error locations. I used the Hosmer-Lemeshow goodness-of-fit statistic to test whether incorporation of telemetry error resulted in a difference in fit compared with the original habitat use model (Hosmer and Lemeshow 1989).

Interpretation of Logistic Regression Models. For categorical variables, the sign of the parameter estimates indicated whether a variable category was used more (+)

or less (-) than expected, whereas the value of the parameter estimate indicated the magnitude of the relationship. The *P*-value for the chi-square test associated with the parameter estimate indicated the statistical significance of this relationship and whether a parameter estimate was different from zero. For continuous variables, the interpretation was the same except that it was dependent on a defined change in value of the variable (e.g., increase of vegetation richness from 2 to 7).

Within the context of the multivariate logistic regression model, the parameter estimates can be used to interpret habitat use patterns related to individual variables. In logistic regression, the exponentiated difference in parameter estimates ($e^{2\beta x}$) of dichotomous variables represents the estimated odds ratio, a useful statistical measure of association (Agresti 1990). The odds ratio approximated how likely it was for the outcome to be present (e.g., a bear location) among observations with $x = 0$ (e.g., elevations below 600 m and above 1,000 m) compared with observations with $x = 1$ (e.g., elevations between 600 and 1,000 m). For continuous variables the interpretation of the parameter estimates is similar to that of dichotomous variables because they also represent estimated log odds ratios. With continuous variables, however, the log odds ratio is dependent upon a defined change in the variable. For categorical variables with more than 2 classes, the parameter estimates have a similar interpretation; for each variable, the difference between a parameter estimate and the parameter estimate of the reference class represents the odds ratio. The odds ratio may be less useful here because the reference class may not be the class of interest. Therefore, I used contrasts of maximum likelihood estimates to compare proportional

bear use of variable categories.

Factor Analysis. I performed a factor analysis on the variables in the overall habitat use models of females and males to facilitate interpretation of the logistic regression models. Factor analysis expresses common elements among the original variables, distinguishes different types of variation (Morrison *et al.* 1992), and may be helpful to interpret patterns of correlation among the habitat variables. I used the PRINQUAL procedure in SAS (SAS Institute, Inc. 1990) to transform the nominal and ordinal variables with Fisher's (1938) optimal scoring method and Kruskal's (1964) secondary least-squares monotonic transformation, respectively. I performed a FACTOR (SAS Institute, Inc. 1990) procedure on the transformed data to calculate the principal factor loadings of each variable. I used maximum likelihood factor analysis because it does not require multivariate normality (Morrison 1990). I used factors with eigenvalues ≥ 1 for interpretation.

Application of Logistic Regression Models. With the logistic regression equation of the best fitting models, the probability of classifying a pixel as a bear location can be predicted from the habitat characteristics of that pixel based on equation (8) (Hosmer and Lemeshow 1989):

$$P = \frac{e^{g(x)}}{1 + e^{g(x)}} \qquad \textbf{(8)}$$

where $g(x)$ is the logit transformation, consisting of the sum of parameter estimates for nominal variables and the estimates of continuous parameters times their observed values. I will refer to this probability as the relative habitat use probability. Thus,

based on the habitat characteristics associated with a certain GIS pixel, the relative habitat use probability represents the probability that the corresponding geographic location is classified as a bear location as opposed to a random location. This probability is not absolute because it is determined through comparisons with random locations and is based on a sample of the bear population during a certain time period. If this value is close to 1.0, the probability of use of the specified habitat type is greater than expected. Conversely, if this value is close to 0, the relative probability of use is less than expected. A relative habitat use probability close to 0.5 indicates that the specified habitat type is used in proportion to its availability.

I used predicted probabilities ≥ 0.90 and ≤ 0.10 to describe habitat types of bear locations that received high and low use, respectively. These probabilities were arbitrarily set. I used GIS modelling procedures in ERDAS (GISMO) to create relative habitat use coverages based on the overall habitat use models for females and males and based on the seasonal female habitat use models. I used these coverages to calculate mean relative habitat use probabilities for each bear by overlaying digitized adaptive kernel home ranges. I compared the mean relative habitat use probability for different contours with paired-difference *t*-tests and linear regression to relate these probabilities to home range size (Snedecor and Cochran 1980). I used a paired-difference *t*-test or a Wilcoxon signed-rank test to compare the mean relative habitat use probability of overlapping home range areas with nonoverlapping areas for paired home ranges of bears tracked during approximately the same periods (Siegel 1956, Snedecor and Cochran 1980). I tested for relationships between relative habitat use

and habitat quality by performing a linear regression of the mean relative habitat use probability of female home ranges against mean weight and physical condition of those females (Snedecor and Cochran 1980). I used weight and physical condition under the assumption that they are indices of habitat quality. I also regressed the mean relative habitat use probability against age of females. To calculate the mean weights and ages, I only used data from summer captures during the tracking period of each bear. Physical condition was classified as poor, fair, good, and excellent and coded as an ordinal variable.

Bait-Station Surveys

The National Park Service conducts annual bait-station surveys throughout GSMNP according to standardized procedures (Johnson 1992). Bait-station surveys provide information on whether bait sites are visited by black bears within a 5-day period. Bait-station locations surveyed from 1990-1992 were digitized into the ERDAS GIS system. To test whether bait sites visited by bears were in frequently used habitats, I overlaid the bait-station locations on the GIS coverages depicting the relative habitat use probability. I used Hosmer-Lemeshow goodness-of-fit statistic to test for differences between estimated expected frequencies at bait stations (based on the predicted probability of habitat use) and observed frequency of bait-station visits (Hosmer and Lemeshow 1989). To obtain adequate sample sizes, I extrapolated the habitat use models to the entire national park so that all bait-station sites could be used for analysis.

Simulation of Habitat Alterations

Although the study area includes only National Park Service lands, where forest management primarily consists of maintenance of the *status quo* (i.e., fire suppression, removal of certain exotic species), I determined the effects of hypothetical forest changes to test the effectiveness of the simulations in detecting changes in female habitat use. I determined the hypothetical effects of cutting 2 xeric oak stands at an early and late successional stage (nonforest and pine, respectively) at 2 different spatial scales. I also determined the hypothetical effects of additional roads and human activity sites (e.g., developed campground) on relative habitat use of females. Based on the changes in habitat classifications, the habitat use model provided different estimates of the relative habitat use probabilities compared with the original habitat conditions. The difference of the old and new probabilities provided a measure of predicted change in relative habitat use of black bears.

CHAPTER IV

RESULTS

Home Range Analysis

Overall Home Ranges. Home ranges of females were smaller than those of males for all methods and contours (after log-transformation: t = 4.51 to 6.16; 11,10 df; P = 0.0004 to 0.0001) (Tables 4 and D.1, Figs. 14 and 15). Mean overlap among 95%, 75%, and 50% adaptive kernel contours of adult female pairs with overlapping home ranges and similar tracking periods was 3.8 km^2 (SD = 3.2, n = 16, range = 0.1-9.5 km^2), 1.8 km^2 (SD = 1.0, n = 7, range = 0.6-3.7 km^2), and 0.5 km^2 (SD = 0.5, n = 6, range = 0.1-1.7 km^2), respectively. This overlap represented 23%, 41%, and 31%, respectively, of the mean female home range contour. The mean area of overlapping ranges represented 31.9% of individual 95% adaptive kernel areas (SD = 32.1, n = 32, range = 0.7-100.0 %).

Mean home range overlap between pairs of adult males with similar tracking periods was 137.7 km^2 (SD = 60.2, n = 16, range = 71.0-277.6 km^2), 42.6 km^2 (SD = 44.2, n = 16, range = 10.5-191.9 km^2), and 10.6 km^2 (SD = 9.8, n = 5, range = 0.3-22.9 km^2), for the 95%, 75%, and 50% adaptive kernel contours, respectively. This overlap represented 50%, 44%, and 61%, respectively, of the mean male home range contours. Overlapping areas averaged 50.8% of the individual 95% adaptive kernel estimates (SD = 28.3, n = 32, range = 10.9-100.0).

Table 4. Estimates of overall home range sizes (km^2) of black bears in Great Smoky Mountains National Park, 1976-1982.

		Females				Males			
	%	$\bar{x}$	SD	*n*	range	$\bar{x}$	SD	*n*	range
Harmonic Mean	100%	47.0	47.3	12	9.8-137.0	1,093.0	1,169.1	11	22.2-3,771.0
	95%	15.1	13.5	12	6.1-43.7	342.7	455.3	11	15.1-1,502.0
	75%	3.3	1.2	12	1.7-5.4	61.6	97.6	11	6.7-346.4
	50%	1.3	0.5	12	0.7-2.3	16.7	16.0	11	1.0-57.7

		Females				Males			
	%	$\bar{x}$	SD	*n*	range	$\bar{x}$	SD	*n*	range
Convex Polygon	100%	20.7	18.6	12	5.3-71.2	388.7	360.6	11	24.5-1,101.7
	95%	11.2	9.5	12	3.6-36.2	250.3	310.3	11	19.7-984.8
	75%	4.8	3.9	12	1.9-14.1	61.6	69.4	11	6.5-197.5
	50%	2.5	3.0	12	0.8-11.6	22.2	22.0	11	1.0-71.8

		Females				Males			
	%	$\bar{x}$	SD	*n*	range	$\bar{x}$	SD	*n*	range
Adaptive Kernel	100%	41.5	39.0	12	10.1-130.1	634.9	544.7	11	40.5-1,787.0
	95%	16.6	11.1	12	5.9-38.4	275.3	299.0	11	24.4-1,047.0
	75%	4.3	2.4	12	1.9-9.26	96.9	146.1	11	8.4-483.0
	50%	1.7	0.7	12	1.0-3.2	17.3	19.4	11	1.2-70.0

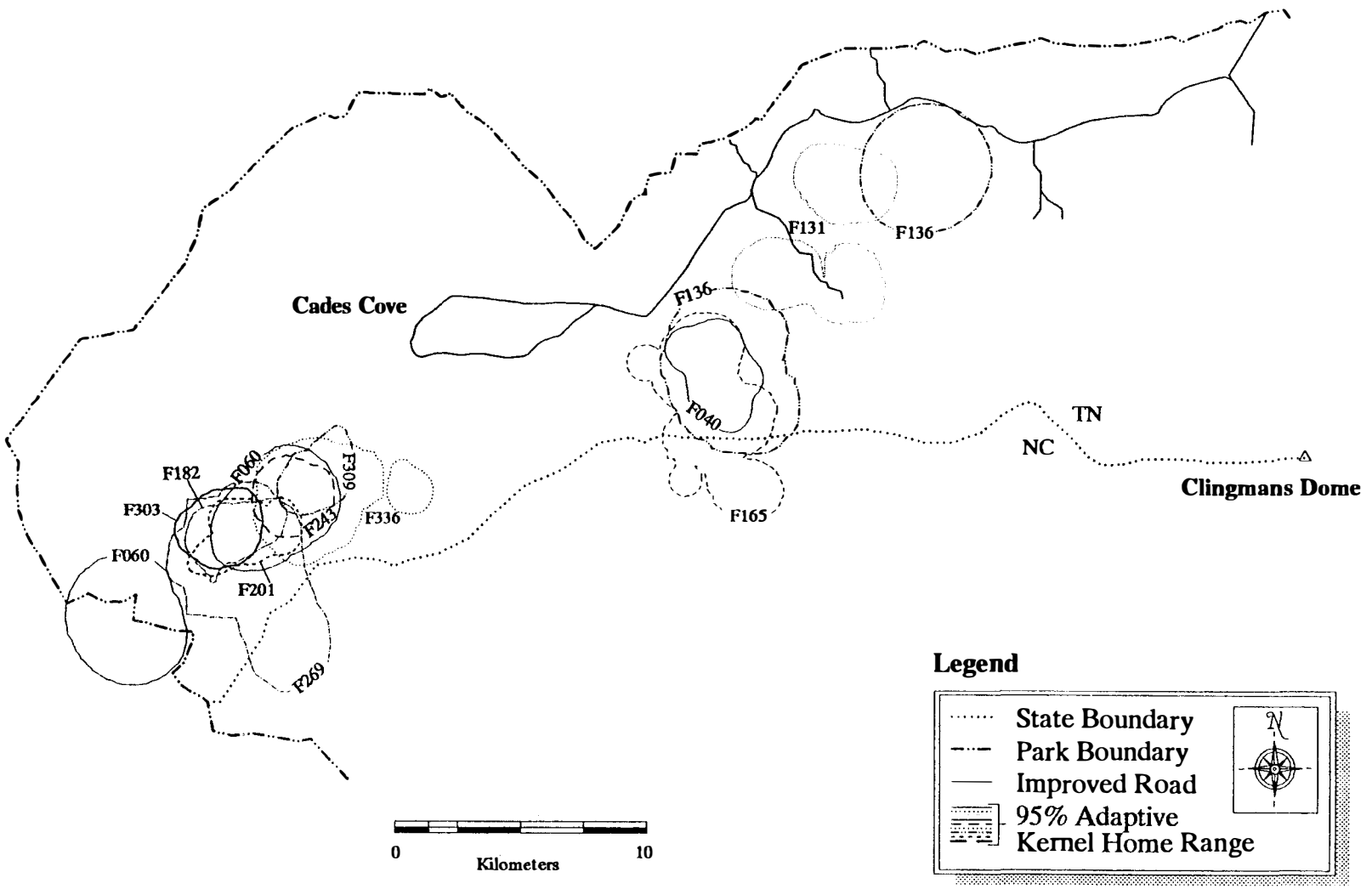


Fig. 14. Overall 95% adaptive kernel home range configurations of female black bears, Great Smoky Mountains National Park, 1976-1982.

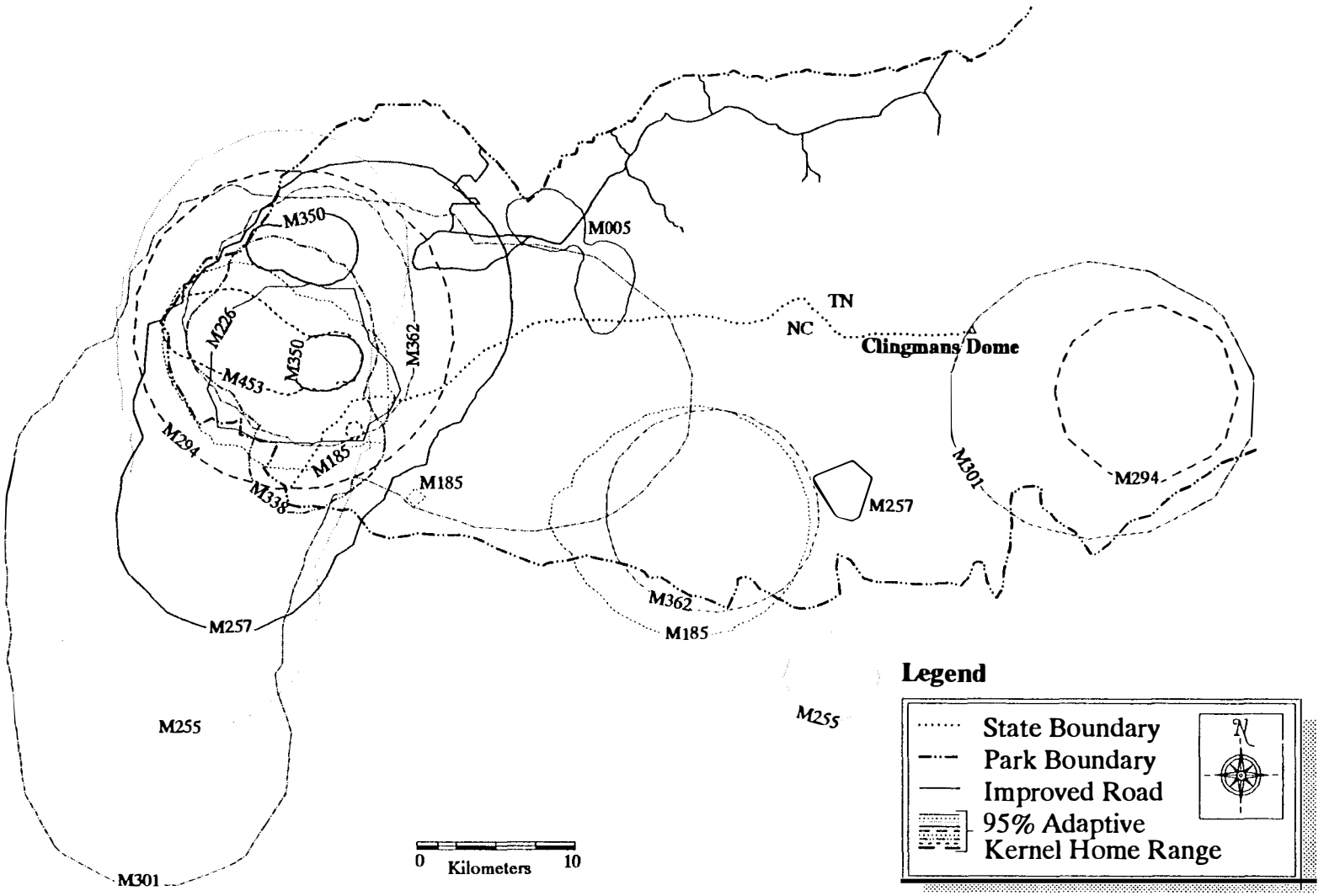


Fig. 15. Overall 95% adaptive kernel home range configurations of male black bears, Great Smoky Mountains National Park, 1976-1982.

Annual Home Ranges. Annual home range estimates for females were calculated for 1977-1981 (Tables C.1-C.5 and D.2, Fig. 16). Annual female home ranges (Table 5) were smaller than overall estimates for all methods and contours (S = 14.0 to 18.0, n = 8, P = 0.0550 to 0.0078) except the 95% harmonic mean and 50% adaptive kernel contours. Annual home range estimates for males were calculated only for 1979 and 1981 (Tables C.3, C.5, and D.2, Fig. 17). Estimates of home ranges for both years combined (Table 5) were smaller than the overall estimates for all methods and contours (t = 2.21 to 3.54, n = 6, P = 0.0782 to 0.0165) except the 95% harmonic mean estimate (t = 2.06, n = 6, P = 0.0948). Mean annual home range estimates were smaller for females compared with males for all methods and contours (Z = 2.94 to 3.64, P = 0.0032 to 0.0003). Home range sizes could not be compared among years in a repeated measures analysis due to small sample sizes. To arrive at some measure of change in annual home range size, I used differences between any pair of annual home range estimates of a certain bear. For females, no differences were detected for any of the home range methods and contours (t = 0.14 to 1.31, n = 11, P = 0.8941 to 0.2202) except the 50% harmonic mean contour (t = 2.21, n = 11, P = 0.0519). Sample sizes for males were too small to compare annual home range estimates.

I found no relationship between age (including subadults) and all adaptive kernel estimates for females (F = 0.21 to 1.38; 1,8 df; P = 0.6618 to 0.2789) or males (F = 0.02 to 1.24; 1,4 df; P = 0.8862 to 0.3473).

Seasonal Home Ranges. For females, seasonal home range sizes were estimated

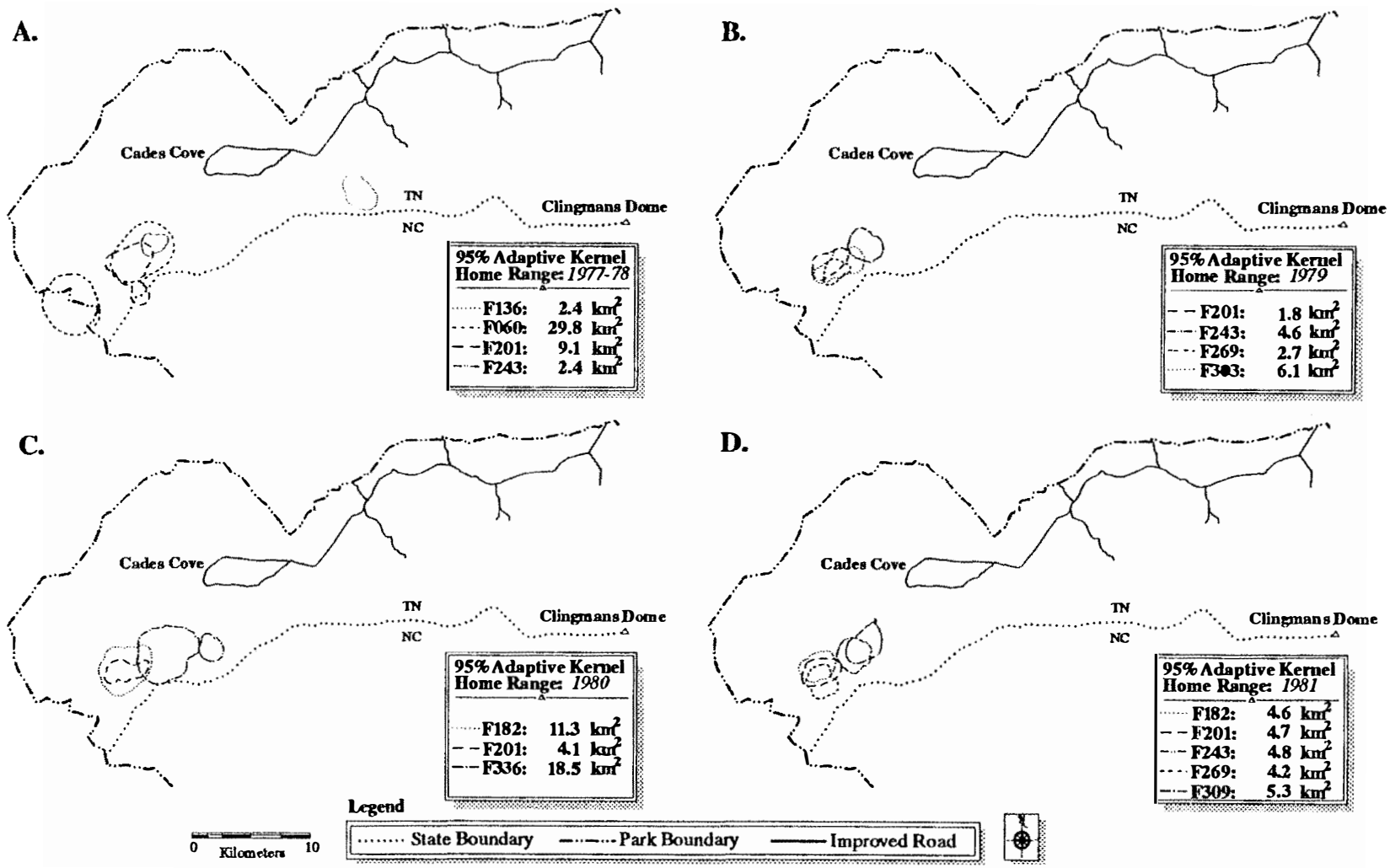


Fig. 16. Annual 95% adaptive kernel home range configurations of female black bears, Great Smoky Mountains National Park, 1977-1981.

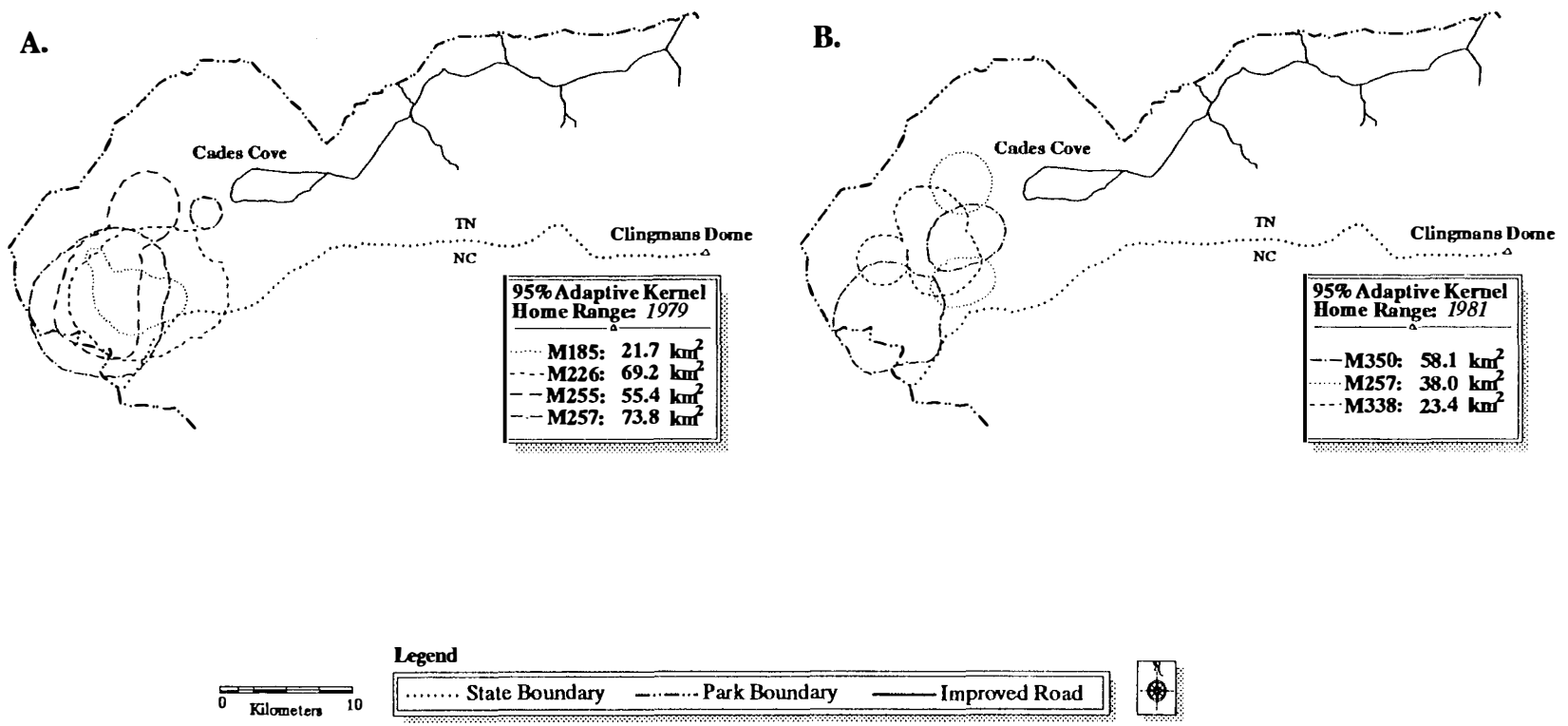


Fig. 17. Annual 95% adaptive kernel home range configurations of male black bears, Great Smoky Mountains National Park, 1979 and 1981.

Table 5. Estimates of annual home range sizes (km^2) of black bears in Great Smoky Mountains National Park, 1977-1981.

		Females				Males			
	%	$\bar{x}$	SD	n	range	$\bar{x}$	SD	n	range
	100%	11.0	11.6	16	3.6-50.4	200.2	316.6	7	23.1-906.3
Harmonic	95%	5.5	4.5	16	1.8-17.2	40.0	21.8	7	15.0-67.1
Mean	75%	1.9	1.1	16	0.8-5.4	13.0	7.2	7	4.3-21.4
	50%	0.8	0.5	16	0.3-2.3	5.2	3.5	7	0.8-10.0

		Females				Males			
	%	$\bar{x}$	SD	n	range	$\bar{x}$	SD	n	range
	100%	6.9	6.8	16	2.3-29.2	51.2	32.9	7	16.0-109.0
Convex	95%	4.3	3.9	16	1.3-17.7	28.3	14.6	7	14.2-51.1
Polygon	75%	2.6	3.1	16	0.7-14.1	12.2	7.5	7	2.1-22.4
	50%	1.5	2.7	16	0.3-11.6	5.2	3.8	7	1.0-11.2

		Females				Males			
	%	$\bar{x}$	SD	n	range	$\bar{x}$	SD	n	range
	100%	14.5	18.1	16	4.3-79.1	107.0	61.7	7	52.2-199.8
Adaptive	95%	7.6	7.1	16	2.4-29.8	48.5	21.1	7	21.7-73.8
Kernel	75%	2.6	1.9	16	1.0-9.3	16.4	8.1	7	6.2-26.4
	50%	1.2	0.6	16	0.5-3.1	6.4	4.0	7	0.9-12.2

for spring, summer, and fall (Tables 6-8 and D.3, Fig. 18). For males, home range sizes were estimated for summer and fall (Tables 7, 8, and D.3, Fig. 19). Spring home range sizes were not estimated for males due to small sample sizes. Fall home range sizes of females were not different from summer home ranges for all methods and contours (t = 1.23 to 2.17, n = 4, P = 0.3065 to 0.1188). No comparisons could be made for female spring home ranges and for all seasonal male home ranges due to small sample sizes.

Annual home range estimates for females were not different from summer or fall estimates for all methods and contours (t = 0.01 to 1.49, n = 4, P = 0.9933 to 0.2324 and S = 3.0 to 5.0, n = 4, P = 0.2500 to 0.1250, respectively). Sample sizes for males were too small to allow comparisons.

Movements. The mean distance between female centers of activity was 536 m (SD = 332, n = 4, range = 138-1,152 m) from spring to summer and 761 m (SD = 528, n = 5, range = 323-1,608 m) from summer to fall (Fig. 20). Distances between overall and seasonal centers of activity averaged 273 m (SD = 264, n = 6, range = 0-302 m) for summer and 613 m (SD = 518, n = 6, range = 250-1,636 m) for fall. The distance between female activity centers of consecutive years averaged 375 m (SD = 223, n = 9, range = 143-815 m). The mean distance from overall to annual centers of activity was 412 m (SD = 672, n = 20, range = 46-3,185 m). Mean distances between summer and fall activity centers of females were not different from distances between annual activity centers (t = 1.12, n = 4, P = 0.3445).

For males, only the mean distance between summer and fall activity centers was

Table 6. Estimates of spring home range sizes (km^2) of black bears in Great Smoky Mountains National Park, 1976-1982.

		Females				Males			
	%	$\bar{x}$	SD	n	range	$\bar{x}$	SD	n	range
Harmonic Mean	100%	3.2	1.1	2	2.5-4.0	-	-	-	-
	95%	1.9	0.7	2	1.5-2.4	-	-	-	-
	75%	0.9	0.4	2	0.6-1.1	-	-	-	-
	50%	0.3	0.1	2	0.3-0.4	-	-	-	-

		Females				Males			
	%	$\bar{x}$	SD	n	range	$\bar{x}$	SD	n	range
Convex Polygon	100%	2.2	0.5	2	1.8-2.5	-	-	-	-
	95%	1.6	0.6	2	1.2-1.9	-	-	-	-
	75%	0.8	0.3	2	0.6-1.0	-	-	-	-
	50%	0.4	0.2	2	0.3-0.5	-	-	-	-

		Females				Males			
	%	$\bar{x}$	SD	n	range	$\bar{x}$	SD	n	range
Adaptive Kernel	100%	4.8	0.7	2	4.3-5.3	-	-	-	-
	95%	2.5	1.0	2	1.8-3.2	-	-	-	-
	75%	1.1	0.4	2	0.9-1.4	-	-	-	-
	50%	0.5	0.1	2	0.5-0.6	-	-	-	-

Table 7. Estimates of summer home range sizes (km^2) of black bears in Great Smoky Mountains National Park, 1976-1982.

		Females				Males			
	%	$\bar{x}$	SD	n	range	$\bar{x}$	SD	n	range
Harmonic Mean	100%	16.4	19.3	4	5.8-45.4	143.9	92.0	3	50.4-234.3
	95%	4.4	0.5	4	3.7-4.9	46.4	24.0	3	20.5-68.0
	75%	1.9	0.4	4	1.6-2.4	8.2	4.5	3	4.4-13.2
	50%	0.9	0.2	4	0.8-1.1	4.2	2.8	3	2.1-7.4

		Females				Males			
	%	$\bar{x}$	SD	n	range	$\bar{x}$	SD	n	range
Convex Polygon	100%	7.3	4.4	4	3.7-13.4	44.2	20.9	3	27.2-67.5
	95%	3.2	0.5	4	2.8-3.8	24.0	9.4	3	15.5-34.1
	75%	1.7	0.2	4	1.5-1.9	7.5	3.8	3	3.2-10.6
	50%	0.9	0.2	4	0.8-1.1	3.9	2.0	3	1.8-5.9

		Females				Males			
	%	$\bar{x}$	SD	n	range	$\bar{x}$	SD	n	range
Adaptive Kernel	100%	9.4	3.4	4	5.7-12.7	83.1	39.5	3	60.0-128.7
	95%	5.2	0.8	4	4.4-5.9	43.0	17.4	3	26.0-60.8
	75%	2.0	0.2	4	1.8-2.2	9.6	4.6	3	4.9-14.1
	50%	1.0	0.02	4	0.9-1.0	4.5	2.7	3	2.5-7.6

Table 8. Estimates of fall home range sizes (km^2) of black bears in Great Smoky Mountains National Park, 1976-1982.

		Females				Males			
	%	$\bar{x}$	SD	n	range	$\bar{x}$	SD	n	range
	100%	88.5	120.8	4	8.8-264.7	749.0	467.2	3	283.7-1,218.0
Harmonic	95%	30.6	38.5	4	7.0-87.7	410.7	249.6	3	122.5-556.7
Mean	75%	5.5	5.9	4	2.3-14.3	88.3	49.3	3	42.1-140.2
	50%	1.5	1.0	4	0.9-2.9	23.2	12.6	3	8.7-30.8

		Females				Males			
	%	$\bar{x}$	SD	n	range	$\bar{x}$	SD	n	range
	100%	24.4	29.7	4	7.9-68.9	511.1	315.6	3	212.7-841.5
Convex	95%	10.1	6.4	4	5.4-19.2	485.6	309.7	3	209.4-820.5
Polygon	75%	3.6	2.4	4	2.1-7.1	63.7	13.5	3	55.2-79.3
	50%	1.4	0.7	4	0.7-2.3	25.4	16.5	3	6.8-38.2

		Females				Males			
	%	$\bar{x}$	SD	n	range	$\bar{x}$	SD	n	range
	100%	42.3	51.1	4	14.7-118.9	857.8	407.0	3	393.3-1,152.0
Adaptive	95%	23.3	27.0	4	7.9-63.7	470.8	218.8	3	220.6-625.9
Kernel	75%	7.0	7.3	4	3.0-17.9	118.8	68.4	3	70.8-197.1
	50%	1.8	1.0	4	1.0-3.3	31.5	21.8	3	9.0-52.6

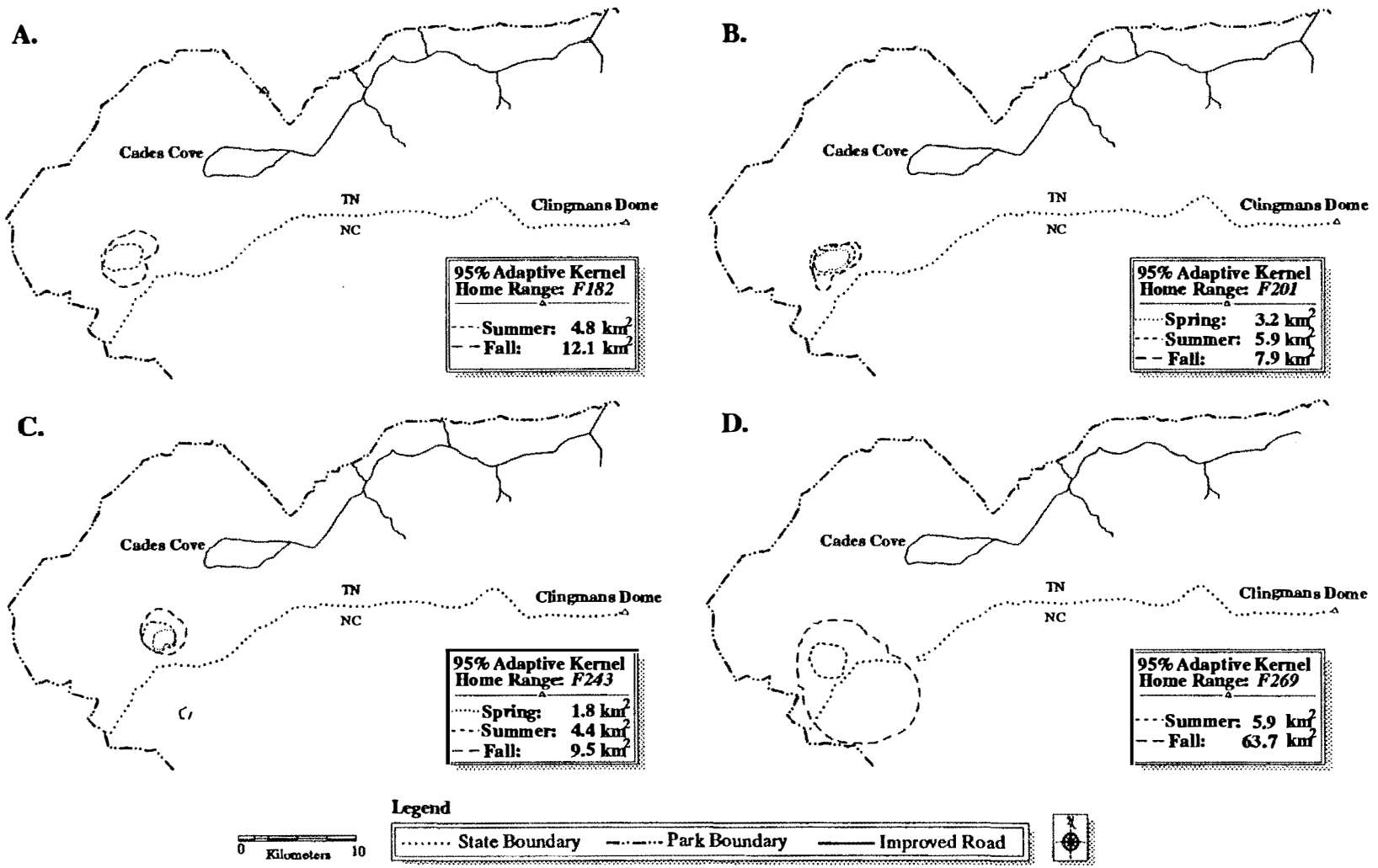


Fig. 18. Seasonal 95% adaptive kernel home range configurations of female black bears, Great Smoky Mountains National Park, 1976-1982.

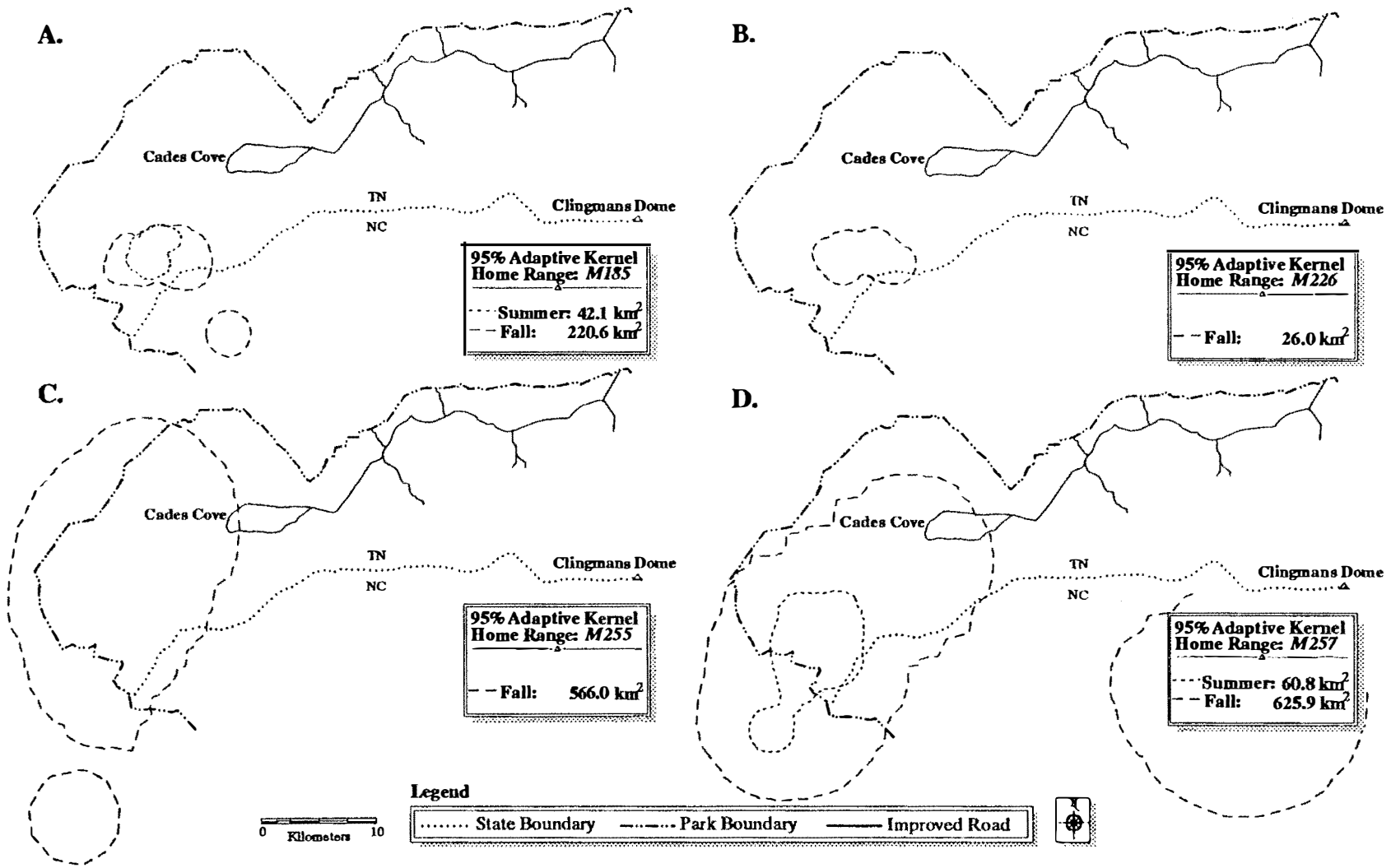


Fig. 19. Seasonal 95% adaptive kernel home range configurations of male black bears, Great Smoky Mountains National Park, 1976-1982.

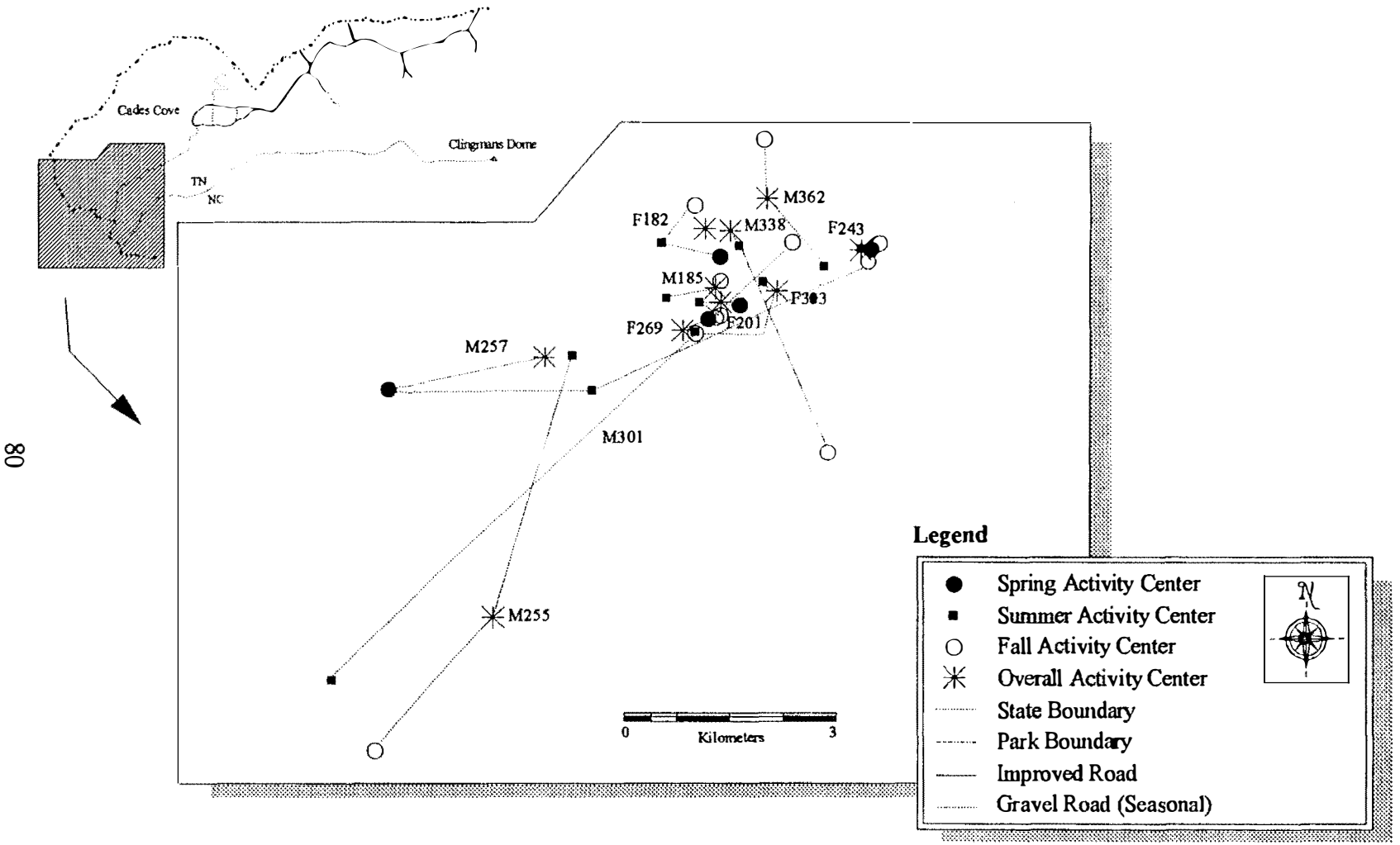


Fig. 20. Seasonal activity centers of black bears in Great Smoky Mountains National Park, 1976-1982.

calculated and was 6,100 m (SD = 4,288, n = 6, range = 962-12,542 m) (Fig. 20). Distances between overall and seasonal activity centers of males averaged 2,660 m (SD = 2,143, n = 8, range = 403-6,240 m) and 4,491 m (SD = 5,167, n = 7, range = 204-15,028 m) for summer and fall, respectively. Distances between male activity centers of consecutive years averaged 3,013 m (SD = 1,716, n = 7, range = 1,397-6,276 m), which was larger compared with females (t' = 4.04, 6.2 df, P = 0.0065). The mean distance from overall to annual centers of activity of males was 2,920 m (SD = 3,689, n = 18, range = 197-14,402 m) and was also larger than that of females (after log-normalization: t' = 5.53, 32.2 df, P = 0.0001). Mean distances between summer-fall and annual activity centers of males were not different (t = 1.11, n = 4, P = 0.3497).

Rates of travel for 11 females and 14 males were determined from 855 and 586 diel locations of 57 and 47 diel periods, respectively. Average time between diel locations was 68.3 minutes (SD = 28.7, range = 39.0-240.0 min) for females and 69.3 minutes (SD = 28.9, range = 37.0-240.0 min) for males. The overall log-normalized mean rate of travel for females ($\overline{x}$ = 2.69 log(m/hr), SD = 0.18, n = 57, range = 2.31-3.10 log(m/hr)) and males ($\overline{x}$ = 2.75 log(m/hr), SD = 0.26, n = 47, range = 2.20-3.28 log(m/hr)) were different (t = 1.96, P = 0.0539).

The mean annual travel rate for females was 477 m/hr (SD = 300, n = 16, range = 254-1,254 m/hr) and 665 m/hr for males (SD = 309, n = 19, range = 200-1,228 m/hr). The mean difference in travel rates between any 2 years was not different from 0 for females ($\overline{x}$ = 50 m/hr, SD = 241, n = 20, range = -211-867 m/hr) (S

= 12.0, n = 20, P = 0.6742) or males ($\bar{x}$ = 135 m/hr, SD = 437, n = 11, range = -568-1,028 m/hr) (S = 1.0, n = 11, P = 0.3306). Mean female and male travel rates were not different for 1978 and 1979 but male travel rates were significantly greater in 1980 and 1981 (after log-normalization: t = 2.84; 21,11 df; P = 0.0077 and t = 2.76; 18,15 df; P = 0.0101, respectively).

Travel rates of females averaged 392 m/hr (SD = 96, n = 3, range = 336-503 m/hr) in spring, 487 m/hr (SD = 177, n = 8, range = 279-871 m/hr) in summer, and 615 m/hr (SD = 362, n = 8, range = 307-1,254 m/hr) in fall. Male travel rates averaged 449 m/hr (SD = 318, n = 2, range = 224-674 m/hr) in spring, 748 m/hr (SD = 356, n = 5, range = 385-1,228 m/hr) in summer, and 335 m/hr (SD = 181, n = 4, range = 189-598 m/hr) in fall. Differences in seasonal travel rates could only be compared for summer and fall and were not different from 0 for females (t = 0.99, n = 8, P = 0.3562) or males (t = 1.34, n = 4, P = 0.2734). Log-normalized female and male travel rates were different for summer and fall (t = 2.96; 38,37 df; P = 0.0042 and t = 2.06; 16,6 df; P = 0.0519, respectively); females had greater travel rates in the fall and males had greater travel rates in the summer.

Repeated measures analysis on normalized mean female travel rates indicated no significant differences among 3-hour periods of the day (F = 1.39; 8,18 df; P = 0.2150) but indicated that patterns of travel rates were different among individual bears (interaction between time period and individual: F = 1.87; 56,126 df; P = 0.0021). For males, these findings were reversed with a significant time effect (F =

3.25; 7,7 df; $P = 0.0065$) but no significant time period-individual interaction ($F = 0.94$; 49,49 df; $P = 0.5918$). For males, greatest travel rates occurred from 6:00 to 20:00. Similar patterns were observed during each season for both sexes.

Mean travel rates only differed between females and males for the 18:00 to 21:00 period in which female travel rates were greater ($Z = 1.86$, $P = 0.0636$). Seasonal mean travel rates were greater for males compared with females for the 9:00-12:00 period in summer ($Z = 1.79$, $P = 0.0734$) and greater for females during the 12:00-15:00 and 18:00-21:00 periods in the fall ($Z = 2.16$, $P = 0.0311$ and $Z = 2.36$, $P = 0.0185$, respectively).

Mean distances between simultaneous locations (i.e., estimated < 8 hours of each other) of females were calculated and compared with mean randomized distances for 11 female pairs with $> 50\%$ home range overlap. For 7 of 11 pairs, mean distances between simultaneous locations were not different from randomized location pairs ($Z = 0.18$ to 1.40, $P = 0.8613$ to 0.1591). For 2 pairs, mean distances were smaller, and for 2 other pairs this distance was larger than expected ($Z = 2.11$ to 2.14, $P = 0.0347$ to 0.0316 and $Z = 4.73$ to 5.21, $P < 0.0001$). This pattern changed slightly by season. In spring, mean distances for 3 pairs were not different from randomized distances ($Z = 0.25$ to 1.55, $P = 0.8028$ to 0.1201) but distances of 4 pairs were greater than expected ($Z = 2.10$ to 3.58, $P = 0.0358$ to 0.0004). In summer, mean distances between simultaneous locations showed no statistical difference from random expectation for 7 animal pairs ($Z = 0.11$ to 1.47, $P = 0.9148$ to 0.1409) whereas mean distances of 3 pairs were greater than expected ($Z = 2.24$ to 5.07, $P <$

0.0253). In fall, mean distances between simultaneous locations of 6 pairs were not different from randomized location pairs (Z = 0.23 to 1.65, P = 0.8181 to 0.0983), whereas 2 pairs had smaller and 3 pairs had larger mean distances than expected (Z = 1.81 to 1.98, P = 0.0703 to 0.0477 and Z = 2.05 to 3.14, P = 0.0407 to 0.0017, respectively).

The mean distance between simultaneous locations of female pairs was 1,706 m (SD = 1,227, n = 7, range = 838-3,862 m) for spring, 1,636 m (SD = 960, n = 10, range = 848-3,643 m) for summer, and 2,733 m (SD = 1,291, n = 10, range = 1,327-5,318 m) for fall. Mean distances between simultaneous locations were greater for fall compared with spring (t = 3.74, n = 7, P = 0.0096) and fall compared with summer (t = 3.37, n = 9, P = 0.0099), but not for spring compared with summer (t = 0.61, n = 7, P = 0.5645).

Mean distances between simultaneous locations of male bears were not different from mean randomized distances for 23 of 35 pairs, smaller for 5 pairs, and larger for 7 pairs (Z = 0.04 to 1.70, P = 0.9688 to 0.0892; Z = 2.63 to 3.66, P = 0.0086 to 0.0003; and Z = 1.85 to 3.66, P = 0.0638 to 0.0003, respectively). As with females, this pattern did not change much by season. In summer, mean distances between simultaneous locations of 28 of 33 pairs were not different from randomized distances (Z = 0.04 to 1.67, P = 0.9650 to 0.0940) whereas 1 was larger and 4 were smaller than expected (Z = 2.17, P = 0.0301 and Z = 2.35 to 3.10, P = 0.0189 to 0.0019, respectively). In fall, mean distances between simultaneous locations of 15 of 29 pairs showed no difference from randomized distances (Z = 0.36 to 1.62, P =

0.7141 to 0.1062) whereas mean distances for 6 pairs were smaller and 8 were larger than expected (Z = 1.82 to 2.91, P = 0.0683 to 0.0036 and Z = 1.82 to 3.95, P = 0.0693 to 0.0000, respectively). Sample sizes for spring were insufficient for analysis. Males had greater distances between simultaneous locations in fall ($\overline{x}$ = 16,044 m, SD = 14,064, n = 29, range = 3,156-54,575 m) compared with summer ($\overline{x}$ = 7,220 m, SD = 4,650, n = 33, range = 639-18,541 m) (S = 179.0, n = 28, $P < 0.0001$).

The log-normalized mean distance between simultaneous locations was greater for males than for females for all locations (males: $\overline{x}$ = 3.92 log(m), SD = 0.32, n = 35, range = 3.31-4.49 log(m); females: $\overline{x}$ = 3.34 log(m), SD = 0.22, n = 17, range = 3.02-3.71 log(m)) (t = 6.62; 35,17 df; $P < 0.0001$), summer locations (males: $\overline{x}$ = 3.75 log(m), SD = 0.33, n = 33, range = 2.80-4.26 log(m); females: $\overline{x}$ = 3.15 log(m), SD = 0.22, n = 10, range = 2.93-3.56 log(m)) (t = 5.34; 33,10 df; $P < 0.0001$), and fall locations (males: $\overline{x}$ = 4.06 log(m), SD = 0.36, n = 29, range = 3.49-4.74 log(m); females: $\overline{x}$ = 3.39 log(m), SD = 0.21, n = 10, range = 3.12-3.73 log(m)) (t = 5.60; 29,10 df; $P < 0.0001$). Samples sizes for spring were insufficient for comparisons.

For 32 female-male pairs with overlapping home ranges, mean distances between simultaneous locations were larger than mean distances between randomized locations for 19 pairs, smaller for 3 pairs, and not different for 10 pairs (Z = 1.80 to 5.23; $P < 0.0722$, Z = 2.40 to 3.17; P = 0.0163 to 0.0015, and Z = 0.10 to 1.40; P = 0.9162 to 0.1614, respectively). During spring, mean distances between simultaneous

locations of 8 of 12 female-male pairs were larger whereas 4 were not different from expected (Z = 1.80 to 4.54, P = 0.0721 to 0.0000 and Z = 0.24 to 1.66, P = 0.8113 to 0.0963, respectively). Eighteen of 30 female-male pairs had larger mean distances between simultaneous summer locations than expected (Z = 1.93 to 4.62, P = 0.0537 to 0.0000) whereas 12 were not different (Z = 0.24 to 0.89, P = 0.8103 to 0.0815). Distances between simultaneous fall locations of female-male pairs were larger than expected from randomized distances for 15 pairs (Z = 1.89 to 3.90, P = 0.0589 to 0.0000), smaller for 3 pairs (Z = 2.08 to 3.22, P = 0.0373 to 0.0013), and not different for 13 pairs (Z = 0.40 to 1.74, P = 0.6912 to 0.0819).

Distances between simultaneous female-male locations averaged 3,851 m (SD = 2,213, n = 12, range = 1,408-8,195 m) for spring, 6031 m (SD = 4,576, n = 29, range = 1,495-17,372 m) for summer, and 14,101 m (SD = 14,104, n = 29, range = 1,398-46,351 m) for fall. Differences between mean simultaneous distances of female-male pairs were greater for fall compared with spring (t = 3.10, n = 12, P = 0.0101) and fall compared with summer (S = 198, n = 29, $P < 0.0001$), but not for spring compared with summer (t = 0.96, n = 12, P = 0.3601).

Habitat Use Analysis

Overall - Females. Both AIC and ICOMP criteria indicated the best fit for relatively high dimensional models; model 1, containing all 9 variables, seemed to be the best model to explain variation in habitat use by bears (Table 9). Addition of the variable proximity to streams to model 1 did not decrease the values of AIC and

Table 9. Summary of best subsets of Akaike's information criterion (AIC) and information-theoretic measure of complexity (ICOMP) values for each level of i (i=no. of independent variables) and all univariate values for logistic regression models of habitat use of female black bears, Great Smoky Mountains National Park, 1976-1982. The global minimum for each criterion is denoted by †.

Model	Habitat Variables[a]									k[b]	-2LogL	$C_1(\hat{F}^{-1})$	AIC	ICOMP
1	VE	VR	EL	SL	AS	DH	TR	HA	RO	21	3,669.6	46.6	**3,711.6†**	**3,762.8†**
2	VE	VR	EL	SL	AS	DH	TR	HA		20	3,682.1	44.7	3,722.1	3,771.5
15	VE	VR	EL		AS	DH	TR	HA		19	3,694.4	41.4	3,732.4	3,777.2
64	VE	VR	EL			DH	TR	HA		15	3,720.9	32.0	3,750.9	3,784.9
177	VE		EL			DH	TR	HA		14	3,750.0	28.8	3,778.0	3,807.6
259	VE	VR	EL				TR			11	3,790.4	26.2	3,812.4	3,842.8
378	VE		EL				TR			10	3,816.5	23.0	3,836.5	3,862.5
470			EL				TR			3	3,882.8	7.1	3,888.8	3,897.0
504	VE									8	3,984.5	20.6	4,000.5	4,025.7
505		VR								2	3,964.7	8.2	3,968.7	3,981.1
506			EL							2	3,957.7	7.4	3,961.7	3,972.5
507				SL						2	4,069.0	9.1	4,073.0	4,087.2
508					AS					5	4,037.5	15.1	4,047.5	4,067.7
509						DH				4	4,028.6	12.6	4,036.6	4,053.8
510							TR			2	3,994.0	3.7	3,998.0	4,001.4
511								HA		2	4,055.9	3.7	4,059.9	4,063.3
512									RO	2	4,066.5	3.7	4,070.5	4,073.9

[a] See Table 3 for explanation of variables codes.

[b] k = no. of estimated parameters including the intercept.

ICOMP. I confirmed the assumption of linearity in the logit for the continuous variables with a graphical technique (Hosmer and Lemeshow 1989). This model included all variables needed to explain variation in habitat use and the variables were scaled appropriately. The Hosmer-Lemeshow goodness-of-fit statistic, $\hat{C}$, for this model ($\hat{C}$ = 12.26, 8 df, P = 0.14) indicated a fair fit of the model to the data. I used regression diagnostics to identify outlying observations with high leverage ($h >$ 0.008). Exclusion of 28 outliers with high leverage resulted in an improvement of the fit of the model ($\hat{C}$ = 7.22, 8 df, P = 0.513). This model was chosen as the operating model. Because of the complexity of the female habitat model, interactions terms could not be included. Based on a probability cut-off point of 0.5, the sensitivity and specificity of the model were 68.8% and 66.9%, respectively, resulting in an overall 67.8% correct classification. The false positive and false negative rates were 34.2% and 30.2%, respectively. The correlation coefficients of the maximum likelihood parameter estimates were relatively small with large correlation coefficients occurring mostly among parameter estimates of the same variable and the constant term (Table E.1).

The results of the logistic regression analysis of this model (Table 10) were used to quantify habitat use patterns of female black bears in the study area, based on equation (8) (page 62). For example, a pixel that corresponds to an area with xeric oak, a vegetation richness of 3, a slope of 20°, at 630 m elevation, southeastern aspect, no historical cuts, 225 m from a trail, 6,705 m from a human activity site, and 3,195 m from an improved road, would have a g(x) = 0.5066 (sum of all

Table 10. Results of logistic regression analysis of overall habitat use of female black bears, Great Smoky Mountains National Park, 1976-1982.

Variable Code	Class	Parameter Estimate	Standard Error	Chi-Square	Prob.
CONSTANT		-1.7252	0.2383	52.40	0.0000
VE1	Northern Hrdwd.	-0.2174	0.2530	0.74	0.3902
VE2	Cove Hrdwd./Pine-Oak	0.4023	0.1280	9.88	0.0017
VE3	Mesic Oak	-2.9101	0.5398	29.06	0.0000
VE4	Mixed Mesic Hrdwd.	0.4402	0.1287	11.70	0.0000
VE5	Tulip Poplar	0.5717	0.1858	9.47	0.0021
VE6	Xeric Oak	0.6704	0.1364	24.15	0.0000
VE7	Pine	0.1413	0.1382	1.05	0.3067
VE8	Nonforest	0.9017	0.3780	5.69	0.0171
VR	Unit: 1 Veg. Type	0.2799	0.0426	43.15	0.0000
SL	Unit: 1 Degree	0.0264	0.00691	14.61	0.0001
EL1	< 600 m, > 1,000 m	-0.4117	0.0616	44.62	0.0000
EL2	600-1,000 m	0.4117	0.0616	44.62	0.0000
AS1	N	0.2284	0.1086	4.42	0.0356
AS2	NE, SE, S, SW, W	0.00309	0.0830	0.00	0.9703
AS3	E	-0.5433	0.1772	9.40	0.0022
AS4	NW	0.2490	0.0949	6.88	0.0087
AS5	Flat	0.0629	0.1744		
DH1	Uncut	-0.9470	0.1171	65.41	0.0000
DH2	Light Cut/Undisturbed	-0.3393	0.1387	5.99	0.0144
DH3	Heavy Cut	0.8859	0.1245	50.66	0.0000
DH4	Settlement	0.4004	0.1370	8.54	0.0035
TR	Unit: 1 Meter	-0.00135	0.000156	75.42	0.0000
HA1	< 5,750 m	-0.4788	0.0694	47.57	0.0000
HA2	≥ 5,750 m	0.4788	0.0694	47.57	0.0000
RO1	< 2,500 m	-0.5509	0.0654	70.92	0.0000
RO2	≥ 2,500 m	0.5509	0.0654	70.92	0.0000

corresponding parameter estimates) and a relative habitat use probability of $e^{g(x)}/(1 + e^{g(x)}) = e^{0.5066}/(1 + e^{0.5066}) = 1.6596/2.6596 = 0.6240$ (Fig. 21).

For the categorical variables, the sign of the parameter estimate indicated whether a variable category was used more (+) or less (-) than expected, whereas the value of the parameter estimate indicated the magnitude of the relationship (Table 10). The *P*-value for the chi-square test associated with the parameter estimate indicated the statistical significance of this relationship and whether a parameter estimate was different from zero (Table 10). For example, use of cove hardwood/pine-oak was more than expected whereas mesic oak seemed to be used less than expected (Table 10).

For elevation, the parameter estimate translated into an odds ratio of 2.3 ($e^{2 \times 0.4117}$), estimating that relative bear use of elevations between 600 m and 1,000 m was 2.3 times more likely than use of elevations $<$ 600 m or $>$ 1,000 m. The parameter estimate for proximity to human activity sites indicated that relative bear use of areas $\geq$ 5,750 m from human activity sites was 2.6 times more likely than for areas $<$ 5,750 m. Relative bear use of areas $\geq$ 2,500 m from improved roads was estimated to be 3.0 times more likely than areas $<$ 2,500 m from improved roads. With every additional overstory vegetation type within a 270 m radius of a location, the predicted probability that bears would use that area increased by a factor 1.3 ($e^{0.2799}$). A 10-° increase of slope resulted in a 1.3 increase in the predicted probability of use. A 100-m increase of proximity to nearest trail decreased the predicted probability of bear use by a factor 0.9.

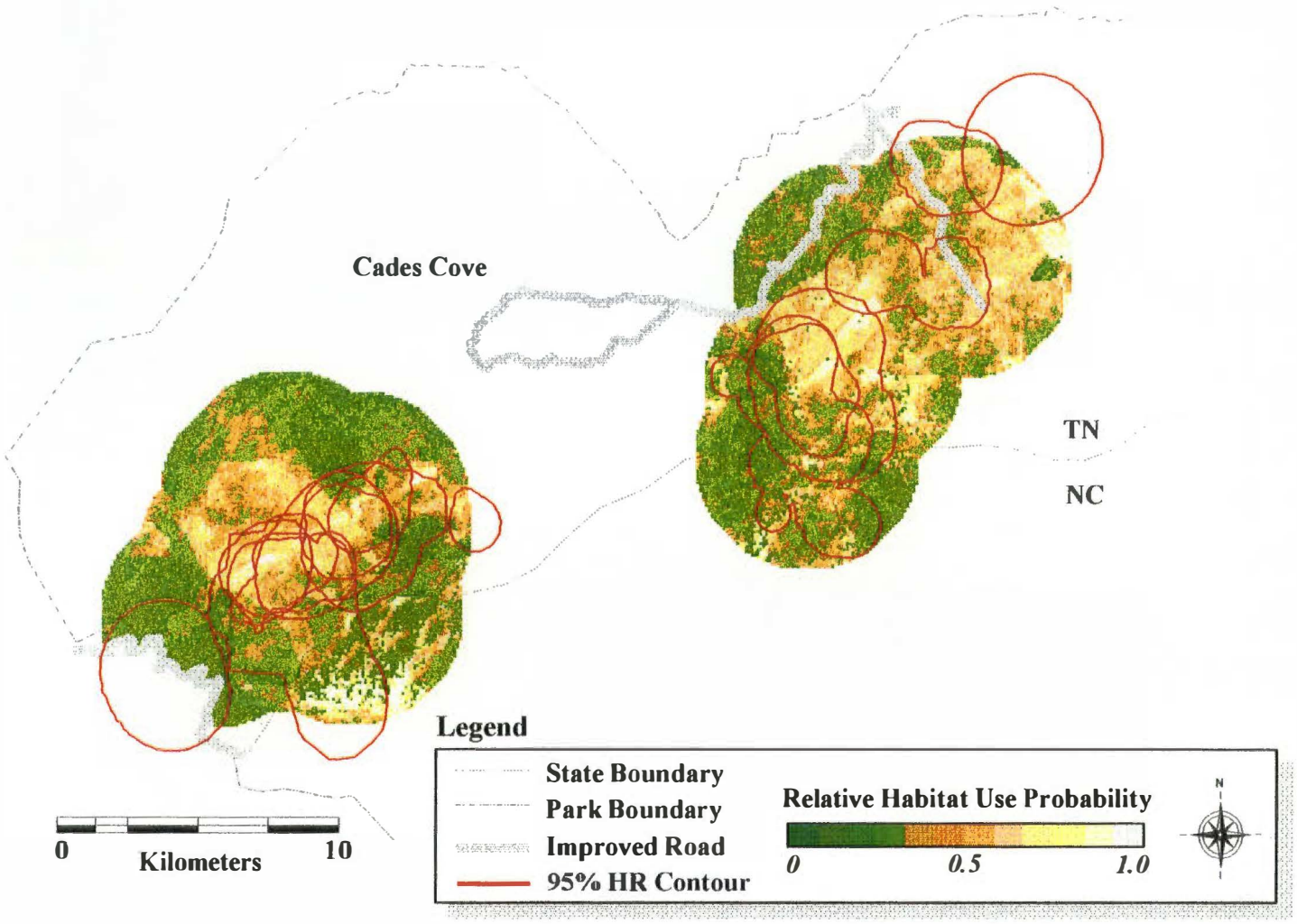


Fig. 21. Relative habitat use probability based on overall habitat use model of female black bears, Great Smoky Mountains National Park, 1976-1982.

For the categorical variables, contrasts of the maximum likelihood estimates revealed which variable categories received more bear use. Northern hardwood was used proportionally more than mesic oak (χ^2 = 17.21, 1 df, $P < 0.0001$) and less than xeric oak (χ^2 = 9.10, 1 df, P = 0.0025), cove hardwood/pine-oak (χ^2 = 5.00, 1 df, P = 0.0254), mixed mesic hardwood (χ^2 = 5.17, 1 df, P = 0.0230), tulip poplar (χ^2 = 5.63, 1 df, P = 0.0177), and nonforest areas (χ^2 = 5.03, 1 df, P = 0.0249). Pine vegetation types were used proportionally less than cove hardwood/pine-oak (χ^2 = 3.73, 1 df, P = 0.0534), mixed mesic hardwood (χ^2 = 5.73, 1 df, P = 0.0167), tulip poplar (χ^2 = 4.82, 1 df, P = 0.0281), xeric oak (χ^2 = 15.94, 1 df, P = 0.0001), and nonforest (χ^2 = 3.09, 1 df, P = 0.0787). Pine was used proportionally more than mesic oak (χ^2 = 23.77, 1 df, $P < 0.0001$), xeric oak more than mixed oak (χ^2 = 33.01, 1 df, $P < 0.0001$), mixed mesic hardwood more than mesic oak (χ^2 = 28.99, 1 df, $P < 0.0001$) and xeric oak (χ^2 = 3.40, 1 df, P = 0.0654), and cove hardwood/pine-oak more than mesic oak (χ^2 = 28.64, 1 df, $P < 0.0001$) but less than xeric oak (χ^2 = 3.98, 1 df, P = 0.0462). Mesic oak was used proportionally less than tulip poplar (χ^2 = 29.41, 1 df, $P < 0.0001$) and nonforest vegetation types (χ^2 = 26.37, 1 df, $P < 0.0001$).

The combination of northeastern, southeastern, southern, southwestern, and western aspects received relatively less use compared with northern aspects and northwestern aspects (χ^2 = 3.15, 1 df, P = 0.0760 and χ^2 = 5.61, 1 df, P = 0.0179, respectively) but more than eastern aspects (χ^2 = 6.01, 1 df, P = 0.0142). Eastern aspects were also used proportionally less than northern, northwestern, and

flat areas (χ^2 = 10.33, 1 df, P = 0.0013; χ^2 = 11.78, 1 df, P = 0.0006; and χ^2 = 4.28, 1 df, P = 0.0386, respectively).

Uncut areas were used proportionally less than light/undisturbed areas, heavily cut areas and settlement areas (χ^2 = 8.60, 1 df, P = 0.0034; χ^2 = 87.44, 1 df, $P <$ 0.0001; and χ^2 = 44.61, 1 df, $P <$ 0.0001, respectively). Heavily cut areas were used proportionally more than light cut/undisturbed areas (χ^2 = 33.22, 1 df, $P <$ 0.0001). Settlement areas were used more than light cut/undisturbed areas (χ^2 = 9.77, 1 df, P = 0.0018) but less than heavily cut areas (χ^2 = 5.17, 1 df, P = 0.0229).

Spring - Females. The spring model was based on 664 locations with the same 9 variables as the overall female habitat use model (Table 11). After exclusion of 18 outliers, this model fit the data ($\hat{C}$ = 11.276, 8 df, P = 0.187). The correlation coefficients of the maximum likelihood parameter estimates generally were small with largest coefficients occurring among parameter estimates of the same variable and the constant term (Table E.2). I calculated and mapped the relative habitat use probabilities for the study area (Fig. 22).

For elevation, the parameter estimate represented an odds ratio predicting that relative use of elevations between 600 m and 1,000 m was 2.1 times more likely than use of elevations < 600 m or > 1,000 m. The parameter estimate for proximity to human activity sites estimated that relative bear use of areas ≥ 5,750 m from human activity sites was 1.5 times more likely than for areas < 5,750 m. Relative bear use of areas ≥ 2,500 m from improved roads was predicted to be 9.0 times more likely

Table 11. Results of logistic regression analysis of spring habitat use of female black bears, Great Smoky Mountains National Park, 1976-1982.

Variable Code	Class	Parameter Estimate	Standard Error	Chi-Square	Prob.
CONSTANT		-1.9155	0.5141	13.88	0.0002
VE1	Northern Hrdwd.	-0.5730	0.4487	1.63	0.2016
VE2	Cove Hrdwd./Pine-Oak	0.4644	0.2160	4.62	0.0316
VE3	Mesic Oak	-1.0281	0.5305	3.76	0.0526
VE4	Mixed Mesic Hrdwd.	0.2614	0.2297	1.29	0.2552
VE5	Tulip Poplar	1.0353	0.3811	7.38	0.0066
VE6	Xeric Oak	0.0693	0.2547	0.07	0.7856
VE7	Pine	-0.9028	0.2735	10.90	0.0010
VE8	Nonforest	0.6735	0.5659	1.42	0.2339
VR	Unit: 1 Veg. Type	0.2485	0.0976	6.49	0.0109
SL	Unit: 1 Degree	0.0455	0.0143	10.14	0.0014
EL1	< 600 m, > 1,000 m	-0.3773	0.1386	7.41	0.0065
EL2	600-1,000 m	0.3773	0.1386	7.41	0.0065
AS1	N	0.4377	0.2495	3.08	0.0793
AS2	NE, SE, S, SW, W	0.3305	0.2116	2.44	0.1182
AS3	E	-1.4815	0.5429	7.45	0.0064
AS4	NW	0.3848	0.2291	2.82	0.0930
AS5	Flat	0.3284	0.4502	0.53	0.4657
DH1	Uncut	-1.0616	0.2815	14.22	0.0002
DH2	Light Cut/Undisturbed	-0.3708	0.2680	1.91	0.1665
DH3	Heavy Cut	0.2739	0.2495	1.21	0.2723
DH4	Settlement	1.1586	0.2624	19.49	0.0000
TR	Unit: 1 Meter	-0.00152	0.000371	16.73	0.0000
HA1	< 5,750 m	-0.2086	0.1654	1.59	0.2074
HA2	$\geq$ 5,750 m	0.2086	0.1654	1.59	0.2074
RO1	< 2,500 m	-1.0972	0.1731	40.16	0.0000
RO2	$\geq$ 2,500 m	1.0972	0.1731	40.16	0.0000

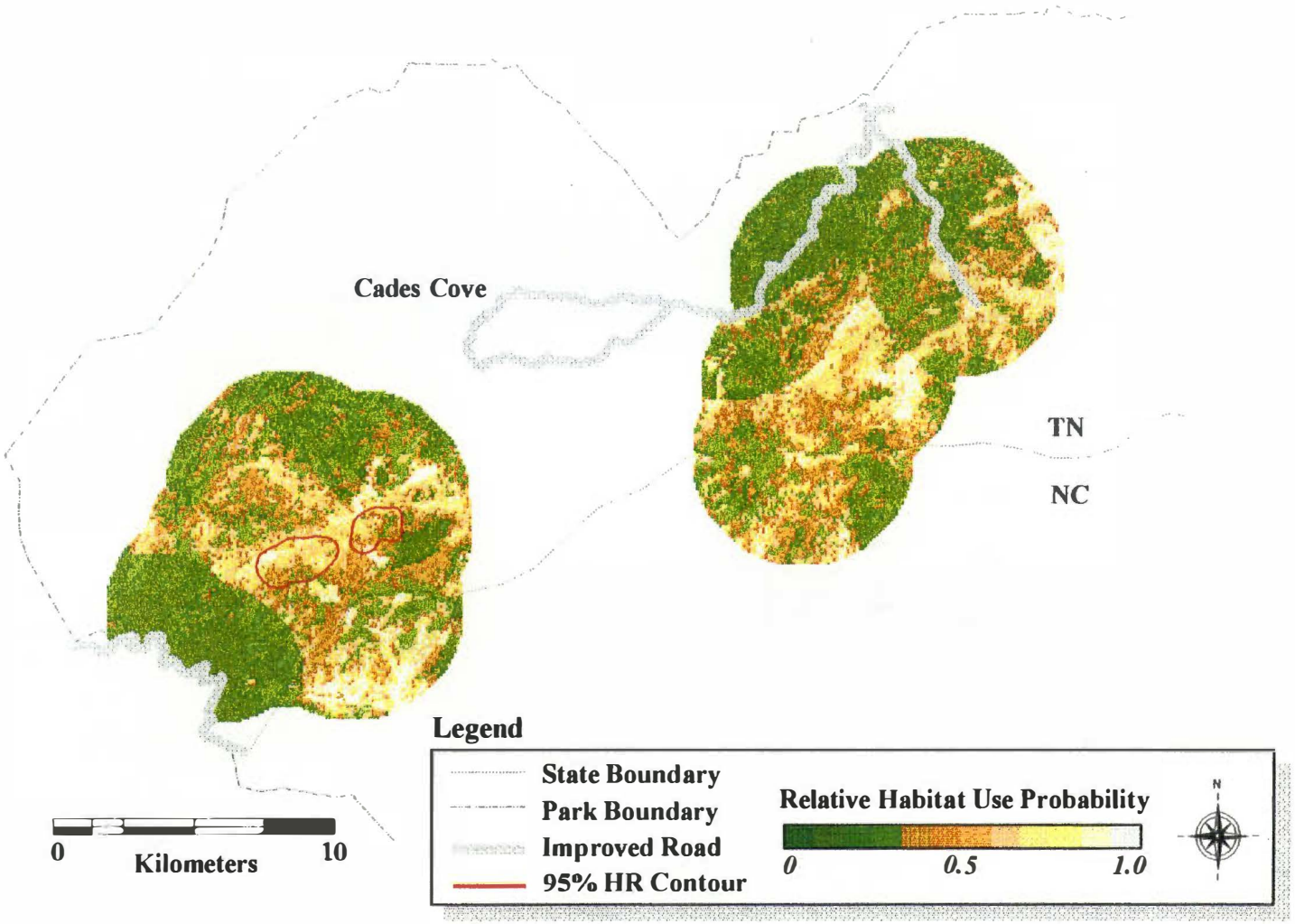


Fig. 22. Relative habitat use probability based on spring habitat use model of female black bears, Great Smoky Mountains National Park, 1976-1982.

than areas < 2,500 m from improved roads. Statistical inferences based on the parameter estimates of the continuous variables indicated that the probability of habitat use increased by a factor 1.3 with each additional overstory vegetation type within a 270-m radius. With every 10-° increase in slope, the probability of habitat use increased by a factor 1.6. Habitat use decreased by a factor 0.9 with every 100-m increase in distance to trails.

Proportional use of tulip poplar vegetation was greater than northern hardwood (χ^2 = 5.79, 1 df, P = 0.0161), mesic oak (χ^2 = 7.85, 1 df, P = 0.0051), mixed mesic hardwood (χ^2 = 3.17, 1 df, P = 0.0751), xeric oak (χ^2 = 4.51, 1 df, P = 0.0337), and pine (χ^2 = 17.30, 1 df, P < 0.0001). Pine was used proportionally less than cove hardwood/pine-oak (χ^2= 17.96, 1 df, P < 0.0001), mixed mesic hardwood (χ^2 = 14.12, 1 df, P = 0.0002), xeric oak (χ^2 = 8.59, 1 df, P = 0.0034), and nonforest (χ^2 = 5.29, 1 df, P = 0.0215). Mesic oak was used proportionally less than cove hardwood/pine-oak (χ^2 = 5.83, 1 df, P = 0.0158), mixed mesic hardwood (χ^2 = 4.01, 1 df, P = 0.0452), and nonforest (χ^2 = 3.82, 1 df, P = 0.0508). Northern hardwood was used proportionally less than cove hardwood/pine-oak (χ^2 = 4.05, 1 df, P = 0.0442).

Eastern aspects were used proportionally less than northern (χ^2 = 7.58, 1 df, P = 0.0059), northwestern (χ^2 = 7.34, 1 df, P = 0.0068), the combination of northeastern with southeastern, southern, southwestern, and western aspects (χ^2 = 7.21, 1 df, P = 0.0073), and flat areas (χ^2 = 4.59, 1 df, P = 0.0322).

Historically uncut areas were used proportionally less than heavily cut (χ^2 = 8.95,

1 df, $P = 0.0028$) and settlement areas ($\chi^2 = 23.56$, 1 df, $P < 0.0001$). Settlement areas were also used proportionally more than light cut/undisturbed areas ($\chi^2 = 11.83$, 1 df, $P = 0.0006$).

Summer - Females. For the summer locations, I fitted a model with the same variables as the overall model (Table 12). This model was based on 1208 locations (34 outliers excluded) and exhibited good explanatory power ($\hat{C} = 2.903$, 8 df, $P = 0.940$). The correlation coefficients of the maximum likelihood parameter estimates generally were small with largest coefficients occurring among parameter estimates of the same variable (Table E.3). Based on the summer model, I calculated and mapped the relative habitat use probabilities for the female study area (Fig. 23).

The parameter estimates for elevation predicted that relative bear use of elevations between 600 m and 1,000 m was 3.4 times more likely than use of elevations $<$ 600 m or $>$ 1,000 m. The parameter estimate for proximity to human activity sites estimated that relative bear use of areas $\geq$ 5,750 m from human activity sites was 3.1 times more likely than for areas $<$ 5,750 m. Relative bear use of areas $\geq$ 2,500 m from improved roads was predicted to be 4.4 times more likely than areas $<$ 2,500 m from improved roads. Based on the parameter estimate for overstory vegetation richness, the relative probability of habitat use increased by a factor 1.2 with each additional vegetation type within 270 m. With every 10-° increase in slope, the probability of habitat use increased by a factor 1.2. The predicted relative habitat use probability decreased by a factor 0.8 with every 100-m increase in distance to trails.

Mesic oak was used proportionally less than cove hardwood/pine-oak ($\chi^2 = 3.64$,

Table 12. Results of logistic regression analysis of summer habitat use of female black bears, Great Smoky Mountains National Park, 1976-1982.

Variable Code	Class	Parameter Estimate	Standard Error	Chi-Square	Prob.
CONSTANT		-1.3060	0.3792	11.86	0.0006
VE1	Northern Hrdwd.	0.0989	0.3931	0.06	0.8013
VE2	Cove Hrdwd./Pine-Oak	0.0218	0.1790	0.01	0.9033
VE3	Mesic Oak	-1.0039	0.4695	4.57	0.0325
VE4	Mixed Mesic Hrdwd.	0.0933	0.1755	0.28	0.5949
VE5	Tulip Poplar	0.2609	0.2856	0.83	0.3609
VE6	Xeric Oak	0.7468	0.1916	15.19	0.0001
VE7	Pine	-0.1281	0.1934	0.44	0.5076
VE8	Nonforest	-0.0896	0.6246	0.02	0.8859
VR	Unit: 1 Veg. Type	0.2156	0.0675	10.21	0.0014
SL	Unit: 1 Degree	0.0157	0.0119	1.76	0.1850
EL1	< 600 m, > 1,000 m	-0.6055	0.1072	31.92	0.0000
EL2	600-1,000 m	0.6055	0.1072	31.92	0.0000
AS1	N	0.1601	0.1749	0.84	0.3601
AS2	NE, SE, S, SW, W	0.1487	0.1309	1.29	0.2560
AS3	E	-0.8033	0.2772	8.40	0.0038
AS4	NW	0.3800	0.1522	6.23	0.0125
AS5	Flat	0.1145	0.2651	0.19	0.6659
DH1	Uncut	-0.9928	0.1863	28.39	0.0000
DH2	Light Cut/Undisturbed	0.3142	0.2346	1.79	0.1805
DH3	Heavy Cut	1.2509	0.2207	32.12	0.0000
DH4	Settlement	0.0560	0.2574	0.05	0.8277
TR	Unit: 1 Meter	-0.00185	0.000253	53.36	0.0000
HA1	< 5,750 m	-0.5634	0.1109	25.81	0.0000
HA2	≥ 5,750 m	0.5634	0.1109	25.81	0.0000
RO1	< 2,500 m	-0.7393	0.1113	44.15	0.0000
RO2	≥ 2,500 m	0.7393	0.1113	44.15	0.0000

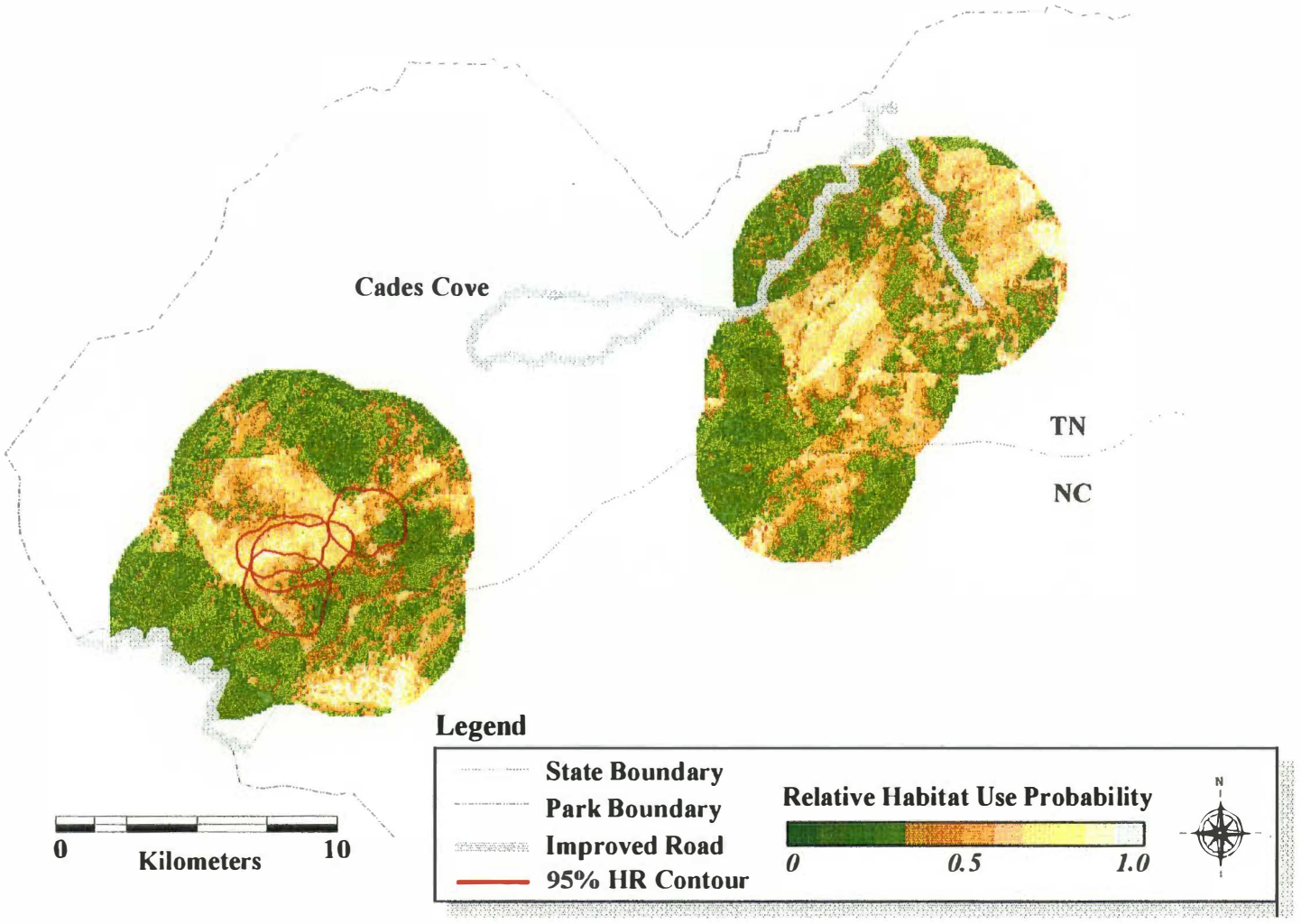


Fig. 23. Relative habitat use probability based on summer habitat use model of female black bears, Great Smoky Mountains National Park, 1976-1982.

1 df, $P = 0.0563$), mixed mesic hardwood ($\chi^2 = 4.04$, 1 df, $P = 0.0444$), and tulip poplar ($\chi^2 = 4.32$, 1 df, $P = 0.0377$). Xeric oak was used proportionally more than cove hardwood/pine-oak ($\chi^2 = 11.05$, 1 df, $P = 0.0009$), mixed mesic hardwood ($\chi^2 = 10.71$, 1 df, $P = 0.0011$), and pine ($\chi^2 = 17.16$, 1 df, $P < 0.0001$).

Eastern aspects were used proportionally less than northern ($\chi^2 = 6.42$, 1 df, $P = 0.0113$), northeastern, southeastern, southern, southeastern, and western aspects combined ($\chi^2 = 7.37$, 1 df, $P = 0.0066$), northwestern aspects ($\chi^2 = 10.63$, 1 df, $P = 0.0011$), and flat areas ($\chi^2 = 4.15$, 1 df, $P = 0.0416$).

Historically heavily cut areas were used proportionally more than uncut ($\chi^2 = 47.21$, 1 df, $P < 0.0001$), light cut/undisturbed ($\chi^2 = 19.13$, 1 df, $P < 0.0001$), and settlement areas ($\chi^2 = 8.66$, 1 df, $P = 0.0033$). Uncut areas were used proportionally less than light cut/undisturbed areas ($\chi^2 = 4.02$, 1 df, $P = 0.0449$) and settlement areas ($\chi^2 = 8.98$, 1 df, $P = 0.0027$).

Fall - Females. The fall habitat use model included all variables of the overall model except aspect (Table 13). This variable seemed to be unimportant in explaining variation in fall locations. The fall habitat use model was based on 1,069 locations and exhibited a good fit ($\hat{C} = 7.022$, 8 df, $P = 0.534$) after exclusion of 13 outliers. The correlation coefficients of the maximum likelihood parameter estimates had largest coefficients occurring among parameter estimates of the same variable and the constant term (Table E.4). Based on the fall habitat use model, I calculated and mapped the relative habitat use probabilities for the female study area (Fig. 24).

The parameter estimates for elevation predicted that relative bear use of elevations

Table 13. Results of logistic regression analysis of fall habitat use of female black bears, Great Smoky Mountains National Park, 1976-1982.

Variable Code	Class	Parameter Estimate	Standard Error	Chi-Square	Prob.
CONSTANT		-1.8615	0.3669	25.74	0.0000
VE1	Northern Hrdwd.	-0.8040	0.5345	2.26	0.1325
VE2	Cove Hrdwd./Pine-Oak	0.4449	0.1967	5.12	0.0237
VE3	Mesic Oak	-1.8786	0.5803	10.48	0.0012
VE4	Mixed Mesic Hrdwd.	0.8352	0.1973	17.91	0.0000
VE5	Tulip Poplar	0.2802	0.2894	0.94	0.3330
VE6	Xeric Oak	0.5548	0.2091	7.04	0.0080
VE7	Pine	0.4979	0.2121	5.51	0.0189
VE8	Nonforest	0.0695	0.6852	0.01	0.9192
VR	Unit: 1 Veg. Type	0.2931	0.0682	18.48	0.0000
SL	Unit: 1 Degree	0.0174	0.0107	2.65	0.1034
EL1	< 600 m, > 1,000 m	-0.3361	0.0940	12.79	0.0003
EL2	600-1,000 m	0.3361	0.0940	12.79	0.0003
DH1	Uncut	-0.6871	0.1799	14.59	0.0001
DH2	Light Cut/Undisturbed	0.2236	0.2244	0.99	0.3191
DH3	Heavy Cut	0.9618	0.2103	20.92	0.0000
DH4	Settlement	-0.4983	0.2561	3.79	0.0517
TR	Unit: 1 Meter	-0.000788	0.00024	10.75	0.0010
HA1	< 5,750 m	-0.4804	0.1078	19.87	0.0000
HA2	≥ 5,750 m	0.4804	0.1078	19.87	0.0000
RO1	< 2,500 m	-0.2254	0.1012	4.97	0.0259
RO2	≥ 2,500 m	0.2254	0.1012	4.97	0.0259

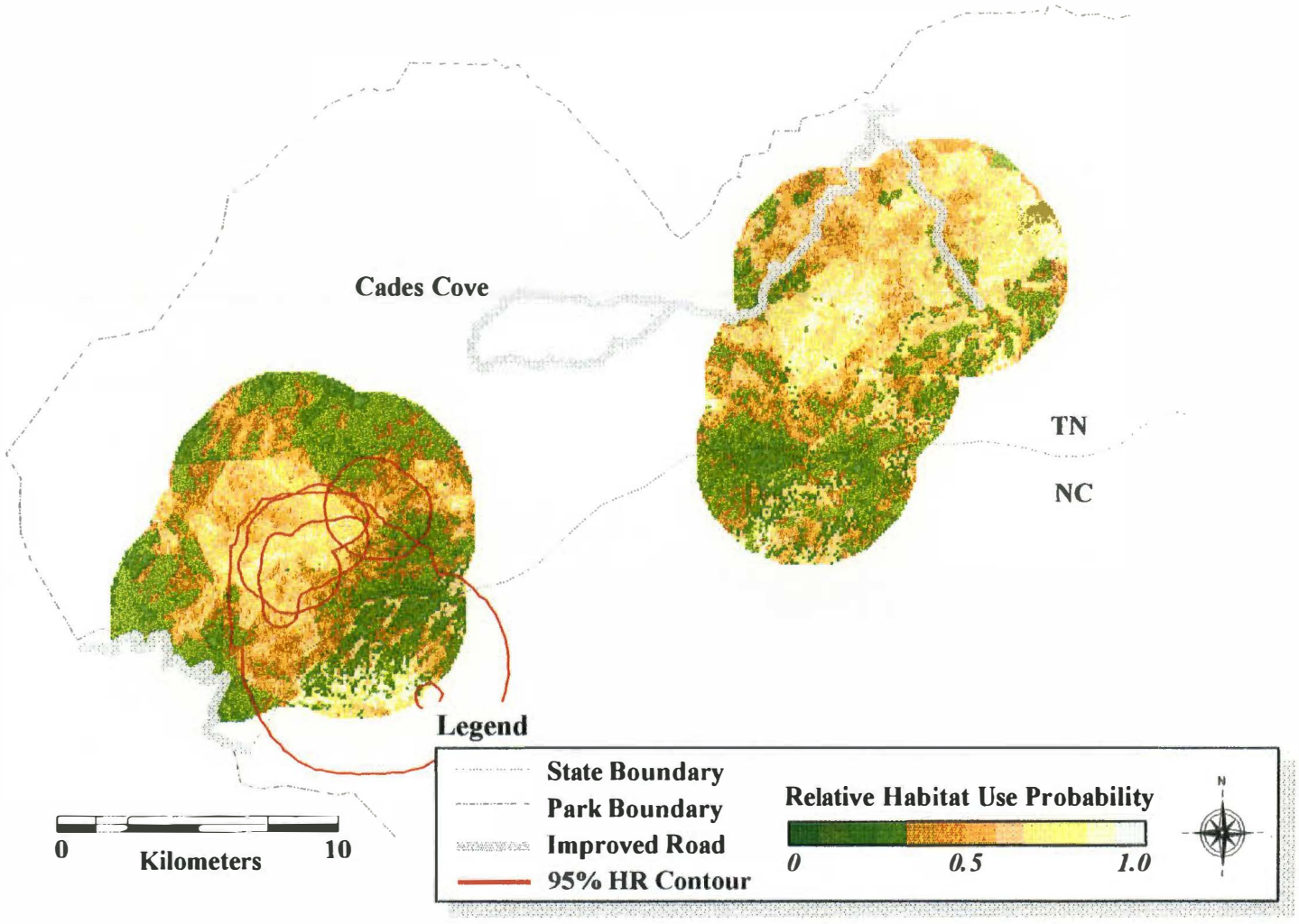


Fig. 24. Relative habitat use probability based on fall habitat use model of female black bears, Great Smoky Mountains National Park, 1976-1982.

between 600 m and 1,000 m was 2.0 times more likely than use of elevations < 600 m or > 1,000 m. The parameter estimate for proximity to human activity sites estimated that relative bear use of areas ≥ 5,750 m from human activity sites was 2.6 times more likely than for areas < 5,750 m. Relative bear use of areas ≥ 2,500 m from improved roads was predicted to be 1.6 times more likely than areas < 2,500 m from improved roads. Based on the parameter estimate for overstory vegetation richness, the probability of habitat use increased by a factor 1.3 with each additional vegetation type within 270 m. With every 10-° increase in slope, the probability of habitat use increased by a factor 1.2. Habitat use decreased by a factor 0.9 with every 100-m increase in distance to trails.

Northern hardwood was used proportionally less than cove hardwood/pine-oak (χ^2 = 4.22, 1 df, P = 0.0399), mixed mesic hardwood (χ^2 = 7.02, 1 df, P = 0.0080), xeric oak (χ^2 = 4.73, 1 df, P = 0.0297), and pine (χ^2 = 4.32, 1 df, P = 0.0377). Mesic oak was used proportionally less than cove hardwood (χ^2 = 12.25, 1 df, P = 0.0005), mixed mesic hardwood (χ^2 = 16.34, 1 df, P = 0.0001), tulip poplar (χ^2 = 9.04, 1 df, P = 0.0026), xeric oak (χ^2 = 12.90, 1 df, P = 0.0003), pine (χ^2 = 12.22, 1 df, P = 0.0005), and nonforest (χ^2 = 3.75, 1 df, P = 0.0529). Mixed mesic hardwood was used more than cove hardwood/pine-oak (χ^2 = 3.95, 1 df, P = 0.0470) and tulip poplar (χ^2 = 3.39, 1 df, P = 0.0658).

Historically heavily cut areas were used proportionally more than uncut (χ^2 = 28.04, 1 df, P < 0.0001), light cut/undisturbed (χ^2 = 4.89, 1 df, P = 0.0271), and settlement areas (χ^2 = 13.25, 1 df, P = 0.0003). Light cut/undisturbed areas were

used proportionally more than uncut areas ($\chi^2 = 7.77$, 1 df, $P = 0.0053$).

Overall - Males. The subset selection procedure based on the lowest AIC and ICOMP values indicated that the variables overstory vegetation richness, slope, and proximity to trails were relatively unimportant in explaining variation among the telemetry and the random locations (Table 14). Models 30 and 42 had AIC and ICOMP values slightly lower than the values for model 105. Addition of the variables slope or proximity to trails to model 105 did not improve the fit. Therefore, I choose model 105 as the operating model because of its lower dimension. However, because model 105 did not fit the data, I explored the inclusion of interaction terms. I included interactions between elevation and vegetation disturbance history, between proximity to human activity sites and vegetation disturbance history, and between proximity to human activity sites and aspect. Inclusion of these terms resulted in a better fit of the model. I excluded 21 outliers with a standardized Pearson residual > 2.0 and an $h > 0.008$. The resulting operational model fit the data (Table 15) ($\hat{C} = 7.777$, 8 df, $P = 0.456$). Based on a cut-off point of 0.5 for the predicted probability, the sensitivity and specificity of the model were 84.4% and 47.9%, respectively, resulting in an overall 72.5% correct classification. The false positive and false negative rates were 23.0% and 40.3%, respectively. The correlation matrix of the maximum likelihood estimates of the parameters in the model showed largest correlations among parameter estimates of the same variable and among the parameter estimates of the interaction terms (Table E.5). I calculated and mapped the relative habitat use probability for males for the male

Table 14. Summary of best subsets of Akaike's information criterion (AIC) and information-theoretic measure of complexity (ICOMP) values for each level of i (i=no. of independent variables) and all univariate values for logistic regression models of habitat use of male black bears, Great Smoky Mountains National Park, 1976-1982. The global minimum for each criterion is denoted by †.

Model	Habitat Variables[a]									k[b]	$-2LogL$	$C_1(\hat{F}^{-1})$	AIC	ICOMP
1	VE	VR	EL	SL	AS	DH	TR	HA	RO	16	1,571.5	32.5	1,603.5	1,636.5
9	VE		EL	SL	AS	DH	TR	HA	RO	15	1,571.5	29.7	1,601.5	1,630.9
30	VE		EL	SL	AS	DH		HA	RO	14	1,571.5	---	**1,599.5**†	------
42	VE		EL		AS	DH	TR	HA	RO	14	1,573.7	27.1	------	**1,627.9**†
105	VE		EL		AS	DH		HA	RO	13	1,573.7	27.2	1,599.7	1,628.1
232	VE		EL			DH		HA	RO	11	1,580.2	22.3	1,602.2	1,624.8
364			EL			DH		HA	RO	6	1,603.3	14.0	1,615.3	1,631.3
392	VE					DH			RO	9	1,617.9	21.2	1,635.9	1,660.3
456	VE					DH				8	1,640.0	18.8	1,656.0	1,677.6
504	VE									6	1,815.5	14.1	1,827.5	1,843.7
505		VR								2	1,884.6	7.5	1,888.6	1,899.6
506			EL							2	1,836.8	6.6	1,840.8	1,850.0
507				SL						2	1,901.5	6.7	1,905.5	1,914.9
508					AS					3	1,890.2	9.3	1,896.2	1,908.8
509						DH				3	1,681.4	9.1	1,687.4	1,699.6
510							TR			2	1,911.1	3.4	1,915.1	1,917.9
511								HA		2	1,911.2	3.3	1,915.2	1,917.8
512									RO	2	1,839.9	6.6	1,843.9	1,853.1

[a] See Table 3 for explanation of variables codes.

[b] k = no. of estimated parameters including the intercept.

Table 15. Results of logistic regression analysis of overall habitat use of male black bears, Great Smoky Mountains National Park, 1976-1982.

Variable Code	Class	Parameter Estimate	Standard Error	Chi-Square	Prob.
CONSTANT		-0.7847	0.1969	15.89	0.0001
VE1	Northern Hrdwd./ Mesic Oak	0.6713	0.2647	6.43	0.0112
VE2	Cove Hrdwd.	0.2367	0.2315	1.05	0.3067
VE3	Mixed Mesic Hrdw./ Tulip Poplar/ Xeric Oak	0.5226	0.1839	8.08	0.0045
VE4	Pine-Oak	0.1674	0.3484	0.23	0.6308
VE5	Pine	0.5409	0.2076	6.79	0.0092
VE6	Nonforest	-2.1389	0.7090	9.10	0.0026
EL1	< 1,015 m	0.5471	0.1210	20.43	0.0000
EL2	≥ 1,015 m	-0.5471	0.1210	20.43	0.0000
AS1	W, NW, N	0.0887	0.0947	0.88	0.3486
AS2	NE, E, SW, W, Flat	-0.1864	0.0945	3.89	0.0485
AS3	SE, S	0.0977	0.1085	0.81	0.3679
DH1	Uncut	0.5303	0.1398	14.38	0.0001
DH2	Light Cut/Undist.	-0.2963	0.1263	5.50	0.0190
DH3	Heavy Cut/ Settlement	-0.2340	0.1452	2.60	0.1071
HA1	< 3,735 m, > 7,965 m	-0.5625	0.0743	57.32	0.0000
HA2	3,735-7,965 m	0.5625	0.0743	57.32	0.0000
RO1	< 5,895 m	0.4513	0.1041	18.78	0.0000
RO2	≥ 5,895 m	-0.4513	0.1041	18.78	0.0000
EL1*DH1		0.4378	0.1375	10.14	0.0014
EL1*DH2		-0.0748	0.1238	0.36	0.5459
EL1*DH3		-0.3630	0.1435	6.40	0.0114
EL2*DH1		-0.4378	0.1375	10.14	0.0014
EL2*DH2		0.0748	0.1238	0.36	0.5459
EL2*DH3		0.3630	0.1435	6.40	0.0114
HA1*DH1		-0.4835	0.1016	22.66	0.0000
HA1*DH2		0.2691	0.0970	7.70	0.0055
HA1*DH3		0.2143	0.1133	3.58	0.0585
HA2*DH1		0.4835	0.1016	22.66	0.0000
HA2*DH2		-0.2691	0.0970	7.70	0.0055
HA2*DH3		-0.2143	0.1133	3.58	0.0585

Table 15. (Cont.)

Variable Code	Class	Parameter Estimate	Standard Error	Chi-Square	Prob.
HA1*AS1		0.1503	0.0908	2.74	0.0980
HA1*AS2		0.0996	0.0947	1.11	0.2929
HA1*AS3		-0.2499	0.1051	5.65	0.0175
HA2*AS1		-0.1503	0.0908	2.74	0.0980
HA2*AS2		-0.0996	0.0947	1.11	0.2929
HA2*AS3		0.2499	0.1051	5.65	0.0175

study area within GSMNP (Fig. 25).

The parameter estimate for elevation predicted that relative use of elevations < 1,015 m by male bears was 3.0 times more likely than use of elevations > 1,015 m. The parameter estimate for proximity to human activity sites indicated that relative bear use of areas between 3,735 m and 7,965 m from human activity sites was 3.1 times more likely compared with areas < 3,735 m and > 7,965 m from human activity sites. Relative bear use of areas < 5,895 m from improved roads was predicted to be 2.5 times more likely than areas ≥ 5,895 m from improved roads.

For the categorical variables, contrasts of the maximum likelihood estimates revealed which variable categories received more bear use. Nonforest areas were used proportionally less than northern hardwood/mesic oak (χ^2 = 10.06, 1 df, P = 0.0015), cove hardwood (χ^2 = 7.45, 1 df, P = 0.0064), mixed mesic hardwood/tulip poplar/xeric oak (χ^2 = 9.85, 1 df, P = 0.0017), pine-oak (χ^2 = 6.26, 1 df, P = 0.0124), and pine (χ^2 = 9.87, 1 df, P = 0.0017). Areas with western to northern aspects were used proportionally more than areas with northeastern, eastern, and southwestern aspects, and flat areas (χ^2 = 3.15, 1 df, P = 0.0758). Male bears used areas with uncut vegetation proportionally more than light cut/undisturbed areas (χ^2 = 13.69, 1 df, P = 0.0002) and heavily cut/settlement areas (χ^2 = 8.94, 1 df, P = 0.0028).

Habitat Use Descriptions

I used relative habitat use probabilities ≥ 0.90 and ≤ 0.10 associated with

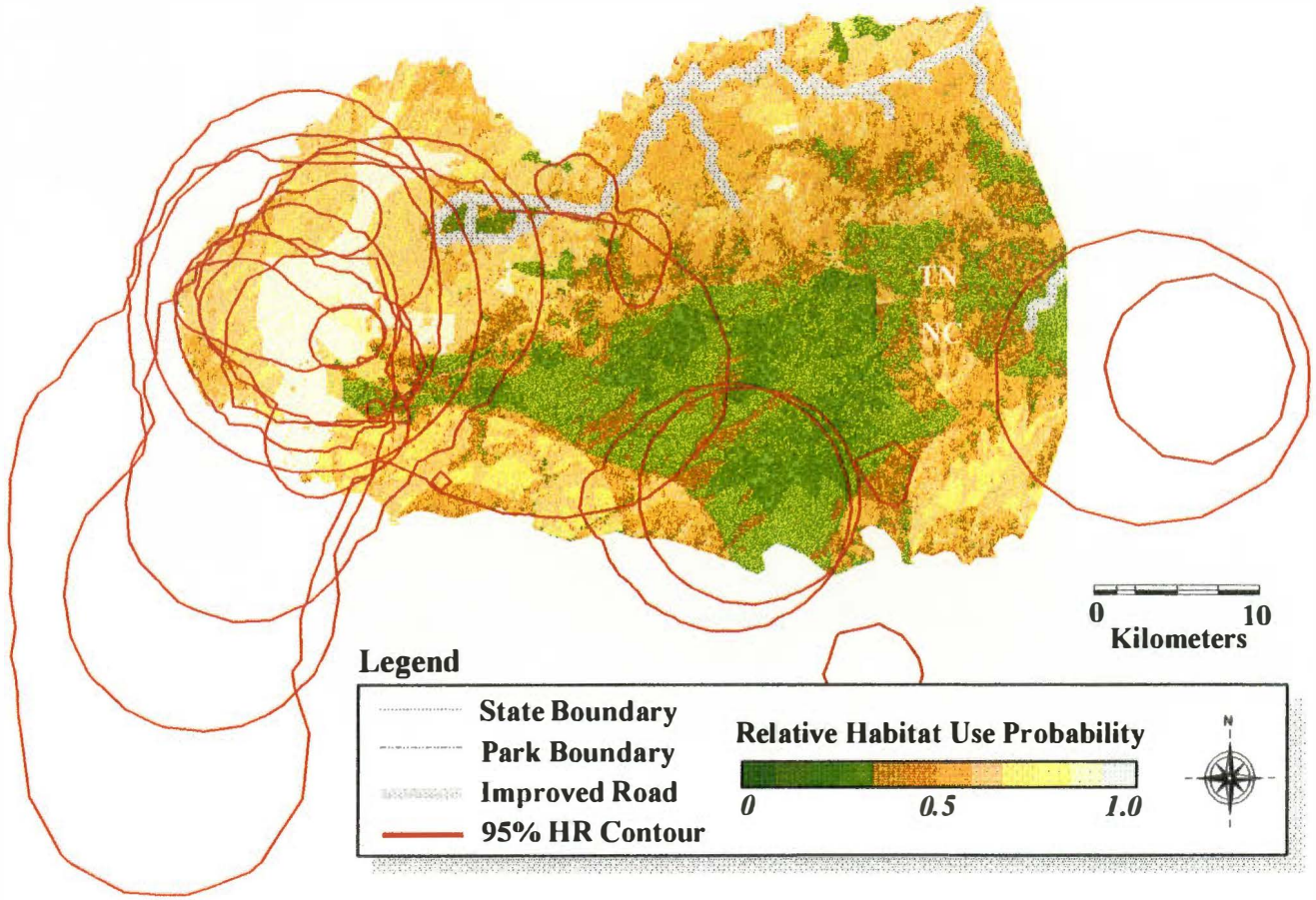


Fig. 25. Relative habitat use probability based on overall habitat use model of male black bears, Great Smoky Mountains National Park, 1976-1982.

telemetry locations of black bears to describe characteristics of habitats with high and low relative use, respectively. Frequently used habitat areas for females were characterized by tulip poplar, mixed mesic hardwood, or xeric oak vegetation types, high vegetation richness ($\geq$ 5 overstory vegetation types), middle elevations (600 m-1,000 m), moderately steep slopes ($\geq$ 15°), northwestern aspects, historic settlement areas, close proximity to trails ($\leq$ 225 m), and large distances from human activity sites ($\geq$ 5,750 m) and improved roads ($\geq$ 2,500 m). These characteristics were similar for spring habitat use except that slopes were generally steeper, northern aspects and historically uncut areas were used more, and distances $<$ 5,750 m from human activity sites and $<$ 2,500 m from improved roads were more common. Characteristics of frequently used summer habitat were similar to overall habitat use except for increased use of xeric oak. Fall habitat use for females also was similar to the overall model except that vegetation richness generally was greater, slopes were not as steep, areas received historically heavy logging, areas were $<$ 5,750 m from human activity sites, and use of areas $<$ 2,500 m from roads was greater.

Habitat areas that received relatively infrequent use by females usually were characterized by mesic oak, low vegetation richness ($\leq$ 4 overstory vegetation types), elevations below 600 m or above 1,000 m, medium slopes (5-15°), all aspects except northwestern and northern, historically uncut, undisturbed, or light cut areas, large distances to nearest trail ($>$ 225 m), and with no distinct patterns of proximity to human activity sites or improved roads. These characteristics changed slightly for spring and summer with pine, mesic oak, xeric oak, and cove hardwood/pine-oak

vegetation and elevations between 600 m and 1,000 m being more common. Low use of fall habitat predicted by the female habitat use model was also similar to that identified by the overall model except that northern hardwood and historical settlement areas also were characteristic, as were areas ≥ 2,500 m from roads.

For male telemetry locations, the habitat use model predicted relatively frequent use of habitats characterized by pine, mixed mesic hardwood/tulip poplar/xeric oak, and cove hardwood vegetation, elevations < 1,015 m, any aspect, historically uncut areas, and areas between 3,735 m and 7,965 m from human activity sites and < 5,895 m from improved roads. The model predicted relatively low use of habitats characterized by nonforest and pine-oak vegetation, elevations ≥ 1,015 m, northeastern to southwestern aspects, heavily logged/settlement and light cut/undisturbed areas, and distances < 3,735 m or > 7,965 m from human activity sites and > 5,895 m from improved roads.

Factor Analysis

Based on the variables in the overall female habitat use model, the first 3 factors explained 62%, 25%, and 13%, respectively, of the common variance. The first factor was primarily related to elevation, vegetation disturbance history, and proximity to human activity sites and improved roads. The second factor was related to overstory vegetation, overstory vegetation richness, and proximity to trails whereas aspect and slope had the greatest loadings on the third factor (Table 16).

For males, the first 2 factors explained 79% and 21%, respectively, of the

Table 16. Results of factor analysis of habitat use by female black bears, Great Smoky Mountains National Park, 1976-1982.

Variable[a]	Factor 1	Factor 2	Factor 3
Eigenvalue	5.9317	2.3501	1.2766
Common Variance Explained (%)	62.06	24.59	13.36
VE	0.31694	0.59219	0.21351
VR	0.27262	0.43659	0.13139
EL	0.54002	0.45393	0.15035
AS	-0.01254	0.23376	-0.46802
SL	-0.07837	-0.36310	0.60946
DH	-0.88022	0.04055	0.01998
TR	-0.06239	-0.08201	0.07054
HA	0.67883	-0.38784	-0.03096
RO	0.46321	-0.36377	-0.17086

[a] See Table 3 for explanation of variable codes.

common variance. The first factor was associated with overstory vegetation type, elevation, and proximity to improved roads. The second factor was mostly related to vegetation disturbance history, and proximity to human activity sites (Table 17).

External Model Validation

Females. The 10-fold validation procedure with Hosmer and Lemeshow's deciles of risk (Hosmer and Lemeshow 1989) resulted in a mean Hosmer-Lemeshow goodness-of-fit statistic of $\hat{C}$ = 20.84 (SD = 9.82, n = 10, range = 5.85-36.47); this statistic approximated the chi-square distribution with 8 df, corresponding to a P-value of 0.0076. Thus, there were differences between observed and predicted outcomes with independent data. The mean sensitivity and specificity were 68.14% (SD = 3.54, n = 10, range = 63.64-74.26) and 66.38% (SD = 4.03, n = 10, range = 55.92-71.13), respectively. The false positive rate was 34.46% (SD = 4.11, n = 10, range = 29.29-44.67) and the false negative rate was 31.07% (SD = 3.65, n = 10, range = 23.97-35.85).

Males. I could not perform external validation of the male habitat use model because the 10% loss of observations in the 10-fold validation procedures resulted in insufficient sample sizes to develop the logistic regression models.

Telemetry Error

I used 1,432 locations, randomly generated within a 150 m radius of all female locations, to determine the effects of telemetry error on the habitat use analysis. The

Table 17. Results of factor analysis of habitat use by male black bears, Great Smoky Mountains National Park, 1976-1982.

Variable[a]	Factor 1	Factor 2
Eigenvalue	4.1990	1.1329
Common Variance Explained (%)	78.75	21.25
VE	0.83506	0.07020
EL	-0.76424	-0.14961
AS	-0.06942	0.20391
DH	-0.34886	0.49636
HA	0.05245	-0.57183
RO	-0.36158	0.32485

[a] See Table 3 for explanation of variable codes.

largest classification difference was for overstory vegetation with 3.9% of the error locations classified differently from the radio-telemetry locations (Table 18). For the continuous variables in the female habitat use model, differences were small (Table 18). Comparison of the habitat classifications of the error locations to those of the original telemetry locations revealed that none of the categorical or continuous variables in the habitat use model showed any significant deviations (P = 0.4239 to 0.9920). Furthermore, fitting the female habitat use model based on the error locations, after exclusion of 23 outliers, resulted in a Hosmer-Lemeshow goodness-of-fit statistic of $\hat{C}$ = 8.89 (8 df, P = 0.3520), indicating that the model fit the data.

Relative Habitat Use and Home Ranges

Mean relative habitat use probability of 12 females was 0.54 (SD = 0.10, range = 0.36-0.70) for the 50% adaptive kernel contour, 0.53 for the 75% contour (SD = 0.097, range = 0.32-0.66), and 0.47 for the 95% contour (SD = 0.075, range = 0.34-0.57). Sample sizes were too small for repeated measures analysis. However, the mean difference in the relative habitat use probability between the 50% and 75% ($\bar{x}$ = 0.017, SD = 0.032, range = -0.048-0.047) was not different from 0 (S = 19.0, P = 0.1514). This probability was different between the 50% and 95% home range contours ($\bar{x}$ = 0.077, SD = 0.050, range = -0.001-0.139), and the 75% and 95% contours ($\bar{x}$ = 0.061, SD = 0.038, range = -0.017-0.095) (S = 36.0 to 39.0, n = 12, P = 0.0024 to 0.0005). The mean relative habitat use probability was not different for the 50% adaptive kernel home range compared with the area extending

Table 18. Classification differences of habitat variables due to telemetry error, female black bears, Great Smoky Mountains National Park, 1976-1982. A. Categorical variables. B. Continuous variables.

A.

Habitat Variable	No. of Locations Classified Differently[a]	%
Overstory Vegetation	56	3.9
Elevation	8	0.6
Aspect	11	0.7
Vegetation Disturbance History	13	0.9
Proximity to Human Activity Sites	3	0.2
Proximity to Improved Roads	1	0.1

B.

Habitat Variable	Mean Difference	Range
Overstory Vegetation Richness (Units)	0.50	0-3
Slope (Degrees)	3.58	0-33
Proximity to Trails (m)	64.55	0-270

[a] Classification based on operational model of female black bear habitat use.

beyond the 50% contour to the 75% contour ($\bar{x}$ = 0.51, SD = 0.095, range = 0.29-0.63) (t = 0.81; 12,12 df; P =0.4285). The mean relative habitat use probability of the 75% adaptive kernel home range was greater than that of the area extending beyond the 75% contour to the 95% contour ($\bar{x}$ = 0.43, SD = 0.059, range = 0.34-0.53) (t = 2.83; 12,12 df; P = 0.0098). The relative habitat use probability of adult females was greater for smaller home ranges for the 95% (F = 10.12; 1,7 df; P = 0.0157), and the 75% (F = 6.47; 1,7 df; P = 0.0385) adaptive kernel contours, but not for the 50% contour (F = 2.66; 1,7 df; P = 0.1471).

Differences between the mean relative habitat use probability of overlapping and nonoverlapping areas of female home ranges were greatest for the 50% adaptive kernel contour ($\bar{x}$ = 0.24, SD = 0.16, n = 6, range = -0.04-0.39) (t = 3.70, P = 0.0140) followed by the 75% ($\bar{x}$ = 0.18, SD = 0.13, n = 7, range = 0.03-0.31) (t = 3.72, P = 0.0098) and 95% contours ($\bar{x}$ = 0.14, SD = 0.06, n = 16, range = 0.04-0.24) (t = 9.31, P < 0.0001) (Fig. 26 provides an example).

For males, the relative habitat use probability was calculated for 9 individuals and was largest for the 50% adaptive kernel contour ($\bar{x}$ = 0.82, SD = 0.14, range = 0.50-0.92), intermediate for the 75% contour ($\bar{x}$ = 0.75, SD = 0.13, range = 0.49-0.85), and smallest for the 95% contour ($\bar{x}$ = 0.62, SD = 0.13, range = 0.46-0.77). Mean differences in the probability of relative habitat use between the 50% and 75% ($\bar{x}$ = 0.07, SD = 0.09, range = -0.025-0.288), 50% and 95% ($\bar{x}$ = 0.020, SD = 0.015, range = 0.022-0.41) and 75% and 95% ($\bar{x}$ = 0.130, SD = 0.13, range = -0.009-0.360) home range contours were > 0 (S = 19.5 to 22.5, n = 9, P = 0.0195

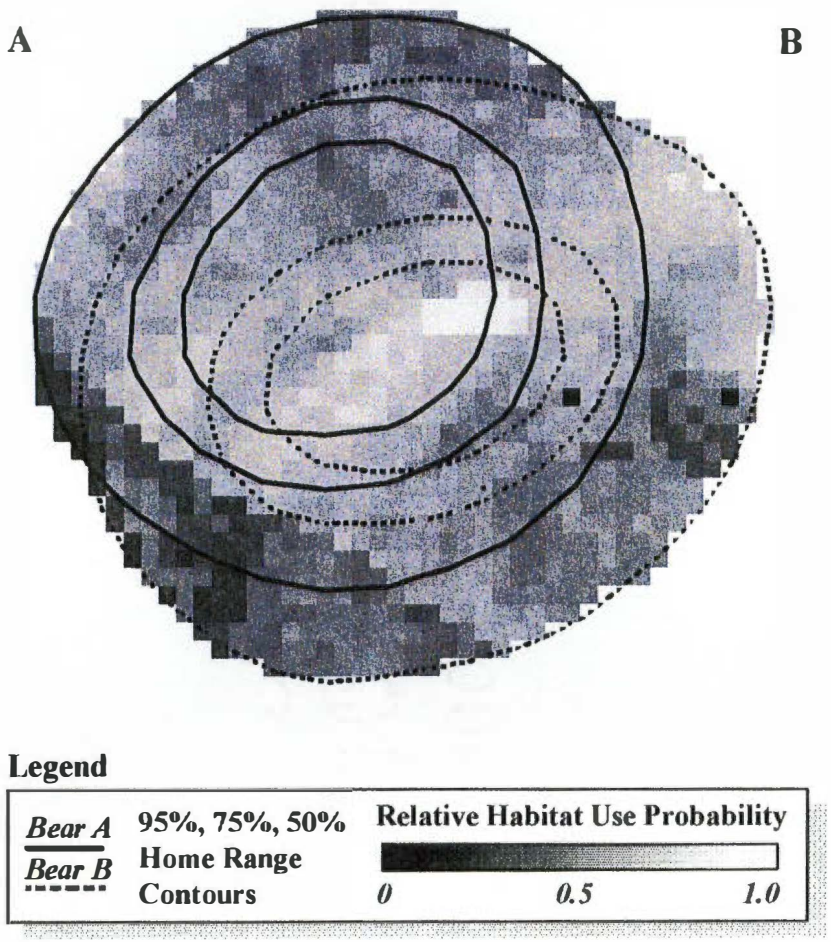


Fig. 26. Example of overlapping home ranges depicted with relative habitat use probability based on overall habitat use model of female black bears, Great Smoky Mountains National Park, 1976-1982.

to 0.0039). The mean relative habitat use probability was different for the 50% adaptive kernel home range compared with that of the area extending beyond the 50% contour to the 75% contour ($\bar{x}$ = 0.73, SD = 0.12, range = 0.48-0.83) (Z = 1.85, P = 0.0637). The mean relative habitat use probability of the 75% adaptive kernel home range was different from that of the area extending beyond the 75% contour to the 95% contour ($\bar{x}$ = 0.58, SD = 0.13, range = 0.43-0.75) (Z = 2.47, P = 0.0134). After removal of one outlier observation (M005), the relative habitat use probability of adult male bears showed a relation to home ranges size for the 95%, (F = 5.21; 1,5 df; P = 0.0712) and 75% (F = 17.47; 1,5 df; P = 0.0087) home range contours, but not for the 50% contour (F = 0.32; 1,5 df; P = 0.5962).

Differences between the mean relative habitat use probability of overlapping and nonoverlapping areas of male home ranges were significant for 95% ($\bar{x}$ = 0.24, SD = 0.06, n = 16, range = 0.11-0.35) (t = 15.31, $P < 0.0001$) and 75% adaptive kernel estimates ($\bar{x}$ = 0.26, SD = 0.08, n = 14, range = 0.13-0.38) (t = 12.27, $P < 0.0001$) but not for the 50% adaptive kernel contour ($\bar{x}$ = 0.26, SD = 0.16, n = 5, range = -0.03-0.34) (S = 6.5, P = 0.1250).

Mean weight, physical condition, and age of female bears exhibited no relationship with the mean relative habitat use probabilities of the 50% (F = 0.31 to 1.39; 1,7 df; P = 0.5936 to 0.2765), 75% (F = 0.03 to 2.14; 1,7 df; P = 0.8738 to 0.1869), and 95% (F = 0.01 to 0.09; 1,7 df; P = 0.9282 to 0.7720) adaptive kernel home range contours.

Bait-Station Surveys

The 1990-1992 frequencies of observed bear visits to bait stations (Fig. 27-29) were significantly different from predicted frequencies based on the overall female and male habitat models ($\hat{C}$ = 1,603.0, 8 df, $P < 0.0001$; $\hat{C}$ = 431.2, 8 df, $P < 0.0001$, respectively). Differences between observed and predicted outcomes were greatest for predicted probabilities $\leq$ 0.6. Above a predicted probability of 0.6, the predicted frequencies corresponded better to bait-station visitation (Table 19).

Simulations of Habitat Alterations

I simulated the construction of an improved road in combination with the addition of a human activity site (e.g., developed campground) for a 32.8 km^2 section of the study area. As a result, the average relative habitat use probability of this area decreased from 0.43 (SD = 0.21, n = 4,047, range = 0.02-0.96) to 0.16 (SD = 0.11, n = 4,047, range = 0-0.82) (Fig. 30A and 30B). An alternative route without addition of the human activity site resulted in less change of relative habitat use (Fig. 30C); the mean relative habitat use probability changed to 0.31 (SD = 0.21, n = 4,047, range = 0-0.94).

In the second example, I simulated how relative habitat use may change after a 35 ha and 58 ha area consisting of xeric oak was cut and replanted with pine (Fig. 31A). I simulated the changes in relative habitat use at an early (nonforest) and a later successional stage (pine). Besides changes in the overstory vegetation type, such action would also affect overstory vegetation richness. Modelling these changes in

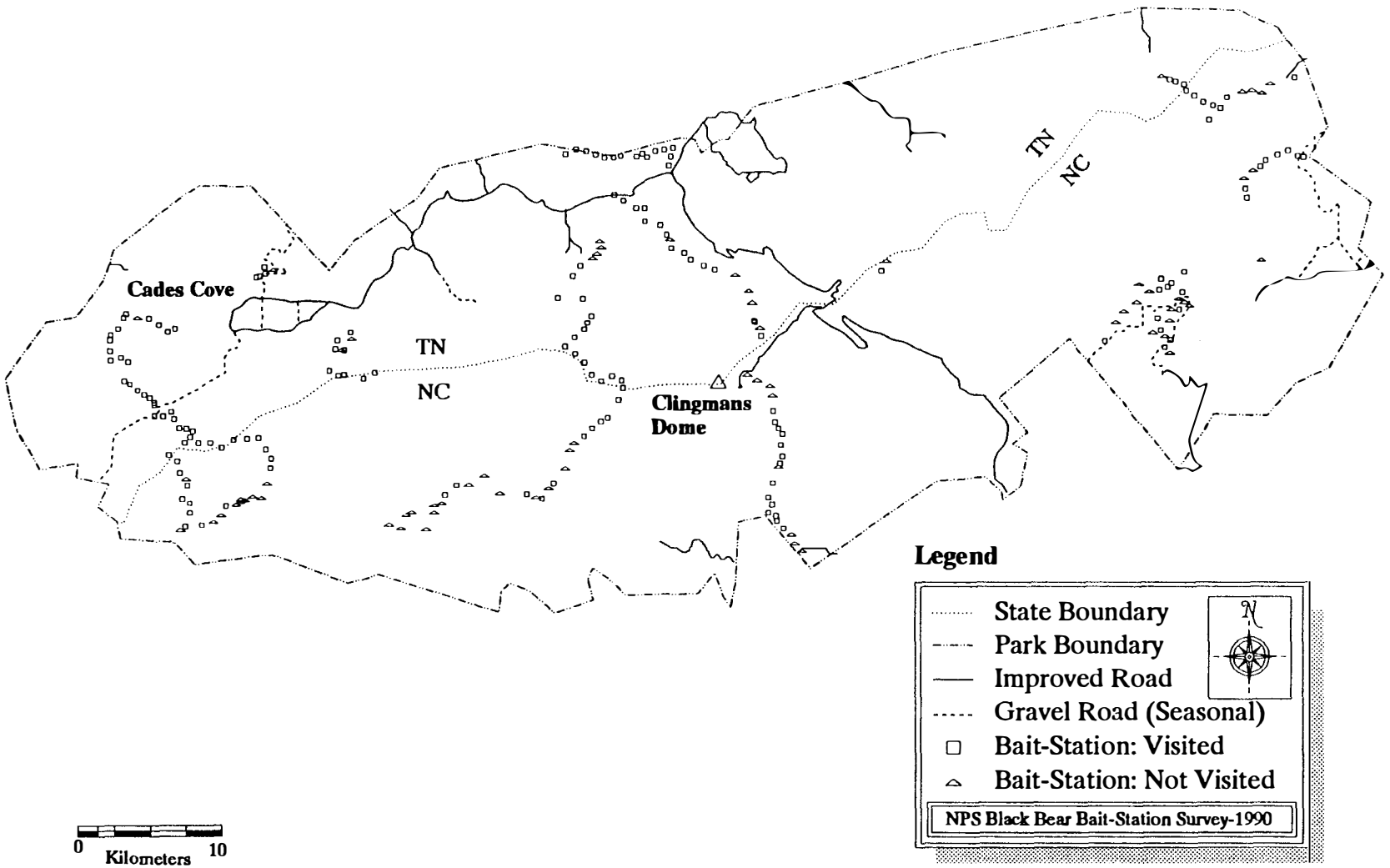


Fig. 27. Results of black bear bait-station survey, Great Smoky Mountains National Park, 1990.

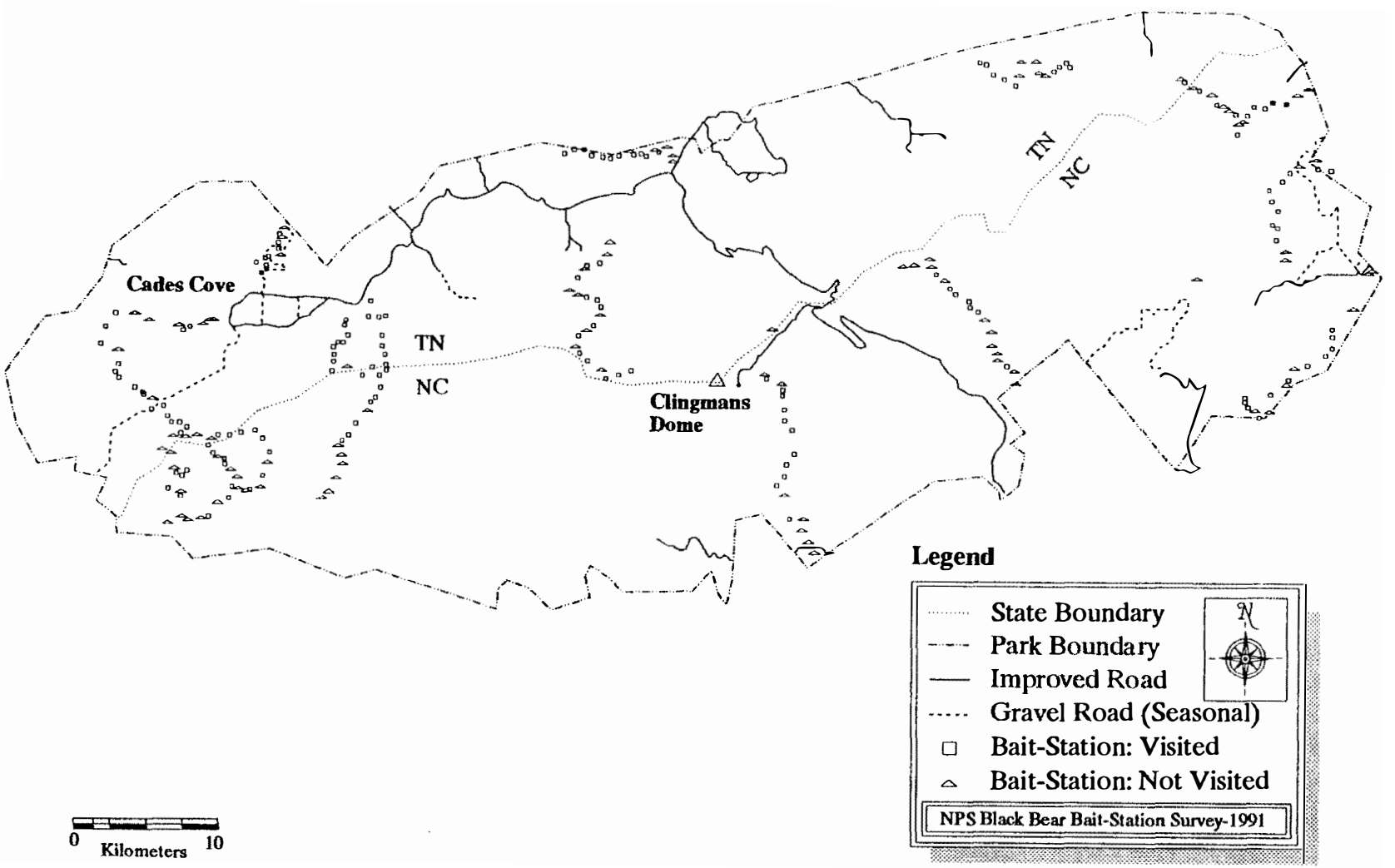


Fig. 28. Results of black bear bait-station survey, Great Smoky Mountains National Park, 1991.

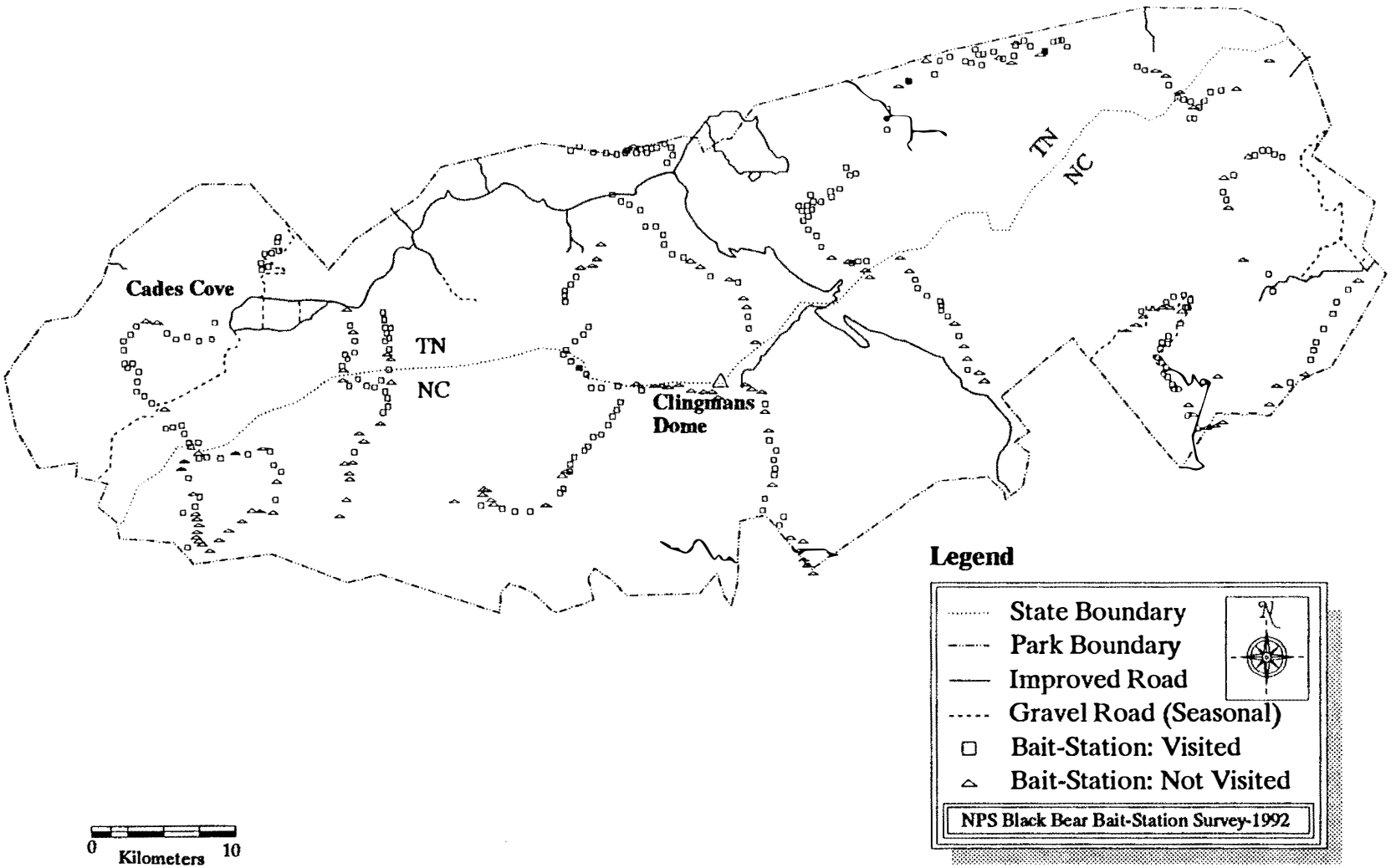


Fig. 29. Results of black bear bait-station survey, Great Smoky Mountains National Park, 1992.

Table 19. Expected and observed frequencies of black bear bait-station visits in Great Smoky Mountains National Park, 1990-1992.

Decile of Risk[a] (Probability range)	Females		Males	
	Expected[a]	Observed	Expected[a]	Observed
1 (0.00-0.10)	1.60	37	11.95	56
2 (0.10-0.20)	6.43	49	20.46	58
3 (0.20-0.30)	13.05	57	25.21	52
4 (0.30-0.40)	20.46	65	30.35	62
5 (0.40-0.50)	26.48	62	35.31	5
6 (0.50-0.60)	32.84	61	39.75	55
7 (0.60-0.70)	39.94	65	44.87	53
8 (0.70-0.80)	48.72	46	49.79	54
9 (0.80-0.90)	58.15	58	54.09	62
10 (0.90-1.00)	71.06	45	69.02	66

[a] Deciles of risk and expected frequencies were based on predicted probabilities from female and male black bear habitat use models, Great Smoky Mountains National Park, 1976-1982.

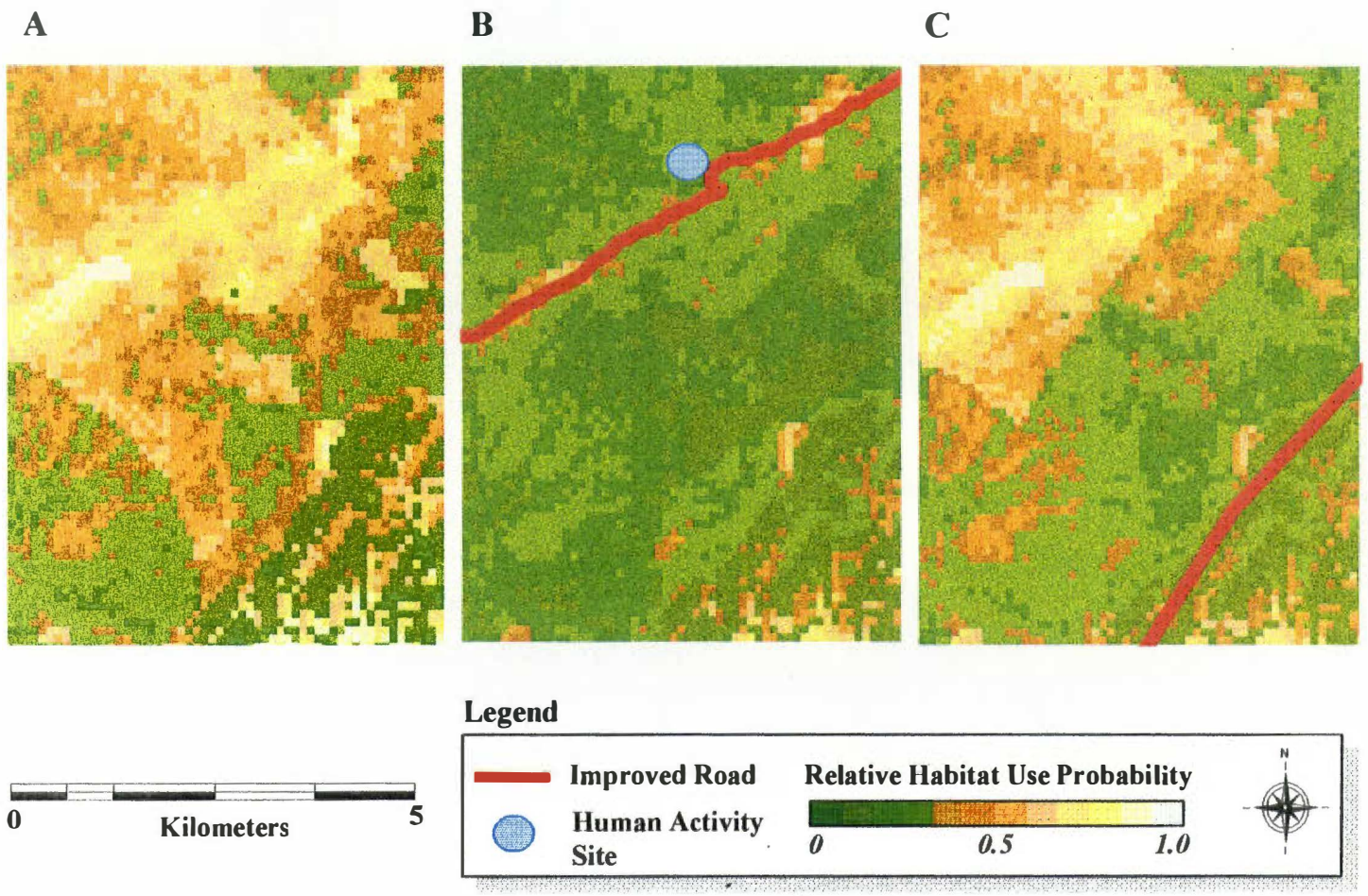


Fig. 30. Predicted changes in relative habitat use probability of female black bears after simulation of road construction and addition of human activity site. A. Before construction. B. After construction of improved road and human activity site. C. After construction of alternative route for new road without development of human activity site.

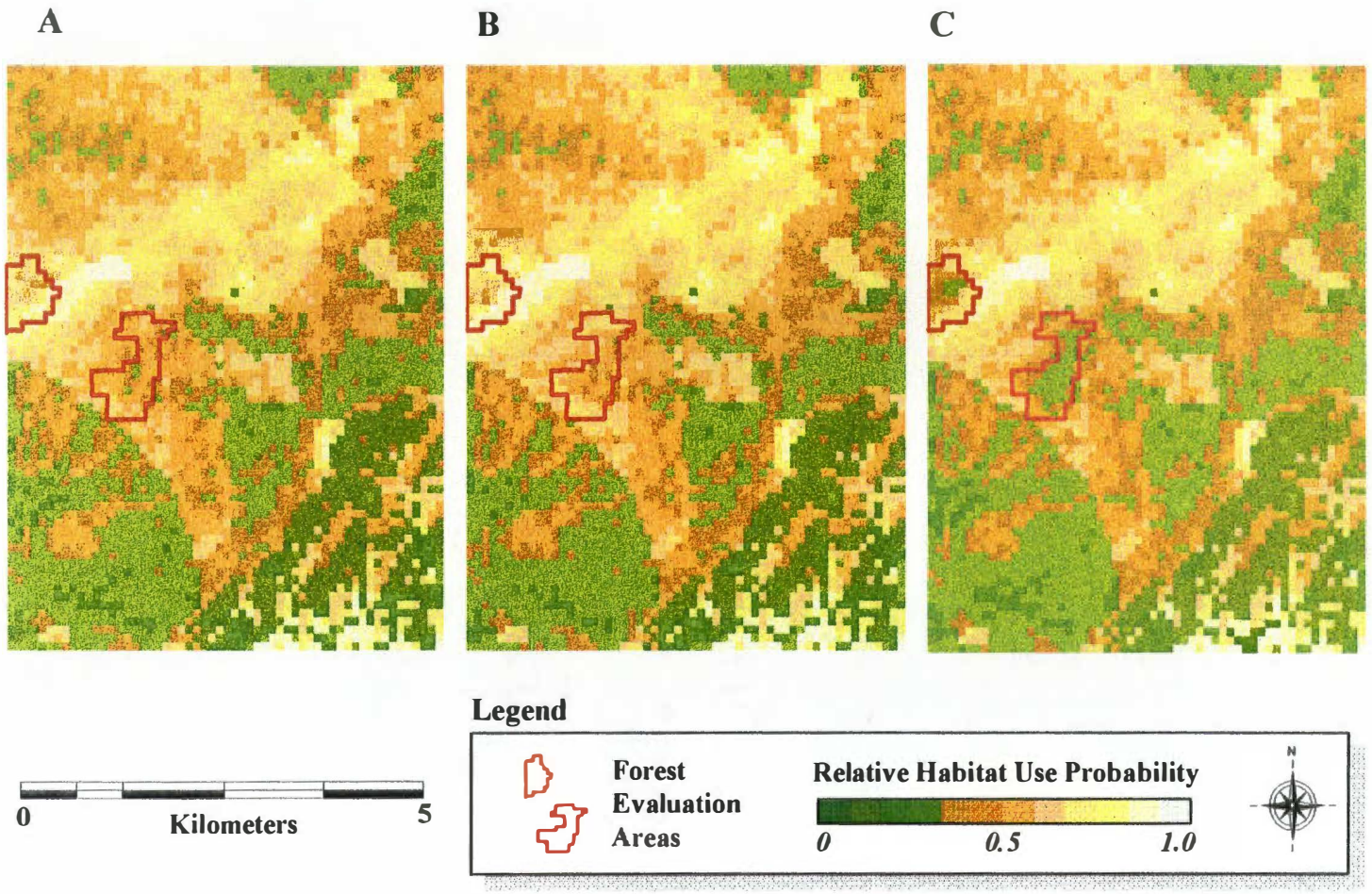


Fig. 31. Predicted changes in relative habitat use probability of female black bears within evaluation area after simulation of logging and converting a 35 and a 58 ha tract of xeric oak to pine. A. Before logging. B. Early stage of succession (nonforest). C. Full regeneration (pine).

both variables revealed that, at an early successional stage, relative habitat use within the forest management areas may not change dramatically: the mean relative habitat use probability changed from 0.57 (SD = 0.14, n = 115, range = 0.28-0.86) to 0.60 (SD = 0.16, n = 115, range = 0.29-0.90) (Fig. 31B). As the management areas mature to pine, however, relative habitat use decreased substantially ($\bar{x}$ = 0.41, SD = 0.15, n = 115, range = 0.18-0.83) (Fig. 31C). For the entire evaluation area, the effects of these forest changes were smaller: the mean relative habitat use probability changed from 0.43 (SD = 0.21, n = 4,047, range = 0.02-0.96) before forest conversion to 0.41 (SD = 0.21, n = 4,047, range = 0.01-0.94) after conversion to pine.

CHAPTER V

DISCUSSION

Home Ranges and Movements

Most bear telemetry locations used in this study were autocorrelated. Some researchers have questioned whether any 2 locations of an individual bear can be truly independent (Powell 1987) considering observations of bears repeatedly returning to certain areas, seemingly for particular resources, and long-distance movements in short time periods (Garshelis and Pelton 1981, Quigley 1982, Carr 1983). The average minimum time difference between consecutive locations within a year was 15.7 hours for females and 19.1 hours for males. Under the assumption that no 2 locations of an individual bear may be truly independent, these location sampling schemes probably resulted in independent locations with regard to minimum time between consecutive locations. Another potential source of autocorrelation may be the time of day that locations were taken. Bears have distinct crepuscular activity patterns that are modified seasonally to more diurnal patterns in summer, and more nocturnal in fall (Garshelis and Pelton 1980). If bear activities are associated with certain habitat types and time periods, a 12- or 24-hour difference in location sampling may contribute to autocorrelated locations. Although more than 90% of female and male locations were collected from 09:00-20:00, the average time between consecutive locations hours suggests that consecutive locations usually were not

collected during the same hour of the day. The bias due to a mostly diurnal sampling regime seems to be small because the probability of activity of black bears from 21:00 to 05:00 usually is low (Garshelis and Pelton 1980).

Estimates of home range size of male bears in this study were not extreme compared with those reported from other black bear studies (Table 20). Sizes of female home ranges, however, were relatively small compared with other regions (Table 20). Besides methodological differences, the large variability in home range estimates may be explained by geographic differences in diets. Gittleman and Harvey (1982) found that among carnivoran species, diet shows a significant influence on home range size, after removal of effects related to metabolic needs.

Many studies reported differences between female and male home range sizes similar to this study (Table 20). Harestad and Bunnell (1979) found that black bears had a high correlation between home range size and body weight compared with herbivores and carnivores; male body weights are greater compared with females, which would correspond to greater home range sizes. The relative home range size of omnivores (including black bears) is correlated with weight according to the equation: $0.059\ W^{0.92}$ (Harestad and Bunnell 1979). Because the average body weight of males in GSMNP is approximately 1.7 times greater than that of females, the average male home range size is predicted to be approximately 1.6 times greater than the female home range size. Thus, based on the home range size differences in GSMNP (Tables D.1-D.3), other factors may play a role. Black bears are promiscuous and males may increase reproductive fitness by fertilizing many females,

Table 20. Estimates of mean home range sizes of black bears in North America. All estimates are from annual 100% convex polygon home ranges.

Location	Home Range Size (km^2)		Study
	Females	Males	
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	112.1	Amstrup and Beecham (1980)
Maine	43.0	1,721.0	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	This Study
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)

which can only be accomplished by large home ranges. Females may increase their fitness by using areas large enough to sustain reproduction and self-maintenance (Amstrup and Beecham 1976, Clutton-Brock and Harvey 1978). Indeed, all male home ranges included at least several home ranges of studied females and most likely other females. Large home range sizes of male bears may also be related to distribution and abundance of food. Widely dispersed and unpredictable food sources may contribute to large home ranges in mammals (Clutton-Brock 1974), conditions that are fairly typical with regard to black bear foods in the southern Appalachians, particularly in the fall. Indeed, differences between female and male home range sizes were proportionally largest in fall. Subadult dispersal may be another contributing factor to large home ranges of male bears (Garshelis and Pelton 1981). However, of 3 subadult males in my study, only 1 (M362) had a relatively large home range.

Although I detected no differences among annual home range sizes, the observed differences between annual and overall home range sizes seem to indicate that the dynamics of spatial use change over a time scale longer than a few years. However, the distances between activity centers of consecutive years and between different seasons indicated some variation in frequency of use within home ranges. As expected, the seasonal home range estimates and differences in distances between seasonal activity centers were similar to those described in the 3 individual studies of Garshelis (1978), Quigley (1982), and Carr (1983). Garshelis and Pelton (1980, 1981) observed seasonal changes in activity and movement patterns and they

hypothesized the following scenario. In spring, bears mostly feed on readily available herbaceous material (Beeman and Pelton 1980), which may cause rapid satiation but provide little nutritive value (Eagle 1979). As a result, activity patterns are crepuscular, movements are limited (Garshelis and Pelton 1981), and home range sizes are small. Also, many females are accompanied by relatively immobile cubs. Summer food of black bears in the study area consists mainly of a variety of fruits (Beeman and Pelton 1980), which are more dispersed than spring foods requiring foraging to continue into the middle of the day. The high caloric value of summer foods (Eagle 1979) provides energy to extend activity periods and supports expenditure of energy for nonfeeding activities such as mating, resulting in home range expansion compared with spring. During fall, bears must build a fat storage in preparation for winter denning and exhibit diurnal and nocturnal activity patterns, feeding on widely dispersed acorns within a patchy distribution of oak stands (Beeman and Pelton 1980). For this reason, bears continually move within and between oak stands, often resulting in increased hourly movements and shifts in activity centers (Garshelis and Pelton 1981, Garshelis *et al.* 1983). Fall ranges tend to vary more from year to year than spring or summer ranges because hard mast production in the southern Appalachians is unpredictable (Carr 1983). Thus, changes in seasonal home range sizes and activity centers may largely be explained by changing activity and movement patterns in response to differences in distribution and nutritive value of seasonally abundant foods (Garshelis and Pelton 1981). These patterns seem to occur on larger scales for males, which may be related to the earlier discussed differences

in home range sizes. Although this hypothesis would predict travel rates to be higher in fall compared with summer, I found no such differences. However, travel rates may not be good indicators of activity patterns because high travel rates do not necessarily imply high activity levels (Garshelis and Pelton 1980).

With the exception of low male travel rates in fall, overall, annual, and seasonal travel patterns of bears in GSMNP were similar to those observed in another study in the southern Appalachians (Garris 1983). Male travel rates were greatest during diurnal hours and varied little among individuals. Female travel rates, however, varied only among individuals, which may be related to presence or absence of cubs or yearlings. Male travel rates were especially great during summer, which may be due to activities associated with mating. Females exhibited greater travel rates than males during the fall, despite less distinct shifts in centers of activity and home range size. Because of the smaller ranges of female bears and competition with males (Garshelis and Pelton 1981), females may have less opportunity to reach good fall foraging areas. Thus, fall food sources available to females may be relatively scarce and dispersed compared with males; high travel rates would increase the probability of encountering such food sources. The mean travel rate of females during fall (665 m/hr) was greater than that observed on CNF (4-year average: 425 m/hr) (Villarrubia 1982, Garris 1983). Availability and production of fall hard mast seem to be greater on national forest areas bordering GSMNP (McLean 1991).

Factors other than food likely influence range sizes and activity patterns. Based on observations in the Bunker Hill study area, Quigley (1982) hypothesized that learning

behavior and social status may result in more efficient use of resources over time and a decrease or stabilization of the home range. Although the annual home range size of several females decreased over time, they increased for other bears (Table D.3). Additionally, the results of my study showed that home range sizes of older bears are not different from younger bears. It seems that annual fluctuations in home range size was mainly the result of high variation of the fall home ranges, which, in turn, seems related to the unpredictable nature of fall mast production. The serial correlation among the location estimates indicated that locations of black bears were not independent of each other, which may be interpreted as an existence of learning behavior in resource use. However, the large seasonal and annual fluctuations in food abundance and dispersion (as indicated by the variation in fall home ranges [Table 8, Table D.3]) may limit the ability to learn in bears.

Small sample sizes did not allow range comparisons among females of different reproductive status. In general, females with cubs or yearlings tend to have small home ranges whereas home ranges of breeding females usually are larger to increase reproductive success (Carr 1983). Subadult females tend to establish a home range within their mother's range whereas subadult males become more or less transient until they find an area to establish a home range (Rogers 1987).

Besides GSMNP, seasonal shifts of activity centers have been observed in other parts of the southern Appalachians (Garris 1983, Clevenger 1986), Virginia (Hellgren and Vaughan 1990), and in Idaho for adult males (Reynolds and Beecham 1980). Although Brody (1984), Beringer (1986), and Seibert (1989) observed comparable

shifts in seasonal activity centers on Pisgah National Forest, North Carolina, they concluded that these shifts were insignificant compared with shifts in activity centers of consecutive years. For both sexes, mean distances between summer and fall centers of activity in GSMNP were approximately 2 times greater than the mean distances between annual centers of activity. Statistical tests, however, showed no differences, possibly due to small sample sizes. Because I used seasonal locations across years to reach adequate sample sizes, the estimated distances between seasonal activity centers essentially reflect long-term dynamics of home range shifts. Thus, the observed summer-fall shifts likely were more distinct than I observed, especially for males. For females, the observed spring-summer and summer-fall shifts were relatively small and corresponded fairly well to those reported by Carr (1983) and Garris (1983) for 1981 but not for 1980, a year of hard mast failure. It seems that shifts in activity centers occur when productive bear foods become patchily distributed (Garshelis and Pelton 1981, Hellgren and Vaughan 1990). In many areas of the southern Appalachians, this often occurs when bears switch from a predominantly soft mast diet in summer and early fall to a diet consisting mostly of acorns in late fall. In areas such as Pisgah National Forest, distribution of oaks is relatively uniform (Brody 1984) and shifts in activity centers may be less pronounced.

Home range overlap was observed for both females and males but was substantially greater among males; this may simply be due to the large male home ranges. Home range overlap may not be a good indicator of territorial behavior because animals may still have different temporal use patterns within overlapping areas. According to

Davies' (1978) definition of territoriality, the test results based on differences between simultaneous and randomized locations did not support the hypothesis that adult females are territorial. Likewise, male bears in GSMNP do not seem to be territorial. However, the results indicated a fairly high occurrence (60%) of mean distances between simultaneous female-male locations that were greater than expected. I used the same techniques as described by Clark (1991) who suggested that females in Arkansas were territorial. Garshelis (1978) and Garshelis and Pelton (1981) reported large home range overlap among females in GSMNP, but also noted different temporal use patterns of these areas. Garshelis and Pelton (1981) also observed substantial overlap among male bears in areas with abundant fall foods. Adult females may decrease the probability of agonistic encounters by avoiding such areas (Garshelis and Pelton 1981). In years of hard mast shortages, increased competition may lead to social intolerance and only the most dominant males may establish home ranges in areas with available hard mast by excluding subordinate bears. Several other researchers observed sharing of home range areas by bears but at different times (Reynolds and Beecham 1976, Lindzey and Meslow 1977, Garris 1983, Clark 1991) and some have suggested that social structure and related behavior may be the organizing force (Poelker and Hartwell 1973, Lindzey and Meslow 1977, Rogers 1977). My observations seem to agree with some of these studies. Although there was substantial home range overlap among female and male bears, there seemed to be differences in temporal use of those areas. Bears of the same sex, however, seemed to use their home ranges independently of each other, although a relatively small

number of bears exhibited temporal differences or similarities in use of overlapping areas.

Habitat Use

Habitat use by black bears in GSMNP was explained with logistic regression models that included 9 variables for females and 6 variables plus 3 interaction terms for males. The logistic regression models performed well in differentiating bear use from random use. With several exceptions, the correlation coefficients of the parameter estimates generally were small, indicating the importance of the variables beyond correlations with other variables in the model. The relatively large number of variables in the habitat models may reflect the complexity of bear habitat use. The necessary rescaling of several variables during the modelling process also may indicate the existence of multi-scale habitat use patterns. The results of the factor analysis seem to confirm this interpretation. For females, the first factor was mostly related to vegetation disturbance history, elevation, and proximity to human activity sites and improved roads. The relatively high correlations among the parameter estimates for these variables confirmed this finding. Combined, these variables seem to explain a macro-scale pattern of habitat use. However, these patterns themselves seem difficult to explain without incorporating the other variables, which were represented in the second and third factors. The second and third factors seem to be more related to micro-scale patterns of habitat use. The factor analysis on the male locations showed that overstory vegetation type, elevation, and proximity to roads

explained most of the variation. Proximity to human activity sites and vegetation disturbance history mostly determined the second factor. Most variables included in the male habitat use model seem to be associated with relatively macro-scale habitat patterns. The pooling of overstory vegetation and aspect classes also indicates a relatively macro-scale use related to these habitat variables. These observations and the results of the home range analyses seem to indicate that male habitat use patterns partly occur on a different scale compared with females.

Telemetry error hardly affected the results of the logistic regression analysis. This was, in part, due to the macro-scale character of many variables in the models. The effect of telemetry error was largest for the micro-scale variables such as overstory vegetation type. Likewise, the effect of error in the GIS coverages probably was largest for the overstory vegetation layer. It is difficult to assess the influence of GIS errors on the analysis. However, because classification error was mostly restricted to relatively uncommon forest types (except for mixed mesic hardwood), the overall effect of this type of error seems to be small.

Although all models explained relative bear use, the external validation of the overall female model indicated that the model is more appropriate for hindcasting than forecasting. Therefore, extrapolations to other areas or time periods may not be appropriate and should be conducted with caution. However, the parameter estimates and associated standard errors of the training sets were similar, indicating the stability of the logistic regression models. Moreover, the sensitivity, specificity, false positive, and false negative rates based on the external validation were almost the

same compared with the internal validation. These rates indicate that approximately 1/3 of the random sites had some characteristics of a female bear location and a similar proportion of bear locations had some characteristics of random use. These observations merely seem to reflect that black bears are extremely mobile and habitat generalists. For all models, the bear locations that I identified as outliers consistently were in areas with a low predicted probability of habitat use. The reverse was true for random locations identified as outliers. These observations were identified as outliers because they severely affected predictive power of the habitat use models.

The logistic regression models explained relative bear habitat use based on the conditions of the study and these habitat use patterns may be used for interpretation and to develop research hypotheses. Because interactions could not be included in the female habitat model, I assume that the effect of a change in one variable (while all other variable classes or values remain the same) is the same for all variables and variable classes. I use seasonal foraging patterns and overstory vegetation types as a logical basis for interpretation and discussion of the results.

After den emergence, bears stay close to the den sites, especially females with cubs. During spring, bears forage mainly on grasses, herbaceous plants, squawroot (*Conopholis americana*), and, in late spring, serviceberry (*Amelanchier arborea*, *A. laevis*) (Eagle and Pelton 1983). Rich herb layers are most characteristic for cove hardwood (Whittaker 1956) whereas squawroot, a parasitic plant that grows from the roots of oak trees (Musselman and Mann 1978), is found primarily in dry oak forests. Serviceberry is especially abundant in cove and northern hardwood forests and along

nonforest areas such as balds (Beeman and Pelton 1980). Thus, from a spring foraging perspective, use of cove hardwood and pine-oak forests and nonforest areas by females seems to agree with these observations. The use of cove hardwood and tulip poplar may also relate to locations of female den sites, which often are associated with large diameter trees of species such as tulip poplar, yellow birch, eastern hemlock, red maple, northern red oak, chestnut oak, and yellow buckeye (*Aesculus octandra*) (Johnson and Pelton 1981, Wathen *et al.* 1983). Large sizes of several of these species (i.e., tulip poplar, red maple, eastern hemlock) are typical for tulip poplar and cove hardwood types (MacKenzie 1991, 1993). Although I was not able to develop a spring habitat use model for males, univariate chi-square analysis of spring locations indicated that males used all vegetation types in proportion to availability. Because males are considerably larger in size and weight, their nutritional requirements in spring may be proportionally less compared with females who often also have the demands of reproduction and lactation. Selective habitat use by females may promote efficient energy intake. In addition, early spring locations may reflect denning habitat more for females than males; females seem to spend more time within the vicinity of the den after den emergence and also seem to be more selective of den sites (Lindzey and Meslow 1976, Johnson and Pelton 1981, Lentz *et al.* 1981). Male bears seem to be less selective of den sites than females and greater travel rates after den emergence may not reflect use of denning habitat.

In early summer, bears continue to feed on squawroot and gradually include fruits and seeds in their diet as summer progresses; huckleberry (*Gaylussacia* spp.),

blueberry (*Vaccinium* spp.), blackberry (*Rubus* spp.), and cherry (*Prunus* spp.) compose the main part of the summer diet (Beeman and Pelton 1980, Eagle and Pelton 1983). Animal foods form a small part of the summer diet and consist mostly of insects such as beetles (Coleoptera), ants (Formicidae), and yellow jackets, wasps, and hornets (Vespidae) (Beeman and Pelton 1980). Based on Whittaker's (1956) and Golden's (1974) descriptions of shrub strata, *Gaylussacia* and *Vaccinium* species are especially common in mesic to submesic hardwood and oak forests (Whittaker [1956]: red oak-pignut hickory, chestnut oak-chestnut; Golden [1974]: red maple-northern red oak, red maple-sweet birch, chestnut oak) and xeric pine and pine-oak forests (Whittaker [1956]: virginia pine, pitch pine heath, table mountain pine heath; Golden [1974] oak-pine). These forest types correspond with MacKenzie's (1991, 1993) mesic oak, mixed mesic hardwood, pine-oak, and pine classifications.

In summer, females used mesic oak much less than expected and mixed mesic hardwood, pine, and pine-oak in proportion to availability. Males, on the other hand, used mesic oak, mixed mesic hardwood, and pine more than expected. Xeric oak received greater than expected use by females and males. Xeric oak may not provide the abundance of summer fruits typical of mesic oak and mixed mesic hardwood. Whittaker's (1956) chestnut oak-chestnut heath, white oak-chestnut forest, and red oak-chestnut forest classification corresponds to MacKenzie's (1991, 1993) xeric oak classification; *Vaccinium* spp. are fairly common for these forest types, especially above 1500 m, but coverage is typically low (Whittaker 1956). Thus, it seems that males used prime summer foraging areas relatively more than females.

During early fall, bears in GSMNP forage on available fruits, especially black cherry (*Prunus serotina*) and fire cherry (*P. pensylvanica*) (Beeman and Pelton 1980, Eagle and Pelton 1983). In late fall (after 15 October), bears forage predominantly on acorns, although hickory (*Carya* spp.) and beech nuts and wild grapes (*Vitis* spp.) often also composed part of the diet (Beeman and Pelton 1980). The diet of black bears in late fall may consist of up to 83% acorns (Eagle 1979). Annual differences in black bear reproductive success, habitat use, and movements have been attributed to annual variations in fall hard mast productivity (Jonkel and Cowan 1971, Rogers 1976, 1987, Garshelis and Pelton 1980, Kelleyhouse 1980, Eiler *et al.* 1989). In the southern Appalachians, fall hard mast abundance seems to influence minimum reproductive age, cub production, and cub survival; abundant white oak mast crops seem to be particularly important (Eiler 1981, Wathen 1983, Eiler *et al.* 1989). In years of a hard mast failure (i.e. 1980 [Carr 1983]), bears may switch to alternative foods, most commonly grapes (Eiler *et al.* 1989). Based on MacKenzie (1991, 1993), xeric oak has the highest occurrence and richness of oak species known to be frequently used by bears in the southern Appalachians whereas the mesic oak type probably has the highest productivity (based on mean basal area) for chestnut oak and especially red oak. Mixed mesic hardwood, pine, and pine-oak seemed secondary in all these characteristics. Beech is essentially restricted to northern and cove hardwood with largest mean basal areas occurring in the northern hardwood type (MacKenzie 1991, 1993). Black cherry is most abundant in cove hardwood and northern hardwood whereas fire cherry occurs mostly in northern hardwood

(MacKenzie 1991, 1993). Grapes occur most frequently in tulip poplar and, to a lesser extent, in mixed mesic hardwood (Whittaker 1956, Golden 1974).

During fall, female bears used mixed mesic hardwood, xeric oak, pine, and cove hardwood/pine-oak more than expected whereas overall habitat use by males indicated frequent use of mixed mesic hardwood, xeric oak, and pine, and, in contrast to females, mesic oak and northern hardwood. Thus, of the forest types that provide productive fall foods, females only used xeric oak to any extent whereas all other productive forest types were used much less than expected. Furthermore, proportional use of xeric oak by females was less compared with summer. It seems that males used the best fall foraging areas whereas females mostly, although not exclusively, used forest types that ranked secondary with regard to fall food production.

Local vegetation richness only played a role in female habitat use, especially in the fall. I hypothesize that the smaller home ranges of females, compared with males, must contain a certain variety of habitat types to meet nutritional demands and provide protective cover, denning habitat, and other key habitat elements. Based on studies in New York, Costello and Sage (1993) suggested that habitat interspersion at the home-range scale may be beneficial for black bears because this may provide foods throughout the seasons of activity and ensure food availability during years of mast failures; this also may be true at a more local scale for female bears in GSMNP. Local vegetation richness may be less important for males because of their large home ranges.

Middle elevations (600 m-1,000 m) were frequently used by both females and males, although elevations < 600 m received relatively more use from males than females. For females, use of the 600 m-1,000 m elevation range was negatively correlated with low use of historically uncut areas, because uncut areas were more common at these middle elevations. In other words, despite the greater occurrence of historically uncut vegetation at the most frequently used elevation range, females tended to stay out of uncut areas. Elevation played an interactive role in male habitat use, which was indicated by the interaction of elevation and vegetation disturbance history in the habitat model. In general, the use of lower to middle elevations by bears was related to use of oak forests, which occur mostly at lower elevations. Use of diverse overstory vegetation by females was correlated with use of the 600 m-1,000 m elevation range where overstory vegetation richness was greatest.

During spring, females were relatively more likely to be found on steep slopes. Because den sites in GSMNP frequently are on steep slopes (> 30° [Johnson and Pelton 1981, pers. obs.]), use of areas around the den after emergence may reflect the significance of the slope variable. In particular, females with cubs will remain within close proximity of the den site long after den emergence. The parameter estimate for slope was positively correlated with the parameter estimate for use of flat areas. Because the parameter estimate for flat areas was not different from zero, this correlation is difficult to interpret.

Females frequently used northern and northwestern aspects during spring and summer but used eastern aspects much less than expected. Use of northwestern

aspects and flat areas was correlated with the slope variable. Slope and aspect together formed the third factor in the factor analysis, which may be interpreted as a physical environment component. Males used all slope aspects in proportion to availability except northeastern, eastern, and flat aspects, which were used less than expected. This pattern was dependent, however, on the proximity to human activity sites, which was indicated by the interaction term.

Frequent female use of historic settlement areas in the spring may be related to abundant herbaceous forage and late spring fruits typical for these open areas. Uncut areas were used less by females than expected during all seasons; this was positively correlated with use of elevations < 600 m and $> 1{,}000$ m and with the parameter estimates for areas $< 5{,}750$ m from human activity sites $\geq 2{,}500$ m from improved roads. Female locations within uncut areas were associated with use of pine, 600 m-1,000 m elevation range, and areas $\geq 5{,}750$ m from human activity sites and $\geq 2{,}500$ m from improved roads. However, despite the frequent occurrence of uncut areas in habitat types that received high relative use, overall use of uncut areas by females was less than expected. It seems that females used uncut areas in proportion to availability where they were common but proportionally less in areas with relatively little uncut vegetation. Frequent use of heavily cut areas by females was negatively correlated with use of areas in close proximity to human activity sites. Despite the relatively low use of areas $< 5{,}750$ m of human activity sites, relative use of heavily cut areas mostly occurred in close proximity to human activity sites. A similar correlation with regard to proximity to roads was present for female use of

areas in spring. That is, most use of settlement areas occurred < 2,500 m from improved roads. These patterns may be explained by the greater occurrence of heavily cut and settlement areas closer to roads and human activity sites.

Overall, males used uncut areas more than expected and light cut/undisturbed areas less than expected. These relationships were strongest at elevations < 1,015 m and in areas 3,735 m-7,965 m from human activity sites. Historically uncut vegetation in GSMNP has many old-growth characteristics (as defined by Thomas *et al.* [1988]) such as a multilayered canopy, different tree species and sizes, dead trees and logs, and small-scale disturbances. Frequent use of historically uncut areas by males may be related to this diversity in vegetation structure and the vegetation itself. Old-growth in GSMNP may be best developed at lower elevations (e.g., the western part of the male study area; Figs. 10 and 25) and production and richness of both soft and hard mast may be large in such areas. Such areas may also provide adequate protection cover and den sites. Thus, males may be able to satisfy many of their year-round habitat needs in these areas, which may also explain why vegetation richness was not an important variable to model male habitat use. Young and Beecham (1986) reported that black bears preferred selectively logged areas during all seasons of activity. In the Adirondack Mountains of New York, uneven-aged, managed forests seemed to be of moderate quality during all seasons, but provided sufficient resources for some bears (Costello and Sage 1993).

Female bears were located closer to trails than expected possibly because bears seem to regularly use trails, abandoned manways, and closed roads, which may be

related to movement efficiency and soft-mast abundance (Hellgren 1988, Brody and Pelton 1989, Beringer *et al.* 1990). In a study of mark trees in GSMNP, researchers observed a proportionally high occurrence of these trees along maintained, abandoned, and animal trails (Burst and Pelton 1980). Males tend to travel in a more circuitous pattern than females (Garshelis 1978), which may explain why proximity to trails was not an important factor for males. Carr and Pelton (1984) suggested that frequent use of areas close to trails or closed roads in the Bunker Hill study area was related to availability of summer fruits. Indeed, the parameter estimate for proximity to trails for females was largest for the summer season. It is possible that areas close to trails represent unique habitats, particularly because the parameter estimate for proximity to trails was not correlated with overstory vegetation types or other variables.

Low use of areas in close proximity to human activity sites and improved roads by females was partly correlated with use of overstory vegetation types and historical vegetation disturbances. For males, frequent use of areas $< 3,735$ m and $> 7,965$ m from human activity sites and areas in close proximity to roads also seemed partly related to use of overstory vegetation types. An additional interpretation of these observations is that female bears avoid areas close to improved roads and human activity sites. Researchers in the southern Appalachians (Brody and Pelton 1989, Beringer *et al.* 1990, Reagan 1991) and Montana (Kasworm and Manley 1990) reported avoidance of roads or human activity areas by black bears, which they attributed to associated disturbance factors. In Idaho, Young and Beecham (1986)

observed such avoidance in female bears but not in males. Tietje and Ruff (1983), however, observed no response of black bears < 2 km of oil development complexes.

Several observations seem to confound the interpretation that areas in close proximity to improved roads and human activity sites were avoided by females due to disturbances. If females avoid roads and human activity sites due to disturbance factors, the question remains why males do not seem to exhibit such behavior. Secondly, there were relatively large correlations among the parameter estimates for vegetation disturbance, proximity to human activity sites, and proximity to improved roads, which may have resulted in the observed patterns of use. As I will discuss, social interactions between male and female bears also may have played a role. Thus, the multivariate analysis identified several potential factors that may have influenced the observed habitat use patterns. The "avoidance" by females of areas close to human activity sites or improved roads was most likely not solely the result of a response to improved roads or human activity sites.

Female use of vegetation types, especially as it relates to summer and fall foraging, was mostly restricted to areas that seemed secondary in food production compared with areas used by males. The importance of vegetation richness for females may be related to this. Given the relatively small home ranges of females, a high vegetation richness may compensate for the use of secondary foraging areas. Where historically uncut vegetation was relatively uncommon (i.e., elevations below 600 m), females used uncut areas less than expected whereas males used those areas more than expected. The old-growth character of uncut areas may offer bears a variety of

life requisites. Competition for important resources would be more severe in areas where those resources are scarce, which, given that uncut areas provided such resources, may explain these observations. The opposite may occur with abundant resources. Xeric oak forests usually provide abundant hard mast in the fall but, because this forest type is common, may not be fully defendable by males. Indeed, xeric oak represented the only productive foraging habitat that females seemed to use to any extent in the fall.

Based on the observations of habitat use and the differences between simultaneous locations of males and females, I hypothesize that female habitat use is partly a result of social interactions with male bears who prevent females from using productive or otherwise important habitat types. Garshelis and Pelton (1981) first suggested the existence of such interactions in GSMNP based on fall movements and other field observations. In 1980, a year of poor hard mast production, Carr (1983) observed that males left summer home ranges earlier than females and subsequently occupied prime oak areas. Carr (1983) interpreted this as an indication of intense competition for areas with productive oaks. In Minnesota (Rogers 1987) and Montana (Jonkel and Cowan 1971) males also were observed to exclude females from productive habitats. Rogers (1977) observed social intolerance by male bears in the fall against females at dump sites. Based on radio-telemetry studies on grizzly bears in Alberta and British Columbia, Canada and Idaho, Wielgus (1993) suggested that adult females avoid the most productive, male-occupied habitats where there were many potentially infanticidal, immigrant males. Finally, Clark (1991) observed that female bears in

the Interior Highlands of Arkansas rarely used clear-cuttings, despite signs of feeding activities; he speculated that these open, food-rich habitats were used primarily by males but avoided by females to prevent agonistic encounters.

Habitat use by black bears in GSMNP seems to be related to a complex set of factors. First of all, social interactions between females and males seem to play a prominent role. Thus, what we perceive as black bear habitat use is most likely a result of habitat characteristics combined with social interactions and factors not measured or identified. Of course, none of the observed habitat use patterns and probabilities are absolute because not all the dynamics of animal behavior and natural systems can be captured into one statistical model and because the analysis used random locations as reference data. However, the distinct habitat use patterns observed in this study suggest the existence of certain patterns.

The general decrease in mean relative habitat use with larger home range contours for both sexes indicates that areas of high relative bear use, as predicted by the habitat use model, were associated with areas of concentrated use according to home range analyses. Although the habitat models were developed based on the same locations used for the home range analyses, relative habitat use predictions for a particular home range contour were based on general habitat use patterns of all bears. Thus, habitat use generally coincided with intensity of use within individual home ranges. Moreover, the mean probability of relative habitat use of overlapping home range areas generally was greater compared with nonoverlapping areas, indicating the existence and possible sharing of certain resources. The size of core areas (50%

home range) of adult bears seemed unrelated to the mean relative probability of habitat use despite differences in the size of core areas. However, the mean probability of relative habitat use decreased with increasing home range sizes for the 75% and 95% home range contours. Several authors have suggested that home ranges of bears are smaller in high-quality habitats and larger in low-quality habitats (Amstrup and Beecham 1976, Lindzey and Meslow 1977, LeCount 1980); this also has been found for other species such as red-shouldered hawks (*Buteo lineatus elegans*) in California (Bloom *et al.* 1993). The results of my study partly agree with these observations but also suggest that the mean probability of relative habitat use in core areas is independent of size. This independence may indicate that there are other factors than habitat use that influence differences in core area size among bears of the same sex. However, this independence also may be related to the small amount of variation in the size of core areas, especially for females.

I observed no relationships between mean weight or physical condition of female bears and the predicted use of habitat within their home ranges. Although sample sizes were fairly small, this may indicate that there is not a direct relationship between habitat use and habitat quality. Of course, it is also possible that weight or physical condition may not reflect habitat quality. Measures of reproductive success may be more appropriate as indices of habitat quality (Chapter VI) but I was not able to use such measures in my analysis.

CHAPTER VI

MANAGEMENT AND RESEARCH IMPLICATIONS

Management Implications

Habitat Use. The results of my study indicate the importance of oak forests in black bear habitat use. Previous studies have emphasized the importance of maximizing mast production from the oak component of the southern Appalachian forests because of the relationship with reproductive success and cub survival (Eiler *et al.* 1989). Uniform distribution of productive oaks and availability of alternative fall foods (e.g., wild grapes) may help reduce the need for extensive movements during the fall and decrease energy expenditure and risk of mortality. Maintenance of oak cover types also would ensure availability of soft mast producing shrubs and trees, especially on submesic to mesic sites. Management for vegetation richness on a small scale (i.e., areas $<$ 30 ha) may allow females to find many life requisites in relatively small areas.

I hypothesized that males may have a substantial influence on female habitat use. Given the validity of this untested hypothesis, management to improve bear habitat may change the sex and possibly age structure of the population within a certain area. Thus, for habitat management plans to be effective, effects on both female and male bears may need to be considered as well as demographic characteristics of the bear population and harvest regimes.

Simulations. The simulation analyses illustrated how predictive habitat use models and GIS may be used to develop hypotheses about relationships among relative habitat use, home range size, home range overlap, and population parameters such as reproductive success. Wildlife managers could use simulation analyses to determine how effects of proposed road construction or other human activities may be minimized. Different temporal and spatial scales can be incorporated into simulations to evaluate predicted changes in relative habitat use. Such information may be used to identify possible spatial and temporal "bottlenecks" in timber harvest regimes that may adversely affect bear habitat use.

The black bear, as a human-sensitive species (Probst and Crow 1991), may be a reliable, landscape-scale indicator of human impacts on forest habitat. GIS-based habitat use models and GIS simulations may be useful for identifying critical habitat areas for land acquisitions, mitigation procedures, and environmental impact statements (EISs). Johnston *et al.* (1988) suggested that GIS-based models will become increasingly important for cumulative impact assessments. EISs often use computer models, such as cumulative effects models and habitat suitability index models, to evaluate effects of different land uses (Schoen 1990). However, these models often are largely hypothetical and lack quantitative data to reliably predict the effects of proposed habitat changes (Schoen 1990).

The results of my study provided biometric, GIS-based habitat use models. Simulations in GIS provided quantitative measures to evaluate the potential effects of proposed habitat alterations on black bear habitat use. The habitat use models may be

applied by natural resource managers in a proactive approach to black bear management and may provide a mechanism for local and regional management of bear habitat.

Bait-Station Surveys. The habitat models did not correlate with visitation to black bear bait stations. The disparity between predicted and observed bait-site visitation occurred primarily for habitat types with a low to medium predicted probability of relative habitat use. The habitat use model predicted bait-station visitation fairly well in habitat types where relative habitat use was predicted to be high. However, regardless of the relative probability of habitat use predicted for bait-station sites, the number of observed visits to bait stations varied little. Because bait-station surveys are based on the use of a food attractant, bait stations with different habitat characteristics temporarily become more similar due to the presence of a high-quality food. Also, bait-station visitation may mostly reflect use of travelways by bears (Garshelis 1990). Moreover, bait sites spaced at 0.8-km intervals may not be independent because one bear may take several consecutive baits (Pelton 1984, Garshelis 1990). Although it is possible that extrapolation of the habitat use models contributed to the poor predictability, the results of the bait-station analysis indicate that bait-station visits may not reflect habitat use.

Application of Habitat Models. Model building is a deductive-inductive process in which models are initially formulated based on ideas, data, or expert opinion. At that early stage, the model represents 1 or more hypotheses, which should then be tested. If predicted outcomes of the model fail to agree with test results, model formulation is

repeated until the model agrees with real-world data (Stormer and Johnson 1986). However, generalization and simplification is inherent when complex and dynamic species-habitat relationships are characterized into statistical algorithms. Even if biological and statistical assumptions of a model are satisfied, application of a model involves extrapolation in time, area, or conditions (Stormer and Johnson 1986). In most instances, statistical habitat models should only be used to hindcast unless they have been validated against independent data (Morrison *et al.* 1992).

Research Implications

I Interpreted habitat use patterns of black bears based on multivariate analyses. Some of the interpretations would have been different when based on separate univariate analyses. By definition, habitat use is a multivariate process, which should be emphasized in habitat use studies.

Although the logistic regression models explained relative habitat use of black bears, the external validation of the overall female model indicated that the model is more appropriate for hindcasting than forecasting. Therefore, extrapolations to other areas or time periods may not be appropriate and should be conducted with caution. Further model building and testing may improve predictive power. The use of random locations may have compromised predictive power because some random sites undoubtedly received bear use. Locations not used by bears would have provided better separation. However, identification of unused habitat types is extremely difficult or such types may be nonexistent and little can be done to improve this

analysis limitation, unless one uses techniques in which the use of random locations is not required (Clark et al. 1993). Other possible factors that may have influenced the predictive power of the habitat use models are: (1) insufficient number of measured variables, (2) insufficient number of bears representative of the population, (3) lack of interaction terms, (4) insufficient number of telemetry locations, (5) social interactions, and (6) inappropriate temporal and spatial scales.

Although additional variables may be important for prediction, it is likely that the resulting models would be extremely complex and biological interpretation would be difficult. The distribution of bear locations in my study underrepresented subadult females and old adult males. Subadult females have small ranges and are relatively unlikely to encounter trap sites whereas old males may be "trap smart". Without an intensive effort to capture, radiocollar, and track specific sex and age classes or all bears in a certain area, a good representation of the bear population may be difficult to achieve.

The male habitat use model seemed to have a relatively high sensitivity, which may be related to the inclusion of interaction terms. Due to the complexity of the female habitat use model in combination with a limiting sample size, interaction terms could not be included although such interactions most likely were present. Thus, larger sample sizes, that allow the fitting of interaction terms, may indirectly affect predictive power.

One finding of this study was that social interactions may play a prominent role in habitat use. Obviously, if habitat use is influenced by conspecifics or through inter-

specific interactions, interpretations of habitat use may reflect such interactions rather than habitat relationships. Studies of black bear habitat use should consider both sexes, different age groups, and, in areas where both black and brown bears occur, brown bear habitat use (Kasworm and Manley 1990).

The habitat models indicated that black bear habitat use may occur at different spatial scales, which may have some implications for research. Although the concepts of spatial and temporal scales have received some attention in wildlife studies (e.g., Buehler *et al.* in press), most studies are designed for, and conducted on, only one scale. For large mammals, this usually means studies on relatively large areas and over relatively large time scales. Bears, however, most likely perceive the graininess of their habitat differently than humans. In my study, habitat use by female black bears seemed to be explained by variables that represented different spatial scales. Although habitat use for several variables could be detected at a resolution of < 1 ha, the question remains whether bears within a huckleberry patch or a stand of equally productive oaks perceive and use their habitat in a fine-grained or coarse-grained manner (MacArthur and Levins [1964]). For example, if bears are highly selective at such scale, models based on habitat use data at a larger scale may lack the desired predictive power. Buehler *et al.* (in press) found that a combination of both macro and micro-scale variables best classified roost sites of bald eagles (*Haliaeetus leucocephalus*). Thus, to understand and predict the dynamics of bear habitat use at larger scales (e.g., landscape scale), we may need a better understanding of habitat use dynamics at the scale of individual food items, bedding sites, protection sites, and

other such habitat features. Indices of food resources of black bears have been developed at a micro-scale (e.g., Noyce and Coy 1990) but few data are available on actual use of such resources due to the secretive behavior of black bears. Although new biotelemetry and global positioning system (GPS) technology may provide new opportunities, the logistical difficulties associated with such research will continue to be a limiting factor. Ultimately, however, knowledge of habitat use at a broader range of applicable spatial and temporal scales may be integrated to improve the predictive power of habitat use models.

I used 2 measures of individual fitness (weight and physical condition) as indices of habitat quality to relate to relative habitat use. Both measures showed no relationship. These variables were only measured during summer trapping efforts and may not be appropriate for this analysis. Other measures of population or individual fitness (e.g., reproductive success, population growth rates, density) may be used for such analyses. Habitat evaluation procedures usually operate under the assumption that species density is positively correlated with habitat quality (Van Horne 1983). Van Horne (1983) suggested that without additional demographic data, density measures may not be sufficient to correlate with habitat quality; this is supported by empirical evidence (Maurer 1986). The ultimate measure of habitat quality may be the ability of a region to sustain viable populations (Lancia *et al.* 1986); this is a difficult criterion to measure because many factors not directly related to habitat (e.g., predation, competition, weather) may influence population dynamics (Schamberger and O'Neil 1986). For bears, measures such as reproductive rate, litter size, cub

survival, and cub growth rates may be useful indices of habitat quality. Future research should attempt to determine relationships between habitat use and population viability on a regional scale.

I hypothesized that male black bears displace females from the most productive habitat areas. Wielgus (1993) described and tested 3 competing hypotheses of sex and reproductive class habitat segregation in grizzly bears. According to Wielgus (1993), there are 2 hypotheses that describe male-induced habitat segregation: the "food competition" model (female and subdominant bears avoid adult males who compete with and cannibalize subdominants for food) and the "sex competition" model of habitat segregation (females with cubs avoid immigrant, adult males because those males may kill cubs to induce estrus and obtain a breeding opportunity). In a third hypothesis, females use different habitats than males simply because of availability or choice; this was termed the "no avoidance" model by Wielgus (1993). To improve reliability and effectiveness of black bear habitat management, hypotheses of habitat segregation in black bears should be tested. Such tests would require an elaborate experimental design with studies of habitat use and population dynamics on a hunted and unhunted population.

CHAPTER VII

SUMMARY

1. I compiled 4,556 radio-telemetry locations of black bears in GSMNP collected during 3 consecutive field studies from 1976 to 1982. I used a minimum of 45 location estimates to calculate home ranges of 12 females and 11 males. Seasonal locations were pooled across years.

2. Overall, annual, and seasonal home ranges of females were smaller compared with males for all methods and contours. Overall estimates of 95% adaptive kernel home ranges averaged 16.6 km^2 for females and 275.3 km^2 for males. Annual estimates of 95% adaptive kernel home ranges averaged 7.6 km^2 for females and 48.5 km^2 for males. For females, spring, summer, and fall estimates of 95% adaptive kernel home ranges averaged 2.5 km^2, 5.2 km^2, and 23.3 km^2, respectively. Summer and fall home ranges of males were 43.0 km^2 and 470.8 km^2, respectively. Mean overlap among 95% adaptive kernel home ranges of bears with similar tracking periods was 3.8 km^2 for female pairs and 137.7 km^2 for male pairs.

3. On average, spring and summer centers of activity of females were 536 m apart and summer and fall centers of activity were 761 m apart. For males, the mean distance between summer and fall centers of activity was 6,100 m. The mean distance between annual centers of activity was 375 m for females and 3,013 for males.

4. The overall log-normalized mean rate of travel for females ($\bar{x}$ = 2.69 log(m/hr)) and males ($\bar{x}$ = 2.75 log(m/hr)) were different. The mean annual travel rate was 477 m/hr for females and 665 m/hr for males. Annual travel rates were greater for males compared with females in 1980 and 1981, but not in 1978 and 1979.

5. Travel rates of females averaged 392 m/hr in spring, 487 m/hr in summer, and 615 m/hr in fall. Male travel rates averaged 449 m/hr in spring, 748 m/hr in summer, and 335 m/hr in fall. For females, there were no differences in travel rates among 3-hour periods of the day although travel rates were different among individual bears. For males, these findings were reversed with a significant time effect but no time period-individual interaction; greatest travel rates occurred from 6:00 to 20:00.

6. Changes in annual and seasonal home range sizes, activity centers, and travel rates may largely be explained by changing activity and movement patterns in response to annual and seasonal variation in distribution, abundance, and nutritive value of foods. These patterns seem to occur on larger scales for males.

7. For 7 of 11 female pairs with > 50% home range overlap, mean distances between simultaneous locations (< 8 hr apart) were not different from randomized locations. For 2 pairs, these mean distances were smaller and for 2 other pairs these distance were greater than expected. Mean distances between simultaneous locations of male bears were not different from mean random distances for 23 of 35 pairs, smaller for 5 pairs, and greater for 7 pairs. For 32 female-male pairs with overlapping home ranges, mean distances between simultaneous locations were larger than mean distances between randomized locations for 19 pairs, smaller for 3 pairs,

and not different for 10 pairs. Differences in mean distances between simultaneous and random locations only changed slightly by season.

8. All bears with at least 30 location estimates were used for habitat use analyses. I used 1517 female (n = 17) and 1144 male (n = 15) locations for the habitat analyses, with an equal number of random location sites as a measure of available habitat.

9. A logistic regression model with 9 variables explained variation in female habitat use. This model included overstory vegetation type, overstory vegetation richness, elevation, aspect, slope, vegetation disturbance history, proximity to trails, proximity to human activity areas, and proximity to improved roads. After exclusion of outlier observation with high leverage, the model fit the data well. Seasonal models of female habitat use were based on the overall model and all fit the data after exclusion of outliers.

10. The male habitat use model was based on 6 variables (overstory vegetation type, elevation, aspect, vegetation disturbance history, proximity to human activity sites, and proximity to improved roads) and 3 interaction terms. After exclusion of outliers, this model exhibited a good fit.

11. The relatively large number of variables in the habitat models may reflect the complexity of bear habitat use. The necessary rescaling of several variables during the modelling process also indicated the existence of multi-scale habitat use patterns; this interpretation was confirmed by factor analysis.

12. For females, the first factor was mostly related to vegetation disturbance

history, elevation, and proximity to human activity sites and improved roads. The relatively high correlations among the parameter estimates for these variables confirmed this finding. Combined, these variables seem to explain a macro-scale pattern of habitat use. However, these patterns themselves seem difficult to explain without incorporating the other variables, which were represented in the second and third factors. The second and third factors seem related to micro-scale patterns of habitat use. The factor analysis on the male locations showed that overstory vegetation type, elevation, and proximity to roads explained most of the variation. Proximity to human activity sites and vegetation disturbance history mostly determined the second factor. Most variables included in the male habitat use model seem to be associated with relatively macro-scale habitat patterns. These observations and the results of the home range analyses seem to indicate that the male bear locations describe habitat use patterns that partly occur on a different scale compared with females.

13. Telemetry error had a negligible effect on the results of the logistic regression analyses, which was partly related to the macro-scale character of many variables in the models. The effect of telemetry error was largest for the micro-scale variables.

14. Although all models explained relative bear use, external validation of the overall female model indicated that the model is more appropriate for hindcasting than forecasting. Therefore, extrapolations to other areas or time periods may not be appropriate and should be conducted with caution.

15. I used the logistic regression models to calculate the relative probability of habitat use based on habitat characteristics of bear locations. Frequently used habitat areas for females were characterized by tulip poplar, mixed mesic hardwood, or xeric oak vegetation types, high vegetation richness ($\geq$ 5 overstory vegetation types), middle elevations (600 m-1,000 m), moderately steep slopes ($\geq$ 15°), northwestern aspects, historic settlement areas, close proximity to trails ($\leq$ 225 m), and large distances from human activity sites ($>$ 5,750 m) and improved roads ($\geq$ 2,500 m). These characteristics were similar for spring habitat use except that slopes were generally steeper, northern aspects and historically uncut areas were used more, and distances $<$ 5,750 m from human activity sites and $<$ 2,500 m from improved roads were more common. Characteristics of frequently used summer habitat were similar to overall habitat use except for increased use of xeric oak. Fall habitat use for females also was similar to that based on the overall model except that the vegetation richness generally was higher, slopes were not as steep, areas received historically heavy logging, areas were $<$ 5,750 m from human activity sites, and use of areas $<$ 2,500 m from roads was more common.

Habitat areas that received relatively infrequent use by females usually were characterized by mesic oak, low vegetation richness ($\leq$ 4 overstory vegetation types), elevations $<$ 600 m or $>$ 1,000 m, medium slopes (5-15°), all aspects except northwestern and northern, historically uncut, undisturbed, or light cut areas, large distances to nearest trail ($\geq$ 225 m), and with no distinct pattern of distances to human activity sites or improved roads. These characteristics changed slightly for

spring and summer with pine, mesic oak, xeric oak, and cove hardwood/pine-oak vegetation and elevations between 600 m-1,000 m more common. Low use of fall habitat predicted by the female habitat use model was also similar to that identified by the overall model except that northern hardwood and historical settlement areas also were characteristic, as were areas $\geq$ 2,500 m from roads.

16. For male locations, the habitat use model predicted relatively high use of habitats characterized by pine, mixed mesic hardwood/tulip poplar/xeric oak, and cove hardwood vegetation, elevations $<$ 1,015 m, any aspect, historically uncut areas, and areas between 3,735 m and 7,965 m from human activity sites and $<$ 5,895 m from improved roads. The model predicted relatively low use of habitats characterized by nonforest and pine-oak vegetation, elevations $\geq$ 1,015 m, northeastern to southwestern aspects, heavily logged/settlement and light cut/undisturbed areas, and distances $<$ 3,735 m or $>$ 7,965 m from human activity sites and $\geq$ 5,895 m from improved roads.

17. Female use of vegetation types, particularly with regard to summer and fall foraging, was mostly restricted to areas that seemed of secondary importance whereas males used areas of mostly primary importance. Xeric oak was the only productive habitat type that females used to any extent. Xeric oak forests usually provide abundant hard mast in the fall but, because this forest type is common, may not be fully defendable by males. Given the relatively small home ranges of females, a high vegetation richness may partly compensate for the use of secondary foraging areas. Bears commonly used low and middle elevations, which was correlated with

oak forest types and high vegetation richness. Use of steep slopes by females was most pronounced in spring and may be related to post-denning activities. The importance of slope aspects in habitat use was partly due to correlations with other variables. Where historically uncut vegetation was relatively uncommon, females used uncut areas less than expected whereas males used those areas more than expected. The old-growth character of uncut areas may offer bears a variety of life requisites. Female bears were located closer to trails than expected possibly because of movement efficiency and soft mast abundance. Unlike male bears, females used areas closed to human activity sites and improved roads less than expected. Because the multivariate analysis identified several other factors that may have influenced these observations, the observed habitat use patterns were most likely not solely the result of a response to potential disturbances associated with improved roads or human activity sites.

18. Based on the observations of habitat use and the differences between simultaneous locations of males and females, I hypothesize that female habitat use is partly a result of social interactions with male bears who prevent females from using productive or otherwise important habitats.

19. The mean relative habitat use probability decreased with larger home range contours for individual bears and with increasing home range areas for the 75% and 95% home ranges. However, the mean probability of relative habitat use in core areas was similar for all bears of the same sex, despite differences in core area size. Thus, other factors than habitat use may influence size differences of core areas.

20. I observed no relationships between mean weight or physical condition of female bears and the mean predicted probability of habitat use within their home ranges, indicating that there may not be a direct relationship between habitat use and habitat quality or that weight and physical condition do not reflect habitat quality.

21. The 1990-1992 frequencies of observed bear visits to bait stations were different from predicted frequencies based on the overall female and male habitat models, indicating that bait-station visits may not be a good indicators of habitat use.

22. Based on the results of my study, management implications are to create and maintain a relatively uniform distribution of productive oak forests. Maintenance of oak cover types also would ensure availability of soft mast producing shrubs and trees, especially on submesic to mesic sites. Availability of alternative fall foods (e.g., wild grapes) may reduce the need for extensive movements during the fall and thus decrease energy expenditure and risk of mortality. Management for vegetation richness on a small scale (i.e., areas $<$ 30 ha) may allow females to find many life requisites in relatively small areas.

23. Given the validity of the untested hypothesis of habitat use segregation between females and males, management to improve bear habitat may change the sex and possibly age structure of the population within a certain area. Thus, for habitat management plans to be effective, effects on both female and male bears may need to be considered as well as demographic characteristics of the bear population and harvest regimes.

24. GIS-based habitat use models may be useful for identifying important

habitat areas for land acquisitions, mitigation procedures, and development and evaluation of forest management plans. Simulation analyses can be performed at different scales, providing a mechanism for local and regional management of bear habitat. GIS may be used to evaluate short-term and long-term effects of proposed forest management actions and other foreseeable habitat changes. Data-based habitat use models may be applied by natural resource managers in a proactive approach to black bear management.

25. Future research should focus on developing efficient and effective regional habitat management regimes for black bears. Such research should consider both sexes and different age groups. A more experimental approach should be emphasized to test different research hypotheses of sex and reproductive class habitat segregation in black bears.

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APPENDICES

Appendix A. Summary of MacKenzie's (1993) overstory vegetation data.

Table A.1. Mean of species basal area (m^2/ha) and number of plots by vegetation type.[a]

Species	Vegetation Type								
	Spruce Fir	Northern Hardwood	Cove Hardwood	Mesic Oak	Mixed Mesic Hardwood	Tulip Poplar	Xeric Oak	Oak Pine	Pine
Acer pensylvanica	1.05	0.43	0.21	0.00	0.18	0.00	0.03	0.00	0.05
Acer rubrum	2.04	2.34	4.60	8.11	5.47	4.86	5.41	2.28	1.89
Acer saccharinum	0.00	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.00
Acer saccharum	0.00	0.75	1.59	0.80	0.58	0.50	0.03	0.00	0.00
Acer spicatum	0.00	0.03	0.01	0.00	0.00	0.00	0.00	0.00	0.00
Amelanchier arborea	0.00	0.00	0.03	0.00	0.00	0.00	0.00	0.00	0.00
Amelanchier laevis	0.00	0.42	0.23	0.28	0.17	0.00	0.06	0.00	0.00
Aralia spinosa	0.00	0.00	0.00	0.00	0.02	0.00	0.00	0.00	0.00
Aesculus octandra	0.36	0.88	1.49	0.46	0.49	0.22	0.03	0.00	0.00
Betula lenta	0.00	3.33	4.61	0.62	1.98	0.35	0.55	0.00	0.08
Betula lutea	17.66	11.54	2.28	0.57	0.86	0.16	0.00	0.00	0.00
Betula spp	0.00	0.17	0.06	0.00	0.00	0.00	0.00	0.00	0.00
Cladastrus kentuckea	0.00	0.00	0.00	0.00	0.00	0.22	0.00	0.00	0.00
Cornus florida	0.00	0.00	0.00	0.00	0.13	0.12	0.41	0.00	0.34
Carpinus caroliniana	0.00	0.00	0.00	0.00	0.15	0.00	0.05	0.00	0.00
Carya cordiformis	0.00	0.00	0.01	0.00	0.10	0.00	0.00	0.00	0.00
Carya glabra	0.00	0.00	0.00	0.28	0.44	0.00	0.54	0.00	0.00
Carya ovalis	0.00	0.00	0.00	0.00	0.03	0.00	0.00	0.00	0.00
Carya pallida	0.00	0.00	0.00	0.00	0.02	0.00	0.00	0.00	0.00
Carya spp.	0.00	0.00	0.03	0.00	0.12	0.16	0.13	0.00	0.00
Carya tomentosa	0.00	0.00	0.00	0.19	0.14	0.00	0.45	0.00	0.33
Castanea dentata	0.00	0.00	0.02	0.00	0.00	0.00	0.00	0.00	0.00
Fagus grandifolia	0.17	5.23	1.58	0.51	0.07	0.00	0.09	0.00	0.00
Fraxinus spp.	0.00	0.00	0.37	0.19	0.23	0.35	0.03	0.00	0.05
Halesi carolina	0.00	1.39	4.25	0.65	0.59	3.66	0.18	0.00	0.05
Hamamelis virginiana	0.00	0.00	0.00	0.00	0.02	0.12	0.03	0.24	0.00
Ilex montana	0.00	0.00	0.06	0.00	0.00	0.00	0.00	0.00	0.00
Ilex opaca	0.00	0.00	0.05	0.00	0.02	0.00	0.00	0.00	0.08
Juglans cinerea	0.00	0.00	0.03	0.00	0.00	0.00	0.00	0.00	0.00
Juglans nigra	0.00	0.00	0.00	0.00	0.08	0.12	0.18	0.00	0.00
Juniperus virginiana	0.00	0.00	0.00	0.00	0.04	0.00	0.00	0.00	0.05
Kalmia latifolia	0.00	0.00	0.00	0.00	0.02	0.00	0.00	0.00	0.00
Liquidambar styraciflua	0.00	0.00	0.00	0.00	0.20	0.00	0.11	0.00	0.34
Liriodendron tulipifera	0.23	0.00	3.24	0.51	10.60	23.56	2.87	0.00	1.47
Magnolia acuminata	0.00	0.00	0.35	0.00	0.18	0.32	0.00	0.00	0.00
Magnolia fraseri	0.00	0.15	1.31	0.53	0.24	0.12	0.12	0.00	0.00
Morus rubra	0.00	0.00	0.00	0.00	0.00	0.00	0.03	0.00	0.00
Nyssa sylvatica	0.00	0.00	0.08	1.87	0.17	0.00	0.22	2.90	0.91
Ostrya virginiana	0.00	0.00	0.02	0.00	0.00	0.00	0.03	0.00	0.00
Oxydendron arboreum	0.31	0.00	0.21	1.04	1.11	0.62	2.42	0.47	1.68
Picea rubens	15.76	2.17	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Platanus occidentalis	0.00	0.00	0.00	0.00	0.08	0.16	0.04	0.00	0.00
Pinus echinata	0.00	0.00	0.00	0.00	0.02	0.00	0.29	0.00	0.94
Pinus pugens	0.00	0.00	0.00	0.00	0.04	0.00	0.19	13.93	11.54
Pinus rigida	0.00	0.00	0.00	0.00	0.71	0.12	1.96	4.25	9.39
Pinus strobus	0.00	0.00	0.02	0.00	0.28	0.00	0.18	0.00	0.37
Pinus virginiana	0.00	0.00	0.00	0.00	0.13	0.00	0.61	0.00	2.47
Prunus pensylvanica	0.65	1.76	0.16	0.00	0.00	0.00	0.00	0.00	0.00
Prunus serotina	0.00	0.53	1.04	0.50	0.14	0.08	0.00	0.00	0.00
Quercus alba	0.00	0.00	0.01	0.63	0.42	0.00	1.84	1.34	0.09
Quercus coccinea	0.00	0.05	0.02	0.50	0.22	0.00	2.05	5.55	2.30
Quercus falcata	0.00	0.00	0.00	0.00	0.00	0.00	0.06	0.00	0.00
Quercus prinus	0.00	0.10	0.59	5.99	2.43	0.00	5.80	2.61	1.28
Quercus rubra	0.00	2.28	3.16	14.68	1.63	0.00	1.62	0.63	0.23
Quercus ellipsoidalis	0.00	0.00	0.12	0.09	0.13	0.00	0.23	0.00	0.00
Quercus velutina	0.00	0.00	0.00	0.00	0.16	0.00	1.67	0.00	0.17
Robinia pseudoacacia	0.33	0.03	0.76	1.75	0.69	1.62	0.49	0.40	0.08
Rhododendron maximum	0.00	0.00	0.02	0.00	0.04	0.00	0.00	0.00	0.00
Rhododendron spp.	0.00	0.00	0.06	0.00	0.00	0.00	0.03	0.00	0.00
Sorbus americana	0.00	0.28	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Sassafras albidum	0.00	0.00	0.17	0.10	0.58	0.27	0.18	0.00	0.00
Tilia heterophylla	0.00	0.51	2.29	1.36	0.43	1.12	0.04	0.00	0.00
Tsuga canadensis	0.32	2.46	7.59	1.28	2.79	1.88	1.57	0.37	1.37
Number of plots	5	40	68	14	40	10	29	2	15

[a] After MacKenzie (1993).

Table A.2. Standard deviation of species basal area and number of plots by vegetation type.[a]

Species	Vegetation Type								
	Spruce Fir	Northern Hardwood	Cove Hardwood	Mesic Oak	Mixed Mesic Hardwood	Tulip Poplar	Xeric Oak	Oak Pine	Pine
Acer pensylvanica	1.56	1.47	0.64	0.00	0.71	0.00	0.16	0.00	0.21
Acer rubrum	3.85	4.18	4.24	4.54	4.92	5.76	4.07	3.22	2.34
Acer saccharinum	0.00	0.00	0.10	0.00	0.00	0.00	0.00	0.00	0.00
Acer saccharum	0.00	1.64	3.50	1.93	1.24	0.87	0.17	0.00	0.00
Acer spicatum	0.00	0.16	0.11	0.00	0.00	0.00	0.00	0.00	0.00
Amelanchier arborea	0.00	0.00	0.23	0.00	0.00	0.00	0.00	0.00	0.00
Amelanchier laevis	0.00	0.84	0.66	0.82	0.81	0.00	0.22	0.00	0.00
Aralia spinosa	0.00	0.00	0.00	0.00	0.13	0.00	0.00	0.00	0.00
Aesculus octandra	0.80	2.41	3.29	1.39	1.27	0.47	0.14	0.00	0.00
Betula lenta	0.00	5.74	5.35	1.34	3.14	0.87	1.28	0.00	0.30
Betula lutea	9.12	11.65	3.39	1.77	2.00	0.50	0.00	0.00	0.00
Betula spp.	0.00	0.66	0.29	0.00	0.00	0.00	0.00	0.00	0.00
Cladastrus kentuckea	0.00	0.00	0.00	0.00	0.00	0.47	0.00	0.00	0.00
Cornus florida	0.00	0.00	0.00	0.00	0.42	0.37	0.91	0.00	0.68
Carpinus caroliniana	0.00	0.00	0.00	0.00	0.80	0.00	0.28	0.00	0.00
Carya cordiformis	0.00	0.00	0.05	0.00	0.51	0.00	0-00	0.00	0.00
Carya glabra	0.00	0.00	0.00	0.73	0.91	0.00	1.47	0.00	0.00
Carya ovalis	0.00	0.00	0.00	0.00	0.18	0.00	0.00	0.00	0.00
Carya pallida	0.00	0.00	0.00	0.00	0.15	0.00	0.00	0.00	0.00
Carya spp.	0.00	0.00	0.17	0.00	0.49	0.49	0.34	0.00	0.00
Carya tomentosa	0.00	0.00	0.00	0.72	0.44	0.00	1.12	0.00	1.29
Castanea dentata	0.00	0.00	0.14	0.00	0.00	0.00	0.00	0.00	0.00
Fagus grandifolia	0.37	6.92	3.25	1.15	0.32	0.00	0.28	0.00	0.00
Fraxinus spp.	0.00	0.00	1.08	0.49	0.57	0.87	0.14	0.00	0.20
Halesi carolina	0.00	3.40	5.44	1.27	1.06	3.66	0.43	0.00	0.18
Hamamelis virginiana	0.00	0.00	0.00	0.00	0.15	0.37	0.16	0.33	0.00
Ilex montana	0.00	0.00	0.48	0.00	0.00	0.00	0.00	0.00	0.00
Ilex opaca	0.00	0.00	0.39	0.00	0.13	0.00	0.00	0.00	0.30
Juglans cinerea	0.00	0.00	0.21	0.00	0.00	0.00	0.00	0.00	0.00
Juglans nigra	0.00	0.00	0.00	0.00	0.38	0.36	0.46	0.00	0.00
Juniperus virginiana	0.00	0.00	0.00	0.00	0.24	0.00	0.00	0.00	0.20
Kalmia latifolia	0.00	0.00	0.00	0.00	0.14	0.00	0.00	0.00	0.00
Liquidambar styraciflua	0.00	0.00	0.00	0.00	1.01	0.00	0.45	0.00	0.92
Liriodendron tulipifera	0.51	0.00	6.18	0.89	9.60	5.68	4.76	0.00	2.29
Magnolia acuminata	0.00	0.00	0.86	0.00	0.46	1.02	0.00	0.00	0.00
Magnolia fraseri	0.00	0.58	2.30	1.49	0.52	0.38	0.41	0.00	0.00
Morus rubra	0.00	0.00	0.00	0.00	0.00	0.00	0.14	0.00	0.00
Nyssa sylvatica	0.00	0.00	0.41	5.36	0.51	0.00	0.55	0.38	1.09
Ostrya virginiana	0.00	0.00	0.14	0.00	0.00	0.00	0.17	0.00	0.00
Oxydendron arboreum	0.70	0.00	0.74	1.48	1.36	1.95	1.89	0.66	1.92
Picea rubens	11.62	3.66	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Platanus occidentalis	0.00	0.00	0.00	0.00	0.49	0.49	0.19	0.00	0.00
Pinus echinata	0.00	0.00	0.00	0.00	0.12	0.00	0.69	0.00	3.64
Pinus pugens	0.00	0.00	0.00	0.00	0.27	0.00	0.71	19.70	13.47
Pinus rigida	0.00	0.00	0.00	0.00	1.65	0.37	2.61	2.64	6.04
Pinus strobus	0.00	0.00	0.19	0.00	0.83	0.00	0.57	0.00	1.44
Pinus virginiana	0.00	0.00	0.00	0.00	0.52	0.00	1.22	0.00	2.65
Prunus pensylvanica	1.46	4.08	1.14	0.00	0.00	0.00	0.00	0.00	0.00
Prunus serotina	0.00	1.59	2.26	1.32	0.74	0.25	0.00	0.00	0.00
Quercus alba	0.00	0.00	0.10	1.76	1.58	0.00	3.21	1.89	0.35
Quercus coccinea	0.00	0.32	0.20	1.87	0.66	0.00	3.19	4.47	2.60
Quercus falcata	0.00	0.00	0.00	0.00	0.00	0.00	0.22	0.00	0.00
Quercus prinus	0.00	0.61	1.84	6.40	4.01	0.00	6.10	3.02	2.64
Quercus rubra	0.00	5.25	4.87	9.22	1.93	0.00	2.54	0.23	0.71
Quercus ellipsoidalis	0.00	0.00	0.70	0.32	0.48	0.00	0.58	0.00	0.00
Quercus velutina	0.00	0.00	0.00	0.00	0.57	0-00	4.53	0.00	0.65
Robinia pseudoacacia	0.74	0.20	1.61	2.64	1.21	1.69	1.01	0.56	0.30
Rhododendron maximum	0.00	0.00	0.14	0.00	0.25	0.00	0.00	0.00	0.00
Rhododendron spp.	0.00	0.00	0.48	0.00	0.00	0.00	0.16	0.00	0.00
Sorbus americana	0.00	1.09	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Sassafras albidum	0.00	0.00	0.73	0.36	1.43	0.45	0.53	0.00	0.00
Tilia heterophylla	0.00	2.97	4.02	3.46	1.12	2.61	0.24	0.00	0.00
Tsuga canadensis	0.72	4.63	9.02	4.78	3.99	2.04	2.47	0.52	3.59
Number of plots	5	40	68	14	40	10	29	2	15

[a] After MacKenzie (1993).

Table A.3. Frequency of species occurrence and number of plots by vegetation type.[a]

Species	Vegetation Type								
	Spruce Fir	Northern Hardwood	Cove Hardwood	Mesic Oak	Mixed Mesic Hardwood	Tulip Poplar	Xeric Oak	Oak Pine	Pine
Acer pensylvanica	2.00	8.00	8.00	0.00	3.00	0.00	1.00	0.00	1.00
Acer rubrum	2.00	16.00	55.00	13.00	35.00	7.00	29.00	1.00	8.00
Acer saccharinum	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00	0.00
Acer saccharum	0.00	9.00	24.00	4.00	12.00	3.00	1.00	0.00	0.00
Acer spicatum	0.00	1.00	1.00	0.00	0.00	0.00	0.00	0.00	0.00
Amelanchier arborea	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00	0.00
Amelanchier laevis	0.00	10.00	9.00	2.00	3.00	0.00	2.00	0.00	0.00
Aralia spinosa	0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00
Aesculus octandra	1.00	7.00	27.00	2.00	6.00	2.00	1.00	0.00	0.00
Betula lenta	0.00	20.00	51.00	3.00	22.00	2.00	8.00	0.00	1.00
Betula lutea	5.00	33.00	40.00	2.00	8.00	1.00	0.00	0.00	0.00
Betula spp.	0.00	3.00	3.00	0.00	0.00	0.00	0.00	0.00	0.00
Cladastrus kentuckea	0.00	0.00	0.00	0.00	0.00	2.00	0.00	0.00	0.00
Cornus florida	0.00	0.00	0.00	0.00	4.00	1.00	6.00	0.00	4.00
Carpinus caroliniana	0.00	0.00	0.00	0.00	2.00	0.00	1.00	0.00	0.00
Carya cordiformis	0.00	0.00	1.00	0.00	2.00	0.00	0.00	0.00	0.00
Carya glabra	0.00	0.00	0.00	2.00	10.00	0.00	4.00	0.00	0.00
Carya ovalis	0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00
Carya pallida	0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00
Carya spp.	0.00	0.00	2.00	0.00	3.00	1.00	4.00	0.00	0.00
Carya tomentosa	0.00	0.00	0.00	1.00	4.00	0.00	5.00	0.00	1.00
Castanea dentata	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00	0.00
Fagus grandifolia	1.00	24.00	23.00	3.00	2.00	0.00	3.00	0.00	0.00
Fraxinus spp.	0.00	0.00	11.00	2.00	7.00	2.00	1.00	0.00	1.00
Halesi carolina	0.00	9.00	45.00	4.00	12.00	9.00	5.00	0.00	1.00
Hamamelis virginiana	0.00	0.00	0.00	0.00	1.00	1.00	1.00	1.00	0.00
Ilex montana	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00	0.00
Ilex opaca	0.00	0.00	1.00	0.00	1.00	0.00	0.00	0.00	1.00
Juglans cinerea	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00	0.00
Juglans nigra	0.00	0.00	0.00	0.00	2.00	1.00	4.00	0.00	0.00
Juniperus virginiana	0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	1.00
Kalmia latifolia	0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00
Liquidambar styraciflua	0.00	0.00	0.00	0.00	2.00	0.00	2.00	0.00	3.00
Liriodendron tulipifera	1.00	0.00	22.00	4.00	34.00	10.00	17.00	0.00	6.00
Magnolia acuminata	0.00	0.00	12.00	0.00	6.00	1.00	0.00	0.00	0.00
Magnolia fraseri	0.00	3.00	25.00	3.00	8.00	1.00	3.00	0.00	0.00
Morus rubra	0.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00
Nyssa sylvatica	0.00	0.00	3.00	3.00	5.00	0.00	5.00	2.00	7.00
Ostrya virginiana	0.00	0.00	1.00	0.00	0.00	0.00	1.00	0.00	0.00
Oxydendron arboreum	1.00	0.00	6.00	6.00	22.00	1.00	27.00	1.00	9.00
Picea rubens	4.00	21.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Platanus occidentalis	0.00	0.00	0.00	0.00	1.00	1.00	1.00	0.00	0.00
Pinus echinata	0.00	0.00	0.00	0.00	1.00	0.00	5.00	0.00	1.00
Pinus pugens	0.00	0.00	0.00	0.00	1.00	0.00	3.00	1.00	9.00
Pinus rigida	0.00	0.00	0.00	0.00	9.00	1.00	14.00	2.00	15.00
Pinus strobus	0.00	0.00	1.00	0.00	6.00	0.00	3.00	0.00	1.00
Pinus virginiana	0.00	0.00	0.00	0.00	3.00	0.00	8.00	0.00	11.00
Prunus pensylvanica	1.00	13.00	2.00	0.00	0.00	0.00	0.00	0.00	0.00
Prunus serotina	0.00	8.00	30.00	2.00	2.00	1.00	0.00	0.00	0.00
Quercus alba	0.00	0.00	1.00	2.00	4.00	0.00	11.00	1.00	1.00
Quercus coccinea	0.00	1.00	1.00	1.00	6.00	0.00	16.00	2.00	10.00
Quercus falcata	0.00	0.00	0.00	0.00	0.00	0.00	2.00	0.00	0.00
Quercus prinus	0.00	1.00	10.00	8.00	17.00	0.00	19.00	2.00	5.00
Quercus rubra	0.00	11.00	35.00	13.00	25.00	0.00	15.00	2.00	2.00
Quercus ellipsoidalis	0.00	0.00	2.00	1.00	3.00	0.00	4.00	0.00	0.00
Quercus velutina	0.00	0.00	0.00	0.00	4.00	0.00	6.00	0.00	1.00
Robinia pseudoacacia	1.00	1.00	18.00	7.00	15.00	6.00	7.00	1.00	1.00
Rhododendron maximum	0.00	0.00	2.00	0.00	1.00	0.00	0.00	0.00	0.00
Rhododendron spp.	0.00	0.00	1.00	0.00	0.00	0.00	1.00	0.00	0.00
Sorbus americana	0.00	3.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Sassafras albidum	0.00	0.00	4.00	1.00	10.00	3.00	3.00	0.00	0.00
Tilia heterophylla	0.00	2.00	26.00	2.00	7.00	2.00	1.00	0.00	0.00
Tsuga canadensis	1.00	18.00	48.00	1.00	25.00	7.00	15.00	1.00	4.00
Number of plots	5	40	68	14	40	10	29	2	15

[a] After MacKenzie (1993).

Appendix B. Estimates of home range size and number of locations.

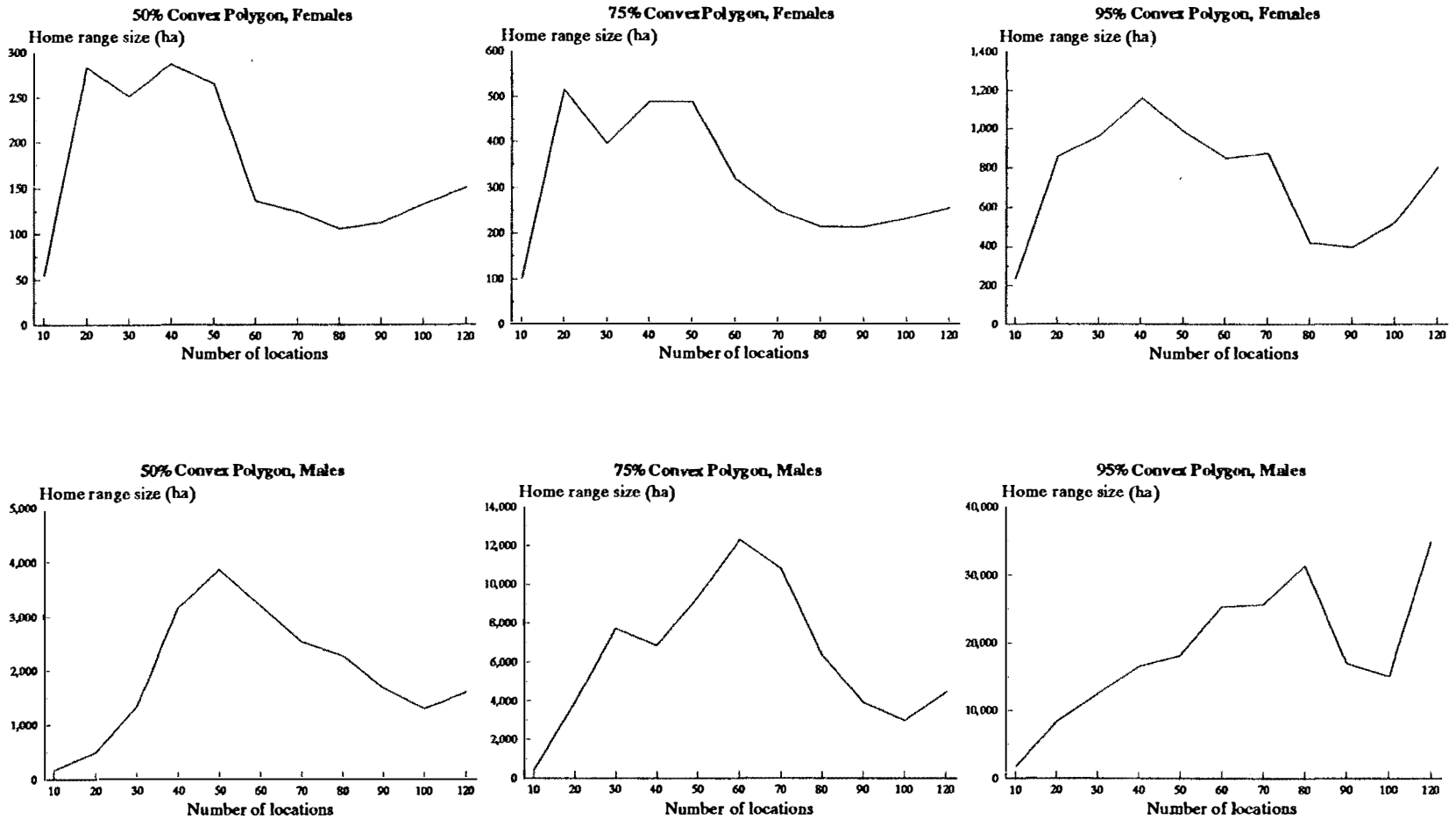


Fig. B.1. Relationships between convex polygon home range size estimates and number of black bear locations, Great Smoky Mountains National Park, 1976-1982.

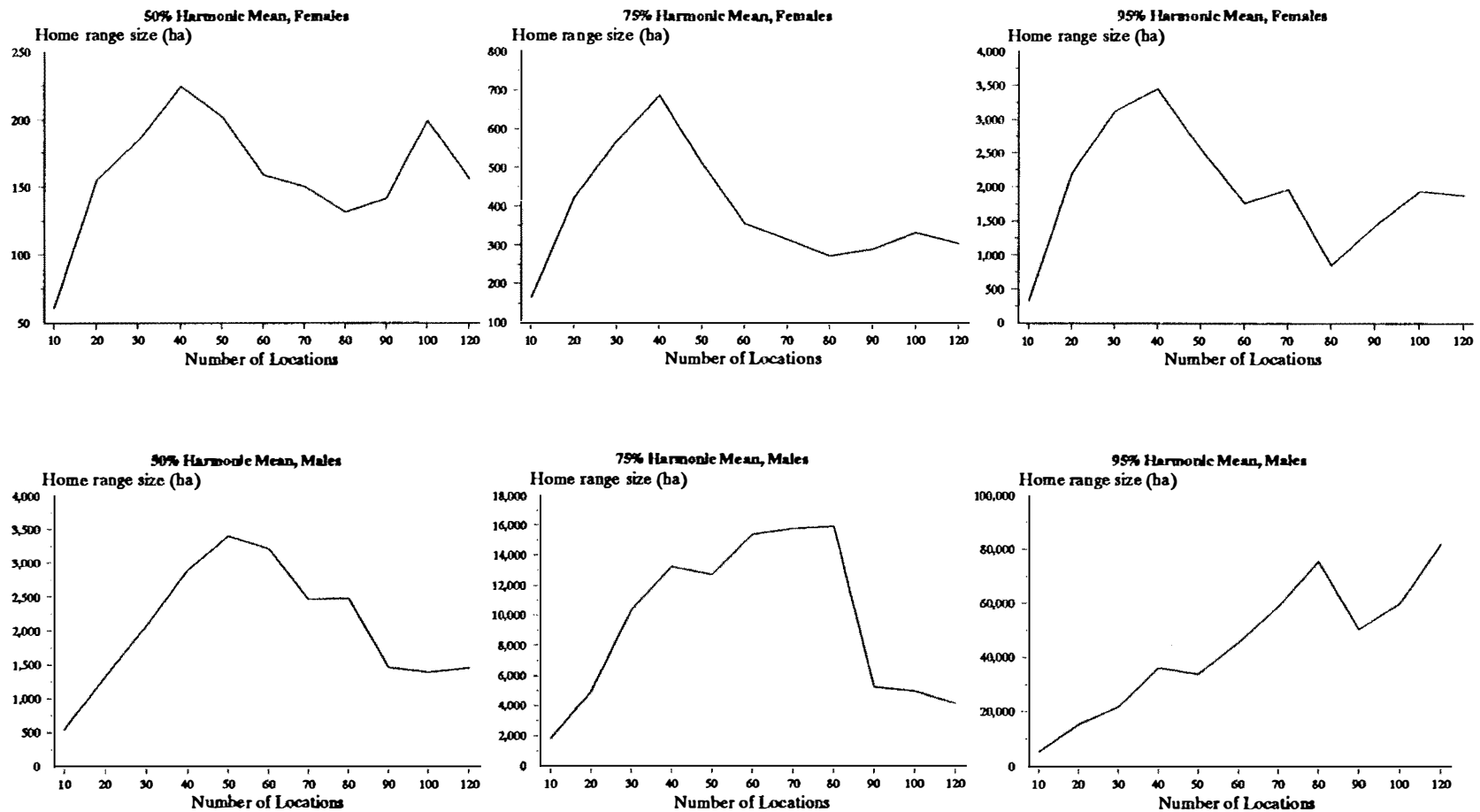


Fig. B.2. Relationships between harmonic mean home range size estimates and number of black bear locations, Great Smoky Mountains National Park, 1976-1982.

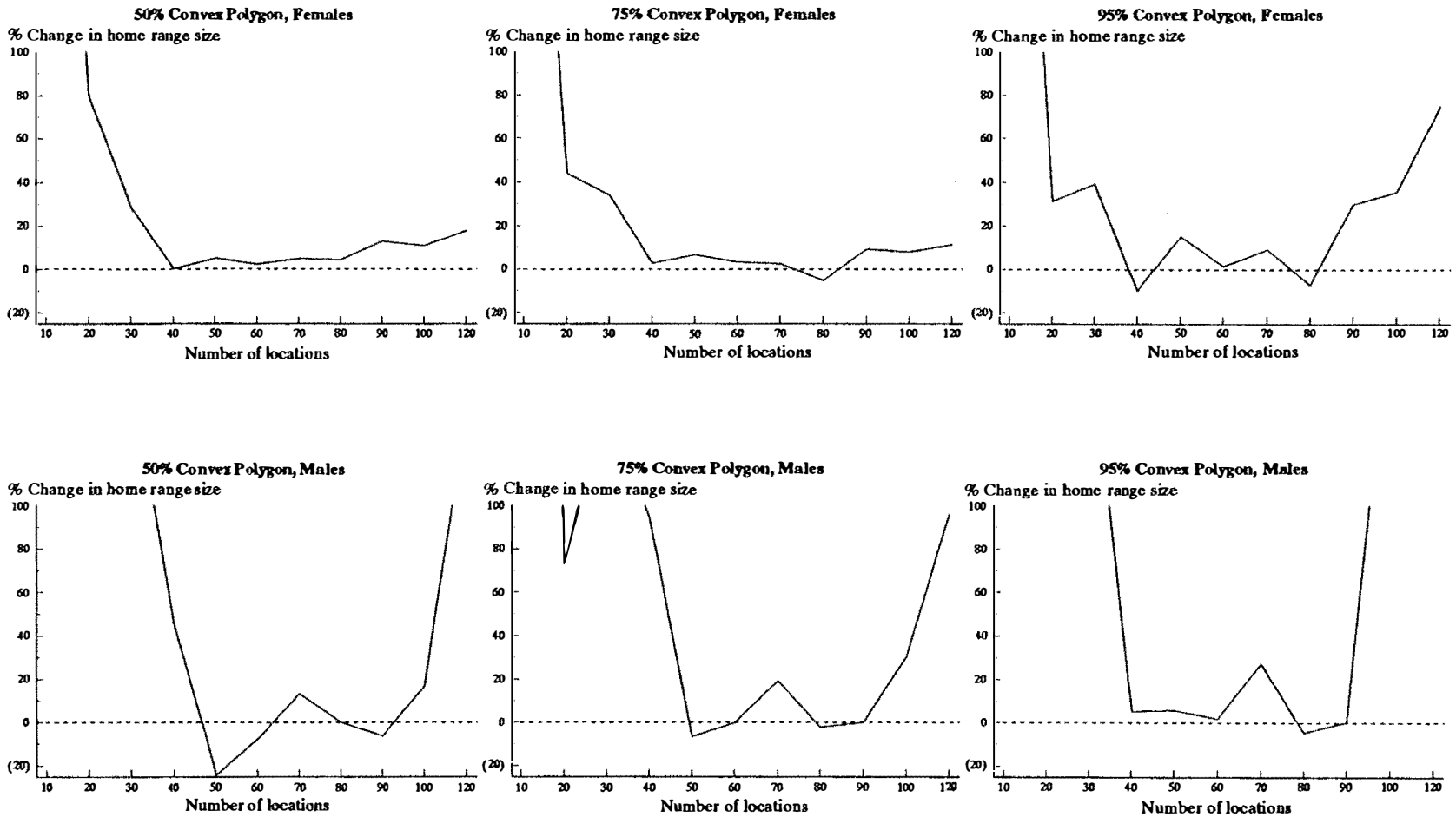


Fig. B.3. Relationships between percent change in convex polygon home range size estimates and number of black bear locations, Great Smoky Mountains National Park, 1976-1982.

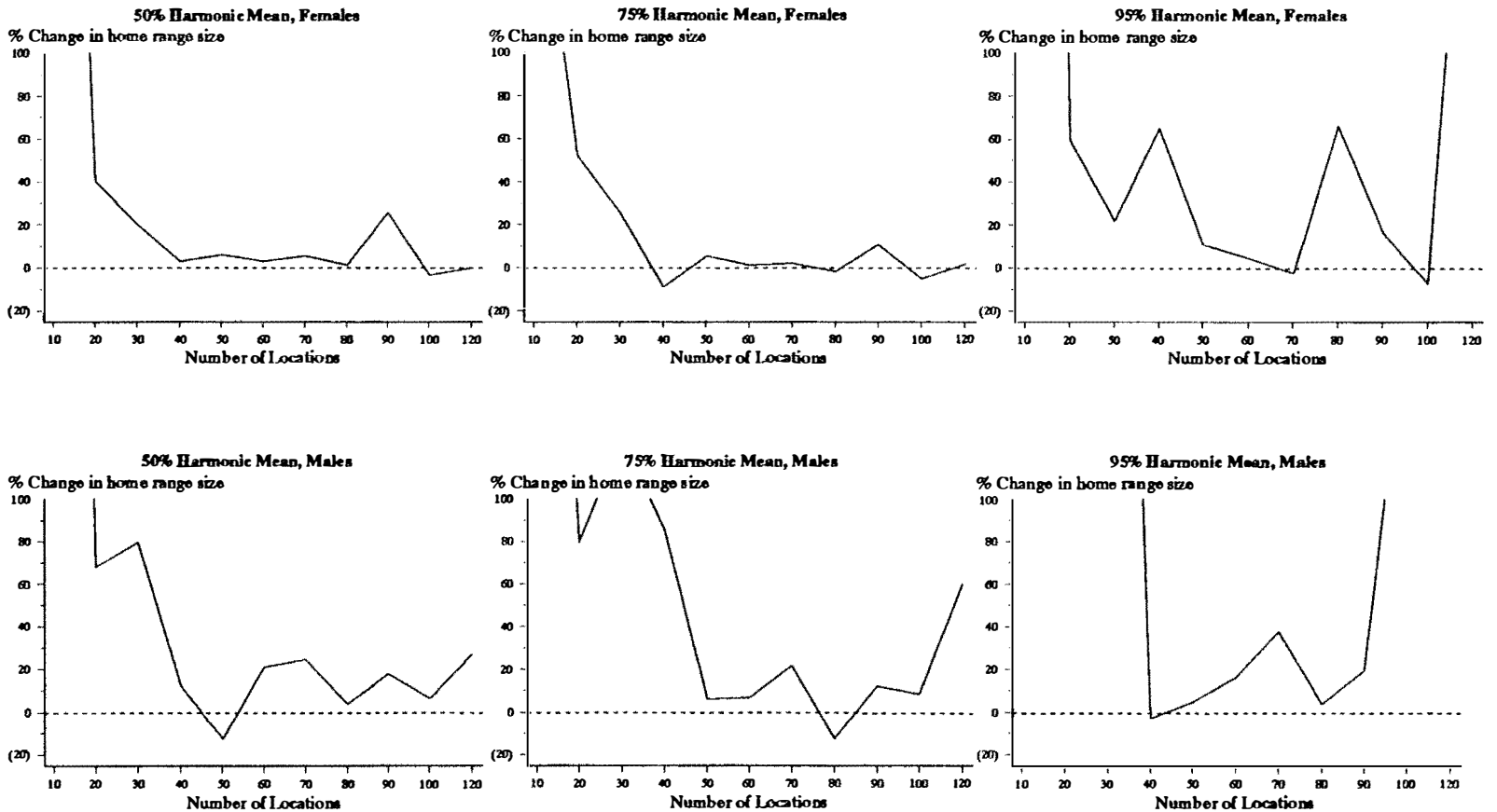


Fig. B.4. Relationships between percent change in harmonic mean home range size estimates and number of black bear locations, Great Smoky Mountains National Park, 1976-1982.

Appendix C. Estimates of annual home range sizes.

Table C.1. Estimates of home range sizes (km^2) of black bears in Great Smoky Mountains National Park, 1977.

		Females				Males			
	%	$\bar{x}$	SD	n	range	$\bar{x}$	SD	n	range
Harmonic Mean	100%	7.5	.	1	.	-	-	-	-
	95%	3.7	.	1	.	-	-	-	-
	75%	1.7	.	1	.	-	-	-	-
	50%	1.0	.	1	.	-	-	-	-

		Females				Males			
	%	$\bar{x}$	SD	n	range	$\bar{x}$	SD	n	range
Convex Polygon	100%	4.8	.	1	.	-	-	-	-
	95%	2.8	.	1	.	-	-	-	-
	75%	2.0	.	1	.	-	-	-	-
	50%	0.9	.	1	.	-	-	-	-

		Females				Males			
	%	$\bar{x}$	SD	n	range	$\bar{x}$	SD	n	range
Adaptive Kernel	100%	11.3	.	1	.	-	-	-	-
	95%	4.8	.	1	.	-	-	-	-
	75%	2.6	.	1	.	-	-	-	-
	50%	1.3	.	1	.	-	-	-	-

Table C.2. Estimates of home range sizes (km^2) of black bears in Great Smoky Mountains National Park, 1978.

		Females				Males			
	%	$\bar{x}$	SD	n	range	$\bar{x}$	SD	n	range
	100%	21.0	25.5	3	4.1-50.4	-	-	-	-
Harmonic		8.1	7.0	3	0.8-15.6	-	-	-	-
Mean	75%	2.7	2.4	3	0.8-5.4	-	-	-	-
	50%	1.1	1.1	3	0.3-2.3	-	-	-	-

		Females				Males			
	%	$\bar{x}$	SD	n	range	$\bar{x}$	SD	n	range
	100%	13.1	14.2	3	2.3-29.2	-	-	-	-
Convex	95%	8.2	8.5	3	1.3-17.8	-	-	-	-
Polygon	75%	5.6	7.4	3	0.7-14.1	-	-	-	-
	50%	4.2	6.4	3	0.3-11.6	-	-	-	-

		Females				Males			
	%	$\bar{x}$	SD	n	range	$\bar{x}$	SD	n	range
	100%	31.8	41.1	3	5.0-79.1	-	-	-	-
Adaptive	95%	13.8	14.2	3	2.5-29.8	-	-	-	-
Kernel	75%	4.5	4.3	3	1.1-9.3	-	-	-	-
	50%	1.5	1.4	3	0.5-3.2	-	-	-	-

Table C.3. Estimates of home range sizes (km^2) of black bears in Great Smoky Mountains National Park, 1979.

		Females				Males			
	%	$\bar{x}$	SD	n	range	$\bar{x}$	SD	n	range
	100%	6.3	3.7	4	3.6-11.6	314.2	398.8	4	46.4-906.3
Harmonic		3.4	1.4	4	2.1-5.3	49.9	22.1	4	20.5-67.1
Mean	75%	1.5	0.6	4	0.8-2.2	14.2	7.3	4	6.5-21.4
	50%	0.6	0.3	4	0.3-0.9	5.7	2.9	4	2.5-8.4

		Females				Males			
	%	$\bar{x}$	SD	n	range	$\bar{x}$	SD	n	range
	100%	3.7	1.2	4	2.4-5.1	65.4	35.6	4	24.7-109.0
Convex	95%	2.8	1.1	4	1.5-4.3	27.7	13.2	4	15.4-41.5
Polygon	75%	1.7	0.6	4	0.9-2.4	13.0	8.1	4	5.0-22.4
	50%	1.0	0.4	4	0.6-1.4	5.2	3.2	4	2.3-8.4

		Females				Males			
	%	$\bar{x}$	SD	n	range	$\bar{x}$	SD	n	range
	100%	7.3	3.4	4	4.3-11.4	136.1	67.8	4	57.7-200.0
Adpative	95%	4.4	1.4	4	2.7-6.1	55.0	23.6	4	21.7-73.8
Kernel	75%	1.9	0.6	4	1.0-2.5	16.5	7.9	4	8.3-24.4
	50%	1.1	0.3	4	0.7-1.5	6.7	3.3	4	2.8-9.8

Table C.4. Estimates of home range sizes (km^2) of black bears in Great Smoky Mountains National Park, 1980.

		Females				Males			
	%	$\bar{x}$	SD	n	range	$\bar{x}$	SD	n	range
Harmonic Mean	100%	14.2	9.4	3	7.4-25.0	-	-	-	-
	95%	9.8	6.6	3	4.4-17.2	-	-	-	-
	75%	2.1	0.5	3	1.7-2.6	-	-	-	-
	50%	0.8	0.2	3	0.7-1.0	-	-	-	-

		Females				Males			
	%	$\bar{x}$	SD	n	range	$\bar{x}$	SD	n	range
Convex Polygon	100%	9.8	6.0	3	5.2-16.5	-	-	-	-
	95%	5.0	1.3	3	3.5-5.8	-	-	-	-
	75%	2.5	0.6	3	1.9-3.1	-	-	-	-
	50%	1.0	0.4	3	0.7-1.5	-	-	-	-

		Females				Males			
	%	$\bar{x}$	SD	n	range	$\bar{x}$	SD	n	range
Adaptive Kernel	100%	16.9	9.7	3	8.9-27.7	-	-	-	-
	95%	11.3	7.2	3	4.1-18.5	-	-	-	-
	75%	3.1	0.7	3	2.4-3.9	-	-	-	-
	50%	1.6	0.6	3	0.9-2.1	-	-	-	-

Table C.5. Estimates of home range sizes (km^2) of black bears in Great Smoky Mountains National Park, 1981.

		Females				Males			
	%	$\bar{x}$	SD	n	range	$\bar{x}$	SD	n	range
Harmonic Mean	100%	7.5	1.6	5	6.6-10.3	48.3	40.6	3	23.1-95.1
	95%	3.5	0.5	5	2.9-4.0	26.9	15.3	3	15.0-44.2
	75%	1.6	0.4	5	0.9-2.1	11.5	8.3	3	4.3-20.6
	50%	0.7	0.3	5	0.4-1.2	4.7	4.8	3	0.8-10.0

		Females				Males			
	%	$\bar{x}$	SD	n	range	$\bar{x}$	SD	n	range
Convex Polygon	100%	4.5	0.7	5	3.8-5.7	32.3	20.4	3	16.0-55.2
	95%	2.9	0.4	5	2.4-3.4	29.2	19.4	3	14.2-51.1
	75%	1.6	0.4	5	1.0-2.1	11.0	8.3	3	2.1-18.4
	50%	0.8	0.3	5	0.5-1.2	5.3	5.3	3	1.0-11.2

		Females				Males			
	%	$\bar{x}$	SD	n	range	$\bar{x}$	SD	n	range
Adaptive Kernel	100%	9.3	3.4	5	6.3-15.1	68.3	24.2	3	52.2-96.1
	95%	4.7	0.4	5	4.2-5.3	39.8	17.4	3	23.4-58.1
	75%	1.9	0.4	5	1.6-2.5	16.2	10.1	3	6.2-26.4
	50%	0.9	0.2	5	0.7-1.3	6.1	5.7	3	0.9-12.2

Appendix D. Estimates of individual home range sizes.

Table D.1. Estimates of overall home range sizes (km^2) of individual black bears in Great Smoky Mountains National Park, 1976-1982.

Bear ID	# of Loc.	Harmonic Mean				Convex Polygon				Adaptive Kernel			
		100%	95%	75%	50%	100%	95%	75%	50%	100%	95%	75%	50%
F040	60	9.8	6.3	3.5	1.4	8.0	6.3	4.2	2.6	13.5	9.0	5.1	2.5
F060	51	50.4	15.6	5.4	2.3	29.2	17.8	14.1	11.6	79.1	29.8	9.3	3.2
F131	53	26.9	16.8	5.2	1.1	23.0	17.8	11.5	2.3	48.6	20.1	8.4	2.0
F136	73	91.8	43.7	4.2	2.1	37.6	36.2	4.6	3.2	94.0	38.4	4.7	2.3
F165	48	19.8	13.3	3.6	0.7	15.9	9.7	4.5	1.0	24.2	23.3	4.1	1.5
F182	157	21.1	6.4	2.9	1.7	9.0	4.9	2.6	1.5	16.6	6.9	3.0	1.6
F201	282	20.3	6.8	2.2	1.1	10.4	6.0	2.4	1.1	17.3	6.7	2.3	1.1
F243	250	137.0	6.1	2.1	0.9	15.5	4.9	1.9	1.0	23.5	6.8	2.1	1.0
F269	173	135.2	41.1	3.6	1.8	71.2	16.7	3.6	2.2	130.1	26.7	3.9	1.9
F303	65	13.5	6.2	2.4	1.3	7.0	5.3	3.1	1.4	12.8	7.8	2.9	1.5
F309	83	11.5	4.4	1.7	0.9	5.3	3.6	1.8	1.0	10.1	5.9	1.9	1.1
F336	56	27.0	14.2	2.8	0.9	16.5	5.8	2.9	0.8	27.6	18.0	3.9	1.2
Mean		47.0	15.1	3.3	1.3	20.7	11.2	4.8	2.5	41.5	16.6	4.3	1.7
St.Dev.		47.3	13.5	1.2	0.5	18.6	9.5	3.9	3.0	38.9	11.1	2.4	0.7
M005	51.0	22.2	15.1	8.0	3.7	24.5	22.0	13.2	7.9	40.5	24.4	12.5	5.0
M185	140.0	584.8	216.2	18.0	18.0	217.0	212.7	21.3	13.4	338.7	249.0	18.7	5.2
M226	70.0	3,771.0	64.0	13.9	7.3	657.8	19.7	10.1	3.3	1,092.0	75.9	18.5	8.1
M255	120.0	1,670.0	801.2	84.4	24.1	841.5	674.1	92.5	29.6	803.3	465.4	102.1	23.0
M257	215.0	1,571.0	544.0	49.2	18.9	574.4	243.9	40.6	25.4	1,040.0	400.8	61.3	19.0
M294	51.0	403.3	216.0	54.3	15.0	273.2	258.7	197.5	71.8	685.9	327.0	249.8	16.3
M301	78.0	2,319.0	1,502.0	346.4	57.7	1,101.7	984.8	185.6	50.6	1,787.0	1,047.0	483.0	70.0
M338	82.0	464.3	113.6	33.7	12.8	145.5	55.7	31.8	9.9	274.7	117.7	34.6	15.2
M350	54.0	30.3	20.9	6.7	1.0	31.1	29.3	12.3	6.5	69.2	28.8	8.4	1.2
M362	88.0	1,108.0	243.7	52.4	24.3	363.0	224.8	66.3	24.5	785.3	249.1	67.6	25.8
M453	46.0	79.6	33.3	10.9	1.1	46.6	27.5	6.5	1.0	66.9	42.8	9.7	1.5
Mean		1,093.0	342.7	61.6	16.7	388.7	250.3	61.6	22.2	634.9	275.3	96.9	17.3
St.Dev.		1,169.1	455.3	97.6	16.0	360.6	310.3	69.4	21.9	544.7	299.0	146.1	19.4
M:F		23.2	22.8	18.7	12.5	18.8	22.3	12.9	9.0	15.3	16.6	22.5	9.9

Table D.2. Estimates of annual home range sizes (km^2) of individual black bears in Great Smoky Mountains National Park, 1977-1981.

Bear ID	# of Loc.	Year	Harmonic Mean 100%	95%	75%	50%	Convex Polygon 100%	95%	75%	50%	Adaptive Kernel 100%	95%	75%	50%
F136	52	1977	7.5	3.7	1.7	1.0	4.8	2.8	2.0	0.9	11.3	4.8	2.6	1.3
F060	51	1978	50.4	15.6	5.4	2.3	29.2	17.8	14.1	11.6	79.1	29.8	9.3	3.2
F201	50	1978	8.6	6.8	1.9	0.7	7.9	5.6	2.1	0.7	11.2	9.1	3.1	0.8
F243	46	1978	4.1	1.8	0.8	0.3	2.3	1.3	0.7	0.3	5.0	2.4	1.1	0.5
F201	71	1979	6.0	3.7	1.6	0.7	4.0	2.6	1.7	1.1	11.4	4.1	1.8	1.0
F243	49	1979	3.6	2.6	1.3	0.5	3.3	2.7	1.7	0.8	4.7	4.6	2.0	1.3
F269	57	1979	4.0	2.1	0.8	0.3	2.4	1.5	0.9	0.6	4.3	2.7	1.0	0.7
F303	49	1979	11.6	5.3	2.2	0.9	5.1	4.3	2.4	1.4	8.8	6.1	2.5	1.5
F182	49	1980	10.3	7.8	1.9	0.7	7.7	5.7	2.4	1.5	14.0	11.3	3.2	2.1
F201	48	1980	7.4	4.4	1.7	0.7	5.2	3.5	1.9	0.7	8.9	4.1	2.4	0.9
F336	46	1980	25.0	17.2	2.6	1.0	16.5	5.8	3.1	0.9	27.7	18.5	3.9	1.7
F182	103	1981	6.9	3.9	2.1	1.2	4.2	3.4	2.1	1.2	6.3	4.6	2.5	1.3
F201	112	1981	7.0	3.4	1.7	0.7	5.7	2.7	1.7	1.0	15.1	4.7	1.8	1.1
F243	109	1981	6.7	4.0	1.6	0.6	4.7	2.9	1.6	0.6	8.4	4.8	1.9	0.7
F269	60	1981	6.6	2.9	0.9	0.4	3.8	2.4	1.0	0.5	8.7	4.2	1.6	0.7
F309	66	1981	10.3	3.3	1.5	0.8	4.3	3.1	1.5	0.6	7.7	5.3	1.8	1.0
Mean			11.0	5.5	1.9	0.8	6.9	4.3	2.6	1.5	14.5	7.6	2.6	1.2
St.Dev.			11.6	4.5	1.1	0.5	6.8	3.9	3.1	2.7	18.1	7.1	1.9	0.7
M185	72	1979	46.4	20.5	6.5	2.5	24.7	15.4	5.0	2.3	57.7	21.7	8.3	2.8
M226	55	1979	906.3	67.1	9.6	3.8	109.0	17.4	7.7	2.7	185.1	69.2	11.2	5.1
M255	67	1979	119.0	45.2	21.4	8.4	52.9	41.5	22.4	7.4	101.8	55.4	24.4	9.1
M257	62	1979	185.0	66.7	19.4	7.9	75.0	36.4	16.8	8.4	199.8	73.8	22.1	9.8
M257	79	1981	95.1	44.2	20.6	10.0	55.2	51.1	18.4	11.2	96.1	58.1	26.4	12.2
M338	47	1981	23.1	21.5	9.5	3.3	25.8	22.4	12.6	3.5	56.5	38.0	16.1	5.3
M350	46	1981	26.7	15.0	4.3	0.8	16.0	14.2	2.1	1.0	52.2	23.4	6.2	0.9
Mean			200.2	40.0	13.0	5.2	51.2	28.3	12.2	5.2	107.0	48.5	16.4	6.4
St.Dev			316.6	21.8	7.2	3.5	32.9	14.6	7.5	3.8	61.7	21.1	8.1	4.0
M:F			18.2	7.2	7.0	6.6	7.4	6.7	4.7	3.4	7.4	6.4	6.2	5.2

Table D.3. Estimates of seasonal home range sizes (km^2) of individual black bears in Great Smoky Mountains National Park, 1976-1982.

Bear ID	# of Loc.	Season	Harmonic Mean				Convex Polygon				Adaptive Kernel			
			100%	95%	75%	50%	100%	95%	75%	50%	100%	95%	75%	50%
F201	59	Spring	4.0	2.4	1.1	0.4	2.5	1.9	1.0	0.5	5.3	3.2	1.4	0.6
F243	56	Spring	2.5	1.5	0.6	0.3	1.8	1.2	0.6	0.3	4.3	1.8	0.9	0.5
Mean			3.2	1.9	0.9	0.3	2.2	1.6	0.8	0.4	4.8	2.5	1.1	0.5
St.Dev.			1.1	0.7	0.4	0.1	0.5	0.6	0.3	0.1	0.7	1.0	0.4	0.1
F182	70	Summer	5.8	4.3	1.7	0.8	3.7	3.0	1.6	0.8	5.7	4.8	2.2	1.0
F201	118	Summer	8.3	4.9	2.0	1.0	7.8	3.8	1.8	0.9	12.7	5.9	2.0	1.0
F243	109	Summer	6.2	3.7	1.6	0.8	4.3	2.8	1.5	0.8	7.3	4.4	1.8	1.0
F269	78	Summer	45.4	4.7	2.4	1.1	13.4	3.4	1.9	1.1	12.0	5.9	2.2	0.9
Mean			16.4	4.4	1.9	0.9	7.3	3.2	1.7	0.9	9.4	5.2	2.0	1.0
St.Dev.			19.3	0.5	0.4	0.2	4.4	0.5	0.2	0.1	3.4	0.8	0.2	0.0
F182	48	Fall	10.7	7.9	2.7	1.0	7.9	6.0	3.0	1.7	14.7	12.1	4.1	1.8
F201	105	Fall	8.8	7.0	2.3	1.0	8.5	5.4	2.2	1.1	16.0	7.9	3.0	1.2
F243	85	Fall	69.8	19.7	2.8	0.9	12.4	10.0	2.1	0.7	19.5	9.5	3.1	1.0
F269	63	Fall	264.7	87.7	14.3	2.9	68.9	19.2	7.1	2.3	118.9	63.7	17.9	3.3
Mean			88.5	30.6	5.5	1.5	24.4	10.1	3.6	1.4	42.3	23.3	7.0	1.8
St. Dev.			120.8	38.5	5.9	1.0	29.7	6.3	2.4	0.7	51.1	27.0	7.3	1.0
M185	59	Summer	146.9	50.7	4.4	2.1	37.8	22.5	3.2	1.8	60.5	42.1	4.9	2.5
M226	48	Summer	50.4	20.5	7.1	3.0	27.2	15.5	8.7	3.9	60.0	26.0	9.7	3.4
M257	83	Summer	234.3	68.0	13.2	7.4	67.5	34.1	10.6	5.9	128.7	60.8	14.1	7.6
Mean			143.9	46.4	8.2	4.2	44.2	24.0	7.5	3.9	83.1	43.0	9.6	4.5
St.Dev.			92.0	24.0	4.5	2.8	20.9	9.4	3.8	2.0	39.5	17.4	4.6	2.7
M:F			8.8	10.6	4.3	4.6	6.1	7.5	4.4	4.3	8.8	8.2	4.7	4.6
M185	70	Fall	283.7	122.5	42.1	8.7	212.7	209.4	55.2	6.8	393.3	220.6	70.8	9.0
M255	69	Fall	1,218.0	552.9	140.2	30.8	841.5	820.5	79.3	38.2	1,152.0	566.0	197.1	52.6
M257	88	Fall	745.3	556.7	82.5	30.2	479.1	427.1	56.7	31.3	1,028.0	625.9	88.6	32.9
Mean			749.0	410.7	88.3	23.2	511.1	485.6	63.7	25.4	857.8	470.8	118.8	31.5
St.Dev.			467.2	249.6	49.3	12.6	315.6	309.7	13.5	16.5	407.0	218.8	68.4	21.8
M:F			8.5	13.4	16.0	15.9	20.9	47.9	17.7	17.6	20.3	20.2	16.9	17.3

Appendix E. Correlation coefficients of logistic regression parameter estimates.

Table E.1. Correlation coefficients of the parameter estimates for logistic regression model of overall habitat use by female black bears, Great Smoky Mountains National Park, 1976-1982.[a]

	Const.	VE1	VE2	VE3	VE4	VE5	VE6	VE7	VE8	VD	SL	EL1	EL2	AS1	AS2	AS3	AS4	AS5	DH1	DH2	DH3	DH4	TR	HA1	HA2	RO1	RO2
Const.	1.00																										
VE1	-0.14	1.00																									
VE2	-0.29	0.05	1.00																								
VE3	0.22	-0.24	-0.54	1.00																							
VE4	-0.25	-0.05	0.55	-0.57	1.00																						
VE5	-0.06	-0.13	0.26	-0.43	0.32	1.00																					
VE6	-0.32	-0.06	0.48	-0.53	0.56	0.28	1.00																				
VE7	-0.30	-0.06	0.49	-0.54	0.56	0.30	0.53	1.00																			
VE8	0.21	-0.22	-0.26	-0.29	-0.24	-0.19	-0.25	-0.24	1.00																		
VD	-0.77	0.09	0.03	0.03	-0.04	-0.09	0.03	0.04	-0.08	1.00																	
SL	-0.37	-0.03	-0.03	0.01	0.02	-0.03	0.10	0.05	-0.02	0.03	1.00																
EL1	-0.20	-0.15	-0.04	-0.02	0.06	0.09	0.08	0.11	0.01	0.33	-0.05	1.00															
EL2	0.20	0.15	0.04	0.02	-0.06	-0.09	-0.08	-0.11	-0.01	-0.33	0.05	-1.00	1.00														
AS1	-0.05	0.01	-0.02	0.04	-0.06	-0.06	0.03	-0.02	-0.02	0.07	-0.18	-0.03	0.03	1.00													
AS2	-0.09	0.03	0.06	-0.02	0.00	0.01	-0.06	-0.04	0.02	0.02	-0.16	-0.01	0.01	0.14	1.00												
AS3	0.15	-0.04	0.03	-0.07	0.08	0.09	0.00	0.09	0.01	-0.10	0.00	0.00	0.00	-0.38	-0.39	1.00											
AS4	-0.15	0.04	-0.03	0.05	-0.06	-0.07	0.06	-0.04	-0.04	0.15	-0.23	0.03	-0.03	0.11	0.32	-0.38	1.00										
AS5	0.01	-0.01	-0.03	0.03	-0.01	-0.02	-0.03	-0.04	0.01	-0.04	0.32	0.00	0.00	-0.37	-0.35	-0.39	-0.38	1.00									
DH1	-0.08	0.23	-0.10	0.15	-0.23	-0.14	-0.23	-0.26	-0.02	0.01	0.03	0.32	-0.32	-0.04	-0.02	-0.06	0.06	0.06	1.00								
DH2	0.03	-0.27	0.07	-0.04	0.15	0.14	0.13	0.10	0.02	0.03	-0.05	-0.09	0.09	0.04	-0.04	0.03	-0.05	-0.10	-0.31	1.00							
DH3	-0.04	0.02	-0.12	0.01	-0.02	-0.01	-0.01	0.01	0.03	0.04	0.06	-0.13	0.13	0.09	-0.01	-0.12	-0.11	0.03	-0.32	-0.30	1.00						
DH4	0.07	0.07	0.12	-0.09	0.06	-0.01	0.07	0.11	-0.03	-0.07	-0.03	-0.06	0.06	-0.08	0.06	0.04	0.09	-0.07	-0.26	-0.47	-0.33	1.00					
TR	-0.15	0.05	-0.10	0.05	-0.03	0.00	-0.03	-0.01	-0.04	0.02	-0.11	0.01	-0.01	0.03	-0.15	0.04	-0.01	0.01	0.03	0.02	-0.08	0.03	1.00				
HA1	-0.07	0.17	-0.06	0.09	-0.13	-0.14	-0.12	-0.15	-0.01	0.03	0.08	0.01	-0.01	-0.04	0.16	-0.14	0.09	0.04	0.56	-0.06	-0.40	-0.05	-0.03	1.00			
HA2	0.07	-0.17	0.06	-0.09	0.13	0.14	0.12	0.15	0.01	-0.03	-0.08	-0.01	0.01	0.04	-0.16	0.14	-0.09	-0.04	-0.56	0.06	0.40	0.05	0.03	-1.00	1.00		
RO1	0.20	0.10	0.02	0.07	-0.05	-0.09	-0.12	-0.16	-0.02	-0.13	-0.09	0.04	-0.04	0.01	-0.06	-0.04	0.06	0.03	0.33	-0.04	-0.21	-0.05	0.13	-0.12	0.12	1.00	
RO2	-0.20	-0.10	-0.02	-0.07	0.05	0.09	0.12	0.16	0.02	0.13	0.09	-0.04	0.04	-0.01	0.06	0.04	-0.06	-0.03	-0.33	0.04	0.21	0.05	-0.13	0.12	-0.12	-1.00	1.00

[a] See Table 10 for variable codes and class descriptions.

Table E.2. Correlation coefficients of the parameter estimates for logistic regression model of spring habitat use by female black bears, Great Smoky Mountains National Park, 1976-1982.[a]

	Const.	VE1	VE2	VE3	VE4	VE5	VE6	VE7	VE8	VD	SL	EL1	EL2	AS1	AS2	AS3	AS4	AS5	DH1	DH2	DH3	DH4	TR	HA1	HA2	RO1	RO2
Const.	1.00																										
VE1	-0.13	1.00																									
VE2	-0.19	-0.09	1.00																								
VE3	0.01	0.03	-0.24	1.00																							
VE4	-0.05	-0.28	0.24	-0.33	1.00																						
VE5	0.06	-0.29	-0.03	-0.29	0.05	1.00																					
VE6	-0.08	-0.27	0.14	-0.30	0.29	0.02	1.00																				
VE7	-0.09	-0.27	0.15	-0.31	0.25	0.01	0.21	1.00																			
VE8	0.21	-0.23	-0.29	-0.26	-0.25	-0.20	-0.24	-0.24	1.00																		
VD	-0.80	0.15	0.14	0.04	-0.05	-0.08	-0.05	0.03	-0.12	1.00																	
SL	-0.35	-0.09	-0.03	-0.05	0.02	0.01	0.12	0.04	0.04	-0.02	1.00																
EL1	-0.18	-0.10	-0.05	-0.12	0.07	0.06	0.14	0.17	0.00	0.31	-0.08	1.00															
EL2	0.18	0.10	0.05	0.12	-0.07	-0.06	-0.14	-0.17	0.00	-0.31	0.08	-1.00	1.00														
AS1	-0.10	0.06	-0.02	0.10	-0.06	-0.08	0.05	-0.04	-0.06	0.00	-0.21	-0.09	0.09	1.00													
AS2	-0.16	-0.06	0.11	-0.01	0.01	0.03	-0.06	0.02	0.01	-0.04	-0.11	-0.03	0.03	0.35	1.00												
AS3	0.20	-0.04	0.03	-0.13	0.05	0.08	0.00	0.08	0.03	-0.02	0.00	0.04	-0.04	-0.48	-0.51	1.00											
AS4	-0.23	0.08	-0.08	0.15	-0.06	-0.09	0.03	-0.03	-0.08	0.10	-0.19	0.02	-0.02	0.34	0.47	-0.51	1.00										
AS5	0.01	0.00	-0.04	0.04	0.00	-0.02	-0.01	-0.07	0.03	-0.01	0.27	0.01	-0.01	-0.32	-0.30	-0.44	-0.30	1.00									
DH1	-0.03	0.37	-0.11	0.18	-0.30	-0.14	-0.21	-0.25	0.01	-0.02	0.01	0.36	-0.36	-0.07	-0.06	-0.02	0.07	0.05	1.00								
DH2	0.06	-0.36	0.16	-0.11	0.21	0.16	0.19	0.12	0.00	-0.01	-0.02	-0.15	0.15	0.04	-0.02	0.01	-0.07	0.01	-0.26	1.00							
DH3	-0.06	0.05	-0.12	-0.03	-0.02	0.00	-0.01	0.03	0.03	0.14	0.01	-0.11	0.11	0.12	-0.04	0.03	-0.12	-0.03	-0.41	-0.35	1.00						
DH4	0.03	-0.08	0.07	-0.05	0.13	-0.01	0.04	0.12	-0.04	-0.11	0.00	-0.13	0.13	-0.09	0.12	-0.02	0.11	-0.04	-0.41	-0.41	-0.15	1.00					
TR	-0.19	0.15	-0.14	0.10	-0.03	-0.03	-0.07	-0.01	-0.09	0.03	-0.12	-0.01	0.01	0.04	-0.07	0.04	0.02	-0.05	0.09	-0.03	-0.12	0.06	1.00				
HA1	-0.10	0.23	-0.08	0.08	-0.12	-0.13	-0.08	-0.17	0.03	0.03	0.10	0.06	-0.06	-0.08	0.02	-0.07	0.08	0.08	0.60	0.02	-0.47	-0.21	-0.06	1.00			
HA2	0.10	-0.23	0.08	-0.08	0.12	0.13	0.08	0.17	-0.03	-0.03	-0.10	-0.06	0.06	0.08	-0.02	0.07	-0.08	-0.08	-0.60	-0.02	0.47	0.21	0.06	-1.00	1.00		
RO1	0.29	0.15	0.04	0.11	-0.13	-0.14	-0.10	-0.07	-0.02	-0.18	-0.19	0.14	-0.14	0.01	-0.02	0.03	0.05	-0.06	0.39	0.03	-0.13	-0.33	0.18	-0.17	0.17	1.00	
RO2	-0.29	-0.15	-0.04	-0.11	0.13	0.14	0.10	0.07	0.02	0.18	0.19	-0.14	0.14	-0.01	0.02	-0.03	-0.05	0.06	-0.39	-0.03	0.13	0.33	-0.18	0.17	-0.17	-1.00	1.00

[a] See Table 11 for variable codes and class descriptions.

Table E.3. Correlation coefficients of the parameter estimates for logistic regression model of summer habitat use by female black bears, Great Smoky Mountains National Park, 1976-1982.[a]

	Const	VE1	VE2	VE3	VE4	VE5	VE6	VE7	VE8	VD	SL	EL1	EL2	AS1	AS2	AS3	AS4	AS5	DH1	DH2	DH3	DH4	TR	HA1	HA2	RO1	RO2
Const	1.00																										
VE1	-0.09	1.00																									
VE2	-0.21	-0.05	1.00																								
VE3	0.01	-0.06	-0.22	1.00																							
VE4	-0.17	-0.17	0.37	-0.28	1.00																						
VE5	0.03	-0.23	0.08	-0.26	0.17	1.00																					
VE6	-0.27	-0.17	0.31	-0.26	0.41	0.12	1.00																				
VE7	-0.24	-0.19	0.31	-0.29	0.44	0.15	0.40	1.00																			
VE8	0.30	-0.30	-0.43	-0.29	-0.40	-0.27	-0.39	-0.37	1.00																		
VD	-0.78	0.08	0.04	0.01	-0.02	-0.10	0.09	0.10	-0.08	1.00																	
SL	-0.40	0.04	0.00	0.02	0.04	-0.01	0.09	0.03	-0.08	0.03	1.00																
EL1	-0.17	-0.20	-0.02	-0.11	0.10	0.13	0.10	0.20	0.04	0.34	-0.09	1.00															
EL2	0.17	0.20	0.02	0.11	-0.10	-0.13	-0.10	-0.20	-0.04	-0.34	0.09	-1.00	1.00														
AS1	-0.05	-0.02	-0.01	0.05	-0.04	-0.06	0.02	-0.01	0.02	0.09	-0.16	-0.01	0.01	1.00													
AS2	-0.11	0.08	0.09	-0.03	0.03	-0.01	-0.06	-0.04	-0.03	0.07	-0.18	0.00	0.00	0.10	1.00												
AS3	0.16	-0.02	-0.02	-0.09	0.03	0.08	-0.03	0.07	0.03	-0.11	-0.01	0.01	-0.01	-0.38	-0.40	1.00											
AS4	-0.15	0.03	0.00	0.07	-0.07	-0.10	0.10	-0.02	-0.03	0.17	-0.24	0.00	0.00	0.07	0.30	-0.38	1.00										
AS5	0.00	-0.01	-0.02	0.04	0.02	0.01	0.00	-0.04	-0.01	-0.07	0.35	-0.01	0.01	-0.35	-0.32	-0.38	-0.37	1.00									
DH1	-0.13	0.20	-0.03	0.22	-0.21	-0.11	-0.20	-0.24	-0.04	0.02	0.05	0.30	-0.30	-0.06	0.00	-0.02	0.04	0.04	1.00								
DH2	0.00	-0.29	0.05	-0.09	0.16	0.13	0.13	0.12	0.05	0.03	-0.05	-0.07	0.07	0.00	-0.08	0.06	-0.03	0.00	-0.28	1.00							
DH3	-0.04	-0.01	-0.12	0.02	0.06	0.02	0.04	0.06	-0.04	0.01	-0.02	-0.11	0.11	0.06	0.01	-0.04	-0.10	0.06	-0.28	-0.23	1.00						
DH4	0.12	0.13	0.08	-0.10	-0.05	-0.06	-0.01	0.01	0.01	-0.05	0.03	-0.06	0.06	-0.01	0.06	0.00	0.09	-0.08	-0.22	-0.51	-0.44	1.00					
TR	-0.15	-0.04	-0.09	0.07	-0.03	0.00	-0.04	0.06	0.00	0.02	-0.10	0.02	-0.02	0.04	-0.18	0.06	-0.02	0.01	0.00	0.06	-0.07	0.00	1.00				
HA1	-0.07	0.18	-0.02	0.10	-0.12	-0.14	-0.11	-0.16	0.00	0.03	0.08	0.06	-0.06	-0.03	0.17	-0.13	0.07	0.03	0.53	-0.07	-0.41	0.03	-0.03	1.00			
HA2	0.07	-0.18	0.02	-0.10	0.12	0.14	0.11	0.16	0.00	-0.03	-0.08	-0.06	0.06	0.03	-0.17	0.13	-0.07	-0.03	-0.53	0.07	0.41	-0.03	0.03	-1.00	1.00		
RO1	0.21	0.08	0.05	0.09	-0.03	-0.08	-0.13	-0.10	-0.02	-0.08	-0.04	0.09	-0.09	0.02	-0.02	-0.07	0.02	0.06	0.27	-0.13	-0.19	0.09	0.08	-0.08	0.08	1.00	
RO2	-0.21	-0.08	-0.05	-0.09	0.03	0.08	0.13	0.10	0.02	0.08	0.04	-0.09	0.09	-0.02	0.02	0.07	-0.02	-0.06	-0.27	0.13	0.19	-0.09	-0.08	0.08	-0.08	-1.00	1.00

[a] See Table 12 for variable codes and class descriptions.

Table E.4. Correlation coefficients of the parameter estimates for logistic regression model of fall habitat use by female black bears, Great Smoky Mountains National Park, 1976-1982.[a]

	Const.	VE1	VE2	E3	VE4	VE5	VE6	VE7	VE8	VD	SL	EL1	EL2	DH1	DH2	DH3	DH4	TR	HA1	HA2	RO1	RO2
Const.	1.00																					
VE1	0.03	1.00																				
VE2	-0.21	-0.21	1.00																			
VE3	0.05	-0.12	-0.29	1.00																		
VE4	-0.25	-0.27	0.50	-0.33	1.00																	
VE5	-0.06	-0.25	0.22	-0.28	0.28	1.00																
VE6	-0.30	-0.27	0.46	-0.32	0.53	0.25	1.00															
VE7	-0.29	-0.27	0.46	-0.33	0.52	0.26	0.52	1.00														
VE8	0.27	-0.27	-0.40	-0.26	-0.38	-0.29	-0.37	-0.37	1.00													
VD	-0.78	0.09	0.00	0.06	-0.02	-0.07	0.00	0.03	0.09	1.00												
SL	-0.42	-0.03	-0.07	0.03	-0.01	-0.06	0.13	0.05	-0.01	0.08	1.00											
EL1	-0.25	-0.11	-0.05	-0.02	0.08	0.11	0.05	0.07	0.01	0.33	-0.01	1.00										
EL2	0.25	0.11	0.05	0.02	-0.08	-0.11	-0.05	-0.07	-0.01	-0.33	0.01	-1.00	1.00									
DH1	-0.08	0.15	-0.14	0.23	-0.21	-0.12	-0.27	-0.29	0.01	0.00	0.02	0.30	-0.30	1.00								
DH2	-0.06	-0.18	0.13	-0.21	0.24	0.17	0.19	0.18	0.03	0.07	-0.08	-0.06	0.06	-0.30	1.00							
DH3	-0.03	0.00	-0.04	0.03	0.01	-0.05	0.04	0.06	-0.02	-0.06	0.03	-0.16	0.16	-0.27	-0.18	1.00						
DH4	0.13	0.05	0.02	0.00	-0.07	-0.02	0.00	0.00	-0.02	-0.01	0.03	-0.02	0.02	-0.22	-0.52	-0.48	1.00					
TR	-0.16	0.05	-0.11	0.03	-0.03	0.02	-0.04	-0.08	0.00	0.02	-0.14	0.02	-0.02	0.02	-0.03	-0.05	0.06	1.00				
HA1	-0.06	0.11	-0.06	0.15	-0.14	-0.11	-0.14	-0.14	-0.03	0.05	0.13	0.06	-0.06	0.52	-0.14	-0.42	0.10	-0.01	1.00			
HA2	0.06	-0.11	0.06	-0.15	0.14	0.11	0.14	0.14	0.03	-0.05	-0.13	-0.06	0.06	-0.52	0.14	0.42	-0.10	0.01	-1.00	1.00		
RO1	0.15	0.10	-0.03	0.09	-0.04	-0.09	-0.16	-0.28	0.04	-0.08	-0.03	-0.03	0.03	0.31	-0.09	-0.30	0.11	0.12	-0.08	0.08	1.00	
RO2	-0.15	-0.10	0.03	-0.09	0.04	0.09	0.16	0.28	-0.04	0.08	0.03	0.03	-0.03	-0.31	0.09	0.30	-0.11	-0.12	0.08	-0.08	-1.00	1.00

[a] See Table 13 for variable codes and class descriptions.

Table E.5. Correlation coefficients of the parameter estimates for logistic regression model of overall habitat use by male black bears, Great Smoky Mountains National Park, 1976-1982.[a]

	Const.	VE1	VE2	VE3	VE4	VE5	VE6	EL1	EL2	AS1	AS2	AS3	DH1	DH2	DH3	HA1	HA2	RO1	RO2	EL1*DH1	EL1*DH2	EL1*DH3	EL2*DH1	EL2*DH2	EL2*DH3	HA1*DH1	HA1*DH2
Const.	1.00																										
VE1	-0.59	1.00																									
VE2	-0.62	0.37	1.00																								
VE3	-060	0.28	0.39	1.00																							
VE4	0.00	-0.09	-0.08	0.07	1.00																						
VE5	-0.42	0.15	0.29	0.62	0.03	1.00																					
VE6	0.70	-0.57	-0.61	-0.70	-0.46	-062	1.00																				
EL1	-0.38	0.39	0.30	-0.21	-0.12	-0.23	-0.06	1.00																			
EL2	0.38	-039	-0.30	0.21	0.12	0.23	0.06	-1.00	1.00																		
AS1	-0.07	0.13	-0.11	0.00	0.08	-0.14	-0.01	0.10	-0.10	1.00																	
AS2	-0.06	0.03	0.07	0.01	0.02	0.00	-0.04	0.05	-0.05	-0.34	1.00																
AS3	0.12	-0.14	0.04	-0.01	-0.09	0.12	0.05	-0.13	0.13	-0.57	-0.57	1.00															
DH1	0.03	0.12	0.02	-008	-0.05	-0.05	0.01	0.01	-0.01	-0.05	0.01	0.03	1.00														
DH2	-0.21	-0.13	0.07	0.05	0.02	0.00	0.00	0.11	-0.11	0.09	0.02	-0.10	-0.41	1.00													
DH3	0.15	-0.01	-0.09	0.04	0.03	0.05	-0.01	-0.11	0.11	-0.03	-0.03	0.06	-0.48	-0.48	1.00												
HA1	0.03	0.08	0.00	0.02	-0.02	-0.03	-0.02	-0.15	0.15	005	-0.07	0.02	-0.03	-0.08	0.10	1.00											
HA2	-0.03	-0.08	0.00	-0.02	0.02	0.03	0.02	0.15	-0.15	-0.05	0.07	-0.02	0.03	0.08	-0.10	-1.00	1.00										
RO1	-0.40	0.16	0.12	-0.02	-0.03	-010	-0.05	0.00	0.00	-0.06	0.00	0.05	0.00	0.16	-0.14	0.14	-0.14	1.00									
RO2	0.40	-0.16	-0.12	0.02	0.03	0.10	0.05	0.00	0.00	0.06	0.00	-0.05	0.00	-0.16	0.14	-0.14	0.14	-1.00	1.00								
EL1*DH1	-0.03	-0.08	-0.03	0.07	0.02	0.03	0.00	-002	0.02	0.00	-0.04	0.04	-0.72	0.29	0.44	0.05	-0.05	-0.04	0.04	1.00							
EL1*DH2	0.10	0.15	-0.01	-0.06	-0.04	-0.05	-0.01	-012	0.12	-0.05	0.05	-0.01	0.33	-0.67	0.27	0.05	-0.05	-0.03	0.03	-0.40	1.00						
EL1*DH3	-0.06	-0.06	0.04	-002	0.01	0.02	0.00	0.13	-0.13	0.04	-0.01	-0.03	0.41	0.30	-0.65	-0.09	0.09	0.06	-0.06	-0.48	-0.48	1.00					
EL2*DH1	0.03	0.08	0.03	-0.07	-0.02	-0.03	0.00	0.02	-0.02	0.00	0.04	-0.04	0.72	-0.29	-0.44	-005	0.05	0.04	-0.04	-1.00	0.40	0.48	1.00				
EL2*DH2	-0.10	-0.15	0.01	0.06	0.04	0.05	0.01	0.12	-0.12	0.05	-0.05	0.01	-0.33	0.67	-0.27	-0.05	0.05	0.03	-0.03	0.40	-1.00	0.48	-0.40	1.00			
EL2*DH3	0.06	0.06	-0.04	0.02	-0.01	-002	0.00	-013	0.13	-0.04	0.01	0.03	-0.41	-0.30	0.65	0.09	-0.09	-0.06	0.06	0.48	0.48	-1.00	-0.48	-0.48	1.00		
HA1*DH1	0.11	-0.06	-0.04	-0.05	-0.03	002	0.06	0.08	-0.08	0.03	0.05	-0.07	0.22	-0.06	-0.16	-0.12	0.12	-0.25	0.25	-0.19	0.04	-0.28	0.19	-0.04	0.28	1.00	
HA1*DH2	-0.12	0.00	0.00	-0.01	0.00	0.00	0.01	0.00	0.00	-0.05	-0.01	0.05	-0.03	0.22	-0.16	-0.23	0.23	0.25	-0.25	0.04	-0.24	0.17	-0.04	0.24	-0.17	-0.35	1.00
HA1*DH3	0.01	0 06	0.04	0.06	0.03	-0.01	-0.06	-0.07	0.07	0.02	-0.04	0.02	-0.17	-0.14	0.28	0.31	-0.31	0.01	-0.01	0.17	0.17	-0.28	-0.17	-0.17	0.28	-0.60	-0.54
HA2*DH1	-0.11	0.06	0.04	0.05	0.03	-0.02	-0.06	-0.08	0.08	-0.03	-0.05	0.07	-0.22	0.06	0.16	0.12	-0.12	0.25	-0.25	0.19	-0.04	0.28	-0.19	0 04	-0.28	-1.00	0.35
HA2*DH2	0.12	0.00	0.00	0.01	0.00	0.00	-0.01	0.00	0.00	0.05	0.01	-0.05	0.03	-0.22	0.16	0.23	-0.23	-0.25	0.25	-0.04	0.24	-0.17	0.04	-0.24	0.17	0.35	-1.00
HA2*DH3	-0.01	-0.06	-0.04	-0.06	-0.03	0.01	0.06	0.07	-0.07	-0.02	0.04	-0.02	0.17	0.14	-0.28	-0.31	0.31	-0.01	0.01	-0.17	-0.17	0.28	0.17	0.17	-0.28	0.60	0.54
HA1*AS1	0.08	-0.08	-0.02	-0 02	0.02	0.00	0.03	-0.08	0.08	0.07	-0.04	0.02	-0 02	-0.04	0.06	-0.17	0.17	-0.01	0.01	0.05	0.02	-0.06	-0.05	-0.02	0.06	-0.10	0.10
HA1*AS2	-0.05	0.09	0.04	0.01	-0.04	-003	-0.02	0.02	-0.02	-0.02	0.02	0.00	0 06	-0.02	-0.04	-0.05	0.05	0.01	-0 01	-0.01	0.03	-0.01	0.01	-0.03	0.01	-0.03	0.07
HA1*AS3	-0.02	-0.02	-0 02	0.01	0.02	0.02	-0.01	0.03	-0.03	0.02	0.02	0.02	-003	0.05	0.05	0.20	-0.20	0.01	-0.01	-0.03	0.04	0.06	0.03	-0.04	-0.06	0.11	-0.14
HA2*AS1	-008	0 08	0.02	0.02	-0.02	000	-0.03	0.08	-0.08	-0.07	0.04	-0.02	0.02	0.04	-0.06	0.17	-0.17	0.01	-0.01	-0.05	-0.02	0.06	0.05	0.02	-0.06	0.10	-0.10
HA2*AS2	0.05	-0.09	-0.04	-0.01	0.04	0.03	0.02	-0.02	0.02	0.02	-0.02	0.00	-0 06	0 02	0.04	0.05	-0.05	-0.01	0.01	0.01	-0 03	0.01	-0.01	0.03	-0.01	0.03	-0.07
HA2*AS3	0.02	0.02	0.02	-0.01	-0.02	-0.02	0.01	-0.03	0.03	-0.02	-0.02	-0.02	0.03	-0.05	-0.05	-0.20	0.20	-0.01	0.01	0.03	-0.04	-0.06	-0.03	0.04	0.06	-0.11	0.14

Table E.5. (Cont.).

	HA2*DH1	HA2*DH2	HA2*DH3	HA1*AS1	HA1*AS2	HA1*DS3	HA2*AS1	HA2*AS2	HA2*AS3
HA2*DH1	1.00								
HA2*DH2	-0.35	1.00							
HA2*DH3	-0.60	-0.54	1.00						
HA1*AS1	0.10	-0.10	-0.01	1.00					
HA1*AS2	0.03	-0.07	0.03	-0.36	1.00				
HA1*AS3	-0.11	0.14	-0.03	-0.60	-0.60	1.00			
HA2*AS1	-0.10	0.10	-0.01	-1.00	0.36	0.60	1.00		
HA2*AS2	-0.03	0.07	-0.03	0.36	-1.00	0.60	-0.36	1.00	
HA2*AS3	0.11	-0.14	0.03	0.60	0.60	-1.00	-0.60	-0.60	1.00

[a] See Table 15 for variable codes and class descriptions.

VITA

Frank Teunissen van Manen was born in Arnhem, The Netherlands, on 15 October 1964. He graduated from the Christelijk Lyceum in Arnhem in 1983 and enrolled at the Agricultural University in Wageningen, The Netherlands, that same year. He received an 'Ingenieur' degree (M. S.) from the Agricultural University in 1989, after a 1½-year internship at the Department of Forestry, Wildlife and Fisheries, University of Tennessee. He started his doctoral research in the Ecology program at the University of Tennessee in the fall of 1989 and was awarded the Ph.D. degree in May 1994. Frank is married to René Thompson and they reside in Maryville, Tennessee, for which he proudly uses the local pronunciation.