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I am submitting herewith a dissertation written by Jennifer Lynn Murrow entitled "An Experimental Release of Elk into Great Smoky Mountains National Park." I have examined the final electronic copy of this dissertation for form and content and recommend that it be accepted in partial fulfillment of the requirements for the degree of Doctor of Philosophy, with a major in Natural Resources.

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**AN EXPERIMENTAL RELEASE OF ELK
INTO
GREAT SMOKY MOUNTAINS
NATIONAL PARK**

A Dissertation

Presented for the

Doctor of Philosophy

Degree

The University of Tennessee, Knoxville

Jennifer Lynn Murrow

August 2007

ACKNOWLEDGMENTS

I would like to extend my sincere appreciation to the many agencies who participated in this study. Financial support was provided by the Rocky Mountain Elk Foundation, Friends of the Smokies, Great Smoky Mountains Association, the National Park Service, the U. S. Geological Survey, and the University of Tennessee, Knoxville. Great Smoky Mountains National Park personnel provided data and logistical support. The interest, cooperation, and support of those agencies were fundamental to this project's success.

Special thanks to my committee members for making this dissertation possible. My major advisor, Dr. Joe Clark, has been a valuable mentor and a friend. I profited from the professionalism he helped me develop throughout the 7 years of this project. Dr. Frank van Manen provided essential input and support on study design, modeling, and statistical analyses. I benefited from Dr. Lisa Muller and Dr. Edward Ramsay's expertise in ungulate ecology and biology, while Dr. Mike Jenkins provided guidance for the intensive vegetation investigation. The support of my committee throughout the process led to a sound research study and to my growth as a scientist and a mature adult.

I am indebted to the help of many people from the National Park Service. I am fortunate to have worked closely with Kim Delozier, Supervisory Wildlife Biologist with Great Smoky Mountains National Park, who provided essential field support and guidance throughout the study. Thanks to Janet Rock for arranging time in her busy schedule to meet and identify plant species. I also appreciate the assistance of Cindy Thatcher and Ann Reed, who providing GIS technical advice and statistical support,

respectively. My fieldwork required the assistance of 15 technicians, and I would not have been able to complete this project without their support and dedication.

My past and present fellow students and coworkers at UT have been a continual source of support and friendship, especially Terry White, Jaime McNutt, Laura Thompson, Shymala Ratnayeke, and Laura and Jared Laufenberg. My experience at the University of Tennessee would not have been the same without them. One person from the University of Tennessee stands above all the rest, Steven Dobey. He has stood the test of time and trial as a true friend, and I have been lucky to have him in my life.

Finally, I would like to thank my family, especially my mother and father, for all of their love and encouragement over the past 7 years. Throughout the course of this study, they have guided me and reminded me that deep roots withstand the greatest storms.

ABSTRACT

I conducted 6 years of field work to evaluate the habitat use and population dynamics of an experimental release of elk (*Cervus elaphus*) into Great Smoky Mountains National Park (Park). Elk exhibited relatively small home ranges (female: 10.4 km² and males: 22.4 km²) and movement distances decreased over time. I calculated survival rates ($\bar{x} = 0.73\text{--}0.93$) and litter production rates ($\bar{x} = 0.73$) for the population. To assess the potential for a long-term elk population, I incorporated those vital rates into the population modeling software Riskman and tested its sensitivity to any given vital rate. The projected population growth was positive (1.03, SD = 0.001) and the probability of extinction in 100 years was minimal (1%, SD = 0.001). However, the model was sensitive to adult female survival, and the simulated annual deaths of only 4 adult females increased the probability of extinction to 45% (SD = 0.021). Compositional analysis detected a strong preference for grassland areas by elk in the Park. I used spatial data to identify potential habitat for elk on a multivariate level by calculating the Mahalanobis distance (D^2) statistic based on the relationship between elk locations and 7 landscape variables. The D^2 model indicated that the best elk habitat primarily occurred in areas of moderate landscape complexity and edge density and gentle slope, and was limited in the Park. At the current small population density, elk had minimal impact on vegetation inside the Park and their diet consisted primarily of graminoids. The elk population at Great Smoky Mountains National Park will likely remain small and vulnerable to extinction for some time due to low growth rates, high environmental stochasticity, and limited habitat. Active management (e.g. predator management, prescribed burning, and

mowing) will be required to maintain this population until the population grows to more sustainable levels.

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CHAPTER I: INTRODUCTION

Historical Elk Distribution

Prior to European settlement, approximately 10 million elk (*Cervus elaphus*) inhabited North America (Seton 1927; Fig. 1; All figures and tables appear in the appendices). Six elk subspecies ranged from Canada to Mexico and from the Atlantic coast to the Pacific coast (O’Gara and Dundas 2002). Naturalist John Madson wrote "...elk were probably the most widespread of all American hoofed species, thriving from central California to the Atlantic savannahs; from Mexico into Canada. The only places thought not occupied originally by elk were the Great Basin, much of New England, eastern parts of the Atlantic coastal states, and sections of the Deep South and Gulf Coast" (Madson 1966:102).

As human settlement advanced westward, elk numbers declined because of large-scale habitat loss, unregulated hunting, and competition with domestic livestock (Christensen 1998, O’Gara and Dundas 2002). By 1922, it was estimated that only 100,000 elk inhabited North America, with core populations restricted to Yellowstone National Park in Wyoming, Olympic National Park in Washington, and the Tule Elk Reserve in California (Bryant and Maser 1982). The eastern (*C. e. canadensis*) and Merriam (*C. e. merriami*) subspecies were extinct by the early 1900s, and only a few isolated populations of the manitoban subspecies (*C. e. manitobensis*) remained in central Canada (Bryant and Maser 1982).

There is moderate historical information on all but the eastern subspecies, which occurred east of the Mississippi River. Murie (1951) and O’Gara and Dundas (2002)

presented species distribution maps, but there are discrepancies in the extent of elk distribution on the eastern seaboard. Radiocarbon dating indicated that elk occurred in the eastern U.S. as early as 9,550 years ago, based on skeletal remains found on Iroquois National Wildlife Refuge in New York in 2004 (Gerhart 2005). William Bartram (Van Doren 1955) observed that eastern elk were abundant prior to European settlement, but numbers began to decline by the late 1700s. Naturalist John James Audubon mentioned that by 1851 a few Eastern elk could still be found in the Allegheny Mountains of Virginia, but they were essentially gone from the remainder of their range (Gerhart 2005).

On a more local scale, the historic distribution of eastern elk in western North Carolina and eastern Tennessee is also unclear. Few records and scarce archaeological evidence exist, so species distribution maps are of limited value. O’Gara and Dundas (2002) presented a distribution map of elk based on previous work by Murie (1951) that indicated the general presence of elk in North Carolina and Tennessee. One author stated that elk were plentiful in the Carolinas as late as the early 1700s (Brickell 1737). Additionally, elk antlers were discovered in the spruce-fir forests of the Black Mountains in North Carolina in the mid-1800s (Cope 1870). Elk were thought to be common throughout Tennessee, remaining in the bottomlands of west Tennessee until the mid-1800s (Rhoads 1897).

Impacts of Elk

Given the effects that elk can have on the habitat they occupy, careful consideration and study should be given to the advantages and disadvantages of reintroducing elk into

unoccupied areas. Depending on the population size, management practices, and habitat occupied, elk may affect vegetative communities, predator populations, and local economics (Beschta 2005, Bergman et al. 2006, Wright et al. 2006). Positive economic impacts include hunting license fees and wildlife-viewing revenue (Manfredo et al. 2004, Fix et al. 2005). However, elk can also have negative economic impacts in the form of crop damage and vehicular collisions. Elk grazing or browsing has the potential to increase or decrease biodiversity depending on the productivity of occupied habitats, intensity of herbivory, and grazing history. In landscape systems with low productivity and biodiversity, heavy grazing by elk may negatively alter biotic relationships such as inter-specific plant competition for light and nutrients, and impede ecological processes such as the soil-plant nutrient cycle (Stohlgren et al. 1997). Conversely, grazing may increase plant species richness in productive systems by removing strong competitors and controlling encroachment into open habitats (Baker et al. 1997, Stohlgren et al. 1997, Olff and Ritchie 1998). Additionally, elk offspring and weak or sick animals may serve as a potential food source for predators such as bears (*Ursus* spp.), mountain lions (*Puma concolor*), and wolves (*Canis lupus*).

Elk in Great Smoky Mountains National Park

In the early 1900s, efforts to restore and protect declining elk populations were enhanced by implementation of harvest restrictions, acquisition of public lands, elk translocations or reintroductions, and habitat restoration (Witmer 1990). As a result, an estimated 1 million elk occupied an expanding portion of their western historic range by 1998 (Bryant and Maser 1982, Christensen 1998; Fig. 2). Most translocation attempts in

the eastern U.S. were considered unsuccessful, however, because of a lack of suitable habitat, excessive and illegal harvest, and diseases and parasites (Witmer 1990, Thorne et al. 2002). For example, 193 elk released in Virginia in the early 1900s gradually disappeared as a result of poaching and disease. In 1933, the U.S. Forest Service introduced 11 elk in the Black Mountain Refuge in Arkansas, the population grew to 125 and then vanished by the late 1950s (Cartwright 1991). However, recent reintroductions in Arkansas, Michigan, North Dakota, Pennsylvania, Oklahoma, South Dakota, and Texas have resulted in relatively small (<300) but established elk populations (Witmer 1990, O’Gara and Dundas 2002, Bender et al. 2005). Since 1995, a renewed interest in reintroducing elk in the eastern U.S. has resulted in releases in Kentucky, Tennessee, and Wisconsin (Phillips 1985, Didier and Porter 1999, McClafferty and Parkhurst 2001, Larkin et al 2004). The most recent successful reintroduction of elk has been in Kentucky, where the herd has now reached >6,500 animals (K. Alexy, Kentucky Department of Fish and Wildlife Resources, personal communication).

The 1916 Organic Act states that the National Park Service (NPS) should conserve the scenery and the natural and historic objects and the wild life in the Park system. Furthermore, the first mission goal states that natural and cultural resources and associated values should be protected, restored, and maintained in good condition and managed within their broader ecosystem and cultural context. The 1982 Great Smoky Mountain National Park (GSMNP; Park) General Management Plan was prepared for compliance with NPS standards. It reflected a direction for natural resources to be

managed in accordance with applicable laws and policies including the possible reintroduction of animal species.

It is NPS policy to restore native animal populations in parks when it is feasible and if the species has been extirpated by human-caused actions. In 1990, the Rocky Mountain Elk Foundation approached officials at GSMNP with an interest of examining the feasibility of reintroducing elk to the Park. Whereas a reintroduction could have many positive ecological and economic benefits, potential risks were also recognized. Therefore, NPS biologists decided to implement an experimental release to assess whether the establishment of a permanent elk herd was possible and practical. GSMNP biologists, supported by national experts on elk and wildlife diseases, developed or assembled hundreds of reports and documents to aid in the decision making process associated with an experimental release of elk in GSMNP.

To evaluate public sentiment towards a potential release, NPS personnel initiated discussions with the public, state agencies, and private organizations in March 2000. Over 800 stakeholders and private citizens participated in those sessions. Federal officials made presentations to educate and address concerns of the local and state agricultural communities. Contacts were made with farm bureaus, livestock associations, and state veterinarians and >2,400 responses were received via internet, letters, comment forms, phone conversations, and direct contact. Upon the conclusion of that investigation, >90% of respondents were in favor of an experimental reintroduction (Kim Delozier, GSMNP, personal communication).

An environmental assessment was conducted to assess potential positive or negative impacts on water resources, soils, vegetation, wildlife, threatened and endangered species, cultural resources, air quality, sound quality, visual quality, socio-economics, and land and people adjacent to GSMNP. Final results from that assessment varied from positive to non-significant, and none were classified as significantly negative.

Finally, disease and parasite risks were synthesized from the “Model Health Protocol for Importation of Wild Elk for Restoration” compiled by the Southeastern Cooperative Wildlife Disease Study at the University of Georgia (Corn and Nettles 1998). There was substantial concern over several diseases that elk can carry and potentially pass to cattle, particularly brucellosis (BC) and bovine tuberculosis (TB). Ultimately, the NPS and the North Carolina State Veterinarian’s Office chose to restrict potential source animals to those originating from Elk Island National Park (EINP) in Alberta, Canada. The decision was based on an extensive disease monitoring history at EINP, including BC and TB. In addition, the elk herd at Land Between the Lakes National Recreation Area (LBL), which was originally stocked with elk from EINP and has since been closed to other importation sources, was approved to serve as a source population for the GSMNP reintroduction.

Because of positive responses from the public and the positive environmental and disease risk assessments, NPS approved an experimental elk release in GSMNP. A plan was developed that authorized the release of 25 elk per year for 3 years (2001–2003). After reviewing potential release sites and recommendations from a panel of elk experts,

Cataloochee Valley, located in western North Carolina, was selected as the acclimation and release site (Kim Delozier, GSMNP, personal communication).

Evaluating the GSMNP Elk Release

There were obvious concerns surrounding reintroducing a large ungulate as discussed previously, and despite extensive precautions taken prior to the release of elk in GSMNP, Park managers remained apprehensive about potential negative biological impacts to GSMNP. Managers sought assurance that the reintroduction would be successful, beneficial, and feasible over the long-term. If that were not the case, problems should be identified early on so that corrective actions could be taken. NPS biologists were most concerned with the viability of the elk herd and potential impacts to vegetative communities and private lands adjacent to GSMNP. To address those questions, I conducted research to evaluate population dynamics (sex and age distribution, mortality rates, natality rates, recruitment), habitat use, home-range size and placement, and the feasibility of establishing a permanent elk population in GSMNP. I developed several hypotheses for testing:

- I. elk in GSMNP have demographic parameters similar to those seen in other wild herds,
- II. elk habitat use is centered on open habitat in GSMNP,
- III. elk have no negative impact on the vegetation of GSMNP, and
- IV. elk are able to establish a viable self-sustaining herd in GSMNP.

Thus, specific objectives of my research were to:

- 1) estimate survival rates and reproductive success, assess home ranges, and identify causes of mortality of reintroduced elk;
- 2) determine whether mortality rates varied by age, sex, or release technique;
- 3) assess habitat use and food habits and evaluate impacts of the elk reintroduction (e.g., impacts to native vegetation or agricultural crops, fence damage, highway mortality); and
- 4) assess the probability of success of releasing elk to establish a permanent, viable population at GSMNP.

CHAPTER II: STUDY AREA

General

GSMNP encompassed approximately 2,105 km² of primarily forested land in eastern Tennessee and western North Carolina. The Park included portions of Blount, Sevier, and Cocke counties along the Tennessee (TN) border, and Haywood and Swain counties in North Carolina (NC). The formation of GSMNP was authorized in 1926 from lands purchased from private landowners and was dedicated as a National Park in 1940 (Campbell 1960). The Park was situated adjacent to an additional 12,141 km² of USDA property that was comprised of Cherokee, Pisgah, and Nantahala national forests. The southern border of the Park was adjacent to the Eastern Band of the Cherokee Indian Reservation.

In 2006, GSMNP was the most visited national park in the country with approximately 9.5 million visits per year (Nancy Gray, GSMNP, personal communication). Developed areas inside the Park included 10 campgrounds, 9 picnic areas, and 99 backcountry campsites including 16 with shelters on site. Popular activities in the Park included picnicking, hiking, wildlife viewing, kayaking, and horseback riding.

This study was conducted in the eastern portion of GSMNP in western North Carolina, centered on Cataloochee Valley in Haywood County (35° 38' 23.000 north latitude and 83° 04' 55.000 west longitude). The nearest major roadway to the release site was US Interstate 40, which traversed the eastern section of the study area (Fig. 3). Several cities were contained within the study area. Newport, TN was located in the

northern section of the study area whereas Maggie Valley and Cherokee, NC were located to the south and southwest, respectively.

Topography, Geology, and Soils

GSMNP was located within the most southerly portion of the Appalachian Highlands (Fenneman 1938). The mountains of the Smokies were created during the late Paleozoic era by crustal movements of the rocks of the Ocoee series that were originally formed during the Precambrian Era (King and Stupka 1950). The mountains have been eroded over time via winds, rains, and streams, leaving the existing compact mountains. Geologists estimate that the mountains have been eroded at a rate of approximately 5 cm per 1,000 years (Matmon et al. 2001).

The region was notable for having extreme variations in topography with >65% of the Park having slopes >15°. Lands within GSMNP were 99% forested, furrowed and relatively steep with elevations ranging from 260 m along Abrams Creek to 2,025 m on the summit of Clingman's Dome (Linzey 1995). The mountainous terrain was composed of peaked-ridges with perpendicular finger ridges, all separated by deep narrow coves and small valleys. The Appalachian Trail traversed 115 km of the primary ridge of GSMNP, which was oriented northeast to southwest.

Soils in the region were medium to highly acidic with moderate fertility and were classified as the Ramsey Association (Soil Survey 1953). These soils were comprised of quartz, feldspar, and slate (King et al. 1968).

Climate and Hydrology

The general area encompassed by GSMNP was classified as a warm-temperate rain forest (Thornthwaite 1948). This section of the Appalachian Highlands was one of the most ecologically diverse temperate areas in North America (Southern Appalachian Man and the Biosphere 1996). The wide variation in topography and climate, coupled with the presence of 9 major riverine systems, contributed significantly to the immense diversity of the area. Several major rivers emerged from the Smokies, including the Little Pigeon, Oconaluftee, and Nantahala.

In GSMNP, there is an inverse relationship between temperature and precipitation with increasing elevation; every 1,000 m change in elevation results in a 4°C change in temperature (Shanks 1954). Mean annual precipitation ranged from 100 to 150 cm per year in low elevations and from 200 to 250 cm in higher elevations. On average, the wettest month was July, and the driest month was October (Stephens 1969). The months of August and January had the highest and lowest temperatures, respectively. Significant cloud cover occurred during most seasons with $\geq 78\%$ of days having significant cloud cover (Larry Nicodemus, National Oceanic and Atmospheric Administration, personal communication). Winter snow accumulation was relatively slight.

Fauna and Flora

The northeast to southwest orientation of the Smoky Mountains allowed species to migrate along the slopes and ridges during interglacial periods. Therefore, the Smokies have become refugia for many species of plants and animals that were isolated from their northern distributions as a result of glacial movements. Consequently,

GSMNP is among the most faunally diverse areas in North America, with >200 species of birds, 80 fishes, 69 amphibians and reptiles, and 66 mammals (King and Stupka 1950).

Historians speculate that subsistence hunting by the Cherokee Indians had minimal impacts on the abundance of animal populations in GSMNP (Linzey 1995). Unfortunately, overharvest by European settlers and changing land use practices did result in the extinction of many species native to this area by the time the National Park was established in 1934. The most well-known of those extirpated species include bison (*Bison bison*), elk, mountain lions, and red wolves (*Canus rufus*).

Variation in topography and climatic conditions created an environment with one of the highest plant diversities in eastern North America (Whittaker 1956).

Consequently, GSMNP was recognized as an International Biosphere Reserve and classified as one of the richest temperate forest regions in the world (Herrman and Bratton 1977) with over 50 uniquely identified plant communities. Approximately 100 species of native trees occurred in the Smokies, which was more than any other North American national park. Almost every forest type found in the eastern United States could be found within GSMNP, including deciduous forest, boreal forest, and unique transitional forest types. Collectively, 32 ferns, 230 lichens, 330 mosses, and 2,000 fungi have been identified within GSMNP (King and Stupka 1950, Stupka 1960). Seventy-six plant species were listed as threatened or endangered in Tennessee and North Carolina. Three federally listed threatened and endangered plant species occurred in the Park: spreading avens (*Geum radiatum*), Virginia spiraea (*Spiraea virginiana*), and rock

gnome lichen (*Gymnoderma lineare*). Approximately 300 species of native vascular plants and 200 of the 450 non-vascular plants were considered rare (NPS 2007).

Cove hardwoods, pine (*Pinus* spp.)-oak (*Quercus* spp.), northern hardwoods, hemlock, and spruce-fir comprised the major forest types in GSMNP. The cove hardwood association consisted of sheltered valleys with rich soils and was the most botanically diverse forest type. Pine-oak forests were dominant on dry, exposed slopes and ridges, and were concentrated in the western section of the Park. Northern hardwood forests comprised of American beech (*Fagus grandifolia*), birch (*Betula* spp.), and maple (*Acer* spp.) dominated middle to upper elevations from 1,067 to 1,524 m in the Park. Eastern hemlock (*Tsuga canadensis*) dominated riparian areas and shady slopes up to 1,372 m in elevation to form almost unmixed stands. Mountain peaks >1,524 m elevation in GSMNP were dominated by Fraser fir (*Abies fraseri*) and red spruce (*Picea rubens*) and formed high-elevation boreal forests. Two other important plant communities were grassy and heath balds. Balds were large treeless areas located at mid to high elevations in the Park. The existence of the balds dates back to the early 1800s, but their exact origin is unknown. Heath balds were composed of shrubs such as mountain laurel (*Kalmia latifolia*), rhododendron (*Rhododendron* spp.), blueberry (*Vaccinium* spp.), and huckleberry (*Gaylussacia* spp.) and occurred primarily in the eastern section of the Smokies. Grassy balds were dominated by grasses and occurred mostly in the western section of the Park. Major non-native, invasive plant species in GSMNP included kudzu (*Pueraria montana* var. *lobata*), mimosa (*Albizia julibrissin*), multiflora rose (*Rosa multiflora*), and Japanese grass (*Microstegium vimineum*).

From the mid- to late 1700s through the 1940s, approximately two-thirds of GSMNP was harvested for timber (Pyle 1988). The drastic vegetative alterations associated with those extensive harvest regimes resulted in major changes in species richness (Linzey 1995). Another major faunal change in GSMNP that significantly affected plant and animal communities was the arrival of the chestnut blight (*Cryphonectria parasitica*) in the mid-1920s. The effects of that fungus were so significant that by 1938, 85% of American chestnut (*Castanea dentata*) trees in GSMNP had been infected or killed (Woods and Shanks 1959). Chestnut mast was a source of forage for many wildlife species, and more variable mast-producing species such as oaks gradually replaced American chestnut forests.

Most of the historic openings in GSMNP had become closed due to an encroaching forest canopy because of lack of fire, discontinued logging, and an absence of large herbivores. Of the 2,105 km² in GSMNP, <1% was in treeless habitat. The center of my study area was the grasslands of Cataloochee Valley which contained approximately 1 km² of open grassland habitat. This was second only to Cades Cove which contained 8 km² of grasslands.

Land Use and Socioeconomic Factors

The area now comprising GSMNP has been occupied by humans beginning with the Paleo Indians and was discovered by European settlers in the 16th century. During the 1800s, Cataloochee Valley was inhabited by the largest human settlement in the region. One of the earliest settlers to Cataloochee Valley was Henry Colwell, who purchased 41 ha in 1814. Other settlers soon arrived resulting in the construction of homesteads,

farms, churches, and a school. Many of those families inhabited Cataloochee until the Park was established in 1934. After the acquisition of GSMNP, the National Park Service burned most of the homes and structures, although a few were preserved for their historical value. To date, the open fields in Cataloochee have been maintained by mowing. Access into Cataloochee Valley was by 2 roads: Cove Creek Road from Jonathan Valley, NC and NC 284 from Big Creek on the NC-TN border.

The Cataloochee study area was located in Cocke County, TN and Haywood County, NC. Haywood County had an estimated human population of 56,482 (U.S. Census Bureau 2005), with Waynesville, NC being the largest city. The median household income was \$34,684 and 13.3% of the population was below poverty level. In Haywood County, 77.7% of residents possessed high school diplomas and 16% had bachelor's degrees (U.S. Census Bureau 2003). Excluding construction, which is not recorded by county, the top 4 private industry employers for Haywood County were retail trade, health care and social assistance, manufacturing, and accommodations and food services sectors. Haywood County had an annual unemployment rate of 4.3% (U.S. Census Bureau 2005).

The estimated human population for Cocke County was 34,929 (U.S. Census Bureau 2005), with Newport, TN being the largest city. The median household income was \$26,251 with 19.4% of the population below poverty level (U.S. Census Bureau 2003). Census data revealed that 61.2% of residents had high school diplomas, and 6.2% possessed bachelor's degrees or beyond. Most residents in Cocke County were employed in the fields of manufacturing, retail trade, health care and social assistance, and

accommodations and food services. Cocke County had an annual unemployment rate of 7.8% (U.S. Census Bureau 2005).

CHAPTER III: METHODS

ELK CAPTURE AND PROCESSING

Source Herd Selection

Only elk originating from EINP, Alberta, Canada were used in the experimental release. Those elk were the Manitoban subspecies (*C. e. manitobensis*) and were considered to be the most geographically and genetically proximal subspecies to the extinct Eastern elk. In addition to EINP, elk from LBL were also considered a source as that herd exclusively originated from elk translocated from EINP in 1995. We translocated the first shipment of elk to GSMNP from LBL in 2001; the second shipment of elk was transported from EINP in 2002. The third shipment of elk scheduled for 2003 was cancelled by the North Carolina Wildlife Resources Commission due to newly imposed cervid importation restrictions to prevent possible chronic wasting disease spread.

Initial Animal Capturing and Processing

During late January 2001, elk from the 2.8-km² enclosure at LBL were darted and immobilized with a carfentanil/xylazine combination, which was administered at dosages of 1.5 mg carfentanil/45 mg xylazine for adult elk (124–269 kg) and 0.9 mg carfentanil/30 mg xylazine for juveniles (91–183 kg). A Pneu-Dart[®] projectile and disposable darts (1.5 cc) were used to administer the anesthetic from <50 meters. Once immobilized, we transported elk to an on-site holding facility where biological data were collected. Age, determined by tooth eruption and wear, and sex were determined for each animal and blood (10–20 ml) was collected from the jugular vein for disease and

pregnancy testing. I marked all elk with a uniquely numbered metal ear tag and a pair of numbered plastic Allflex[®] (Allflex USA, Inc., Dallas, Texas, USA) ear tags that corresponded to tattoo identification placed on the inside of the ear. I removed a small section (1 mm³) of tissue from the ear to aid in future genetic analyses. While the elk were still anesthetized, antlers were removed from bulls to reduce injury during transport. I recorded body measurements that included chest girth, head length, 1 foreleg length, and total body length. All adult cows' blood serum was tested for pregnancy prior to shipment from their source herd and again prior to release. Pregnancy was determined using the Protein-B specific test (BioTracking[®], Moscow, Idaho, USA). I administered an antagonistic reversal consisting of naltrexone (150 and 100 mg for adults and juveniles, respectively) and yohimbine (30 and 20 mg for adults and juveniles, respectively) half delivered intravenously and the other half intramuscularly to reverse the effects of the immobilization drugs.

A USDA veterinarian tested all elk for TB by shaving a small portion of hair from the mid-cervical region of the left side of the neck of each elk. A measurement of the skin was taken using calipers, and bovine TB antigen was injected on the left side of the neck. Elk were treated orally with Curatrem[™] (8.5% clorsulon = 85 mg/ml) at a dosage of 7.5 ml per 91 kg for immature and adult liver flukes (*Fasciola hepatica*). The same volume of water was administered orally to ensure the full dose of Curatrem was ingested. Each also received a subcutaneous injection of ivermectin as a general anti-parasitic agent at a dosage of 10 mg/50 kg body mass. To reduce potential for capture

myopathy, all elk received a subcutaneous injection of vitamin E (136 micrograms/ml) and selenium (2.5 mg/ml) at a dosage of 1 ml/45 kg body mass.

Three days following treatments with the TB antigen, elk were again processed to assess any reaction at the site of inoculation. TB injection site was measured with calipers and comparing it to the first measurement. All elk displaying a positive reaction to the bovine TB antigen ($n = 1$) were given the avian TB antigen on the opposite side of the neck, and checked again after 3 additional days. If swelling was noted at the injection site of the avian TB antigen, the animal was not considered for shipment to GSMNP ($n = 1$). Prior to transportation, elk were provided with an electrolyte solution and alfalfa pellets in a holding corral.

In 2002, processing techniques similar to those used at LBL were used at the elk holding facility at EINP. Chemical immobilization was not necessary at EINP, however, because hay was used to lure elk into corral traps. Elk were then loaded into trailers and driven to a facility where biological data were collected and TB tests were administered.

Animal Acclimation and Processing

A period of confinement was thought to aid in maintaining elk herd cohesiveness and minimize post-release movements; this confinement is termed a soft release (Parker 1991). Consequently, after elk were transported to GSMNP in cattle or horse trailers, the animals were placed in a holding facility constructed at the Cataloochee release site. The facility was approximately 0.01 km² in size and equipped with hay feeders, a flowing water tank, and a livestock-handling system to enable handling of elk prior to final

release. Elk were maintained in this facility for up to 60 days before release into Cataloochee Valley.

Two weeks before each scheduled release into the wild, elk were again processed using the corral/squeeze chute system attached to the acclimation pen. The general condition of each elk was assessed, and all animals were equipped with VHF or GPS radio collars. To prevent constriction due to growth and swelling of the neck during the rut, radiocollars of all male elk were attached with 2 modified expandable spacers (Telonics Incorporated, Mesa, Arizona, USA). All VHF and GPS collars were equipped with on-board mortality sensors that were set to activate after 2 hours of motionless activity. VHF collars were replaced on bulls at 3 years of age to accommodate natural growth and neck swelling during the breeding season.

Vaginal radio-transmitters (Advanced Telemetry Systems, Inc, Minnesota, USA) were placed in all female elk for which pregnancy tests returned positive results and pregnancy was confirmed with rectal palpation. Blood samples were collected and all animals were again treated with Curatrem[™] for liver flukes.

TELEMETRY

Radio Telemetry and GPS Collars

I located VHF and GPS collared elk from the ground using a model TR-4 receiver (Telonics Incorporated, Mesa, Arizona) and H-antenna (Telonics Incorporated, Mesa, Arizona) or 5-element Yagi antenna (Wildlife Materials, Carbondale, Illinois). I attempted to obtain ground locations using the “loudest signal method” (Springer 1979, Mech 1983), based on ≥ 3 azimuths $\geq 45^\circ$ apart collected within 20 minutes. Aerial

locations were collected from a Cessna 182 fixed-wing aircraft using the TR-4 receiver and a toggle box that made it possible to switch between the H-antenna mounted on each wing strut. Aerial locations were obtained by flying in increasingly tighter circles over radiocollared elk. Once directly over the animal, a location was recorded using a GPS (GPS III; Garmin International, Olathe, Kansas). All GPS locations were recorded in Universal Transverse Mercator (UTM) North American Datum 1983 (NAD83) coordinates.

GPS telemetry is a relatively new technique in wildlife research and has had only limited use in temperate forests (Rodgers 2001, Taylor 2002, Janeau et al. 2004). However, GPS collars can produce substantially more data than is generally feasible with VHF technology (Gau et al. 2004). Therefore, Lotek[®] 2200L GPS collars were deployed on selected elk throughout the study (Lotek Wireless Incorporated, New Market, Ontario, Canada). Collars were programmed to collect locations every 2 or 3 hours and those data were stored on board the collars. This sampling regime was designed to equally span a 24-hour time period and to maximize data collection during the limited transmitter battery life. On occasions that GPS collar batteries failed, those elk were chemically immobilized, when possible, and the collars were retrieved.

GPS collars required 3 satellites to fix a 2-dimensional (2D) position (X and Y) and ≥ 4 satellites to record a 3-dimensional (3D) location, which included an elevation estimate. In general, 2D fixes are less accurate than 3D fixes (Rempel et al. 1995, Moen et al. 1996, Rempel and Rodgers 1997, Edenius 1997, Bowman et al. 2000, D'Eon et al. 2002). When a location was estimated by the on-board GPS, the software also recorded

the horizontal dilution of precision (HDOP). Dilution of precision is a measure of the geometric configuration of the satellites in the sky at the time the location was recorded. For example, a low HDOP value indicated good satellite configuration and increased accuracy of that individual location. A high value suggested that satellites were clumped or likely positioned too low on the horizon for more accurate triangulation. Overall, HDOP represented the potential for location error associated with individual fixes (Rempel et al. 1995, Moen et al. 1996, Dussault et al. 1999, Cain et al. 2005). Additionally, HDOP provided means for censoring data with probable location error by using an established threshold (Moen et al. 1996, Cain et al. 2005) or a reported acceptable error. Fieldwork from previous studies using Lotek[®] GPS collars indicated that any DOP below 6 for 2D and 3D locations was acceptable for analyses of habitat use (Adrian Gyulay, Lotek[®] Wireless Incorporated, personal communication). Therefore, I removed all recorded locations with a DOP >6.0.

Assessing GPS Telemetry Bias

Malfunctioning collars, location error, and fix-rate bias associated with GPS telemetric systems are commonly reported in the literature (Cain et al. 2005). Habitat analyses can be biased when locations have a lower probability of collection in certain habitats or if there is potential for location error. However, certain habitats and terrains are known to limit the ability of collars to obtain locations, and the GPS data may reflect a habitat bias that is not ameliorated by large sample sizes (Rempel et al. 1995, Dussault et al. 1999, Frair et al. 2004, Cain et al. 2005). For example, successful fix rates have been inversely related to tree height (Dussault et al. 1999, Janeau et al. 2004), basal

diameter, density, and canopy closure (Rempel et al. 1995, Moen et al. 1996, Edenius 1997, Obbard et al. 1998).

Although it is difficult to account for every type of GPS bias, fix-rate biases represent the greatest problem when using GPS locations for habitat analyses (Rempel et al 1995, D'Eon et al. 2002, D'Eon 2003). Consequently, there have been several approaches designed to address location error and fix-rate bias associated with GPS systems. One such approach involved buffering locations with error polygons so that the bias associated with location error may be addressed (Rettie and McLoughlin 1999, Frair et al. 2004). A second technique weighted existing locations or replaced missing locations based on a fix-rate bias model developed from field trials (D'Eon 2003, Cain et al. 2005, Sager 2006). Most often researchers have attempted to account for the bias using test collars and this may be the only way to account for the potential fix-rate bias without an exhaustive analysis of the variables that most influence fix-rate success in a specific study area (Graves and Waller 2006). Depending on the study area and species being investigated, extremely large datasets may dampen fix rate biases (D'Eon 2003).

I used stationary GPS collars in field trials to conservatively assess the ability of collars to acquire locations under different environmental conditions within my study area. This was done to reduce the effect of any systematic fix-acquisition bias associated with location data obtained from GPS collars. I utilized only remotely sensed variables to model the bias in the fixed GPS collars to enable future adjustment of elk locations used in habitat analyses.

Failure rate, or the rate at which GPS collars were unsuccessful at acquiring positional fixes, was assumed to vary according to habitat and landscape features present within the home ranges of elk. I used sample locations from treeless, deciduous, mixed, and evergreen cover types. The treeless cover type had 4 replicates. The remaining cover types were sub-sampled based on slope and canopy cover with low and high classifications for each. My goal was to sample 4 replicate stands of each of the 3 habitat types and slope canopy combinations, resulting in a total of 52 sites. I programmed test collars to attempt a GPS fix once every 2 hours and placed them at the pre-selected locations for at least one 24-hour period. I placed collars at randomly chosen locations <2 km from roads or trails in GSMNP. All collars were placed approximately 1 m above ground with the GPS antenna facing upward, affixed to a self-standing metal support rod. At each sampling site, I documented cover type (deciduous forest, coniferous forest, mixed forest, or treeless), slope, aspect, elevation, and percent canopy cover. I measured slope and aspect from the center of each selected site using a clinometer and compass, respectively. Canopy cover was estimated using a spherical densiometer (Lemmon 1956) from the center of each plot and in the 4 cardinal directions 2 m from the plot center. All measurements were recorded in the summer during the "leaf-on" season and again in the winter during the "leaf-off" season. At each site, I used a GPS Pathfinder[®] Geo-Explorer XM (Trimble Navigation Limited, California, USA) to average $\geq 1,000$ points and record a differentially corrected UTM coordinate to provide the reference ground coordinates. The unit provides locations with <1-m accuracy.

I treated individual sites as independent sample units in the analysis. Because repetitive terrain and vegetative attributes at each site would reduce independence of individual locations, I converted locations obtained from GPS collars to a probability of collar failure for each site. I used linear regression to model the probability of failure as a function of environmental characteristics; percent location failure was treated as the dependent variable. After establishing a correlation between the habitat attributes measured at the site and the parameters obtained from remotely sensed data (elevation, aspect, slope, habitat type, canopy cover class, and topography curvature), those data formed the pool of predictor variables in the model. Statistical analyses were performed using SAS 9.1.3 software (SAS Institute, Cary, North Carolina). I used linear regression to determine which parameters were associated with GPS collar failure (Harrell 2001). I developed 2 separate models, 1 for summer and 1 for winter. I used Proc Reg in SAS to develop all possible models and the Akaike Information Criterion to select the best predictors (Harrell 2001).

HOME RANGES AND MOVEMENTS

Study Area Delineation

Because of the striking differences in cover type within and outside of the Park, a potential bias in the habitat analysis may arise if the defined study area was too large and encompassed habitat types that rarely occurred within the Park. For example, the habitat analysis may indicate that elk are not using a given habitat that is located in abundance outside of the Park when the small population of elk has not yet accessed that habitat. To create a study area, I calculated a minimum convex polygon (MCP) that included only

locations used in annual and seasonal home range calculations (Fig. 3). The study area I delineated was 335 km² in size, and was used for the habitat analysis and the habitat modeling.

Home Range Analysis

Home range is defined as the area of use where an animal gathers food, hunts, mates, and rears young, excluding occasional movements outside the area (Burt 1943). I used the 95% fixed kernel method (Worton 1989) to estimate seasonal and annual home ranges of GPS-collared elk. All home range estimates were calculated using the Animal Movement Extension (Hooge and Eichenlaub 1997) in ArcView[®] Geographic Information System (GIS; Environmental Systems Research Institute, Redlands, California, USA).

Autocorrelation occurs in a telemetry dataset when there is a direct relationship from one consecutive telemetry location to the next. Consequently, there is a low probability that the subsequent location is truly random. Historically, researchers have attempted to reduce that bias by increasing the collection time between locations until they are statistically independent from one another. However, removing biologically significant data in efforts to attain statistical independence results in no improvement of home range estimates (Anderson and Rongstad 1989, Reynolds and Laundre 1990, Gese et al. 1990, de Solla et al. 1999, Otis and White 1999, and Blundell et al. 2001). Research indicates that the intensity of sampling of an animal's use of habitat is more important than concerns regarding statistical independence of data points (Otis and White 1999, Kernohan et al. 2001) and furthermore, kernel home range estimators are robust to

autocorrelation particularly with decreasing sampling intervals (Swihart and Slade 1997, deSolla et al. 1999). Therefore, I considered all GPS locations obtained as available for all analyses.

The kernel method is nonparametric and provides a home range utilization distribution (UD), which represents the probability of use within the area used by an animal. Higher probabilities occur where there are higher concentrations of radiolocations, and lower probabilities occur where there are fewer locations (Worton 1989). Within the kernel estimations, I used the default or *ad hoc* method for estimation of the smoothing parameter (Silverman 1986, Worton 1989, Seaman and Powell 1996).

Annual home ranges were calculated for animals with >500 locations distributed across ≥ 9 months within a calendar year. I calculated seasonal home ranges for spring (March-May), summer (June-August), autumn (September-November), and winter (December-February); elk with <250 locations per season were excluded from seasonal analyses. Those strict dataset requirements for annual and seasonal home range size ensured an adequate representation of the area used.

I compared the size of annual home ranges by sex and year of release. I compared LBL elk in 2002 to all elk in 2004 to compare animals that had been released for 1 year to animals that had been released ≥ 2 years. I also compared seasonal home ranges by sex, elk origin, and year. I then compared the same parameters within a smaller dataset that excluded all locations collected during the first year after release. That was done to assess whether exploratory movements in the first year affected home range size. I performed an analysis of variance (ANOVA) on ranks, which negates the

assumption of normality, to compare overall home range sizes in most tests. After assessing normality of the distribution of home range sizes, I utilized a paired t-test to identify differences in home range size by year for all elk in which estimates existed for consecutive years, and I used the Wilcoxin Rank Sum test to compare overall home range sizes between LBL and EINP.

Movements

Post-release movements were important to evaluate elk behavior after release and to assess site fidelity. I used location data collected from GPS collars to estimate the average distance moved between consecutive GPS locations, the average distance moved between days, and net distance traveled. I also documented the linearity of movements after GPS-collared elk were released at time intervals of 2 weeks, 3 months, and 6 months. The time period of 2 weeks was selected to analyze immediate movements after release. I chose 3 months as a time period that should have encompassed most immediate exploratory movements and any movements from calving, without including possible seasonal shifts in habitat use (Rob Kay, Parks Canada, personal communication). Because movements of some elk were represented by GPS datasets that spanned <1 year, I chose 6 months as the longest time period to analyze movements. I documented and analyzed site fidelity and centers of activity by season using the Animal Movement Extension (Hooge and Eichenlaub 1997) in ArcView[®] GIS.

I calculated the average distance moved between consecutive GPS locations as the average distance recorded between each consecutive location each day, and I calculated the average distance moved between days by averaging the distance between

the first location acquired on consecutive days. I excluded days when the GPS collar acquired no locations from all analyses. I used the straight-line distance between starting and ending locations of the respective time periods to calculate net movement. Circuitry or linearity is a measure of the overall straightness of an animal's movements with values ranging from 0 to 1. A value of 0 indicates the animal returned to the original release site or beginning location or never left it, whereas a value of 1 indicates the animal moved away from the release site in a linear fashion. Movement parameters were calculated using Microsoft Excel and the Animal Movement extension in ArcView[®] GIS. I compared movements based on origination site of elk (LBL and EINP), 1st and 2nd years after release, and sex using an ANOVA based on ranks.

I estimated site fidelity by comparing the observed movement patterns to random movement patterns generated with the Animal Movement extension in ArcView[®] GIS. Site fidelity was categorized into 3 classes: constrained movements, random movements, or dispersal movements. I analyzed site fidelity for the first 2 weeks, 3 months, and 6 months post-release to determine if elk demonstrated site fidelity or if site fidelity differed between elk origin (LBL versus EINP). The *P* value reported for this test was equal to the proportion of generated movement paths with higher mean standard deviation values, and is not equivalent to *P* values reported with other statistical tests. If site fidelity was close to the 95% cutoff, I increased the replicates of generated paths from 100 to 1,000. Lastly, I calculated seasonal centers of activity for elk using the harmonic mean point theme in the Animal Movement extension in ArcView[®] GIS. Distances from centers of seasonal activity were calculated based on distance from the

release site and those from corresponding seasons in different years. When sample sizes were sufficient, distances between seasonal centers of activity were compared based on elk origin (LBL and EINP), 1st and 2nd years after release, and sex using an ANOVA based on ranks.

DEMOGRAPHICS AND POPULATION GROWTH

Population Size

All elk were radiocollared at release and monitored from 2001 to 2006. In 5 years, I only documented 1 elk collar that dropped off with no obvious explanation (i.e., animal sighting or accompanying carcass). As such, the fates of most elk in this study were known. Likewise, visual observations of elk throughout this period of study enabled researchers to further document the fates of remaining collared and uncollared animals. Most calves were successfully captured and collared each year, and adults were recollared as needed. Consequently, radio telemetry and visual observation provided an accurate estimate of the standing population size of elk during and at the conclusion of this study.

Reproduction

All adult cows received pregnancy tests prior to shipment from their source herd and again prior to release (PSPB test; BioTracking[®], Moscow, Idaho). I determined the reproductive status of radio-equipped females from those pregnancy tests, rectal palpation, and visual observations. Additionally, pre-parturient cow elk usually isolate themselves before calving, and I used this movement pattern as an indicator of pregnancy (Larry Bryant, USDA Forest Service, personal communication). When female elk

separated themselves from the herd and were suspected to be pregnant, a calf search was performed 1–2 days following the observed movement. Field personnel initiated searches by radio-locating the expectant female via her radiocollar or vaginal transmitter using triangulation. We then hiked to the location and systematically searched a grid of approximately 150 m in every direction from that site. If initial search efforts proved unsuccessful, the search was repeated a few hours later and again the following day, allowing breaks for calf feedings. Searches were continued until the calf was estimated to be >4 days of age, at which time the searches were terminated.

Calves that were successfully located were physically restrained and blindfolded to minimize stress. We then moved the calf to a blanket that had been washed in scent remover. All field staff wore latex gloves to minimize any transfer of human scent to the calf. I recorded body measurements, body mass, and sex of the calf, and each calf was fitted with an expandable breakaway collar. Handling of the calf was limited to <10 minutes. To ensure we immediately detected calf mortalities, newly collared calves were radio located every day for ≥ 2 weeks.

Survival

Field personnel used telemetry to monitor adult and subadult elk 3–6 times per week to estimate annual and seasonal survival. Annual survival rates were determined for subadult (1–2 years) and adult (≥ 3 years) males and females using the Kaplan-Meier staggered entry procedure (Pollock et al. 1989). The survival function was

$$\hat{S}(t) = \prod \left(\frac{1 - d_j}{r_j} \right),$$

$$\frac{j}{a_j} < t, \text{ where}$$

$\hat{S}$ is the probability of survival, d_j is the number of deaths up to time j , r_j is the number of animals at risk at time a_j , a_j is a particular time of death, and t is the time interval (Pollock et al. 1989). Estimates of variance (var) were

$$\text{var}[\hat{S}(t)] = \frac{[\hat{S}(t)]^2 [1 - S(t)]}{r(t)}.$$

Assumptions were that all animals were randomly sampled, survival times were independent for individuals, capturing or radio-collaring elk did not influence future survival, censoring mechanisms were random, and survival functions for newly collared elk were the same as those for previously collared elk.

Calf survival was calculated as a proportion of animals that survived within the first year given that all calves were born at approximately the same time of year. Survival rates for uncollared calves were estimated based on periodic visual observations throughout the summer. Survival rates were compared by sex and age using a Log-rank test (Pollock et al. 1989).

We physically retrieved radio collars that switched to mortality mode to determine whether the collar malfunctioned, broke away from the animal, or if there was a mortality. Field necropsies/assessments were performed on all dead elk to determine causes of death. When predation was suspected as the likely cause of death, I assigned a predator classification based on physical signs on or around the remains using standardized procedures (Wade and Bowns 1993). When feasible, entire elk carcasses

were immediately collected and taken to the University of Tennessee College of Veterinary Medicine (UTCVM). UTCVM personnel performed laboratory necropsies to determine official cause of death, animal health, and the presence of any diseases or parasites of concern. Necropsy results were made available to state veterinarians and biologists from North Carolina, Tennessee, and NPS.

Population Growth

I used a population model (RISKMAN, version 1.5.413; Ontario Ministry of Natural Resources, Toronto, Ontario, Canada) to estimate population growth and extinction probabilities. This individual-based model required estimates of calf survival, subadult male and female survival, adult male and female survival, and reproductive rates. I classified calves as any elk <1 year of age, subadult were elk ages 1–2, and adults were ≥ 3 years of age. Age-specific reproduction was defined as the probability that a female in reproductive condition (i.e., ≥ 3 years of age) would produce a calf. I calculated subadult litter production from 3-years-old females and adult litter production from females >3 years of age. Survival rates and variances for the simulations were based on the Kaplan-Meier estimates. I calculated the annual process variation of each model parameter to incorporate temporal variation into the error terms of the stochastic trials (White et al. 2002). This technique attempts to separate process variation, such as variation in space or time, from sampling variation, the variance associated with statistical estimation from a sample. I did not include density effects in the simulations. I used the 2002 and 2006 standing age distribution to initiate simulations, and conducted 50 stochastic simulations to establish standard deviations. The start of the model year

was prior to parturition; therefore, a 3-year-old female (subadult) would breed and then give birth on her 4th birthday. The model recorded an extinction event if the simulated population decreased to <10 animals.

To evaluate demographic response of elk to simulated changes in model parameters, I conducted a sensitivity analysis by analyzing multiple scenarios of the projected population for the next 100 years (White 2000). I manipulated the model based on the 2006 age distribution model by reducing the parameter means and standard errors, such as female survival and adult reproduction, by 5 and 10% to evaluate the response of the projected population growth and extinction probability. Finally, I determined which of those parameters had the greatest impact on population growth rate and extinction probability.

ELK HABITAT

Habitat Use

I used compositional analysis (Aebischer et al. 1993) to determine whether some vegetation cover types were disproportionally selected by elk in GSMNP. Compositional analysis alleviates several statistical problems such as non-independence of habitat delineations, differential habitat use by groups of animals, inflated sample sizes caused by using locations as the sampling unit, and arbitrary definitions of habitat availability (Aebischer et al. 1993, Katnik and Wielgus 2005). I compared use and availability at two levels: home range placement within the study area (2nd order selection) and resource use based on radio locations within the home range (3rd order selection; Johnson 1980). This technique is based on ranking land cover according to relative use and determination of

statistical differences. I performed 1,000 iterations of the randomization test required when the dataset was non-normal, and replaced missing values or zeros that occurred when an animal did not use one of the designated habitats with 0.3 to limit type I error (Bingham and Brennan 2004). I pooled locations for animals tracked for >1 year, and home ranges were recalculated for those animals.

I used multi-resolution Land Cover (MRLC) data from 2001 (Homer et al. 2004) for the habitat selection analysis. Using ArcView[®] GIS, I reclassified the original National Land Cover Data (NLCD) digital map layer (30- x 30-m resolution) into 6 cover types: treeless/grassy habitat, scrub/shrub, deciduous forest, evergreen forest, mixed forest, and human/barren (Table 1, Fig. 4). The treeless classification combined the grassland/herb, pasture/hay, and woody wetlands classes. The treeless cover type represented areas with high levels of herbaceous forage cover, and comprised <1.75% of the available habitat. The human disturbance classification included low- and high-density residential areas, commercial areas, bare rock/sand/clay, and row crops. That classification represented areas assumed unsuitable for elk because of lack of resources or high probability of human-elk conflict. Those pooled classes contributed <3% of the total study area.

Habitat Model

There have been tremendous advances in habitat modeling techniques that allow a better representation of multivariate animal-landscape relationships over large spatial scales (Clark et al. 1993, Donovan and Thompson 2001, Dettmers et al. 2002). Many advanced modeling methods have been designed and tested for a wide variety of plants

and animals, including elk (Eby and Bright 1985, Van Deelen et al. 1997, Didier and Porter 1999, Johnson et al. 2000, Telesco et al. 2007). In addition to the univariate analysis using compositional analysis, I used the Mahalanobis distance method (Clark et al. 1993) to create a predictive multivariate model that allowed me to identify areas that possessed potential multi-faceted habitat conditions suitable for elk in GSMNP based on existing elk locations. I did this analysis for individual elk locations, and included all locations that met the requirements for inclusion in the home range analyses ($n = 12$). I used elk locations instead of home ranges because of the low number of elk equipped with GPS collars, and I assumed any bias from GPS location error and time of day would be minimal. There were 3 individuals that had less than half of the average number of locations. Regardless, I included these animals because there was substantial overlap with other home ranges for one animal, suggesting that habitat use was not unusual. The other 2 were EINP elk making exploratory movements in their first year of release, and may actually enhance the population level representation of the model by incorporating locations during exploration. Furthermore, all 3 represented only 1 year of telemetry data as opposed to the majority of the other elk, which had locations collected over 2 years.

The Mahalanobis distance statistic is a measure of dissimilarity between pixel values associated with animal locations representing “ideal” habitat characteristics and the remaining pixel values in a landscape. Therefore, low D^2 values indicate landscape conditions similar to those where elk were located (Knick and Rotenberry 1998). The habitat characteristics for each variable are defined by the range of values for a suite of variables associated with elk locations. Mahalanobis distance (D^2) is represented by:

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

where $\bar{\underline{x}}$ is the vector of habitat measures associated with each pixel in a grid layer, $\underline{\hat{u}}$ is the mean vector of habitat measures estimated from elk locations, and Σ^{-1} is the inverse covariance matrix, also estimated from the elk locations. Assumptions of this technique are that the study animals distribute themselves in the best habitats on the study area (Knick and Rotenberry 1998).

Mahalanobis distance offers several advantages over other commonly used modeling techniques such as logistic regression or discriminant function analysis. Mahalanobis distance does not require absence data, thus avoiding potential biases because of false negatives (Clark et al. 1993). Mahalanobis distance does not require a delineation of available habitat, and thus avoids many biases caused by study area delineation (Knick and Rotenberry 1998). Additionally, the distance values are uncorrelated, standardized scores; correlated variables are adjusted by the variance-covariance matrix, and distributional assumptions do not have to be met (Clark et al. 1993).

Model Variables

I began the variable selection process by identifying parameters that might influence elk habitat use (Haines-Young and Chopping 1996, Turner et al. 1993, Telesco et al. 2007). However, no information was available regarding elk behavior and habitat use in the southern Appalachians, and I considered large-scale variables because of elk's large space requirements and generalized habitat needs (Edge et al. 1987, Turner et al. 1993, Cooperrider 2002, Lyon and Christensen 2002). Although Mahalanobis is not

sensitive to correlated variables, I limited the number of variables to facilitate interpretation of the habitat model. The variables I selected to calculate Mahalanobis distance were created in ArcInfo[®] GIS (Environmental Systems Research Institute, Redlands, California, USA) and FRAGSTATS (McGarigal et. al. 2002). Source maps and subsequent calculations were converted to grids with a 30- x 30-m resolution, and projected into NAD83, UTM Zone 17 North.

The quality and availability of forage and cover are recognized as the primary critical components of elk habitat (Cook 2002, Skovlin et al. 2002). Depending on year, season, and habitat, elk diets consist of grasses, forbs, shrubs, and woody browse (Cook 2002, Jost et al. 1999). Both grasslands and forest provide forage whereas forest cover mainly provides thermal protection by modifying temperature extremes and security from predators and human disturbance (Wisdom et al. 1986, Skovlin et al. 2002). I assumed that landscapes with a higher diversity of land-cover types would contain higher quantities of cover and forage (Didier and Porter 1999, Telesco et al. 2007). To evaluate the overall availability of forage, I used Simpson's diversity index (SIDI). SIDI is an intuitive measure of diversity that is relatively insensitive to rare class types (McGarigal and Marks 1995). The index represents the probability that any 2 cells selected at random would be different land-cover types, considering both richness and evenness of land cover types. I calculated SIDI on the same cover type classifications as the habitat analysis.

Many studies have shown that elk use ecotones more than the interior of a patch (Wisdom et al. 1986, Johnson et al. 2000, Roloff et al. 2001, Skovlin et al. 2002).

Ecotones between forests and open fields have a higher diversity and quantity of forage, and reduce the distance between forage and security cover (Wisdom et al. 1986, Skovlin et al. 2002). Amount of edge, a proxy for ecotone, is influenced by the size, density, and shape complexity of patches. Therefore, ecologists have developed broad-scale landscape metrics to quantify patterns of edge and patch configuration (McGarigal and Marks 1995, Haines-Young and Chopping 1996, Turner et al. 2001). I calculated patch richness (PR), edge density (ED), perimeter-area ratio (PARA), fractal dimensions (FRAC), and contagion (CONTAG; Table 2) to characterize the spatial configuration of elk habitat in my study area. Those metrics were calculated from a land-cover grid of forest and fields. The forest category represented cover habitat and was comprised of all forest types. The field category represented treeless habitat and was comprised of the pasture/hay/grassland cover type. Whereas row crops are often palatable and desirable to elk (Herner-Thogmartin 1999), they were not included in the field class because there is a high probability of elk-human conflict associated with this cover type. Consequently, row crops were grouped with habitat types representing urban and barren areas, which had little value to elk. Those habitat types were considered as background with no value and were not used in calculations.

PR and ED are 2 of the simplest measurements of spatial landscape relationships. I used PR to calculate the number of unique habitats patches over the total landscape area within a window. ED, the length of edge for forest and field patches divided by the total landscape area within a window, was calculated to approximate a distance to edge measurement (Wisdom et al. 1986, Johnson et al. 2000, Roloff et al. 2001). PARA is

easily interpreted; the longer the perimeter compared to its area, the more complex the shape (McGarigal and Marks 1995). However, PARA is size dependent. Conversely, FRAC is a measure of shape complexity, but is not size dependent and can be difficult to interpret. However, FRAC can capture a characteristic of complexity that other metrics cannot. The theory behind fractals is complex, and based on the idea that increasing resolution exposes details previously undetected (Mandelbrot 1983, Turner 2001). I calculated PARA and FRAC by using the area-weighted mean over all patches (Schumaker 1996). Finally, I calculated CONTAG, which is a measure of both dispersion and interspersed patches and is inversely related to edge density (McGarigal and Marks 1995).

Finally, I used slope as a variable for my elk habitat model (Unsworth et al. 1998, Skovlin et al. 2002). Elk generally select gentle to moderate slopes (<40%), exhibiting differences in slope use among seasons and years (Edge et al. 1987, Unsworth et al. 1998, Skovlin et al. 2002). I calculated mean percent slope using the Neighborhood Statistics tool in the Spatial Analyst extension of ArcGIS®.

Variable and Scale Selection

The spatial scale of habitat models can affect the outcome, validity, and interpretation of landscape-level analyses (O'Neill et al. 1996, Riitters et al. 1997, Turner et al. 2001, Telesco et al. 2007). Because elk may select habitat at multiple spatial scales, the most appropriate scale to measure habitat use may depend on the individual variable. For that reason, I used methods described by Riitters et al. (1997) to create and incorporate landscape metrics at multiple scales, based on a moving window analysis.

Using ArcGis® (Environmental Systems Research Institute, Redlands, California, USA), I first placed a window of fixed size over a raster grid representing a landscape feature. That window was moved across the grid, one pixel at a time. The value of the habitat measure was calculated for the landscape within the window and placed in the center pixel. This process resulted in a new grid in which the value of each pixel characterized the habitat for an area equal to the window scale. I repeated the process for multiple window sizes so that each habitat measure was calculated at multiple scales. For each variable, I chose the scale with the least amount of variation based on the elk locations. When a landscape metric had low variation compared to the variation of the metric across the entire study area, I assumed the metric may be more relevant to the model.

I identified 4 scales based on telemetry data collected on elk in GSMNP; these scales loosely represent the order of habitat selection described by Johnson (1980). The areas of the 4 window sizes were 0.2 km², 4 km², 12 km², and 36 km². The 0.2-km² window represented the localized area of Cataloochee Valley, where most elk resided. The 4-km² window represented the mean core home range size for males. The 12-km² window approximated the average female annual home range and the average male seasonal home range. The largest window represented the size of the largest male seasonal home range (autumn; 36 km²), which approximates the smallest area required by an elk to acquire adequate resources (Herner-Thogmartin 1999). I chose to use circular windows, rather than the square windows, to represent natural animal movements.

I generated 25 different variables based on the combination of 7 landscape measures and 4 measurement scales. To determine which variables were most

biologically applicable for elk, I eliminated variables with high variation among elk locations. I determined this by examining the mean, coefficient of variation, and frequency distributions of variable values at all elk radiolocations. Although the modeling technique handles repetitive variables, I did not include the same variable at multiple scales or highly correlated variables to avoid redundancy. From the remaining variables, I selected variables with low variation compared to their variation across the study area.

Model Testing

After calculation of D^2 , I tested for differences between cumulative frequency distributions of D^2 values for a set of random locations and the original elk locations using a Kolmogorov-Smirnov test. I established a cutoff value for suitable habitat by determining the point where the cumulative frequency distribution for the D^2 values associated with the elk and random locations differed most (Browning et al. 2005). I considered pixels with suitably low Mahalanobis values to represent suitable elk habitat.

VEGETATION ANALYSES

Microhistological Analysis

Dietary information on free-ranging ungulates is useful for assessing the composition, quality, and seasonal differences in nutrient and forage in a given area (Adams 1957, Short et al. 1969, Smith and Shandruk 1979, Hodgman et al. 1996). The most commonly used method of food habits analysis for ungulates is microhistological fecal analyses. This technique quantifies compositions of herbivore diets by identification of plant species from epidermal characteristics of ingested flora (Smith and

Malechek 1974, Holechek et al. 1982). Microhistological analysis has been used throughout the U.S. to quantify diets of ungulates such as white-tailed deer, black-tailed deer (*Odocoileus hemionus columbianus*), mule deer (*Odocoileus hemionus hemionus*), and elk (Keegan et al. 1989, Johnson and Dancak 1993, Kirchhoff and Larsen 1998, Zielinski 1999, Myers 2001).

I collected fecal pellets from 2003 to 2005 in treeless areas and forested areas to determine the principal diet of elk at GSMNP. I defined fecal pellet groups as those that consisted of ≥ 10 pellets. I used only fresh fecal pellet groups as determined by moisture content and lack of feeding activity by insects. All samples were frozen upon collection. Once >50 fecal pellet groups had been collected each year, I combined them into a composite sample for analysis by season (spring: March–May, summer: June–August, autumn: September–November, and winter: December–February). Samples were analyzed by the Wildlife Habitat Nutrition Laboratory at Washington State University for vegetation content at the genus or, if possible, species level, identifying all possible plants in the feces. I chose to have the lab use 200 microscope views of the fecal contents to determine the makeup of composite seasonal diets. Samples collected from distinctive areas with small sample sizes, or areas not covered by the separate vegetation analysis, were analyzed as individual samples with 100 microscope views ($n = 20$).

Fecal nitrogen is frequently used as an assay of diet quality (Kie and Burton 1984, Leslie and Starkey 1987, Wehausen 1995). In trials where digestible energy intake were controlled, Hodgman et al. (1996) showed that the indices of fecal nitrogen and fecal 2,6 diaminopimelic acid (DAPA) were the best indicators of diet quality. More than 80% of

a ruminant's energy from food comes from volatile fatty acids produced by bacterial fermentation in the rumen. The concentration of DAPA in feces is an index of the rate of bacterial growth in the rumen and hence is an index of the rate at which energy is delivered to the rumen. Several studies showed that fecal DAPA levels fluctuated to reflect seasonal changes in forage quality in free-ranging moose (*Alces alces*) and white-tailed deer (Leslie et al. 1989), mule deer (Kie and Burton 1984), and elk (Davitt et al. 1985). Neutral detergent fiber (NDF) is an estimate of a plant's cell wall content. Lignin content. NDF is considered an indicator of how much forage an animal will eat because NDF typically decreases with increasing lignin content. Percent oven dry matter, percent fecal nitrogen, DAPA, and neutral detergent fiber analyses were performed on all composite and individual fecal samples (Bruce Davitt, Washington State University, personal communication).

Vegetation Monitoring

I developed vegetation-sampling methods to determine if major changes in vegetation cover occurred as a result of browsing and grazing by elk. From 2002 to 2005, I compared vegetative characteristics between treatment and control plots in areas used by elk.

I used stratified sampling techniques to assign plot locations based on a landform measure (i.e., cove, slope, or ridge), aspect, elevation, and vegetation diversity (Mike Jenkins, GSMNP, personal communication). Sites for paired plots were randomly selected within those strata. Strata characterized with higher variability based on percent herbaceous cover, sapling density, and understory richness were assigned more plots,

with a minimum of 5 plots per strata (Table 3). For plots located in treeless areas, I selected sites that would minimize visual obtrusiveness to visitors.

I used polypropylene deer fencing (Benner's Gardens[®], Conshohocken, Pennsylvania) to construct a 12- x 12-m enclosure at each site to serve as a control area. Rebar rods were driven into the ground to secure the fencing. All fencing was raised 0.5 m above ground to allow feeding in enclosures by animals other than elk, including deer. A 10- x 10-m sampling plot was established using rebar stakes and centered within each 12- x 12-m enclosure. The approximate 1-m buffer zone created around the 10-m² sampling plot within each enclosure helped avoid edge effects from elk browsing along the fence line. Control plots were located ≤ 50 m from each treatment plot in areas with similar aspect, topography, and plant communities. The down-slope side of each plot was designated as the first line, and transects were established at 2-m intervals perpendicular to the slope (Fig. 5). Within all forested enclosures, a 3.2- x 3.2-m subplot was positioned in the right up-slope corner of the plot for woody seedling density measurements. In "treeless" plots, where the ground was typically level, subplots were located on the right-hand corner of the control plot facing the nearest tree line. The sampling protocol was designed to allow 2 data collectors to complete the sampling regime in 1 field season. Sampling began with plots at the lowest elevations and those which had the southernmost exposures, because vegetation emerges earliest in the season at these locations. UTM coordinates, elevation, slope, and aspect, as well as notes on disturbance of either the treatment or control plots were recorded during both years of sampling.

Vegetation Plot Sampling

I used the line intercept method to estimate percent cover for species within the forested 10- x 10-m plots. I measured the horizontal coverage of vegetation ≤ 1.4 m in height along transects. Vertical height of vegetation was also measured and placed into the following classes: class 1 (0 to 25 cm), class 2 (>25 to 50 cm), class 3 (>50 to 75 cm), and class 4 (>75 to 140 cm). When vegetation spanned ≥ 2 vertical height classes, the tallest class was recorded. If a transect line bisected vegetation >1.4 m in height (e.g., tree trunk), the length along the transect was measured and recorded as a stem.

Treeless treatment and control plots were sampled to estimate vegetative cover and diversity using a slightly different line intercept method than that used in forested plots. The height and class of vegetation that contacted a small-diameter pole was recorded at every 0.5-m position along each line transect, totaling 19 samples per transect or 95 samples per exclosure. When vegetation spanned ≥ 2 vertical height classes, the tallest class was recorded (Mike Jenkins, National Park Service, personal communication).

All woody stems >1.4 m tall and <10 cm diameter at breast height (DBH) within 10- x 10-m plots were measured and counted. Woody stems were tallied in the following size classes: class 1 (0 to 1 cm), class 2 (>1 to 2.5 cm), class 3 (>2.5 to 5 cm), and class 4 (>5 to 10 cm). If multiple stems arose from 1 plant, each stem was counted separately.

I measured woody seedling density in each 3.2- x 3.2-m subplot. The height of each seedling present in a subplot was measured and tallied by species into 1 of the

following 4 height classes: class 1 (0 to 5 cm), class 2 (>5 to 20 cm), class 3 (>20 to 50 cm), and class 4 (>50 to 140 cm). Tree species >1.4 m in height were not recorded.

The DBH of all trees >10 cm DBH within the 10- x 10-m plot were measured and identified to species. Each tree was assigned a ranking for canopy position (dominant, codominant, intermediate, or suppressed) and tree condition (no dieback, 1-25% dieback, 26%-50% dieback, 51%-75% dieback, and >75%).

Vegetation Analysis

Vegetation data from the paired plots were compared to determine if there was an overall effect from feeding by elk between 2002 and 2005. Woody stem density, woody seedling density, and herbaceous cover (line intercept method) were each classified into 7 relevant vegetation groups (deciduous tree, deciduous shrub, evergreen tree, evergreen shrub, grass and sedges, forb, or fern). After collapsing species into the 7 categories, differences between the 2 sampled years were calculated and ranked. The average height or counts for 2002 were subtracted from those for 2005 for each plot. The ranked difference scores were tested for normality with the Shapiro-Wilk W statistic and with the Levene's test for homogeneity of variance. Using the ranked difference scores between 2002 and 2005 as the dependent variable, I performed an analyses of variance with a randomized block design to determine if differences in total plant counts or individual species group abundance occurred between years in the treatment or control. Specifically, I identified any change in overall plant abundance or change in general plant group composition over time. If temporal changes were detected with ANOVA, I used the least significant difference mean separation technique to determine whether those

changes differed between treatment and control plots. I compared vegetation data from the paired plots by each individual stratum (Table 3). Then I combined all strata (strata 3–9) and compared means of all parameters. Finally, I combined the cove strata (strata 7 and 8) and made vegetative comparisons. I used an alpha value of 0.1 for all vegetation statistics to minimize Type II errors and maximize the probability to detect any impacts of elk browsing.

CHAPTER IV: RESULTS

ELK CAPTURE AND PROCESSING

From 24 to 26 January 2001, personnel from UT, NPS, and LBL chemically immobilized 25 (13M:12F) elk in the Elk and Bison Prairie at LBL. On 1 February 2001, 3 cattle trailers were used to transport those 25 elk to GSMNP. There were no injuries associated with the transport process and all elk were transferred into the holding facility upon arrival to Cataloochee Valley. Access to the facility was restricted to project personnel and contact with elk occurred only when feed was brought into the pen. On 2 February 2001, we herded all elk into the holding facility's chute system to facilitate the pre-release workup of individual animals. During that process, all elk received individually numbered ear tags and were equipped with radio tracking devices. Nineteen (11M:8F) elk were equipped with MOD-600 VHF radio collars (Telonics Incorporated, Mesa, Arizona, USA) with an 8-year battery life, and 6 (3M:3F) elk received 2200L GPS/VHF collars (Lotek Wireless Incorporated, New Market, Ontario, Canada). Eight female elk with positive results for previously administered pregnancy tests were equipped with vaginal VHF transmitters. No sedation was required for the pre-release workup and all elk exited the chute without injury. On 2 April 2001, the holding facility was opened and all 25 elk were released into Cataloochee Valley.

On 14 January 2002, personnel from UT, NPS, and Department of Parks Canada corralled 27 (8M:19F) elk in Elk Island National Park. Cattle trailers containing the 27 elk departed from EINP on 1 February 2002 and arrived in Cataloochee Valley on 4 February 2002. No injuries to elk occurred during the transport process and all animals

were safely transferred into the holding facility. Seven (3M:4F) elk were equipped with GPS collars and VHF radio collars were deployed on the remaining animals (5M:15F). All 7 adult female elk that tested positive for pregnancy in 2002 were equipped with vaginal VHF transmitters. After this release, vaginal transmitters were not used again. On 20 April 2002, the holding facility was opened and elk from EINP were released into Cataloochee Valley.

TELEMETRY

Radio Telemetry and GPS Collars

Collection of location data from VHF collars was hampered by terrain, weather, and limited vehicle access in GSMNP. Consequently, location data used for determination of home-range dynamics, movements, habitat use, and habitat modeling were restricted to those collected from GPS collars. When possible, GPS collars were refurbished and redeployed on elk throughout the duration of the project. Of approximately 50,000 locations that my GPS collars were programmed to record (which excluded potential locations from malfunctioning collars), I obtained 31,861 locations from 14 (7M:7F) elk including redeployment of refurbished collars. Those collars had either collected locations the entire time of deployment or had a partial collection because they had stopped collecting locations sometime during the deployment. Data associated with 3 (2M:1F) elk could not be retrieved due to complete collar malfunction. After removing locations with DOP >5.9, the data set contained 30,672 locations. From those data, 12 (6M:6F) study animals had sufficient locations to calculate annual home ranges

(24,623 locations) and 14 (7M:7F) had sufficient data to calculate seasonal home ranges (27,127 locations)

Assessing GPS Telemetry Bias

I created 2 linear regression models to quantify the potential GPS collar bias in summer and winter. I detected a correlation between percent canopy cover at test sites and percent canopy cover obtained from remotely sensed data (summer: $\text{corr} = 0.61$, $P < 0.001$; winter: $\text{corr} = 0.47$, $P < 0.002$). Therefore, I was able to evaluate remotely sensed canopy cover data and other remotely sensed variables that were associated with failure of GPS collar to obtain locations. The best model fit for the summer period ($n = 46$, $P < 0.003$) was obtained using a 2-variable model that included slope ($\beta = 0.00563$, $\text{SE} = 0.0024$) and cover type ($\beta = 0.15553$, $\text{SE} = 0.048$ adjusted $R^2 = 0.2031$). For the winter period ($n = 42$), fix rate success was best explained by a 2-variable model that included landform curvature ($\beta = -0.03238$, $\text{SE} = 0.014$) and cover type ($\beta = -0.10042$, $\text{SE} = 0.025$ adjusted $R^2 = 0.3312$). Due to the small β and R^2 values and the high success rate of the fixed trial collars, the linear regression models developed from trial collars only resulted in an adjustment of 1–3% of the original locations that my GPS collars failed to record (61%). Therefore, I did not use the regression equation to adjust location data collected from GPS radio collars.

HOME RANGES AND MOVEMENTS

Home Range Analysis

Annual home-range sizes calculated from 2001 to 2004 averaged 10.4 km^2 for females ($n = 9$, $\text{SE} = 5.2$) and 22.4 km^2 for males ($n = 8$, $\text{SE} = 6.8$; Fig. 6). The mean

annual home range of females was approximately half that of males, although the ANOVA failed to detect differences by gender or year ($F_{1,6} = 0.960$, $P = 0.365$ and $F_{2,6} = 1.378$, $P = 0.322$, respectively). Because of limited battery life associated with GPS collars, only 5 (2M:3F) animals had consecutive years of location data after their release. Of those, no differences in home-range size were detected between the 1st and 2nd years after release ($t = 1.36$, $P = 0.245$). I could not make comparisons between elk from LBL and EINP by sex or age classes or among age classes across years because of an insufficient number of animals. However, across years and sex, EINP animals had home ranges that were 2.5 times larger than LBL ($\bar{x} = 26.0$, $n = 5$, $SE = 10.6$ and $\bar{x} = 9.8$, $n = 11$, $SE = 3.8$, respectively) yet did not statistically differ ($W = 2.314$, $P = 0.314$).

I estimated home ranges for males ($n = 30$) and females ($n = 25$) for all seasons and year combinations with sufficient sample sizes (Table 4). The ANOVA tests indicated that there was an overall difference in home range size by season ($F_{3,8} = 4.692$, $P = 0.006$), with autumn home ranges being largest ($\bar{x} = 27.3$, $n = 15$, $SE = 8.2$). However, no difference in seasonal home ranges size between males and females was detected ($F_{3,8} = 8.44$, $P = 0.477$). As with annual home ranges, I could not compare seasonal home ranges between elk from LBL and EINP or different age classes because of insufficient sample sizes.

Movements

Locations collected for the 12 elk for which annual home ranges could be estimated were used for all movement, linearity, and site fidelity calculations for the 3

time periods (Table 5). The furthest straight-line distance of an elk traveling during the 6-year period was 65 km. However, such movements were rare.

During the first 2 weeks after release, average distances moved between consecutive GPS locations, which averaged 4.3 (SE = 0.02) hours apart, were less for LBL elk ($\bar{x}$ = 98 m, n = 4, SE = 24) than EINP elk ($\bar{x}$ = 206 m, n = 3, SE = 27; $F_{1,5}$ = 9.01, P = 0.030). The average distances moved between consecutive days during the first 2 weeks after release were less for LBL elk ($\bar{x}$ = 190 m, n = 4, SE = 57) than EINP elk ($\bar{x}$ = 485 m, n = 3, SE = 66; $F_{1,5}$ = 11.57, P = 0.020). For LBL elk only, the distances between consecutive locations were greater in 2002 ($\bar{x}$ = 489, SE = 100) than 2001 ($\bar{x}$ = 190, SE = 57; $F_{1,3}$ = 19.20, P = 0.020). The consecutive locations differed between LBL animals in 2002 and all animals in 2004 ($F_{1,7}$ = 8.35, P = 0.020), with smaller distances between consecutive locations for 2004 ($\bar{x}$ = 221, SE = 26). When these same comparisons were made between sexes no differences were detected. Linearity differed between 2001 LBL animals and 2002 EINP animals, with EINP animals moving in a more linear direction away from the release site ($F_{1,5}$ = 7.62, P = 0.040). The 2 week linearity calculations between 2001 and 2002 for LBL animals became more circuitous ($F_{1,3}$ = 54.86, P = 0.010), as did the linearity of movements when comparing 2002 LBL animals and all 2004 animals ($F_{1,7}$ = 10.83, P = 0.010).

During the first 3 months after release, the average distance moved between consecutive GPS locations for elk from LBL ($\bar{x}$ = 420 m, n = 4, SE = 21) were higher than EINP ($\bar{x}$ = 303 m, n = 3, SE = 25; $F_{1,5}$ = 12.71, P = 0.020). No other paired movement calculations for the 3-month time period differed. When these same

comparisons were made between sexes, daily movements were larger for females ($F_{1,6} = 8.69$, $P = 0.030$). Within the 3-month calculations, the linearity between 2001 and 2002 for LBL elk decreased ($F_{1,3} = 96.0$, $P = 0.002$).

No differences were detected for the 6-month movement comparisons. However, when home ranges were averaged over the 6-month period and the distance from release site was compared between LBL elk in 2001 and EINP elk in 2002, there was a significant difference ($F_{1,4} = 10.94$, $P = 0.030$). Overall, animals from EINP displayed home range centers that were further from the release site in 2002 than LBL elk in 2001. When these same comparisons were made between sexes no differences were detected. The 6-month linearity decreased between 2001 and 2002 LBL animals ($F_{1,3} = 25.00$, $P = 0.020$). The linearity between the 2002 LBL elk and all 2004 elk also decreased ($F_{1,7} = 360.48$, $P < 0.001$).

For elk originating from LBL, the average difference between individual spring centers of activity from 2001 to 2002 was 1,701 m ($n = 4$, $SE = 373$, range = 589–2,156 m). Distances between centers of activity during the summer of 2001-2002 differed by an average of 546 m ($n = 4$, $SE = 277$, range = 91–1,274 m). The average difference between autumn centers of activity from 2001–2002 was 320 m ($n = 4$, $SE = 130$, range = 71–643 m). Small sample sizes precluded analyses of distance between centers of activity during winter months. When season centers were averaged across animals, there was a significant difference between the seasonal centers of LBL elk in 2001 and EINP elk in 2002 ($F_{1,3} = 1,393$, $P = < 0.001$) and from distance to the release site ($F_{1,4} = 10.94$,

$P = 0.030$) but no differences were detected between LBL elk in 2001 and 2002 or between males and females.

The average differences between centers of activity for LBL elk in 2001 was 5,343 m ($n = 4$, $SE = 3,325$, range = 1,759–15,314 m) from spring to summer, 2,355 m ($n = 4$, $SE = 2,241$, range = 71–9,076 m) from summer to autumn, 1,648 m from autumn to winter ($SE = 1,464$, $n = 4$, range = 98–6,035 m), and 931 m from winter to 2002 spring ($n = 4$, $SE = 489$, range = 51–1,857 m). In 2002, the average difference between seasonal centers of activity for elk originating from LBL in 2002 was 3,372 m ($n = 5$, $SE = 2,537$, range = 47–13,469 m) from spring to summer, and 2,724 m ($n = 5$, $SE = 1,670$, range = 98–8,834 m) from summer to autumn. The average difference between centers of activity for EINP elk in 2002 was 3,186 m ($n = 3$, $SE = 2,537$, range = 1,636–5,042 m) from summer to autumn. Differences between centers of activity for 2002 could not be determined between any other seasons because of insufficient sample sizes. The average difference between centers of activity for all elk for 2004 was 425 m ($n = 3$, $SE = 272$, range = 72–958 m) from spring to summer and 4,426 m ($n = 4$, $SE = 2,836$, range = 459–12,565 m) from summer to autumn; there were no statistical differences between consecutive seasonal centers of activities by release origin, year, or sex.

DEMOGRAPHICS AND POPULATION GROWTH

Population Parameters

At the conclusion of fieldwork in 2006, I estimated the size of the GSMNP elk herd to be approximately 65 animals (31M:34F), 56 (27M:29F; Table 6) of which were radio-collared. Between 2001 and 2006, we investigated 60 potential calving events and

calves were successfully located within 1–5 weeks of birth on 41 (23M:17F) occasions, 30 of which were immediately radio-collared. The average sex ratio of calves radio-collared within their first year was 0.553 male (SE = 0.13) and the average mass of all calves within the first month of birth was 18 kg (SD = 3.4 kg). Three-year-old females had an average annual pregnancy rate of 0.72 ($n = 9$, SE = 0.26), whereas the rate for adult elk (>3 years) was 0.73 ($n = 45$, SE = 0.13). Calving periods ranged from May to August, with the most concentrated birth pulse occurring during the first 2 weeks of May in and around the grasslands of Cataloochee Valley.

I equipped 77 (36M:41F) adult and subadult elk with radio collars during this study. From 2001 to 2006, I documented 19 adult mortalities and 6 subadult mortalities (Table 7). None of those mortalities were attributed to predation, although many carcasses were fed upon by predators after death. The parasitic nematode, meningeal worm (*Parelaphostrongylus tenuis*), was judged responsible for approximately half (48%) of the documented mortalities. Eleven calf mortalities were documented quickly enough to determine cause of death. Of those 11 deaths, 7 calves were killed by black bears, 3 calves were killed by dogs or coyotes, and 1 died from pneumonia. Overall, the average annual survival rate for calves in GSMNP was 0.73 (95% CI = 0.55 to 0.91, range = 0.33 to 1.0).

Composite annual survival curves were almost identical for male and female elk in GSMNP ($\chi^2 = 0.005$, $P = 0.944$). When pooled across years, average annual survival was approximately 0.89 for both adult males (95% CI = 0.82 to 0.96) and adult female elk (95% CI = 0.83 to 0.95; Table 8). Among years, annual survival rates ranged from

0.82 to 1.0 and 0.56 to 1.0 for adult males and females, respectively (Table 9). I found no difference in survival rates between subadult males and females. Among years, annual survival rates ranged from 0.83 to 1.0 and 0.42 to 1.0 for subadult males and females, respectively and did not differ by sex ($\chi^2 = 0.33$, $P = 0.566$). Similarly, I did not detect a difference in survival between adult and subadult elk ($\chi^2 = 1.96$, $P = 0.162$). There was a difference in survival between female elk from LBL and EINP in their respective release years ($\bar{x} = 0.90$, 95% CI = 0.71 to 1.0 and $\bar{x} = 0.625$, 95% CI = 0.32 to 0.93, respectively; $\chi^2 = 40.32$, $P < 0.001$).

When deaths within the first year after an animal was released were censored, average annual survival rates increased for female elk ($\bar{x} = 0.90$, 95% CI = 0.77 to 1.0), but no difference was detected between sexes ($\chi^2 = 1.15$, $P = 0.284$). There were no deaths of males in their 1st year after release.

Population Growth

I performed population growth simulations using estimated demographic parameters (Table 8) and standing age distributions from 2002 and 2006 (Table 6). During 2002, all elk had been released, and each animal was collared, including all calves from 2001. Therefore, I used that distribution because it was the most accurate snapshot of the elk age distribution and should be more conservative than later distributions. There was only a 0.009 (SD = 0.001) chance of extinction under this scenario, and the average growth rate of the population over the 100 years was 1.03 (SD = 0.002). When I performed simulations with the 2006 age distribution there was a 0.019 (SD = 0.001) chance of extinction, and the average growth rate of the population over the next 100

years was 1.02 (SD = 0.002). Therefore, both age distributions produced similar population projections.

Given the small size of this population and the variability of the survival rates, it was necessary to evaluate the sensitivity of the population to changes in vital rates. Based on slight increases or decreases in average annual survival and reproductive inputs, the population growth rate and probability of extinction were most sensitive to changes in the reproductive rate of adult females. That parameter was closely followed by the survival rate of subadult females. Population growth had only slight responses to decreases in calf, subadult reproduction, and adult reproduction, and all 3 responses were similar. There was a 0.20 (SD = 0.011) chance of extinction and a population growth rate of 1.004 (SD = 0.002) when adult female survival was lowered from 0.889 to 0.845 (5%) and a 0.90 (SD = 0.020) chance of extinction and a population growth rate of 0.985 (SD = 0.003) when adult female survival was lowered to 0.800 (10%; Fig. 7).

When I performed simulations reducing subadult female survival from 0.889 to 0.845 and 0.800, there was a 0.12 (SD = 0.010) and 0.457 (SD = 0.032) chance of extinction, respectively. The average growth rate of the population over the next 100 years using these survival rates were 1.005 (SD = 0.008) and 0.994 (SD = 0.003), respectively.

ELK HABITAT

Habitat Use

I pooled annual home ranges and evaluated habitat use across all years to reach an adequate sample size for the compositional analysis ($n = 12$). Examination of the dataset

for 2nd-order selection indicated the distribution did not differ from normal ($W = 0.97$, $P = 0.2246$) and that selection occurred ($F_{5, 7} = 7.06$, $P = 0.0117$). Treeless habitat, primarily in the form of grasslands, ranked highest among the 6 available classifications (Table 10) although it accounted for <3% of available habitat in GSMNP. Elk showed a preference for that habitat type over all others considered.

The 3rd-order selection dataset was not normal ($W = 0.90$, $P = 0.0001$). Therefore, I used randomization tests, which indicated that selection occurred within home ranges ($F_{\text{val}} = 1.50$, $F_{\text{obs}} = 62.73$, $P < 0.0001$). Treeless habitats ranked highest and were used more than all other available habitat classes (Table 10). Human use/barren areas were selected more than other habitats, excluding treeless and scrub-shrub. Finally, deciduous habitat was used more than mixed habitat.

Second and 3rd-order selection was evident for all seasons except 2nd-order selection in autumn (Tables 11–14). Initial examination of the spring dataset for selection at the 2nd-order indicated that it was non-normally distributed ($W = 0.84$, $P < 0.0001$) and the randomization test indicated that selection was occurring ($F_{\text{val}} = 1.79$, $F_{\text{obs}} = 100.07$, $P = 0.0117$). The spring 3rd-order dataset did not differ from normal ($W = 0.96$, $P < 0.05$). The GLM test indicated that selection was occurring within home ranges ($F_{5, 6} = 7.76$, $P < 0.0135$). The summer dataset for selection at the 2nd-order was non-normally distributed ($W = 0.92$, $P < 0.0006$) and the randomization test indicated that selection was occurring ($F_{\text{val}} = 1.27$, $F_{\text{obs}} = 5.58$, $P = 0.018$). The summer 3rd order dataset also was non-normal ($W = 0.94$, $P < 0.003$). The overall randomization test indicated that selection was occurring within home ranges ($F_{\text{val}} = 1.42$, $F_{\text{obs}} = 10.47$, $P =$

0.002). The 2nd order analysis for autumn indicated that it was normally distributed ($W = 0.98$, $P < 0.69$) and the GLM test indicated that selection was not occurring ($F_{5,6} = 1.79$, $P = 0.22$). The autumn 3rd order dataset also was also normally distributed ($W = 0.96$, $P < 0.06$). The GLM test indicated that selection was occurring within home ranges ($F_{5,6} = 6.44$, $P < 0.02$). Lastly, the winter dataset for selection at the 2nd order was non-normally distributed ($W = 0.87$, $P < 0.0003$) and the randomization test indicated that selection was occurring ($F_{\text{val}} = 5.95$, $F_{\text{obs}} = 375.52$, $P = 0.002$). The winter 3rd order dataset also was non-normal ($W = 0.93$, $P < 0.01$). The overall randomization test indicated that selection was occurring within home ranges ($F_{\text{val}} = 2.72$, $F_{\text{obs}} = 64.08$, $P = 0.003$).

The 2nd-order seasonal analyses exhibited the same patterns as overall habitat use; treeless habitats were selected over all other habitat classes followed by the human use/barren class. The 3rd-order seasonal analyses showed that treeless areas were selected over all other habitat types. Human use/barren or scrub-shrub categories were also used more than deciduous, mixed, and evergreen habitats in every season.

Habitat Model

Only 6 variables remained in my habitat model after removing those that were highly correlated and including each of the remaining variables at only the scale, that showed the least variation among elk locations (Table 15). Overall correlation among the 6 landscape variables was low ($|r| < 0.47$). Although slope and PARA were highly correlated ($|r| = 0.72$), slope was kept in the model because it has been shown to be biologically important to elk (Unsworth et al. 1998, Skovlin et al. 2002). The principal components analysis indicated that the first 4 eigenvalues of the correlation matrix

explained 90% of the variation (Table 16). Each variable exhibited a strong relationship with at least one component, so I retained the 6 variables in the model.

Mahalanobis distance (D^2) values for the study area ranged from 0.80 to 139.07, whereas Mahalanobis distance values for individual elk locations ranged from 0.80 to 50.53 ($\bar{x} = 6.0$, $SE = 0.04$; Fig. 8). Ninety percent of the elk locations had D^2 values <15.0 , 75% of locations were characterized by values of <10.0 , and 50% of the locations had D^2 values <4 . A random sample of 21,176 D^2 values generated within the study area differed from the original elk locations ($D = 0.04$, $P < 0.01$), suggesting that elk habitat selection differed from random. The largest separation between the 2 cumulative frequency distributions occurred at a D^2 value of 8 and 73% of elk locations occurred at pixels with D^2 value ≤ 8 (Fig. 9).

VEGETATION ANALYSES

Microhistological Analysis

I performed fecal analyses for composite diets for all seasons from 2003 to 2005 ($n = 12$). The primary component of the elk diets were grasses, making up 66% of the ingested flora (Table 17). Forbs comprised 11% and a combination of sedges and rushes averaged 9% of the overall composite diets. Shrubs, conifers, ferns, and the other category each encompassed $\leq 5\%$ of fecal content.

Fecal nutrient contents were calculated seasonally from 2003 to 2005 (Table 18). The average percent oven dry matter was 91.5%. The average fecal nitrogen was 3.0%, whereas DAPA was 0.7%. The average fecal neutral detergent fiber was 62.3%.

Although there was slight variation among years, overall fecal nutrient levels were within normal ranges for elk.

Vegetation Analysis

Fifty-four sample plots were available for vegetation analysis; I removed 1 paired plot from the analysis because of inappropriate stratum classification. Normality assumptions were avoided by using ranked means, and in most cases, the assumption of equal variances was met. All comparisons were made between 2002 and 2005.

For south-facing slopes, overall abundance of seedlings did not change over time ($F_{1,6} = 1.86$ $P = 0.18$), but plant composition showed a change between years ($F_{3,42} = 2.31$ $P = 0.09$). When deciduous and evergreen tree and shrub seedling abundances were analyzed separately, there was an increase in deciduous tree and shrub seedlings in the treatment plot. The increased species consisted mainly of *Acer rubrum*, *Amelanchier arborea*, *Carpinus caroliniana*, and *Gaylussacia* spp.

There was an overall difference in abundance and composition of woody stems in acid coves over time ($F_{1,7} = 6.09$, $P = 0.02$, $F_{3,49} = 2.58$, $P = 0.06$, respectively). In general, there was a decrease in the deciduous woody stem abundance in the treatment and a gain in the control.

When the cove strata were combined differences in seedling abundance and composition were detected ($F_{1,9} = 7.17$, $P = 0.03$, $F_{2,96} = 2.46$, $P = 0.09$, respectively). There was a significant gain in total counts in the experimental plots but not in the control. Additionally, there was change in the plant composition between the

experimental and control plots. The treatment plots had an increase in deciduous tree seedling density that accounted for the change in abundance and composition.

The only difference detected for the treeless paired plots was in the abundance of grass. Mean grass counts differed overall between treatment and control over time ($F_{1, 17} = 4.88, P = 0.03$). The total amount of grass increased over time in both plots, and although not significant from the increase in the exclosures, the treatment had the greatest increase in 2005. However, total counts of species experienced relatively small changes, and the biological significance of this finding is relatively minor.

When all strata were combined, line intercept data reflected the overall herbaceous understory and had a negative trend across time. However, the large standard deviations obscured any significant effects.

HUMAN-ELK CONFLICT

There were 10 major instances of human-elk conflict during the first 6 years of the experimental reintroduction project. Those events required intervention by NPS personnel, which included public education, placement of animal deterrents, aversive conditioning, fence construction, elk removal, and euthanasia. Elk were using private pastures or grasslands outside of GSMNP in all cases of nuisance activity. However, 7 of those events occurred in 1 localized area. Of the 10 instances, 5 involved cattle and 3 involved damage to vegetation or agricultural crops. During this study, I documented only 1 vehicle collision. It resulted in the death of a female elk; no human injuries occurred.

CHAPTER V: DISCUSSION

TELEMETRY

Because erroneous conclusions can occur when locations have a lower probability of collection in certain habitats, I developed a linear regression to model the potential GPS bias associated with diminished fix-rate success. The linear regression model developed from test GPS collars explained only approximately 3% of missing locations. Therefore, a 1–3% adjustment was insufficient to justify altering the telemetry dataset. Regardless, the 3rd- and 2nd- order habitat analyses produced similar results, with the latter analysis (home range placement on the landscape) being relatively robust to a habitat-influenced acquisition bias. Because of those similar results, the large dataset, and >50% of locations were collected in forested areas, my conclusions that grasslands were preferred are probably realistic. Nevertheless, the test collar data apparently did not represent the bias of GPS collars on elk because the difference in acquisition rates between animal (61%; SE = 4.5) and test collars (92%; SE = 1.0) was substantial. The fixed collars may have had a higher acquisition rate because they were stationary. Animal behavior may also play a role in the ability of a GPS collars to acquire fixes (D'Eon et al. 2002). In general, GPS collars placed on free-ranging wildlife experienced lower fix-success rates than stationary collars, with the discrepancies attributed primarily to changes in GPS antenna orientation caused by various animal behaviors (i.e., feeding and bedding; Sager 2006). In Mississippi, Bowman et al. (2000) found the ability of GPS collars to collect locations was affected by the behavior of white-tailed deer (*Odocoileus virginianus*). That study concluded that collars on moving deer acquired the greatest

number of fixes with the lowest positional error, whereas collars on bedded deer obtained the least number of fixes. The same pattern of lowered fix-rate success has been documented by GPS collars on bedded moose (*Alces alces*; Moen et al. 1996).

HOME RANGES AND MOVEMENTS

Spatial characteristics of elk typically reflect complex trade-offs associated with foraging behaviors, group dynamics, predator avoidance, and thermal regulation (Anderson et al. 2005). Furthermore, body size, sex, and age are known to influence the area over which elk range. I expected to see distinct differences in male, female, and seasonal home ranges. However, the number of animals available for analysis was low. Whereas individual home ranges were thoroughly represented by large datasets, variability among individuals produced large standard deviations. For example, there were 2 females that displayed large annual home ranges (44 and 30 km²) whereas 2 males had small annual home ranges (1 and 2 km²). My dataset reflects the potential variability and individuality displayed within an elk population; the variability was likely increased because this was an introduced herd originating from different geographic sources.

Numerous home-range estimates for North American elk have been published in the literature (Craighead et al. 1973, Hershey and Leege 1982, Jenkins and Starkey 1982, Irwin and Peek 1983, Edge et al. 1985). However, limitations in GIS technology prevented many older studies from using the fixed kernel method. Furthermore, research on elk inhabiting eastern deciduous forests has been minimal. Minimum Convex Polygon home ranges for elk within the western United States varied from 1 km² in coastal Oregon to 90 km² on the Olympic Peninsula, Washington (Schroer 1987). During

my study, home-range size varied from 1 to 53 km² (95% fixed kernel). Larger home ranges were typically characteristic of dominant, reproducing males or older EINP females in their first year of release. Dominant males usually roamed further in search of reproducing females. Also, EINP elk were less accustomed to human activity, which was common in Cataloochee Valley, possibly resulting in greater movement.

Annual home ranges were relatively small in GSMNP, but were within ranges reported from other elk populations (Franklin et al. 1975, Witmer and deCalesta 1985, Pope 1994, Millspaugh 1995, Cole et al. 1997). For example, Storlie (2006) reported an average annual 95% fixed kernel home range estimate of female Roosevelt elk of 43 km², whereas average female home range in GSMNP was only 10 km². In comparison to western herds, elk in GSMNP did not migrate and this likely contributed to the small home ranges. Although home-range dynamics of elk are influenced by the ability to traverse different habitat types (Craighead et al. 1973, Anderson and Rongstad 1989) and movements related to breeding and parturition (Craighead et al. 1973), variation in resource distribution seemed to be the main determinant of size and placement of home ranges in GSMNP. Because treeless habitat accounted for <3% of all available habitat in GSMNP, and most of the home ranges centered on the grasslands in Cataloochee Valley, the preference for open habitat and grass forage and the lack of migration explain the small home ranges of elk.

Elk typically exhibit seasonal shifts in home ranges coinciding with the breeding season. During autumn, home ranges increase as males seek out females to breed and herding males influence the movements of female (Geist 2002). GSMNP elk displayed

that behavior as autumn home ranges typically tripled in size. Elk researchers in the western U.S. do not usually report seasonal home ranges because of migration patterns of western elk. However, Bauman et al. (1999) and Millspaugh et al. (2004) in South Dakota reported seasonal male and female 95% kernel home range size ranging from 20 to 50 km². Across all seasons, I documented seasonal home ranges from 0.4 to 76 km². There was large variation with several outliers, but the general pattern appeared to be initial exploratory movements and then a settling into a pattern of small home ranges that expand during autumn. For example, the largest seasonal home range documented was 76 km² for an autumn range of a newly released EINP female elk, but her home range was only 2 km² that following winter. On the other hand, 2 female elk and 2 subdominant male elk from LBL consistently exhibited small home ranges, regardless of season. Those elk restricted their movements almost exclusively to Cataloochee Valley.

Regardless of the seasonal shift in size, my study documented some of the smallest seasonal home ranges reported in the literature. Collectively, I speculate this was a result of small population size, the soft-release technique, limited grazing area, and the natural history of the LBL elk and their rapid acclimation to Park visitors. Elk have a remarkable ability to adapt to human disturbance (Craighead et al. 1973, Yerex 1979). That adaptability allowed elk to settle in the Cataloochee Valley, despite increased rates of visitation by Park visitors.

When assessing the long-term persistence of a small translocated population, every individual may be vital. Translocated elk are known to make long-distance movements in efforts to return to source areas (Anderson 1958). Therefore, release site

location, site fidelity, and the extent of post-release movements by elk were critical. Elk movements are affected by topography and often move parallel to major drainages or streambeds (Kie et al. 2005). Whereas daily distances traveled during the 2-week time period post-release was greater when compared to subsequent years, the net distance traveled usually shortened, likely reflecting initial elk exploration movements and eventual establishment into the area. Elk originating from EINP typically exhibited statistically larger initial movements than LBL elk. That was consistent with my expectations because EINP elk came from a much larger facility and were unaccustomed to human activity. Travel rates between the 2 release groups seemed to stabilize in the 6 months after release but net distance traveled by EINP elk remained more than twice that of elk from LBL. However, 2004 movements for all 3 time periods were similar between EINP and LBL elk. Therefore, as time progressed and elk became established, all elk settled into the area and extensive dispersal movements lessened in occurrence. This was supported by the difference between 2001 and 2002 LBL elk movements and the 2002 LBL versus 2004 movements. Increasing site fidelity among elk was further supported by the linearity and site fidelity analyses. Across all 3 time periods and years, both release groups showed decreasing linearity and increased site fidelity, ultimately stabilizing in 2004. Elk did not show homing behavior or extensive movements, such as those documented by Allred (1950) and Anderson (1958), likely because of the source herds' natural history, existing herd cohesiveness, the long distance of relocation, and the restricted area of grasslands in GSMNP. The soft-release technique and funneling of elk into the grasslands was probably a crucial element in limiting exploratory movements.

Although statistical power was limited, seasonal analyses showed progressively smaller distances from centers of activity between years and from season to season. I believe this reflected the acclimation of elk to the area and the higher site fidelity to the grasslands in Cataloochee Valley in autumn and winter (Smith and Robbins 1994). As I stated previously, this herd did not show shifts in seasonal movement as a result of migration but did exhibit typical behavior of elk by habitually using the same travel routes within the study area (Allred 1950, Herner-Thogmartin 1999). GSMNP has mild weather compared with the western U.S., so the need to migrate along elevational gradient was limited. Although, elk have been in GSMNP a limited amount of time and may not yet have established distant areas for feeding, previously introduced elk in the eastern U.S. have not shown migratory movements either (Moran 1973). I documented other movement patterns typical of elk in western states, however, such as female movements during the calving season and dispersal among young males.

DEMOGRAPHICS AND POPULATION GROWTH

Primiparity in elk is strongly correlated with body mass and condition (Hudson et al. 1991) and pregnancy rates reported in the literature are highly variable (48–100%), depending on the condition of the mature cow elk 5 to 8 months before breeding (Hudson et al. 1991, Stussy 1993, Kohlmann 1999). Reintroduced elk populations in the eastern U.S. have shown moderate to high litter production rates (40–92%), depending on winter severity, predator density, and time since release (Cogan 1996, Larkin et al. 2003). During my study, litter production rates for 3-year-old and 4+ year-old elk were similar to those observed in the Pennsylvania (Cogan 1996) but lower than in Kentucky herd

(Larkin et al. 2003). There was one instance of a possible 2-year-old female being pregnant in GSMNP but that was never confirmed. I also documented instances of individual females losing calves to predators, and successfully rearing newborns in subsequent years by moving to calving grounds outside of Cataloochee Valley. Both herds originated from areas with no significant calf predators, and over time, the reproducing females may be more adept at avoiding calf predation.

Adult and subadult survival estimates for radiocollared elk in my study (0.89–0.93) were similar to other unhunted elk herds (Unsworth et al. 1993, Stussy et al. 1994, Eberhardt et al. 1996, Ballard et al. 2000, Larkin et al. 2003). However, results from my population model indicated that, given the small population size, the death of even a single elk significantly impacted annual survival rates. For example, 4 adult female deaths in 2002 lowered mean adult female survival that year from 0.90 to 0.56 (SE = 0.03) and 2 subadult female deaths in 2004 lowered subadult female survival from 1.0 to 0.42 (SE = 0.32). Conversely, survival rates in 2005 and 2006 were high with only 1 female death in 2005, 1 subadult male death in 2005, 2 male deaths in 2005, and 1 male death in 2006.

Survival of juvenile elk in the 1st summer and autumn is a complex interaction between maternal condition, predator abundance, time of birth, and birth weight (Clutton-Brock et al. 1982). In the GSMNP elk herd, calf weights and sex ratio were consistent with those from other free-ranging elk populations (Singer and Harting 1997, Smith and Anderson 1998). Elk mortality within the first 2 days after birth can range up to 40% (Rearden et al. 2005). Unfortunately, that survival percentage is difficult to determine

given the challenges in locating calves during that period. Survival of captured and radio-collared calves in GSMNP was relatively low but within the range documented for elk (Thorne et al. 1976, Oldemeyer et al. 1990). GSMNP officials initiated short-term predator management in 2006 as a response to limited calving habitat, high calf predation by black bears in 2005, and the cancellation of the 3rd release of elk. Fourteen black bears were captured and translocated from Cataloochee Valley to other areas of GSMNP during the concentrated calving season of 2006. Calf survival increased from 33% (SE = 0.06) to 85% (0.04) but it is not known whether the relationship is causal.

The largest source of mortality for subadult and adult elk was from cerebrospinal encephalitis related to meningeal worm; of the documented mortality experienced by this elk herd, 12 of 25 were due to cerebrospinal encephalitis. Although it has been hypothesized that meningeal worm limits elk populations in areas where elk are conspecific with white-tailed deer, it is the degree of exposure, age of elk, individual and population experience with meningeal worm, and environmental moisture level which effects the gastropod populations. All of those influence the potential severity of this parasite (Bender et al. 2005). However, elk have been successfully reintroduced to areas with sympatric high-density white-tailed deer populations (Bender et al. 2005). White-tailed deer in GSMNP are known to be a frequent host of meningeal worm, which do not seem to affect deer but are pathogenic to elk and other cervids (Anderson and Prestwood 1981). Although meningeal worm accounted for approximately half of the documented mortalities, its impacts on the elk herd in GSMNP were small. However, the deaths attributed to meningeal worm seemed mainly confined to subadults. This is a typical

characteristic of meningeal worm infections (Larkin et al. 2003, Alexy 2004) and can result in a population that is biased towards older age classes. Conversely, calf survival was high in 2006 creating the largest subadult cohort to date; however, my sample sizes were too small to draw any conclusions regarding the long-term impact of meningeal worm on the subadult age class.

Population modeling indicates the GSMNP elk population should persist, but the GSMNP elk herd is small and slight changes in adult survival have been documented to have dramatic effects on the rate of increase in elk populations (Nelson and Peek 1982). For the GSMNP herd, the effect of small changes in fecundity and survival was illustrated in the dramatically increased probabilities of extinction projected by the population models. However, such small changes in demographic parameters are difficult to detect as they are occurring, and management options are limited with small populations, except raising the population size above a critical threshold with additional releases of elk.

Nelson and Peek (1982) reported that survival rates in elk had a greater impact on rates of increase than fecundity rates. In GSMNP, extinction and growth rates of the population model were mostly impacted by changes in adult female survival. When adult female survival was reduced by 5%, a starting population size of approximately 90 animals was required prevent the extinction rate from exceeding 10% in 100 years. Whereas given a 10% reduction in adult female survival, a population size of 325 animals was required. The 5% and 10% reduction in adult female survival could be achieved with the deaths of only 4 and 9 females, respectively. Thus, managers must keep in mind

the small size of this population and the variability of the survival and reproductive rates. Elk density-independent mortality factors, such as moisture level effects on meningeal worm, operate at random. Therefore, 2 consecutive years of high elk mortality due to meningeal worm could have dramatic effects on the viability of the population.

ELK HABITAT

Given the large telemetry dataset ($n = 24,622$), the percentage of elk tracked (23%), and the time period covered ($n = 4$ years), the delineation of my study area provided a good estimate of habitats available to elk. Thus, the likelihood of bias toward preferred habitats because of a large study area was reduced (Clark 1991). Although previous studies showed that bull and cow elk use habitats differently (Clutton-Brock et al. 1982, Unsworth et al. 1998, Geist 2002), I pooled all home ranges and evaluated habitat use across all years. This increased the sample size but may have reduced precision of estimates of habitat selection due to an increase in variation.

Whereas elk often make use of all available habitats (Irwin and Peek 1983, Skovlin et al. 2002), they typically select open grazing habitat (Jenkins and Wright 1988, Suter et al. 2004). Elk selected treeless areas during my study, both annually and seasonally, but only 1–3% of GSMNP consists of such openings. Minimum elk habitat was thought to be comprised of 15–20% forest openings (Rob Kay, Elk Island National Park, personal communication), so the lack of sufficient forest openings was initially considered a potential problem associated with repatriating elk to GSMNP. Elk habitat guidelines recommend approximately 60% foraging area and a 40% mix of thermal and security cover as an optimal configuration (Peek et al. 1982, Hillis et al. 1991,

Christensen et al. 1993, Cook and Irwin 1998). Although open grassland areas in GSMNP are well below those guidelines, at the current population level, open habitat seem to be adequate. As the population grows, however, this limited area will likely force elk to disperse outside of the Park onto adjacent private property.

The second ranked habitat for elk in GSMNP was typically the human/urban land-cover type, which often is associated with increased human activity. Human/urban areas (e.g., roadways, homesites) in GSMNP typically were adjacent to treeless areas. So the apparent selection for human/barren areas may be associated with the selection for treeless cover types. However, elk can be attracted to roadsides along secondary roads where thinning or mowing improves the abundance and quality of available forage (Cooper and Millspaugh 1999). Likewise, a similar relationship seemed to exist with scrub/shrub habitat in GSMNP. Consequently, use of among human/urban and scrub/shrub habitats in GSMNP may be a result of the strong preference for grasslands.

Seasonally, elk tend to alter habitat use to meet different physiological, biological, and behavioral requirements (Irwin and Peek 1983, Edge et al. 1987, Skovlin et al. 2002). Although I documented slight shifts in habitat selection of elk in GSMNP, there were no major differences in seasonal use. Given the mild summer and winter weather, elk generalist feeding habits, and small population size, this seems reasonable.

Elk use of balds or spruce-fir forests was limited. The nearest bald to the release site was on the Park boundary and 3 elk used that area for short periods of time throughout the project. Balds make up a very small part of the study area and sufficient low-elevation grazing areas likely did not necessitate their use. Furthermore, many small

balds in GSMNP are succeeding to forest cover, reducing their value to elk. At the current population level, elk likely would not be able to re-establish balds or assist in their maintenance. Spruce-fir forests contain substantial herbaceous vegetation that could provide quality forage for elk. However, these areas are highly degraded by the Balsam Woolly adelgid (*Adelges piceae*), and increased use by elk would warrant more monitoring of this already damaged plant community. As populations increase, there may be more pressure for elk to use spruce-fir forests and balds.

Data availability and quality are considered the primary limiting factors of GIS-based models (Corsi et al. 2000). The effect of misclassification errors in my spatial data were reduced because landscape measures mainly represented larger areas (0.2 km^2 – 36 km^2) rather than actual pixel values (Didier and Porter 1999). Essentially, the reclassification at a larger window size filtered out potential misclassifications. Additionally, reclassification of land-cover data into more general categories further reduced effects of misclassification error. Thus, the habitat model likely was not sensitive to error associated with elk locations or GIS source data.

As opposed to creating multiple models at each scale of interest (Ritters et al. 1997), I created a model that incorporated multiple scales (Telesco et al. 2007). The final model consisted of 3 scales representing local movements (0.2 km^2), core male home ranges (4 km^2), and largest seasonal home ranges (36 km^2). Therefore, habitat selection by elk was presumably influenced by environmental conditions at different scales.

Elk are generalists which can be more difficult to model than specialists (Boetsch et al. 2002). Of the 6 variables included in my model, fractal dimensions, contagion, and

patch richness were the least variable and seemed to be influential. At a finer scale (4 km²), elk used areas that were a matrix of moderately fragmented forest and field habitats. The Fractal dimensions parameter indicated at this fine scale, elk selected a moderately complex landscape. Contagion of forests and fields, which is inversely related to edge density, was important at the largest scale (36 km²). Elk seemed to be selecting areas with a moderate forest-field edge density but such areas are limited in GSMNP. Patch richness, considered a simple measure of landscape composition, was calculated using the 5 major habitat types in GSMNP. Elk selected areas that had a high number of habitats in the moderate window size (1,128 m), reflecting their preference for availability of multiple habitat types within a relatively small area. These interpretations of each individual variable may change somewhat when all parameters are considered together, as additional multivariate relationships likely exist.

The comparison of cumulative frequency distributions of elk and random locations indicated the model identified site characteristics associated with elk presence. There was separation between the cumulative frequency distributions, which indicated elk were selecting a different range of habitat characteristics from what was generally available in the landscape. Because different combinations of habitat conditions can produce equivalent D^2 values, it is difficult to interpret which variable contributed most to habitat suitability. In addition, the model has a continuous range of values so that no clear delineation exists between suitable and unsuitable habitat. However, the cumulative frequency distributions indicate that choosing a general D^2 cutoff value ≤ 8 best separates elk habitat from habitat available within the study area.

The results of my study indicate that habitats selected by elk were associated with areas of moderate landscape complexity at a fine and coarse scales, moderate area of edge habitat, gentle slopes ($<10^\circ$), and high patch richness. This was logical because elk are often associated with patches of interspersed habitat, which provide direct access to forage and cover (Wisdom et al. 1986) and greater selection and quantity of forage (Skovlin et al. 2002). Human disturbance was not considered in this model, and areas of elk use were often associated with human disturbance. Elk interact with a large number of annual visitors to Cataloochee Valley, all of which have been non-threatening, and such habituation can be an advantage to elk in winter (Thompson and Henderson 1999). However, elk habituation to human activity may increase the potential for elk-human conflict, especially in areas outside of GSMNP. My habitat model is not applicable to areas outside of the general study area because of the great contrast in habitat types and land uses.

VEGETATION ANALYSES

Forage availability and nutritional quality impact elk survival and reproduction (Cook 2002, Skovlin et al. 2002). Likewise, plant communities and topographic land features influence selection of foraging areas. Numerous researchers have evaluated the food habits of elk and other large ungulates (e.g., Kufeld 1973, Cook 2002, Sandoval et al. 2005) and have shown large variation by year of study, location, species, and research techniques. Edgerton and Smith (1971) found that elk and mule deer diets consisted of 58% grasses and sedges, 27% forbs, and 15% shrubs during summer. Korfhage et al. (1980) and Leckenby (1984) found that elk diets in the Blue Mountains of northeastern

Oregon were evenly balanced among all major vegetative components. In GSMNP, fecal analyses were typical of many western elk herd diets with the primary component being graminoids (Kingery et al. 1996). The analyzed elk diets consisted of $\leq 5\%$ plant material from deciduous or evergreen browse. Although GSMNP is primarily forest, elk are not utilizing forest areas as a major food source at the current population level. My results indicate that elk in this eastern deciduous forest prefer open grazing land with interspersed cover.

Average fecal NDF was relatively consistent across seasons, indicating there was no season in which food intake changed substantially. Presumptively, elk would have increased forage intake if they were not receiving enough quality nutrients. Composite FN was highest in spring and summer when there was an abundance of new green plant growth; it declined steadily as the summer progressed and forage became senescent with higher lignin content and lower digestibility. The seasonal decline (range = 1.91–4.50) suggested that FN was a sensitive indicator of diet quality, because as lignin content increases, diet quality decreases. These values were within the ranges reported in the literature (Leslie and Starkley 1987, Schoenecker et al. 2004, Walter 2006). To a lesser degree, I observed this same pattern in the DAPA measurements, but FN appeared to better track the changes in diet quality.

I detected little change in the vegetation biomass and composition on my study area that could be attributed to elk. These findings were probably because the elk herd was relatively small and had a low impact on vegetation. Also, my statistical tests likely had low power due to high variability associated with vegetation sampling.

Elk exhibited limited use of ridge tops, and I documented no impacts on ridge vegetation. South-facing slopes had an overall decrease in understory vegetation in both plots and an increase in deciduous seedling in the experimental plots.

Coves were heavily used by this small population of elk. I detected no change in rich coves, but woody stems decreased in acid coves in the experimental plot, particularly deciduous species. Given the recruitment of deciduous woody stems and seedlings seen in other landform classes, this may represent a significant impact from elk. When cove strata were combined, the treatment plots had slightly more seedlings than the control, but the woody stem decrease was not detected.

In the grassland plots, no changes were detected that could be attributed to elk. At low densities, elk likely have limited impacts on grass abundance. However, net aboveground primary plant production can increase with low to moderate levels of elk grazing by compensatory plant growth (Stewart et al. 2006). Conversely, Lacey and Van Poolen (1981), in a review of field studies in the western United States, concluded that net primary production on grazed areas averaged 68% lower than that on protected areas. Plants may only be able to tolerate certain levels of herbivory. The amount and frequency of plant tissue removed influences a plant's ability to recuperate. At low to moderate population densities, elk may facilitate increased plant growth. However, at high densities, plants may be repeatedly grazed, allowing little opportunity for tissues to recover and produce new growth (Webster et al. 2005). As the elk population increases in size, however, those effects of elk on vegetation communities would need to be reevaluated.

CHAPTER VI: MANAGEMENT IMPLICATIONS

When considering a permanent elk herd in GSMNP, managers must consider their biological needs and elk-human conflict issues (Witmer 1990, Lyon and Christensen 2002, Larkin et al 2004). Until this experiment was completed, Park officials were unsure what habitat requirements, disease issues, and public response would be with a reintroduction of elk. During the 6 years since the initial release, elk primarily remained within the general release area, no major diseases of concern have been detected in the herd, and the small population shows positive growth despite the presence of meningeal worm. Additionally, there have been relatively few human-elk conflicts, although addressing elk nuisance complaints required extensive commitments of time and money. The release technique was successful and probably limited elk movements.

An additional release of 25 elk was planned for 2003 but was not possible because of concerns regarding chronic wasting disease. Demographic estimates would have been more precise had more animals been released and the population likely would have been more resilient to stochastic events. This population should be viable but could change if there is any catastrophe or multiple years of high mortality occur. The addition of more female elk to this herd would greatly increase the probability of population persistence. Based on available habitat and current vital rates, there is a good chance that this population will be at low levels and have a significant risk of extinction for many years.

Meningeal worm was the main cause of mortality for subadults and adults whereas black bear predation was the main cause of calf mortality. Although a healthy predator population could potentially keep growth of a large population of elk in check, growth of

the small reintroduced elk population was negatively affected by bear predation. Calf survival increased concurrently with the predator management initiated by GSMNP biologists, and continued bear management during the calving season maybe warranted in the short term.

The current population of elk in GSMNP has minimal impacts on the vegetation. As the population increases in size, this impact would need to be reevaluated. For this reason, I suggest maintaining a subset of the vegetation exclosures for future evaluations.

It seems feasible to maintain a small population of elk in GSMNP. However, population abundance of elk will be severely limited because of a lack of forest openings. Managers of most elk programs indicated that grasslands were important and that they must be maintained by mowing, burning, or disking. Suitable openings in GSMNP only were found at high elevation grassy balds, Cades Cove, and Cataloochee Valley. Those areas represent a small portion of the total land area of GSMNP. Elk extensively used Cataloochee Valley, and maintenance and expansion of open areas would be essential if a larger elk population is desired. It would be beneficial to create or maintain other areas for elk in the eastern portion of GSMNP; this could be accomplished by manually reopening selected areas or frequent burning at high intensity to promote major opening of the forest canopy.

The probability of establishing a permanent elk population in GSMNP is relatively high, if current management continues until the population becomes more established. That management includes monitoring elk survival, prevention of predation on calves during the calving season, rotational burning in and around Cataloochee Valley to

maintain and create openings, and responding to human-elk conflicts. Long-term viability of the GSMNP elk herd will be reliant on the maintenance and expansion of open grasslands and the forest-grassland ecotone.

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APPENDIX A: TABLES

Table 1. Land-cover types of the 1992 National Land Cover Data (NLCD) and classifications for generating land cover variables for the elk habitat analysis and model calculated for Great Smoky Mountains National Park, North Carolina, 2001–2006.

NLCD cover type	Forage/cover classification	Natural types classification
Open water	Other	Other
Low intensity residential	Other	Human/barren
High intensity residential	Other	Human/barren
Commercial/industrial/transportation	Other	Human/barren
Bare rock/sand/clay	Other	Human/barren
Deciduous forest	Forest	Deciduous forest
Evergreen forest	Forest	Evergreen forest
Mixed forest	Forest	Mixed forest
Shrubland	Forest	Shrub/scrub
Grasslands/herbaceous	Field	Treeless
Pasture/hay	Field	Treeless
Row crops	Other	Human/barren
Woody wetlands	Other	Treeless
Emergent herbaceous wetlands	Other	Treeless

Table 2. Measures used to calculate landscape-scale variables for characterizing elk habitat in Great Smoky Mountains National Park, North Carolina, 2001–2006.

Measure ^a	Calculation	Units	Range
Simpson's diversity	$SIDI = 1 - \sum_{i=1}^m P_i^2$		
Probability that any 2 pixels selected at random would be different patch types	P_i = proportion of the landscape occupied by class i m = number of classes present in the landscape	none	$0 \leq SIDI < 1$
Patch richness	$PR = m$		
Number of patch types in the landscape	m = number of type of patches in the landscape	none	$PR \geq 1$, without limit
Edge density	$ED = \frac{\sum_{k=1}^m e_{ik}}{A} (10,000)$		
Edge density of a given cover class	e_{ik} = total length of edge in landscape involving class i A = total landscape area	m/ha	$ED \geq 0$, without limit

Table 2. Continued.

Measure ^a	Calculation	Units	Range
Perimeter-area ratio, area-weighted mean A measure of shape complexity equal to the ratio of the patch perimeter to area	$PARA = \sum_{j=1}^n \left[\frac{P_{ij}}{\sum_{j=1}^n a_{ij}} \right]$ $P_{ij} = \text{perimeter of patch } ij$ $a_{ij} = \text{area of patch } ij$	none	$PARA > 0$
Fractal dimension index, area-weighted mean A scale independent measure of shape complexity	$FRAC = \sum_{j=1}^n \left[\frac{2 \ln(0.25 p_{ij})}{\ln a_{ij}} \left(\frac{a_{ij}}{\sum_{j=1}^n a_{ij}} \right) \right]$ $p_{ij} = \text{perimeter of patch } ij$ $a_{ij} = \text{area of patch } ij$	none	$1 \leq FRAC \leq 2,$

Table 2. Continued.

Measure ^a	Calculation	Units	Range
Contagion	$CONTAG = \left[1 + \frac{\sum_{i=1}^m \sum_{k=1}^m \left[P_i \left(\frac{g_{ik}}{\sum_{k=1}^m g_{ik}} \right) \right] \ln P_i \left(\frac{g_{ik}}{\sum_{k=1}^m g_{ik}} \right)}{2 \ln(m)} \right] (100)$	%	$0 < CONTAG \leq 100$
The observed contagion over the maximum possible contagion for a given number of patch types	P_i = proportion of the landscape occupied by class i g_{ik} = number of adjacencies between pixels of classes i and k m = number of classes present in the landscape		
^a All measures are from McGarigal et al. (2002). Refer to McGarigal et al. (2002) for more detailed explanations of the calculations, uses, and limitations for these measures.			

Table 3. Stratified sampling scheme for paired plots used in monitoring vegetation for elk use in Great Smoky Mountains National Park, North Carolina, 2001–2006.

Landform	Exclosures	Stratified random locations
North ridges	5	Landform and aspect
South ridges	5	Landform and aspect
North slopes	9	Landform and aspect
South slopes	7	Landform and aspect
Rich coves	10	Landform and geology
Acid coves	8	Landform and geology
Treeless	10	National Park Service opinion

Table 4. Annual home range sizes (km²) and standard error (SE) for male and female elk in Great Smoky Mountains National Park, North Carolina, 2001–2004.

	Female		Male	
	$\bar{x}$	SE	$\bar{x}$	SE
Spring	2.9	0.9	6.9	3.5
Summer	4.4	1.9	5.5	4.2
Autumn	15.8	12.0	35.0	10.7
Winter	2.1	0.2	2.0	0.4

Table 5. Movements (m), linearity [means and standard error (SE)], and site fidelity calculated for elk in Great Smoky Mountains National Park, North Carolina, 2001–2004.

	Movement Parameter							
	Average within daily movement		Average between daily movement		Net	Linearity		Site fidelity (<i>n</i>)
	Mean	SE	Mean	SE		Mean	SE	
2001 L ^a 2 weeks	98	24	190	57	1,787	0.24	0.065	R ^b (4)
2001 L 3 months	420	21	644	59	4,316	0.07	0.003	C ^c (3) R (1)
2001 L 6 months	368	21	553	44	4,844	0.06	0.005	C (3) R (1)
2002 L 2 weeks	315	38	489	100	877	0.03	0.014	C (5)
2002 L 3 months	430	39	677	74	3,956	0.03	0.013	C (4) R (1)
2002 L 6 months	386	26	606	50	3,405	0.05	0.002	C (4) R(1)
2002 E ^d 2 weeks	206	27	485	66	2,646	0.03	0.005	R (2) D ^e (1)
2002 E 3 months	303	25	636	68	10,974	0.39	0.024	R (3)
2002 E 6 months	344	33	732	87	8,963	0.06	0.003	R (2) C (1)
2004 2 weeks	221	26	645	109	726	0.10	0.004	C (3) R (1)
2004 3 months	306	28	736	93	2,476	0.06	0.020	C (4)
2004 6 months	315	27	736	81	8,820	0.01	0.002	C (4)

^aElk released in 2001 from Land between the Lakes National Recreational Area

^bRandom movements

^cConstrained movements

^dElk released in 2002 from Elk Island National Park

^eDispersed movements

Table 6. Sex and age distribution of radio-collared elk in Great Smoky Mountain National Park, North Carolina, 2002 and 2006.

2002	Female	Male
Calf	3	3
Yearling	2	2
2	2	2
3	0	5
4+	21	16
Total	28	28
2006	Female	Male
Calf	5	5
Yearling	2	0
2	1	2
3	1	5
4+	20	15
Total	29	27

Table 7. Sub-adult and adult elk mortalities in Great Smoky Mountains National Park, North Carolina, 2001–2006.

Age Class	Mortality					
	Parasitic disease	Stress	Vehicle collision	Nuisance	Capture related	Unknown
Sub-adult males	2	0	0	0	0	1
Sub-adult females	3	0	0	0	0	0
Adult males	3	0	0	2	0	3
Adult females	4	3	1	1	1	1
Total	12	3	1	3	1	5

Table 8. Survival rates and reproductive rates calculated for elk for population modeling in Great Smoky Mountains National Park, North Carolina, 2001–2006.

Parameter	Status (process standard error)
Simulation years	100
Simulations	1000
Calf survival	0.733 (0.19)
Subadult female survival	0.889 (0.13)
Adult female survival	0.889 (0.14)
Subadult male survival	0.927 (0.06)
Adult male survival	0.891 (0.06)
Litter production	3 years of age: 0.722 (0.264) 4+ years of age: 0.734 (0.131)
Calf sex ratio	0.553 (0.13)

Table 9. Yearly survival rates of elk in Great Smoky Mountains National Park, North Carolina, 2001–2006.

	Annual Survival Rates									
	Sub-adult female		Adult female		Sub-adult male		Adult male		Calves	
	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE
2001	1.00	0.00	0.90	0.04	1.00	0.00	1.00	0.00	0.80	0.07
2002	0.92	0.03	0.56	0.04	1.00	0.00	1.00	0.00	0.75	0.09
2003	1.00	0.00	0.89	0.03	0.93	0.04	0.88	0.03	0.80	0.05
2004	0.42	0.13	0.86	0.03	0.83	0.06	0.82	0.03	1.00	0.00
2005	1.00	0.00	0.95	0.02	0.83	0.05	0.88	0.03	0.33	0.06
2006	1.00	0.00	1.00	0.00	1.00	0.00	0.93	0.03	0.85	0.04

Table 10. Ranking matrices for annual resource selection by elk at the second- and third-order selection scale (placement of home range within the study area and resource use within the home range, respectively), Cataloochee study area, Great Smoky Mountains National Park, North Carolina, 2001–2006.

Second-order selection							Rank
Vegetation association	Treeless	Human	Evergreen	Deciduous	Scrub/Shrub	Mixed	
Treeless		+++ ^a	+++	+++	+++	+++	1
Human	---		+ ^b	+	+	+	2
Evergreen	---	-		+	+	+	3
Deciduous	---	-	-		+	+	4
Scrub/shrub	---	-	-	-		+	5
Mixed	---	-	-	-	-		6

Third-order selection							Rank
Vegetation association	Treeless	Human	Scrub/Shrub	Deciduous	Evergreen	Mixed	
Treeless		+++ ^a	+++	+++	+++	+++	1
Human/barren	---		+ ^b	+++	+++	+++	2
Scrub/shrub	---	-		+	+	+	3
Deciduous	---	---	-		+	+++	4
Evergreen	---	---	-	-		+	5
Mixed	---	---	-	---	-		6

^a A triple sign indicates significant deviation from random at $P \leq 0.05$.

^b A single sign indicates a relationship that was not statistically significant at $P \leq 0.05$.

Table 11. Ranking matrices for spring resource selection by elk at the second- and third-order selection scale (placement of home range within the study area and resource use within the home range, respectively), Cataloochee study area, Great Smoky Mountains National Park, North Carolina, 2001–2006.

Vegetation association	Second-order selection						Rank
	Treeless	Human	Deciduous	Evergreen	Scrub/Shrub	Mixed	
Treeless		+++ ^a	+++	+++	+++	+++	1
Human	---		+ ^b	+	+++	+	2
Deciduous	---	-		+	+++	+	3
Evergreen	---	-	-		+	+	4
Scrub/shrub	---	-	---	-		+	5
Mixed	---	-	-	-	-		6

Vegetation association	Third-order selection						Rank
	Treeless	Human	Scrub/Shrub	Evergreen	Deciduous	Mixed	
Treeless		+++ ^a	+++	+++	+++	+++	1
Human	---		+ ^b	+	+++	+++	2
Scrub-Shrub	---	-		+	+++	+++	3
Evergreen	---	-	-		+++	+	4
Deciduous	---	---	---	---		+	5
Mixed	---	---	---	-	-		6

^a A single sign indicates a relationship that was not statistically significant at $P \leq 0.05$.

^b A triple sign indicates significant deviation from random at $P \leq 0.05$.

Table 12. Ranking matrices for summer resource selection by elk at the second- and third-order selection scale (placement of home range within the study area and resource use within the home range, respectively), Cataloochee study area, Great Smoky Mountains National Park, North Carolina, 2001–2006.

Second-order selection							Rank
Vegetation association	Treeless	Human	Deciduous	Scrub/Shrub	Evergreen	Mixed	
Treeless		+++ ^a	+ ^b	+	+++	+++	1
Human	---		+++	+	+++	+++	2
Deciduous	-	---		+	+	+++	3
Scrub/shrub	-	-	-		+	+	4
Evergreen	---	---	-	-		+	5
Mixed	---	---	---	-	-		6

Third-order selection							Rank
Vegetation association	Treeless	Scrub/Shrub	Human	Deciduous	Evergreen	Mixed	
Treeless		+++ ^a	+++	+++	+++	+++	1
Scrub/Shrub	---		+ ^b	+	+++	+++	2
Human	---	-		+	+++	+++	3
Deciduous	---	---	-		+	+++	4
Evergreen	---	---	---	-		+++	5
Mixed	---	---	---	---	---		6

^a A single sign indicates a relationship that was not statistically significant at $P \leq 0.05$.

^b A triple sign indicates significant deviation from random at $P \leq 0.05$.

Table 13. Ranking matrices for autumn resource selection by elk at the third-order selection scale (resource use within the home range), Cataloochee study area, Great Smoky Mountains National Park, North Carolina, 2001-2006.

Vegetation association	Third-order selection						Rank
	Treeless	Scrub/ Shrub	Human	Deciduous	Evergreen	Mixed	
Treeless		+++ ^a	+++	+++	+++	+++	1
Scrub/Shrub	---		+ ^b	+	+	+	2
Human	---	-		+	+++	+++	3
Deciduous	-	-	-		+++	+	4
Evergreen	---	-	---	-		+++	5
Mixed	---	-	---	-	---		6

^a A single sign indicates a relationship that was not statistically significant at $P \leq 0.05$.

^b A triple sign indicates significant deviation from random at $P \leq 0.05$.

Table 14. Ranking matrices for winter resource selection by elk at the second- and third-order selection scale (placement of home range within the study area and resource use within the home range, respectively), Cataloochee study area, Great Smoky Mountains National Park, North Carolina, 2001–2006.

Vegetation association	Second-order selection						Rank
	Treeless	Human	Deciduous	Scrub/Shrub	Evergreen	Mixed	
Treeless		+++ ^a	+ ^b	+	+++	+++	1
Human	---		+	+	+++	+++	2
Deciduous	-	-		+	+	+++	3
Scrub/shrub	-	-	-		+	+	4
Evergreen	---	---	-	-		+	5
Mixed	---	---	---	-	-		6

Vegetation association	Third-order selection						Rank
	Treeless	Human	Scrub/Shrub	Evergreen	Mixed	Deciduous	
Treeless		+++ ^a	+ ^b	+	+	+++	1
Human	---		+	+	+	+++	2
Scrub/Shrub	-	-		+	+	+	3
Evergreen	-	-	-		+	+	4
Mixed	-	-	-	-		+	5
Deciduous	---	---	-	-	-		6

^a A single sign indicates a relationship that was not statistically significant at $P \leq 0.05$.

^b A triple sign indicates significant deviation from random at $P \leq 0.05$.

Table 15. Mean ($\bar{x}$), coefficient of variation (CV), and range (R) of values associated with elk locations for landscape-scale variables included in the elk landscape model, GSMNP 2001–2004. SIDI: Simpson’s diversity index; PR: Patch richness; PARA: Perimeter to area ratio; FRAC: Fractal dimensions; and CONTAG: Contagion.

Variable	Cover class(es)	Window radius (m)	Elk Locations		
			$\bar{x}$	CV	R
SIDI	All natural types	1,128	0.33	0.35	0–0.66
PR	All natural types	1,128	4.43	0.13	1–5
PARA	Forest and field	250	255.37	0.37	112.24–586.85
FRAC	Forest and field	1,128	1.11	0.03	1.02–1.22
CONTAG	Forest and field	3385	93.73	0.04	75.03–100
SLOPE	–	Original scale (900 m ²)	9.1	0.99	0–47.80

Table 16. Principal component loading vectors of metrics calculated for Mahalanobis Distance model of elk landscape use in Cataloochee study area, Great Smoky Mountains National Park, North Carolina, 2001–2006. SIDI: Simpson’s diversity index; PR: Patch richness; PARA: Perimeter to area ratio; FRAC: Fractal dimensions; and CONTAG: Contagion.

Variable	Window radius (m)	Component loading vectors			
		1	2	3	4
SIDI	1128	0.44	-0.33	0.26	0.66
PR	1128	0.14	0.43	0.86	-0.22
PARA	250	0.59	0.04	-0.22	-0.23
FRAC	1128	0.33	0.52	-0.18	0.47
CONTAG	3385	0.05	-0.64	0.30	-0.02
SLOPE	30 m ²	-0.57	0.13	0.12	0.49

Table 17. Microhistological analysis results of annual elk diet composition for elk in Cataloochee study area, Great Smoky Mountains National Park, North Carolina, 2003-2005.

Forage Type	2003	2004	2005	Average
Grasses	63%	69%	67%	66%
Forbs	14%	14%	6%	11%
Sedges/rushes	11%	6%	11%	9%
Conifers	5%	5%	4%	5%
Shrubs	5%	5%	3%	4%
Ferns	2%	1%	8%	4%
Others	0%	0%	1%	1%

Table 18. Seasonal elk diet fecal nutrients for elk in Cataloochee study area, Great Smoky Mountains National Park, North Carolina, 2003-2005.

Nutrient Value	%ODM ^a	%FN ^b	DAPA ^c mg/gm	%FNDF ^d
Spring 2003	92.04	3.02	0.70	62.08
Summer 2003	91.02	2.94	0.75	64.71
Autumn 2003	91.75	2.08	0.57	63.93
Winter 2003	91.69	1.91	0.44	63.37
Spring 2004	91.46	4.02	0.77	64.72
Summer 2004	91.15	3.12	0.66	61.49
Autumn 2004	91.03	3.05	0.91	58.08
Winter 2004	91.46	1.95	0.55	63.13
Spring 2005	92.05	4.50	0.82	58.71

^a Percent oven dry matter

^b Percent fecal nitrogen

^c Fecal 2,6 diaminopimelic acid

^d Fecal neutral detergent fiber

APPENDIX B: FIGURES

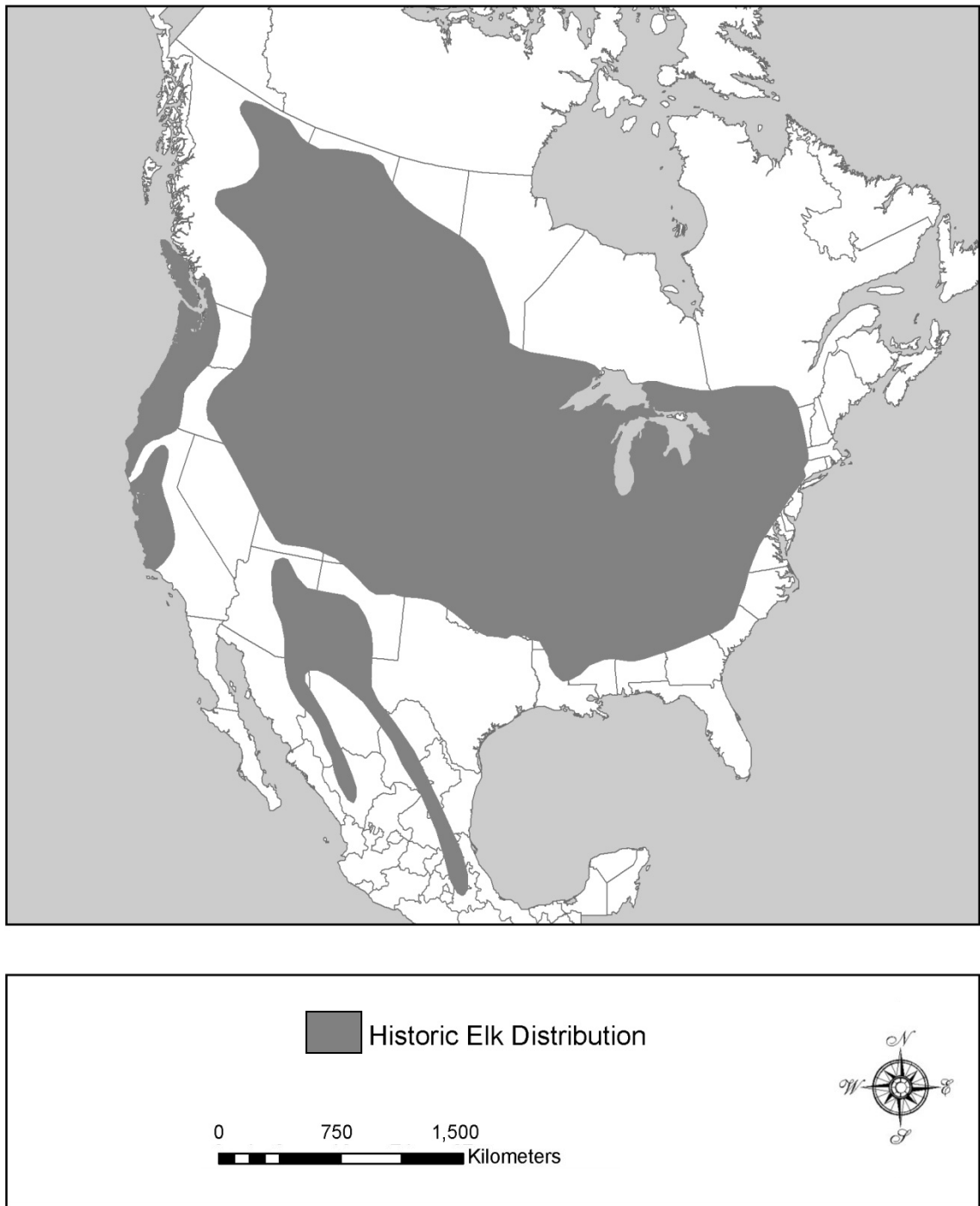


Figure 1. Historic distribution of North American elk (updated from Bryant and Maser 1982).

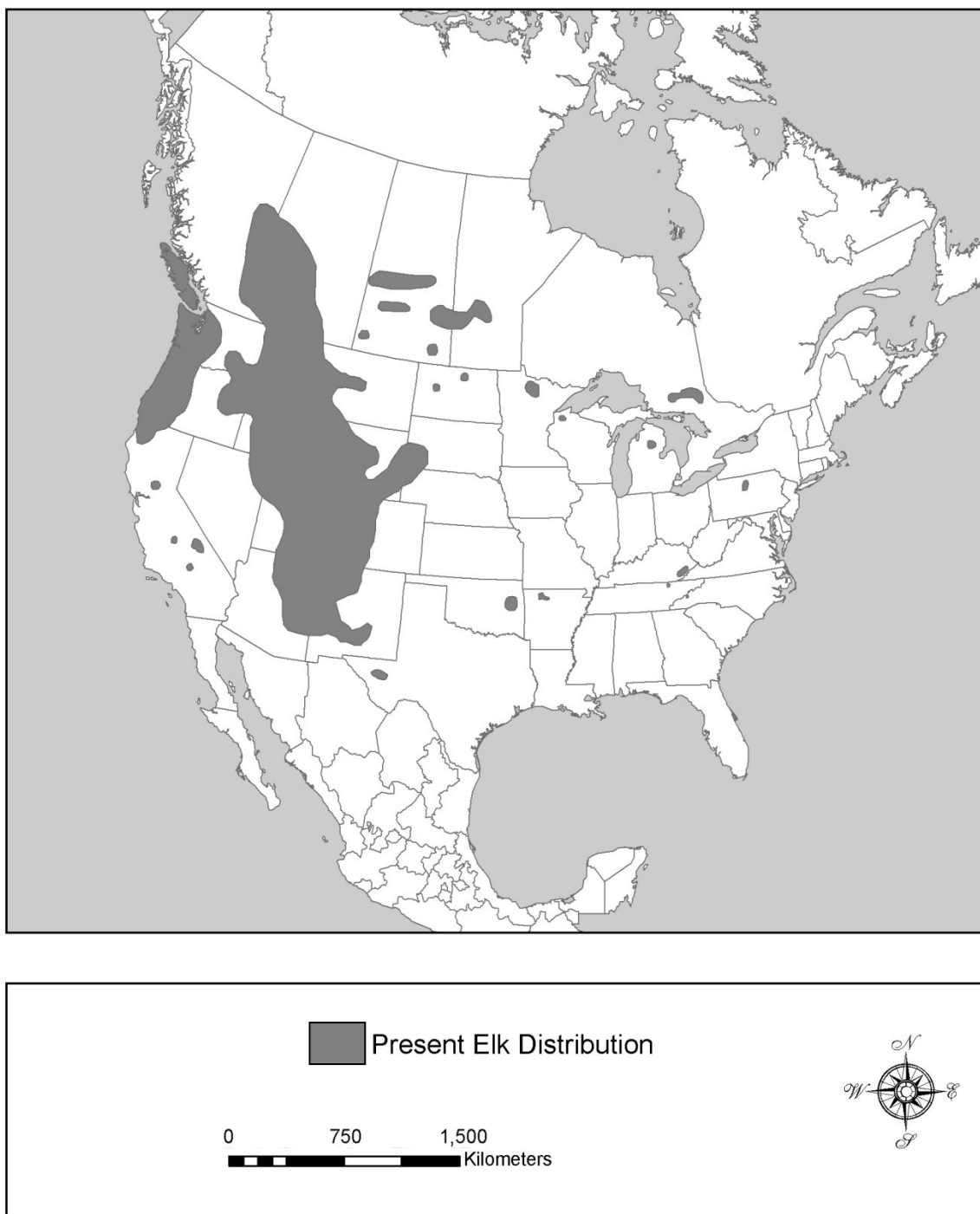


Figure 2. Present distribution of North American elk (updated from Bryant and Maser 1982).

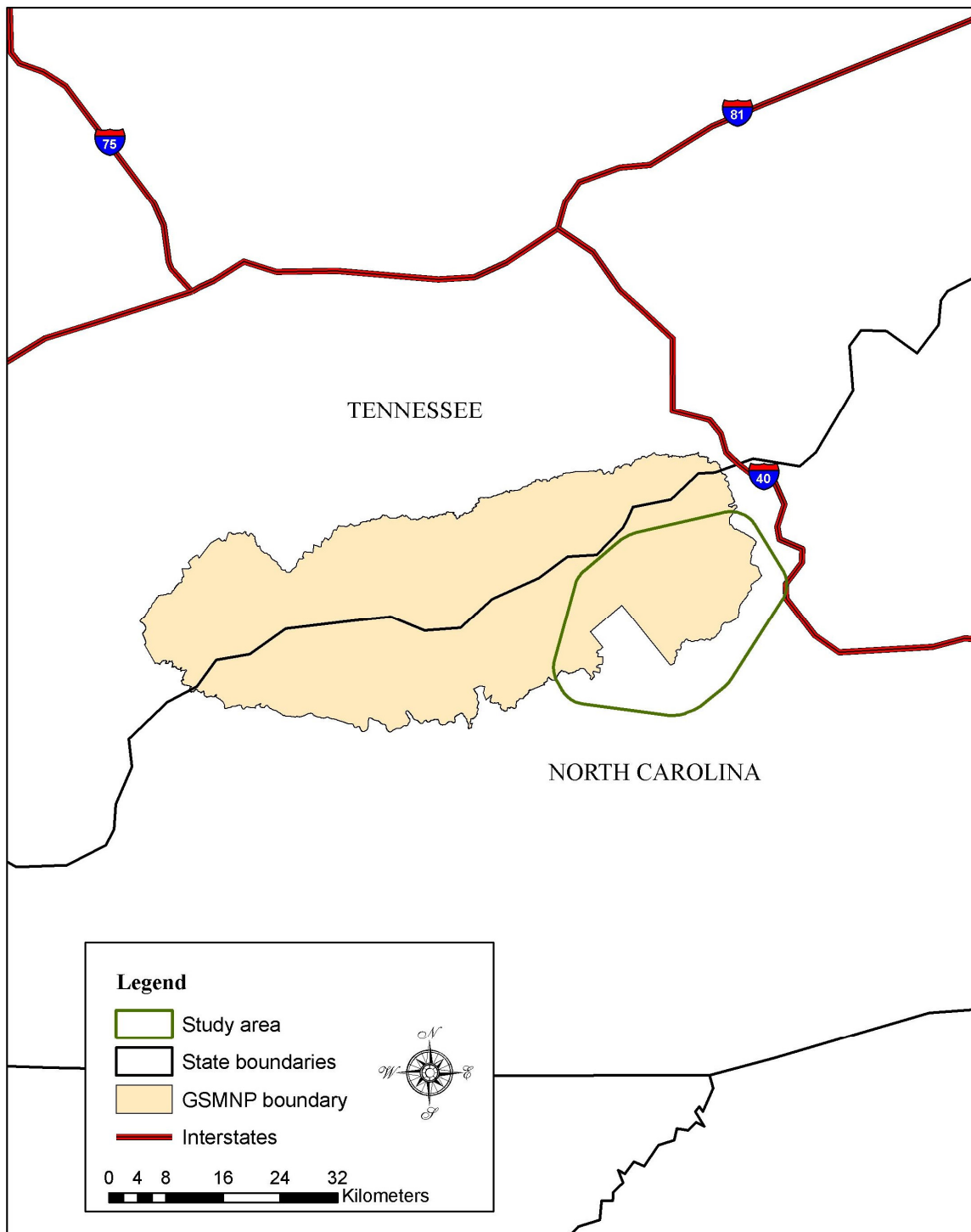


Figure 3. Cataloochee study area for experimental release of elk into Great Smoky Mountains National Park, North Carolina, 2001–2006.

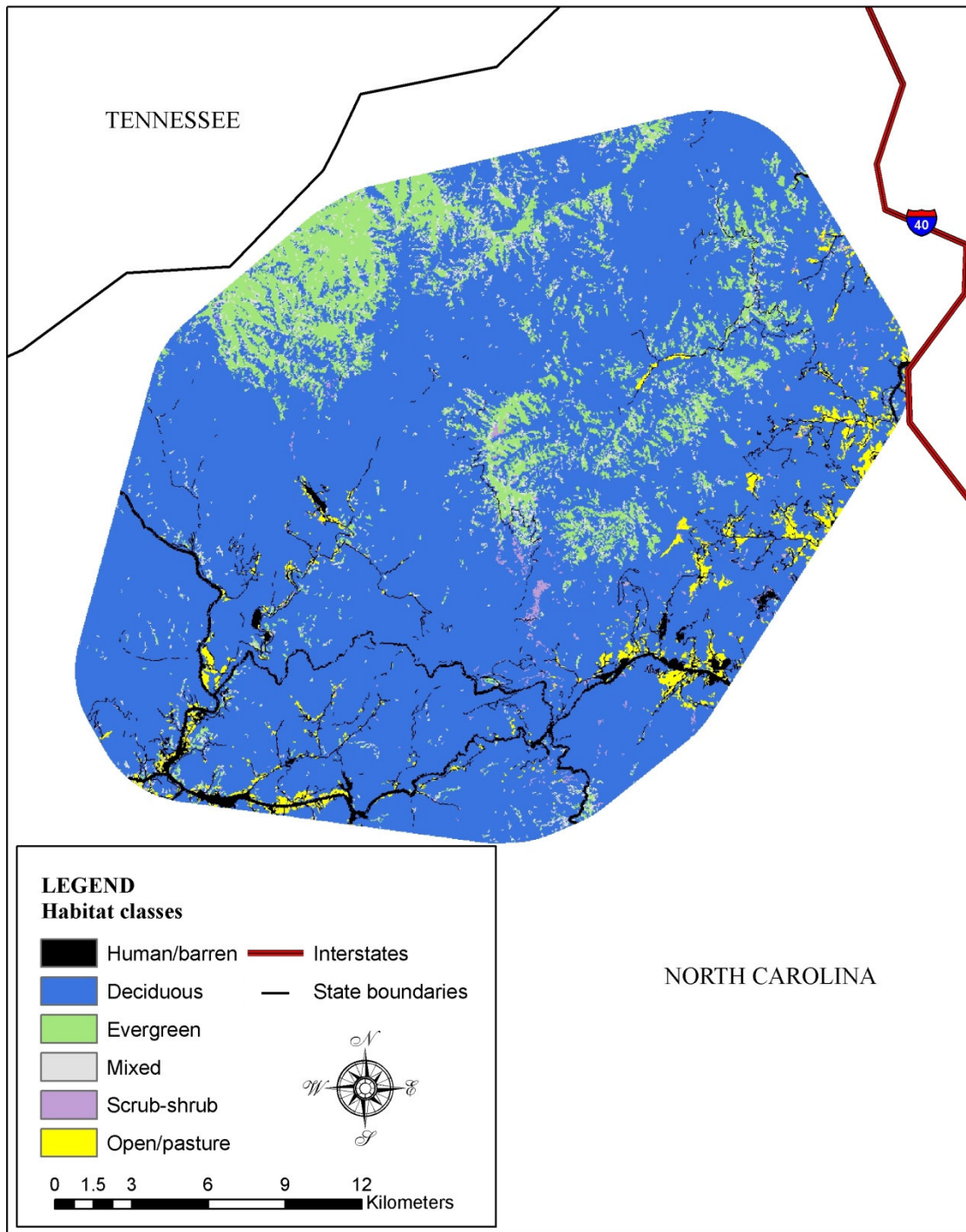


Figure 4. Composition of cover types in the Cataloochee study area, Great Smoky Mountains National Park, North Carolina, 2001–2006.

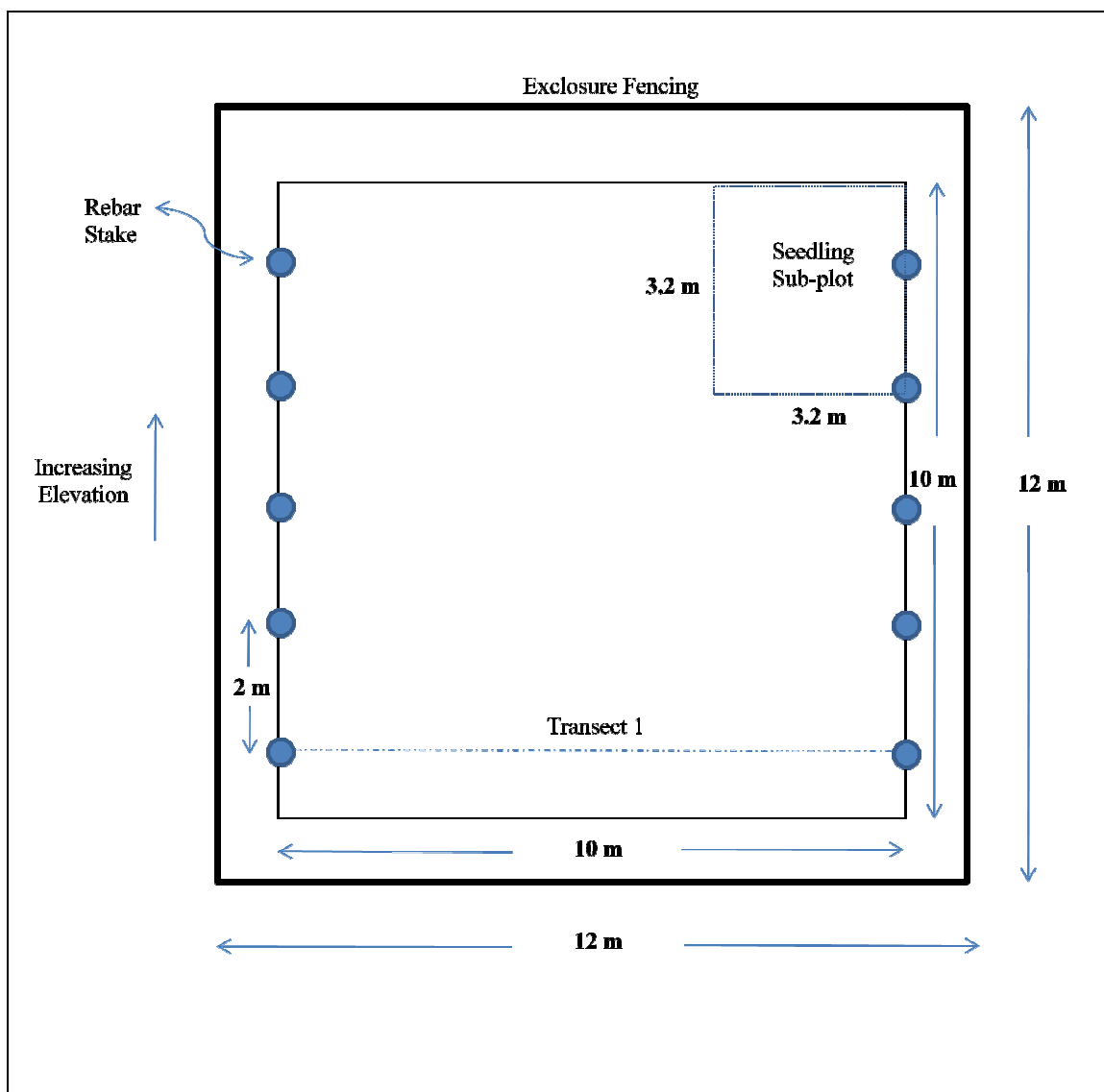


Figure 5. Vegetation exclosure layout (control plots) used to monitor elk impacts on vegetation in Great Smoky Mountains National Park, North Carolina, 2001–2006.

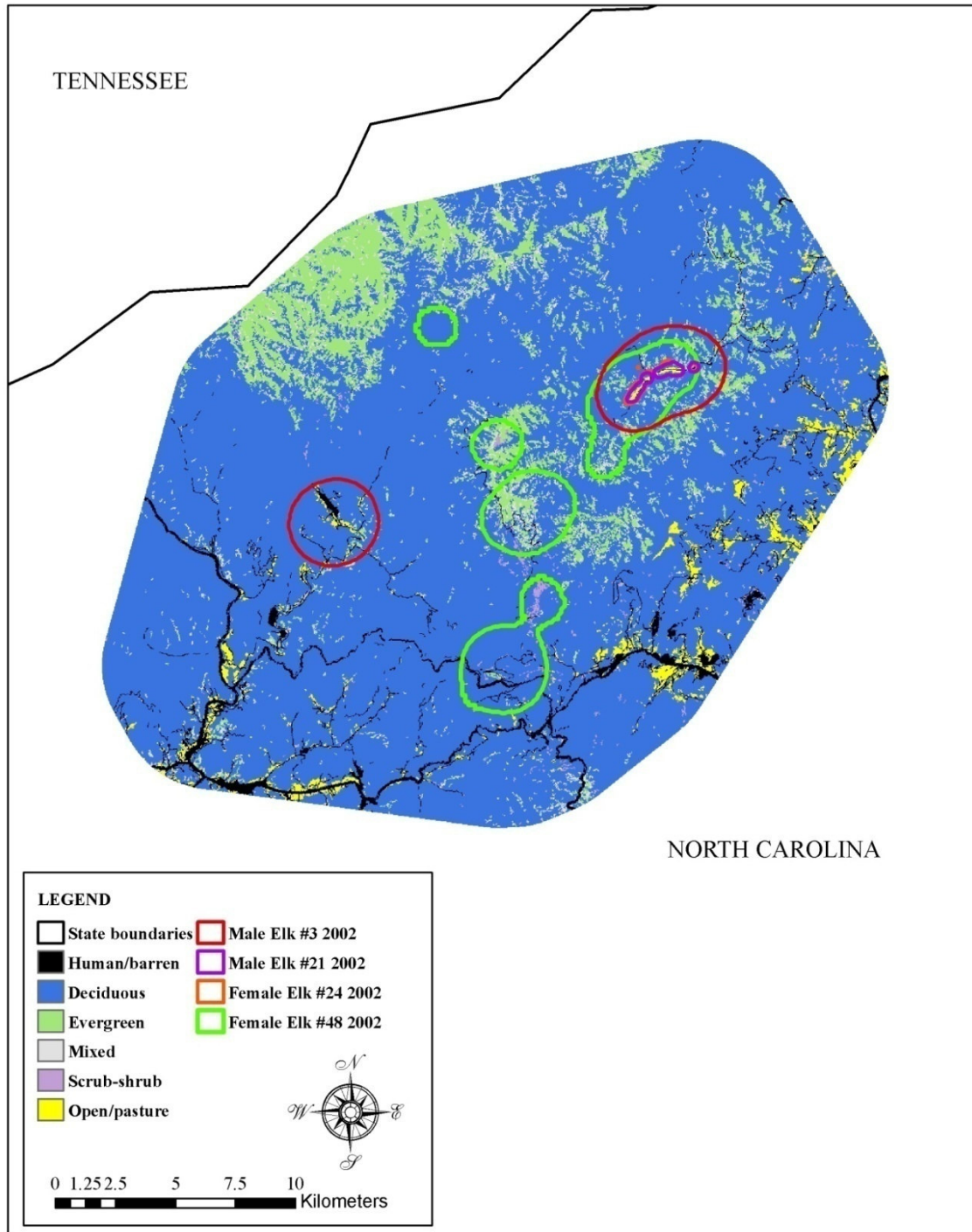


Figure 6. Four examples of home ranges from 2 male and 2 female elk in Cataloochee study area, Great Smoky Mountains National Park, North Carolina, 2002.

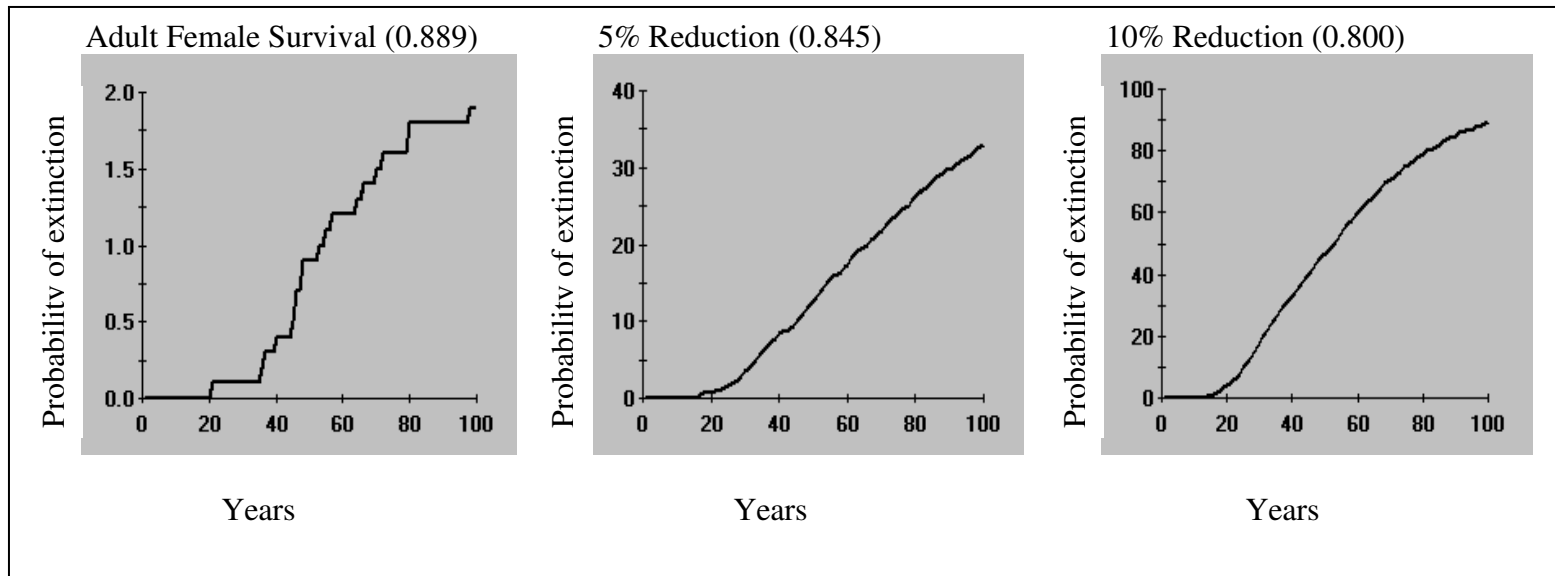


Figure 7. Probability of extinction in 100 years given an adult female survival rates of 0.889, a 5% reduction (0.845), and a 10% reduction (0.800) for elk in Great Smoky Mountains National Park, North Carolina, 2006.

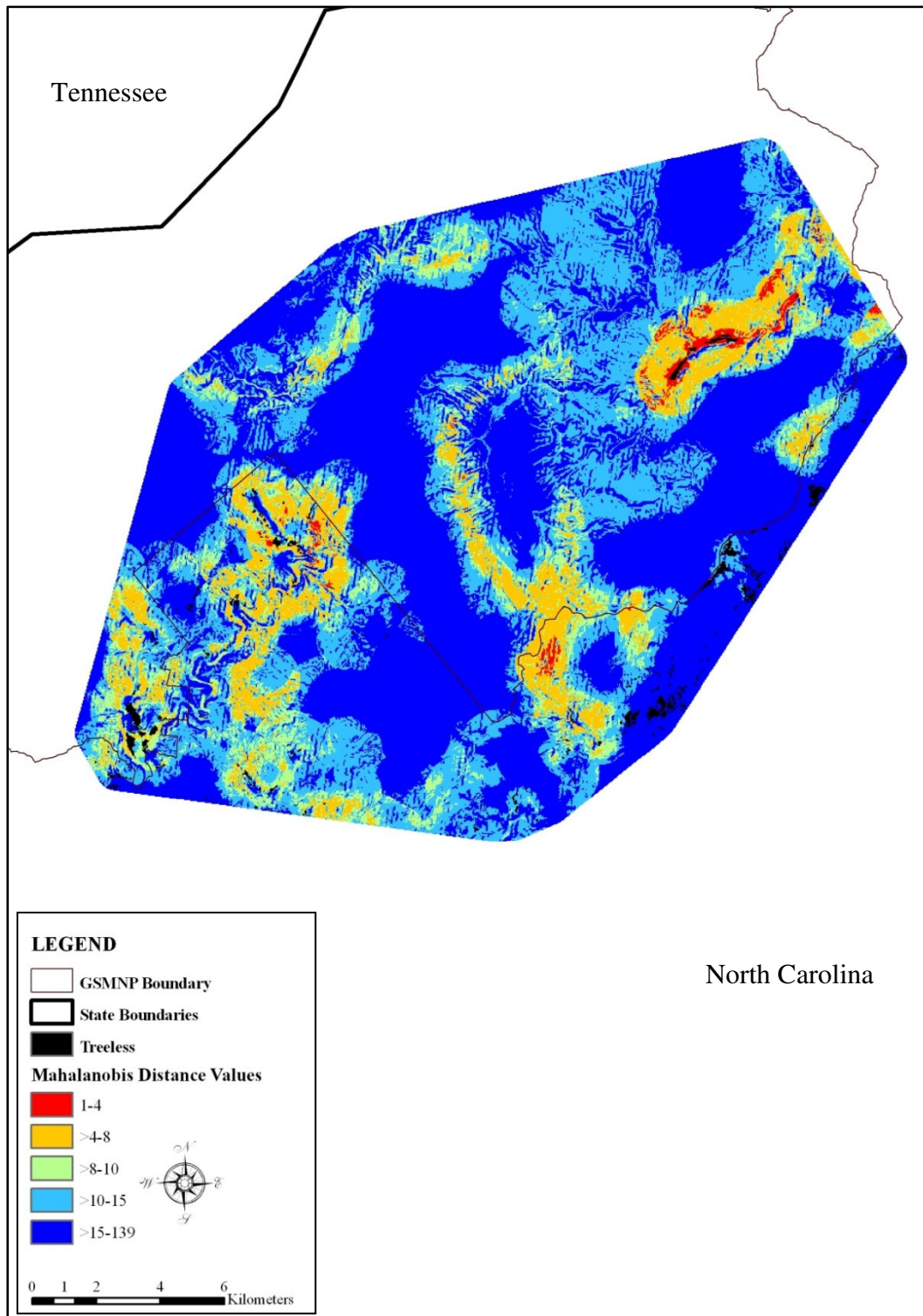


Figure 8. Mahalanobis distance model of elk habitat in Cataloochee study area, Great Smoky Mountains National Park, North Carolina, 2006.

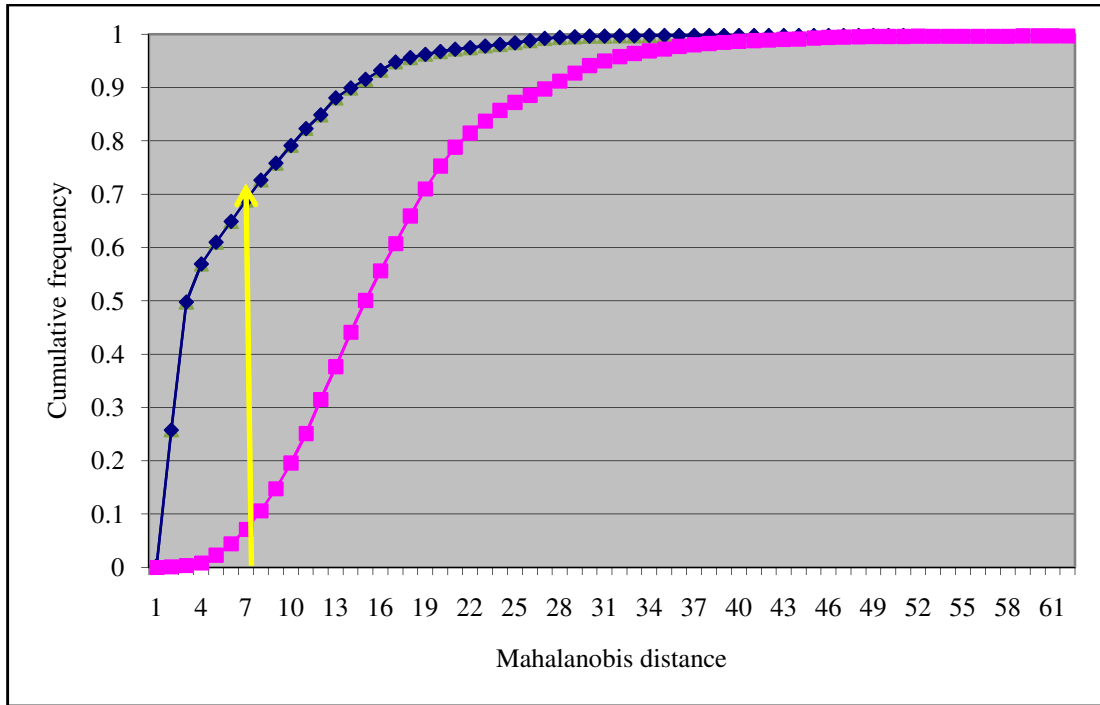


Figure 9. Cumulative frequency distributions of Mahalanobis distance values for elk locations (blue) used to design the model and randomly generated points (red) ($n = 21,761$). The yellow arrow designates the cutoff value of ≤ 8 representing quality elk habitat based on telemetry locations.

VITA

Jennifer Lynn Murrow was born in Charleston, South Carolina, on 28 August 1976. The daughter of Linwood Murrow and Charlotte Murrow Taylor, she was raised in Hanahan, South Carolina, where she graduated from Bishop England High School in 1994. She received her Bachelor of Science Degree in May 1998 from Clemson University, with a major in Aquaculture, Fisheries, and Wildlife. She received her Master of Science Degree in Wildlife and Fisheries Science with a minor in Statistics and Environmental Policy in May 2001. Her research interests are mammalian and landscape ecology.