ELK (*Cervus elaphus* L.) HABITAT SELECTION IN GREAT SMOKY MOUNTAINS NATIONAL PARK

A thesis submitted to the faculty of the Graduate School of Western Carolina University in partial fulfillment of the requirements for the degree of Master of Science in Biology

By

Elizabeth M. Hillard

Director: Dr. Laura E. DeWald Professor of Biology

Committee Members: Dr. Beverly Collins, Biology Dr. Ronald Davis, Natural Resource Conservation and Management

June 2013

ACKNOWLEDGEMENTS

This study would not have been possible without the help from multiple organizations and I would like to extend my sincere gratitude and thanks to the Rocky Mountain Elk Foundation, specifically Kim DeLozier, Conservation Program Manager and Western Carolina University for the financial support of this project. Great Smoky Mountains National Park personnel were fundamental in providing logistical support and the necessary equipment to insure my safety during field work. A special thanks to Joe Yarkovich, Wildlife Biologist, for his guidance, expertise, and provision of field support when needed.

I would like to thank my committee members and director for making this thesis possible. In particular, my director Dr. Laura DeWald who has been an incredible mentor and whose encouragement and investment in my professional future kept me motivated throughout this study. I benefited greatly from my committee member Dr. Beverly Collins for her expertise in plant community ecology and committee member Dr. Ron Davis for his knowledge of wildlife ecology and GIS analysis. I would also like to thank Dr. Tom Martin for his statistical expertise and for reading my final draft and providing helpful comments.

I had a fantastic experience as a graduate student at WCU and would like to thank all of the graduate students and faculty for their support and the learning opportunities they offered along the way. I owe a huge thank you to my best friend and fellow graduate student Scott Abla for his field assistance, patience, support, and humor throughout this project. A final thanks to my family, whose love and support makes anything possible.

ii

TABLE OF CONTENTS

LIST OF TABLES	iv
LIST OF FIGURES	v
ABSTRACT	vi
CHAPTER 1: INTRODUCTION	1
CHAPTER 2: LITERATURE REVIEW	4
Natural History and Distribution	4
Habitat Selection	
Food	7
Cover	9
Disturbance	10
Elk as Ecosystem Modifiers	11
Habitat Management	
Elk in GSMNP	
CHAPTER 3: ELK HABITAT SELECTION (Cervus elaphus L.) in GSMNP	16
Introduction	
Methods	20
Study Area	
Quantifying Elk Habitat Selection	
Data Analysis	
Results	
Discussion	48
Management Implications	
LITERATURE CITED.	

LIST OF TABLES

TABL	.E PAGE
1.	Forest cover types paraphrased from Madden et al. (2004) used
	to assess forest cover type selection by elk in GSMNP25
2.	Understory density classes from Madden et al. (2004) used
	to assess understory density class selection by elk in GSMNP26
3.	Disturbance use history classes from Pyle (1988) used
	to assess disturbance history selection by elk in GSMNP26
4.	Sampling sizes used to measure habitat variables and woody
	Browse in 47 plots of varying elk selection
5.	Habitat variables measured in 315m ² plots used to assess forage
	and cover characteristics in Cataloochee Valley, GSMNP
6.	Browse survey calculations for each plant species
	identified during an elk browse survey, GSMNP
7.	Number of 15m transects with pellet group counts ranging from 0 to 835
8.	Elk habitat selection versus available habitat in Cataloochee Valley, GSMNP39
9.	Means (S.E.) values for habitat variables measured in 315m ² plots in
	four forest types of varying elk selection in Cataloochee Valley, GSMNP40
10.	Mean size and density of dominant woody species in 315m ² plots in
	four forest types of varying elk selection in Cataloochee Valley, GSMNP40
11.	Analyses of variance comparing forest canopy structure, ground cover,
	understory foliage density, and litter-soil variables among plots
	with varying elk pellet group selection categories $(0, 1-2, >2)$
	in Cataloochee Valley, GSMNP
12.	Spearman rank correlation coefficients (r) between measured plot variables
	and pellet group frequencies from 47 plots in Cataloochee Valley, GSMNP44
13.	Woody browse availability and use by elk in the Cataloochee Valley, GSMNP46
14.	Browse variation among forest types and pellet group selection
	categories in the Cataloochee Valley, GSMNP

LIST OF FIGURES

FIGURE	PAGE
1. Elk trails in the Cataloochee Valley area, Great Smoky Mountains	
National Park, Haywood County, NC	22
2. Probability of detecting elk fecal pellet groups near nonforested	
areas in Cataloochee Valley, GSMNP	36
3. Relationship of elk fecal pellet frequency to distance to nonforested	
areas in Cataloochee Valley, GSMNP	37
4. NMDS ordination of forest structure variables among plots of varying	
elk fecal pellet group selection categories (0, 1-2, >2)	42
5. NMDS ordination of ground cover, understory foliage density, and	
litter-soil habitat variables among plots of varying elk pellet group	
selection categories $(0, 1-2, >2)$	42

ABSTRACT

ELK (*Cervus elaphus* L.) HABITAT SELECTION IN GREAT SMOKY MOUNTAINS NATIONAL PARK

Elizabeth M. Hillard, M.S.

Western Carolina University (June 2013)

Director: Dr. Laura E. DeWald

Evaluating how the established herd of elk (*Cervus elaphus* L.) is using forested areas in Great Smoky Mountains National Park (GSMNP) is important for the health and management of the elk, and for the protection of the diverse flora within the park. I assessed habitat selection of forest cover type, understory density class, disturbance use history, and distance to nonforested areas using GIS raster layers and fecal pellet counts. Elk trails were mapped and fecal pellet counts were used to index habitat selection. Plots were established to determine if there were relationships between elk selection and habitat components related to food and cover. Elk in GSMNP selected successional and floodplain forest types, ericaceous understory classes of light to medium density, areas with concentrated settlement use history, and forests close to areas of open fields and recent human disturbance. These selected areas have histories of disturbance and contained preferred forage that was produced by more open canopies and that lacked overly dense understory vegetation. Woody browse species were also an important factor driving elk habitat selection. Elk browsed 10 of the 28 identified browse species in greater proportions than their availability. Pellet group density correlated positively with woody browse use. Species specific aspects of browse appear to be more important than

browse abundance. Plots with one or more pellet groups had relative browse use in greater proportions then browse available but plots containing zero pellet groups had relative browse use less then browse available despite having the highest abundance of browse due to fewer preferred browse species. Availability of species specific browse also appears to be a driver for forest type selection with successional forests containing the highest percentage of elk preferred browse species. Elk in GSMNP are selecting forested areas with understory classes of light/medium densities of *Kalmia* that provide adequate cover and allow easier movement and ground cover for forage and not selecting understory classes with heavy densities of *Rhododendron* and *Kalmia* where movement costs are high and the herbaceous layer is sparse.

In summary, elk in GSMNP are selecting areas that have more open forest canopies maintained by disturbances, and selecting undisturbed continuous forests less because they do not contain preferred or abundant forage. Future monitoring that detects pellets in more closed continuous forests could indicate depletion of food sources in preferred younger forests indicating that more intensive habitat management strategies should be considered. This understanding of resource selection by elk will be used to implement management practices that promote a healthy self-sustaining elk population and the monitoring of sensitive park resources.

viii

CHAPTER 1: INTRODUCTION

In 2001 and 2002 an experimental elk (Cervus elaphus L.) herd from Elk Island National Park, Alberta, Canada, and Land Between the Lakes National Recreational Area, Kentucky were released in the eastern portion of Great Smoky Mountain National Park (GSMNP) in western North Carolina. Located in Cataloochee Valley in Haywood County, the elk population was 52 at the time of introduction (Murrow et al. 2009) and has slowly increased to an estimated 150+ individuals (Joe Yarkovich, GSMNP, personal communication). Research during the experimental phase of the reintroduction from 2001 to 2008, evaluated population dynamics, habitat use, impacts to park resources, and projections for future herd sustainability (Murrow 2007, Murrow et al. 2009, Yarkovich et al. 2011). Currently, the GSMNP elk show a positive growth rate, recruitment, and body condition indicating they have high quality habitat for food and cover (Joe Yarkovich, GSMNP, personal communication). In the experimental phase, the 52 elk had limited impact on vegetation, were grazing in open fields, and were not utilizing forested areas in GSMNP as a major food source (Murrow et al. 2009). Fecal microhistological analyses from 2003 to 2005 concluded the primary component of the elk herd diet in all seasons was graminoids and habitat research results from GPS collars indicated elk in GSMNP preferred open grazing land with interspersed cover (Murrow 2007, Murrow et al. 2009). However, of the 210,500 hectares in GSMNP, less than 1% is treeless habitat with the Cataloochee Valley containing approximately 1 km² of the preferred open grassland (Murrow 2007). Although no fecal analysis was conducted from 2006 to 2008, field necropsies of several elk indicated they were heavily using acorns (Quercus rubra L.) as a food source during the fall and winter (GSMNP-EA

2011). This may indicate a change in elk forage behavior from introduction to adaptation, as the elk have learned what food sources are available in the Park. This species is opportunistic and can move to take advantage of locally abundant food resources (Skovlin et al. 2002). Elk in ecosystems outside of GSMNP have been documented to forage on herbaceous vegetation, shrubs, and tree saplings (Binkley et al. 2003). While elk typically choose more open habitat, elk in GSMNP are showing they are capable of doing well in predominately forested habitats (GSMNP-EA 2011), and evaluation of movements found they did not migrate and used relatively small annual home ranges (Murrow et al. 2009).

A current estimated average annual population growth rate of 1.07 (Yarkovich et al. 2011) indicates a stable elk population has been established and triggered the development of a long-term management plan. The GSMNP elk management plan is adaptive, and relies on information from research to implement management practices that allow a healthy self-sustaining elk population at a level that has minimal negative impacts to other Park resources (GSMNP-EA 2011) such as reduction in plant productivity and growth rates (Schoenecker et al. 2004). An extensive literature review (GSMNP-EA 2011) concluded western US vegetation monitoring methods to assess impacts by elk may not be applicable to the GSMNP ecosystem because vegetation in the park is dissimilar. In addition, the appropriate spatial scale for monitoring is unknown in GSMNP. Herbivore population management requires both a large and small-scale approach (Gordon et al. 2004) because density dependent processes associated with population structure of large mammals may interact with ecosystem functioning to increase or decrease plant productivity depending on the relationship of herbivore populations relative to the carrying capacity of the ecosystem (Stewart et al. 2009). Since elk are now using forested areas for foraging, reevaluation of the potential influences that these animals are having on the forested areas of GSMNP is important for both the health/management of the elk and the preservation of the diverse flora within the Park. Identifying elk selection of forage and cover is a key aspect of understanding how these animals could be shaping this southern Appalachian ecosystem.

The purpose of this project was to add information to our knowledge of elk habitat selection in GSMNP and identify where monitoring should be focused to mitigate undesirable changes to park resources. These results will provide important information for the development of a long-term monitoring plan needed to manage elk habitat. By identifying areas of high elk selection, the Park Service will be able to prioritize areas that need to be closely monitored for impacts on vegetation as made necessary in the GSMNP Environmental Assessment (GSMNP-EA 2011).

Chapter 2 in this thesis is a literature review of elk habitat selection, and Chapter 3 is a manuscript based on the research results that will be submitted to the Journal of Wildlife Management or similar journal. All literature citations are in Chapter 4.

CHAPTER 2: LITERATURE REVIEW

Natural History and Distribution

Elk (*Cervus elaphus* L.) are even-toed ruminant ungulates belonging to the deer family Cervidae and are one of the largest and most valued mammals of North America (Peek 2003). They are popular with the general public and hunters as both a game species and for recreational viewing, and thus a focal species that generates management income and tourism dollars.

From hoof to shoulder, elk can vary in height from 0.75 to 1.5 m (Hudson and Bubenik 2002). Males have wide branching antlers with terminal tines set in a single plane. Antlers average 1.5 m in length and are used as rank indicators and weapons during intraspecific competition for females (Geist 2002). Male elk (bulls) are polyamerous and manage and protect a harem of female elk (cows) (Raedeke et al. 2002). Bulls attract cows and advertise territory and status through a vocal display called bugling (Hudson and Bubenik 2002). Elk have thick coats that vary in color from dark brown to tan. Their predominate mane, head, and legs are dark in color, while the body remains light. Bulls average 331kg compared to the average female 241 kg (Hudson and Bubenik 2002). Gestation generally lasts between 240 and 262 days and results in a single birth (Raedeke et al. 2002).

The elk genus evolved and diversified in Eurasia during the Pliocene around 4.5 to 1.8 million years ago (Lister 1987). Fossil remains indicate that during the Late Pliocene or Early Pleistocene about 1.8 million years ago *C. elaphus* were spread over a large part of the former USSR, Europe, western Siberia and midcentral Asia (Flerov 1952,

4

Lundelius et al. 1987). Though little physical evidence exists, it is thought this was the same time elk entered North America from Asia through what is now the Bering Straits (Geist 1998). The oldest documented North American fossil of *C. elaphus* is dated at about 40,000 years before present (Guthrie 1966) and although few elk fossils exist from the Late Pleistocene, they become numerous throughout the Holocene (~10,000 to 500 years ago) because of the importance of elk as a resource for prehistoric humans. These fossils provided a better understanding of elk historic distribution as remains were preserved and identified in archeological sites. These numerous fossils showed adaptability and tolerance of elk to a wide variety of habitats.

The historic range of elk in the US and Canada included the coniferous rainforests of the Pacific Northwest, the dry chaparral mountains of the Southwest, shrub forests of the Great Lakes Region, the North American prairie, and the mixed conifer/hardwood forests of the eastern US and southeastern Canada (Murie 1951). Overhunting and habitat loss from European colonization led to reduced populations, extirpation, and the extinction of two subspecies (*C. e. canadensis, C. e.merriami*) (O'Gara and Dundas 2002). Colonization and expansion westward reduced the natural range of North American elk to Manitoba, Saskatchewan, and the northern Rocky Mountains, the Canadian West Coast provinces and the north and western United States (Bryant and Maser 1982). In the 1920s the North American elk population was estimated to be approximately only 100,000 individuals. Relocation efforts and re-introductions have helped elk populations to recover from the low population numbers of less than a century ago and now approximately 1,000,000 elk occur in 25 states and 7 provinces (Peek 2003).

Habitat Selection

Of the North American ungulates, elk are among the most widely distributed and moststudied species. The specific components elk use for food and cover vary depending on geographic area (Skovlin et al. 2002, Strohmeyer and Peek 1996, Sawyer et al. 2007), vegetative type (Beck and Peek 2005), and season (Jenkins and Starkey 1993, Beck and Peek 2005, Walter et al. 2006). Elk are successful generalists and thrive in areas with varying food and cover. For example, southwestern deserts and other arid habitats once considered marginal for elk (Skovlin et al. 2002) currently have thriving populations in areas including Texas (Carpenter and Silvy 1991), Idaho (Strohmeyer and Peek 1996), and Wyoming (Sawyer et al. 2007). Elk success in diverse areas with different food and cover is representative of their current range which includes a variety of ecosystems with contrasting ecological communities ranging from prairies (Conard and Gipson 2012), sagebrush steppe (Strohmeyer et al. 1999), coniferous rainforests (Schroer et al. 1993), and forests in various stages of succession (Lepardus et al. 2011, Murrow et al. 2009). The main drivers of elk habitat selection are forage quality and biomass as well as cover that provides shelter from predators and weather (Frank and McNaughton 1993, Zeigenfuss et al. 2002, Schoenecker et al. 2004).

Despite the varied ecosystems where elk occur, throughout their range elk are known to prefer areas characterized by edge habitats where quality forage and forest cover are in close proximity (Thomas et al. 1988, Irwin and Peek 1983, Grover and Thompson 1986, Reynolds 1966, Coop 1971). Meadows and fields are primarily used for grazing while forested areas are utilized for forage, thermal cover, escape from predators, and as calving areas (Thomas et al. 1988, Irwin and Peek 1983, Grover and Thompson 1986). Elk habitat use has been shown to decrease with increased distance from the interface of forest and nonforest communities (Reynolds 1966, Coop 1971, Creel and Winnie 2005).

Food

Food habits of elk vary depending on the ecosystem. Elk forage on plants ranging from forbs, woody stems, and young grasses to less digestible mature grasses and sedges (Cook 2002). Elk consume the flowers, stalks, seeds, and pods of grasses and forbs. They eat the stems, leaves, and bark of trees and shrubs. They also eat lichens, mosses, and ferns (Harper et al. 1967, Smith and Anderson 2001, Cook 2002). In addition to quantity, quality of forage can influence condition, reproductive success, and rates of growth of elk populations (Bender and Haufler 1999), and Cook (2002) suggested nutrition was the primary driver of elk distribution, abundance and productivity. Elk diets show great plasticity, although they have similar nutritional value across a variety of habitats where there can be large variation in quality of forage resources (Baker and Hobbs 1982). Maximizing net intake of energy and nutrients appears to be the basic foraging goal of elk (Hanley et al. 1989) and as intermediate feeders, they can move between the spectrum of grazing and browsing. Patterns of forage use vary in response to availability and seasonal changes in quality and quantity (Jenkins and Starkey 1993, Beck and Peek 2005, Walter et al. 2006) because availability and nutritive value change with plant phenology. Although general patterns in forage occur seasonally throughout elk ranges, overall, graminoids dominate elk diets (Christianson and Creel 2007) and graminoids are important for elk in all seasons when available (Jenkins and Wright 1986,

Jones and Hudson 2002). Forb and shrub use increases in late spring and early summer with the dormancy of forbs in the fall causes an increased use of shrubs (Kufeld 1973, Cook 2002). In the winter, elk consume significantly lower amounts of forage and diets consist of mostly grasses or browse depending on availability (Kufeld 1973).

Availability of different plant life forms is generally confounded by geographic area, and thus elk forage use patterns and diets vary depending on the ecological community inhabited. For example, graminoids and forbs were seasonally important for elk in the forested regions of the Olympic Peninsula, Washington but conifers and ferns made up the majority of their winter diets where grasses were limited and contributed to only a small part of the annual diet (Jenkins and Starkey 1991). Elk in the aspen (Populus tremuloides Michx.) -sagebrush (Artemisia spp. L.) communities of northeastern Nevada were found to forage on forbs (59%-78%) in the summer, while diets in the spring varied between graminoids (18%-60%), forbs (30%-55%) and browse (10%-35%) (Beck and Peek 2005). In the coastal prairies of northern California, grasses made up the majority of the annual diet, with rare utilization of conifers and ferns (Jenkins and Starkey 1991). In contrast, elk ate evergreen browse extensively during the winter in the pinyon pinejuniper (Pinus edulis-Junipernus) woodlands of New Mexico (Short et al. 1977). With more moderate winters and minimal snow fall compared to the western US, grasses and forbs dominated diets of introduced elk in both winter and spring on reclaimed surface mine sites in the southern Appalachian Mountains of Kentucky, where the annual diet was composed of almost equal proportions of grasses (24%), forbs (27%), and browse (32%) (Schneider et al. 2006).

<u>Cover</u>

Elk forage-site selection is affected by proximity of the foraging sites to vegetation that provides cover (Skovlin et al. 2002). Cover is vegetation structure usually composed of varying flora and overhead tree cover that provides security from disturbances, predators, and to amend the effects of weather during extreme variations of heat and cold (Marcum and Scott 1985, Nelson and Burnell 1975, Leckenby 1984, Strohmeyer et al. 1999). Security cover is important for females and newborn calves to hide from predators and effective birthing sites are also associated with sufficient forage to support increased energetic demands associated with lactation and recovery from gestation (Carl and Robbins 1988). In North America, there are few successful freeranging elk herds not associated with forested lands because of the cover they provide (Allen 1972). In the Blue Mountains of Oregon, 80% of elk used summer open grassland forage areas occurring within 300 yards of the forest (Leckenby 1984).

Crown density of forest overstory influences elk use of cover. Marcum and Scott (1985) related summer range feeding and bedding activities of elk in western Montana to four crown cover classes and showed the most frequently used bedding sites occurred in high (75%-100%) cover. In contrast, feeding occurred most often in low (0%-25%) cover. Nelson and Burnell (1975) found highest elk use of cover in the heaviest (75%-100%) crown canopies in a central Washington summer range. Elk bedding sites in Idaho sage-brush steppe where forest cover is absent were restricted to vertical and horizontal cover provided by shrubs (Strohmeyer et al. 1999).

In addition to cover provided by forest canopies, understory foliage density and the vertical and horizontal structure of the understory also help ameliorate extreme temperatures but more importantly it lowers the chance of detection from predators (Mysterud and Ostbye 1999, Skovlin et al. 2002, Strohmeyer et al. 1999, Seward 2003, White et al. 2010). In eastern Kentucky, pregnant cows chose calving areas in closed-canopy hardwood forest within 152 m of a forest/grassland interface and females selected sites with a higher percentage of woody saplings and thicker vegetation between 1.0 - 2.25 m in height (Seward 2003). However, the density of understory vegetation can also impede escape. In north-central Idaho elk calf recruitment was negatively correlated with high percent shrub cover surrounding calf locations because calves 14 days or younger had difficulty negotiating dense shrub fields. This lack of mobility reduced escapement and increased vulnerability to predation by bears (*Ursus americanus* Pallas.) (White et al. 2010).

Disturbance

Overstory stand density and canopy cover determine understory herb productivity of foraging areas within forested habitats (Skovlin et al. 2002). Because elk use several different kinds of habitat seasonally and geographically, the distribution and interspersion of plant communities and successional stages is a critical component of elk selection. Disturbance regimes (fire, logging, extreme weather) can alter the quality, availability, and distribution of forage resources for wildlife. In early successional forest created or maintained by disturbance, the nutritional quality and rates of primary production of herbaceous forage is higher because the reduced tree canopy cover (Basile 1979, Singer 1979, Metlen et al. 2004, Van Dyke and Darragh 2006) increases availability of nutrients and light to the forest floor (Grogan et al. 2000). For example, elk carrying capacity in the summer increased from 8 to 28 elk/100 km² within 12 years after prescribed burning of 5,200 ha of subalpine coniferous forests and mixed shrub-herb plant communities in Banff National Park, Canada where graminoid and forb biomass was higher in burned than unburned conifer forests (Sachro et al. 2005).

Although elk use habitats in all stages of succession and show considerable plasticity in their response to changes in habitat (Merrill et al. 1995), throughout their range undisturbed continuous forests do not support high elk densities (Basile 1979, Singer 1979, Van Dyke and Darragh 2006). In New Mexico when pinyon pine-juniper woodland canopy was dense, production of understory browse and ground herbs were reduced and elk use of that habitat diminished (Short et al. 1977). Early successional seres usually have the best forage, while middle and late successional seres provide the best shelter (Romme et al. 1995). These early successional areas where forest canopies are open and that provide important elk foraging sites are very short lived (10-20 years) and the period of optimum forage production may last only 5 to 10 years without reoccurring disturbance (Toweill and Ward 2002). In general, postfire succession of herbs and shrubs in young forests provide excellent forage and cover for elk for 20 to 30 years until forest canopy shade reduces the understory (Skovlin et al. 1983).

Elk as Ecosystem Modifiers

The majority of studies have shown that large mammalian ungulates can shape the structure, diversity, and functioning of terrestrial ecosystems though herbivory (Frank and McNaughton 1993, Schoenecker et al. 2004), vegetation trampling (Rooney and Waller 2003), seed dispersal (Danell et al. 2003), soil compaction (Packer 1963), primary productivity (McNaughton 1979, Frank and McNaughton 1993, Augustine and McNaughton 1998), changes in nutrient cycling, (Pastor et al. 1998, Schoenecker et al.

2004, Stewart et al. 2009), and changes in plant species composition (Augustine and McNaughton 1998, Danell et al. 2003). Low to intermediate levels of herbivory and habitat use from low ungulate population densities can initiate positive feedbacks on plant communities resulting in increases in plant production and enhanced nutrient cycling. For example, moderate grazing in Tanzania's Serengeti National Park stimulated productivity up to twice the levels in ungrazed control plots. However, productivity was maintained at control values even under very intense grazing showing that overgrazing can also increase primary productivity in these arid grassland plant-herbivore systems (McNaughton 1979). Conversely, high population densities of large herbivores that compete for limited resources often lead to declines in plant species diversity and composition and changes in nutrient cycles which can have cascading effects on other trophic levels in ecosystems (Cox 2011). Interactions between moose (Alces alces L.) and the Boral forests of Isle Royale, Michigan show negative feedback on nutrient cycles through selective browsing of early successional nutrient-rich species such as aspen and birch (Betula papyrifera Marsh.), causing a shift in community structure to un-favored species such as spruce (*Picea* Dietr.) and fir (*Abies* Mill.) (Pastor et al. 1998). Similarly, heavy elk herbivory in Rocky Mountain National Park, Colorado caused nitrogen deposition to decline in willow (*Salix* sp. L.) stands. The nitrogen was transported from preferred willow feeding areas to preferred bedding habitat in conifer stands though fecal deposits and trampling (Schoenecker et al. 2004). These redistributions of nitrogen can alter plant growth rates and change plant species composition over time (Danell et al. 2003).

Habitat Management

Management strategies must consider what components of forage and cover are adequate for the health and survival of elk (Holthousen et al. 1994). Elk densities must be kept within carrying capacity limits in order to avoid detrimental effects on populations and alterations to vegetation composition and ecosystem function (Anderson and Katz 1993, Holthousen et al. 1994, GSMNP-EA 2011). Large populations can cause forage and cover to be limited, improving habitat by increasing understory forage vegetation through canopy reduction can reduce negative impacts by ungulates (Anderson and Katz 1993, Webster et al. 2005, Shaw et al. 2010, Lashley et al. 2011). Disturbance can also increase habitat for elk by promoting forage growth and by creating ecotones between areas of dense cover and more open feeding areas (Shaw et al. 2010, Lashley et al. 2011). Therefore, forest disturbance can be managed for elk and other ungulates to maintain a diversity of vegetation types and age classes (Shaw et al. 2010). For example, forest canopy reducing treatments on upland hardwood stands in the Southern Appalachians in Tennessee improved the availability and cover for deer (Odocoileus virginianus Zimmerman.) (Lashley et al. 2011). Similarly, in the Nez Perce National Forest, Idaho herbaceous forage production for elk increased 176% from prefire levels two growing seasons after prescribed fire (Leege and Godbolt 1985).

Much of the increase in elk numbers during the 1900s was due to a combination of human translocations of elk, improved conservation and management efforts, lack of predators, natural range expansion, and extensive wildfire and logging that resulted in abundant foraging habitats (Peek 2003, Toweill and Ward 2002). Maintaining a mosaic of burned (early successional) and unburned (late successional) habitat is beneficial to elk because it provides the necessary cover and forage needed for survival and thus increases carrying capacity (Leege and Godbolt 1985, Long et al. 2008, Lashley et al. 2011). Elk in GSMNP

The eastern sub-species of elk (Cervus elaphus canadensis Erxleben.) were extirpated from its eastern North American range in the late 1800s as a result of overharvest and habitat loss from agriculture and urbanization (Bryant and Maser 1982). Little information exists on the morphological distinctiveness or ecological function of this eastern sub-species in the landscapes of the east (Cox 2011). In 2001 and 2002 an experimental population of elk from Elk Island National Park, Alberta, Canada, and Land Between the Lakes National Recreation Area, Kentucky were released in to the eastern portion of Great Smoky Mountain National Park (GSMNP) centered in the Cataloochee Valley in western North Carolina. The elk population was 52 at the time of introduction (Murrow et al. 2009) and increased to an estimated 150+ individuals (Joe Yarkovich, GSMNP, personal communication). Murrow et al. (2009) evaluated population dynamics, habitat use, impacts to park resources, and projections for future herd sustainability during the experimental phase of the introduction from 2001 to 2008. At this time, with the population size at 52, elk had limited impact on vegetation and were not utilizing forest areas in GSMNP as a major food source (Murrow et al. 2009). Furthermore, habitat research results from GPS collars indicated that elk in GSMNP preferred open grazing land with intermixed cover and fecal microhistological analyses determined that the primary component of the elk herd diet in all seasons was graminoids (Murrow 2007, Murrow et al. 2009). Currently, the elk show positive recruitment and body condition indicating that they have high quality habitat for food and cover (Joe Yarkovich,

GSMNP, personal communication). While elk typically elect more open habitat, elk in GSMNP are showing they are capable of doing well in predominately forested habitats (GSMNP-EA 2011). However, evaluation of movements found elk did not migrate and used relatively small (female: 10.4 km² and males: 22.4 km²) annual home ranges (Murrow et al. 2009). A current estimated average annual population growth rate indicates a stable elk population has been established (Yarkovich et al. 2011). As a result, a long-term management plan for maintaining a healthy self-sustaining elk population at a level that has minimal negative impacts to other Park resources was developed and is being implemented (GSMNP-EA 2011).

With the now established larger elk herd, small home range size, and implications they are using forested areas for forage, reevaluating the impact that these animals are having on the forested areas of GSMNP is important for both the health and management of the elk and the protection of the diverse flora within the Park. An extensive literature review (GSMNP-EA 2011) suggested western US vegetation monitoring methods to assess impacts by elk may not be applicable to the GSMNP ecosystem because recent research has shown that fundamental herbivore/vegetation interactions driving landscape change are localized (often at scales of a few meters) (Gordon et al. 2004), identifying the spatial and temporal behavior of the elk in GSMNP is also important for understanding how these animals are interacting with the ecosystem. Understanding availability and use of elk forage and cover in GSMNP is important for elk management planning and for the protection of the unique diversity of plants and plant communities in the Park.

CHAPTER 3: ELK (Cervus elaphus L.) HABITAT SELECTION IN GSMNP

Introduction

Historically, elk (Cervus elaphus, L.) occurred throughout much of the contiguous United States (Murie 1951, O'Gara and Dundas 2002). They inhabited diverse ecosystems including the temperate rainforests of the Pacific Northwest, dry chaparral mountains of the Southwest, shrub forests of the Great Lakes Region, the North American prairie, and mixed conifer/hardwood forests of eastern North America (Murie 1951). Elk were extirpated from large parts of this historic range due to habitat loss and overhunting during the westward expansion of Euro-American settlers in the late 1800s and early 1900s. By 1922, it was estimated that only 100,000 elk inhabited North America, mostly in Yellowstone National Park in Wyoming, Olympic National Park in Washington, and the Tule Elk Reserve in California (Bryant and Maser 1982). As a result of wildlife management, conservation efforts, reintroductions, and reduction in predators the current elk population in North America is estimated to be near 1,000,000 (Peek 2003). Currently, the largest populations of elk are in western North America inhabiting a range from Vancouver Island east to southern Saskatchewan, and in the US westward from Texas north to North Dakota.

Currently, in North America most free-ranging elk herds are associated with forested lands (Allen 1972) and forest ecotones with grassland or meadow communities (Thomas et al. 1988, Irwin and Peek 1983, Grover and Thompson 1986, Skovlin et al. 2004). Elk habitat use relates closely to the availability and spatial arrangement of food, cover, water, and space (Frank and McNaughton 1993, Zeigenfuss et al. 2002,

Schoenecker et al. 2004); as intermediate feeders and they can switch between grazing primarily on grasses to browsing on woody species depending on forage availability (Short et al. 1977, Baker and Hobbs 1982, Cook 2002). Elk forage-site selection is also affected by the proximity of cover created by midstory and understory woody species that provide security from disturbances, predators, and to moderate extreme temperatures (Skovlin et al. 2002). Landscape with a cover:forage ratio of 60:40 is the most suitable habitat for elk in western Oregon and Washington (Holthousen et al. 1994). Habitat preferences differ with geographic area, however as well as with vegetation type, and season (Cook 2002). Elk habitat selection in the Buffalo National River area of Arkansas is associated with areas of high landscape heterogeneity, heavy forest cover, gently sloping ridge tops and valleys, low human population density, and low road densities (Telesco et al. 2007). In the Blue Mountains of eastern Oregon and Washington elk select size and spacing of cover and forage differently when snow is present or absent, when roads are open to traffic, and seasonally they move to where plants are more abundant (Thomas et al. 1988).

Elk are generalists and thus able to thrive in a wide variety of environmental conditions (Frank and McNaughton 1993, Zeigenfuss et al. 2002, Cook 2002, Schoenecker et al. 2004). Analysis of resource use and niche partitioning in Yellowstone National Park revealed that elk had a wide range of resource use (Feranec and Stable 2007). This ability to use a variety of resources has facilitated reintroductions of elk in the eastern US; for example, the successful herd in the Land Between the Lakes National Recreation Area between Tennessee and Kentucky has high survival and reproductive rates (Larkin et al. 2004). As a result of these successful reintroductions and because elk meet National Park Service (NPS) criteria for restoring extirpated native plant and animal species (GSMNP-EA 2011), elk were reintroduced into the Great Smoky Mountains National Park (GSMNP). In 2001 and 2002 elk from populations in Elk Island National Park, Alberta, Canada, and Land Between the Lakes were introduced into the Cataloochee Valley of GSMNP (Murrow et al. 2009).

Because large mammalian ungulates such as elk do not use habitat uniformly (Neu et al. 1974), they can function change structure, diversity, and functioning of ecosystems, particularly where they have been reintroduced to, or if densities are high. Low or intermediate levels of large ungulate herbivory can initiate positive feedbacks on plant communities by increasing plant production and enhancing nutrient cycling (McNaughton 1979, Stewart et al. 2006). Changes can occur as a result of herbivory (Frank and McNaughton 1993, Zeigenfuss et al. 2002, Schoenecker et al. 2004), vegetation trampling (Frank and McNaughton 1993, Rooney and Waller 2003), seed dispersal (Danell et al. 2003), soil compaction (Packer 1963), primary productivity (Stewart et al. 2006), nutrient cycling, (Frank and McNaughton 1993, Augustine and McNaughton 1998, Danell et al. 2003, Stewart et al. 2009) and plant species composition (Augustine and McNaughton 1998, Webster et al. 2005, Griggs et al. 2006). Stewart et al. (2006) described density dependence of elk and plant responses to herbivory in the Blue Mountains of Oregon where forested areas with low densities of elk had greater net above ground primary productivity and forage quality than plots with no herbivory. Conversely, areas with high elk densities showed declines in net above ground primary productivity and forage quality. Altered plant communities can lead to changes in nutrient distributions causing cascading effects on other trophic levels (Cox 2011, Schoenecker et

al. 2004, Danell et al. 2003), demonstrating the importance of understanding elk habitat selection and use.

Growth of the elk population in GSMNP from 52 at the time of introduction to the current size of more than 150 individuals suggests they are finding quality food and cover habitat in the Park. Fecal microhistological analyses from 2003 to 2005 of reintroduced elk in GSMNP concluded the primary component of their diet was graminoids (Murrow et al. 2009). Field necropsies of several elk from 2006 to 2008 indicated they were heavily utilizing acorns (*Quercus rubra* L.) (GSMNP-EA 2011) suggesting elk are using forested areas as well as grasslands for forage and cover during autumn and winter.

At introduction elk in GSMNP selected open fields for forage and research indicated the herd was having limited impact on the vegetation resources of GSMNP (Murrow 2007, Murrow et al. 2009), of the 210,500 ha in GSMNP, less than 1% represents treeless habitat dominated by graminoids and the Cataloochee Valley (site of the introduction) contains only 1 km² of preferred open grassland (Jenkins 2007, Murrow et al. 2009). When dense ungulate populations compete for limited resources, degradation of vegetation communities can result. For example, heavy herbivory by white-tailed deer (*Odocoileus virginianus* Zimm.) in the Cades Cove area of GSMNP altered cover, diversity, and population demographics of forest herbs (Webster et al. 2005) and suppressed tree regeneration (Griggs et al. 2006). With the now established larger elk herd, small home range size, and implications they are using forested areas for forage and cover, reevaluating habitat selection and use in the forested areas of GSMNP is important for both the health and management of the elk, and for the protection of the diverse flora within the Park. Identifying spatial and temporal behavior of habitat selection by the elk in GSMNP will also help managers understand the role these large ungulates could have in shaping this Southern Appalachian ecosystem. The purpose of this study was to investigate elk habitat selection in relation to food availability and cover within GSMNP. I hypothesized that elk would select vegetation community types that contain and produce higher amounts of forage in greater disproportions then their availability in the study area and that forage and cover habitat variables would differ with different levels of elk selection.

Methods

Study Area

The study took place in the Cataloochee Valley which is located in the southeastern portion of GSMNP (35° 38' 23.000 north latitude and 83° 04' 55.00 west longitude) in Haywood County, North Carolina. The area used for this study was a 92,076 km² section of the Valley with general boundaries defined by the GSMNP park boundary to the south and east, Mount Sterling to the north, and Henitooga road to the west. Before establishment of GSMNP in 1910, approximately 1,200 people lived in this mountain valley. Most made their living by farming, including commercial apple growing (Pyle 1985). This study area was selected because annual and seasonal home range calculations from radio collar locations indicated high use by elk, and this area was used for population modeling and habitat analysis in previous elk studies in the Park (Murrow et al. 2009, Yarkovich et al. 2011). The study area is dominated by montane *Quercus-Carya* (oak-hickory) forest (Jenkins 2007) with 1 km² of open grassland habitat maintained by mowing (Murrow et al. 2009). The forest overstory is dominated by

northern red oak (*Quercus rubra* L.) with lesser amounts of chestnut oak (*Q. montana* Willd.) and white oak (*Q. alba* L.). The shrub layer is relatively open usually containing a substantial component of heaths, but also contain many non-ericaceous species. The herbaceous component is relatively diverse, but often patchy and composed of both acidophiles and species characteristic of moderately fertile soils (Jenkins 2007).

Quantifying Elk Habitat Selection

To determine if elk were selecting areas in proportion to their availability, elk trails were used to design a line transect sampling scheme to survey elk fecal pellets as an indicator of habitat selection throughout different forest types in the study area. The elk trails served as a preliminary survey from which pellet-group sampling was conducted (Neff 1968). In addition, understanding elk movements relative to forest cover types helps explain the dynamic processes influencing the distribution of individuals in space for assessment of habitat selection (Leblond et al. 2011). GSMNP trails, roads, and field edges were visually surveyed for presence of elk trails. Trails containing elk tracks and fecal pellets were walked from January 2012 – May 2012 and mapped using a Garmin GPS unit. In the field, trails were classified into three categories based on visual observations: 1) high use trails -obvious trail with numerous tracks, frequent elk pellets and trail often trenched; 2) moderate use trails - trail evident with tracks and pellets often but diffuse; 3) low use trails -trail indistinct with tracks and pellets scarce but showing one route of movement. The GPS trail data were downloaded into ArcMap using GPX formatting and labeled by use (Figure 1). These trails of varying elk use were used to establish transects for

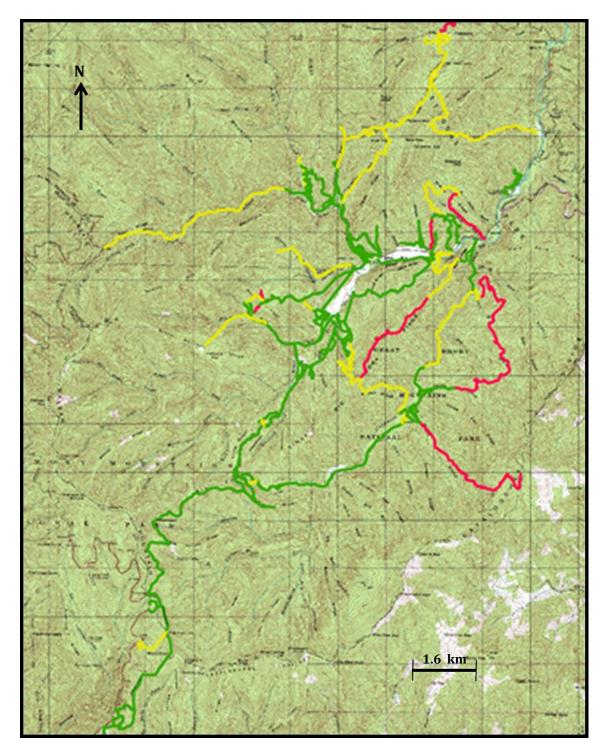


Figure 1. Elk trails in the Cataloochee Valley area, Great Smoky Mountains National Park, Haywood County, NC. Green = high use trails, yellow = moderate use trails, red = low use trails based on visual observation of frequency of elk tracks and elk fecal pellet groups.

fecal pellet distance sampling following the methods of Buckland et al. (1993) and Buckland et al. (2001).

Fecal pellet distance sampling can be used to determine population densities (Neff 1968, Buckland et al. 1993, Buckland et al. 2001). The perpendicular distances of detected elk fecal pellets from the transect line are measured to determine the detection function. With the detection function, deposition rate, and pellet group decay rate a populations density can be estimated (Buckland et al. 1993, Buckland et al. 2001). I originally set out to convert pellet counts into elk density numbers to assess selection. However, the decay rate of elk pellet groups in GSMNP was highly variable, with the length of time to pellet group decay ranging from < 10 days to > 300 days. Because the variable decay rate would lead to unreliable density estimates, pellet group counts were instead used as an index of habitat selection. Because pellet groups are deposited most where the elk spend greater time (Neff 1968), their frequency will usually vary considerably between areas of differential habitat selection (Van Etten 1959). In the Buffalo National River area of Arkansas, patterns of elk pellet group counts were similar to 10 years of elk density measures using helicopter surveys (Telesco et al. 2007).

Transect sampling of fecal pellet groups was conducted May 2012 – June 2012. Using ArcMap, 161 transect locations were placed 400 m apart along a subsample (80%) of the mapped elk trails and uploaded into a GPS unit. At each location 15 m transects were surveyed perpendicular to the elk trail, and numbers of elk fecal pellet groups (including zeros) were counted. Only pellet groups containing 16 or more pellets were counted as a group to reduce the risk of counting a widely spread pellet group as two groups, which would lead to overestimation of selection (Marques et al. 2001). Pellet groups beyond 2 m from the transect line were not counted (Buckland et al. 1993). Habitat selection was evaluated by overlaying the 161 transect locations of various pellet counts with GIS data layers that represented the vegetative environment within the study area. Vegetation map layers provided by GSMNP were used to assess forest cover type, understory density classes defined by Madden et al. (2004) (See Tables 1 and 2) and disturbance use history described by Pyle (1985 and 1988) (See Table 3). The disturbance history of forested areas provided an estimate of plant community patterns related to the size, frequency, and persistence of the disturbance (Elliot et al. 1998). Using ArcMap, GIS raster layers of forest cover type, understory density class, and disturbance history were superimposed over the 161 transect locations. Forest cover type, understory density class, and disturbance history were recorded for each transect location. The forest cover type layer was also used to measure the distance of each transect from nonforested areas of recent human disturbance or open fields.

Herbivore/vegetation interactions driving landscape change can often be localized at scales of only a few square meters (Gordon et al. 2004), and hence may not be discernible using larger scale assessments (Palmer et al. 2003). Therefore, a subset of transect locations (n=47) were chosen to establish plots. Four of the eight forest types described in Table 1 had multiple transects with groups of 0, 1-2, and > 2 pellet groups. These replicate pellet group classes suggested differing elk selection (Neff 1968, Schaublin and Bollmann 2011). These three categories of pellet group counts were used to index habitat selection (Neff 1968), assuming no/ low (0), moderate (1-2), and high (>2) selection, to examine differences in forage and cover variables at the microhabitat

Forest Cover Type	Description		
Oak-Hickory	Uneven-aged, with old trees present. Reproduction occurs primarily in canopy gaps. Canopy dominated by mixtures of <i>Quercus</i> and <i>Carya</i> .		
Floodplain	Flood sediment provides nutrient input as a natural disturbance, sometimes frequently enough to keep the forests in early successive. Forests have an open to dense shrub layer with a sparse to dense her layer. Canopy a mixture of bottomland and mesophytic tree species usually <i>Tsuga canadensis</i> and <i>Platanus occidentalis</i> .		
Hemlock	<i>Tsuga</i> dominates the canopy along with three or fewer associates. Acid loving species like heath family members are common. <i>Rhododendron</i> frequently dominates the understory. At maturity, <i>Tsuga</i> dominates exclusively. The hemlock wooly adelgid (<i>Adelges tsugae</i> Annand.) is presently decimating this forest type.		
High Elevation Oak	Uneven-aged forests with reproduction occurring in canopy gaps. Closed to somewhat open canopy dominated by <i>Quercus rubra</i> and often with <i>Quercus montana</i> , <i>Acer rubrum</i> , <i>Liriodendron tulipifera</i> , and various northern hardwood species.		
Montane-Cove	Stable, uneven-aged, late successional forests, with trees up to several centuries old. Dense forest canopy with a diverse mixture of mesophytic trees, including <i>Liriodendron tulipifera</i> , <i>Tilia americana</i> , <i>Acer saccharum</i> , <i>Aesculus flava</i> , <i>Betula lenta</i> .		
Northern Hardwood	Uneven-aged, late successional forests with reproduction occurring in canopy gaps. Canopy dominated by combinations of mesophytic tree species, primarily <i>Fagus grandifolia</i> , <i>Betula alleghaniensis, and Aesculus flava</i> .		
Successional	Canopy dominated by mesophytic trees, primarily <i>Liriodendron</i> <i>tulipifera</i> , <i>Fagus grandifolia</i> , <i>Acer spp.</i> , and <i>Quercus rubra</i> . Under natural conditions these forests are uneven-aged, with old trees present		
Pine	Canopy dominated by <i>Pinus strobus</i> , with or without associated trees such as <i>Tsuga canadensis</i> or <i>Quercus montana</i> . The shrub layer is ofter dense. Shrubs include <i>Vaccinium</i> spp., <i>Rhododendron</i> spp., and <i>Gaylussacia</i> spp.		

Table 1. Forest cover types paraphrased from Madden et al. (2004) used to assess forest cover type selection by elk in GSMNP.

Understory Density Class	Description
Herbaceous/Deciduous	Non-woody plant species that undergo periods of dormancy seasonally, of varying density
Kalmia (L,M)	<i>Kalmia latifolia</i> , light to medium density (> 20% to 100% of ground surface visible from aerial photographs)
Kalmia (H)	<i>Kalmia latifolia,</i> heavy density (0 to 20% of ground surface visible from aerial photographs)
Rhododendron (L,M)	<i>Rhododendron</i> spp., light to medium density (> 20 to 100% of ground surface visible from aerial photographs)
Rhododendron (H)	<i>Rhododendron spp.</i> , heavy density (0 to 20% of ground surface visible from aerial photographs)
Other	Tsuga and Pinus understory with varying density

Table 2. Understory density classes from Madden et al. (2004) used to assess understory density class selection by elk in GSMNP

Table 3. Disturbance use history classes from Pyle (1988) used to assess disturbance history selection by elk in GSMNP

Disturbance Use History Concentrated settlement	Description Areas where many settlers had buildings and cleared fields, clusters of homeplaces or cleared areas covering more than half a given area. The present vegetation can be expected to show unmistakable signs of past clearing and remnants of cabins, stone walls, old roads, and signs of past fire.
Corporate logging	Areas that had logging operations with corporate ownership, usually large in scale. Construction of railroads and use of mechanized skidders were economically feasible. Corporate logging usually resulted in large areas of even-aged regeneration because the majority of the overstory trees were removed in a short period of time.
Diffuse disturbance	Disturbance with boundaries difficult to define. On a broad scale level, a tract of land with 20 isolated farms in 10,000 hectares might be said to have farming impacts diffused throughout. Areas generally have a mixture of broad scale and fine scale disturbance but stands of large trees still exist.
Primary forest	No direct or indirect effects of human activities are found. Attributes may include, but are not limited to, big trees, old trees, and absence of evidence of logging or homesteading.

scale. Replicated plots of these three selection categories were established in each of the four forest cover types to examine habitat components related to cover and forage. The number of plots per forest type and selection category is listed in Table 4. A total of 47 plots each with a 10 m radius (area = 314 m^2) were established and habitat variables related to food and cover described in Table 5 were measured in July 2012 – August 2012. Habitat information was collected for four strata in each plot (1) forest canopy structure, (2) understory, (3) ground cover, and (4) litter-soil. Forest canopy variables were measured on woody vegetation > 4.5 cm diameter at breast height (DBH). Data collected included species, DBH, crown position in the canopy, and midstory light exposure as described by Bechtold (2003) for each overstory tree in the plot. In addition, a densiometer was used to measure percent canopy cover for the plot by walking the 20 m diameter of the plot and collecting densiometer data every 1 m using methods described by Hayes et al. (1981). These overstory canopy structure variables were selected because they influence the amount of sunlight available for forage growth and relate to how well forest stands provide both forage and cover (Miller et al. 1999).

Understory was defined as vegetation < 2.5 m tall and < 4.5 cm DBH. Understory vertical cover was measured using a vegetation profile board 2.5 m tall divided into 0.5 m sections. As described by Nudds (1977), the board was placed on the ground in the center of the plot and examined from a 15 m distance to record average cover for each vertical layer of understory vegetation. This percent understory foliage variable was used to assess available cover for providing protection from calf predation, cold, and shading from the sun (Nudds 1977). Ground cover and seedling variables were

	Forest Type			
Elk Selection Category	Successional	Montane-Cove	Montane Oak-Hickory	Hemlock
(# Pellet Groups)	# Plots	# Plots	# Plots	# Plots
0	6	3	4	4
1-2	6	4	4	1
> 2	5	3	3	4
Total # Plots	17	10	11	9

Table 4. Sampling sizes used to measure habitat variables and woody browse in 47 plots of varying elk selection. See Table 1 for definition of forest types.

Variable	Definition
Forest Canopy Structure	Measured on trees > 4.5cm DBH
Avg. Basal Area (m ² /plot)	Average amount of an area (m ² /plot) occupied by tree stems
Tree species richness	Number of different tree species
Canopy Cover	Percentage of points with overstory vegetation, from 20 vertica GRS densiometer sightings along a 20m transect
Proportion Midstory trees	Proportion of trees identified in the canopy zone to be midstory
Proportion Overstory trees	Proportion of trees identified in the canopy zone to be overstory
Proportion Superstory trees	Proportion of trees identified in the canopy zone to be superstory
Midstory Light Exposure	Total number of sides and the top $(n=5)$ of each midstory tree crown that receives direct light
Understory	Vegetation < 2.5m tall and < 4.5 DBH
% understory foliage	Total percent vertical cover of all vegetation profile board sections
Ground Cover	
% total vegetation cover	Visual estimation of total percent plant horizontal cover
% grass cover	ר
% forb cover	
% fern cover	 Visual estimation of percent horizontal cover of each life form
% sedge/rush cover	
% shrub cover	
% seedling cover	
Seedling species density	Total number of seedlings per plot
Seedling species richness	Number of different seedling species
Litter-soil	
Litter depth (cm)	Depth of penetration (≤ 10 cm) into soil material using a metal ruler
Soil-bulk density	Dry-weight density (g/cm ³) of litter-soil core (4x4 cm) sample, after oven drying at 45 ^o C for 48 hours
General	
Slope (%)	Slope angle was measured at the center of the plot using a clinometer
Aspect	Directional degrees of the slope was recorded using a compass

Table 5. Habitat variables measured in 315m² plots used to assess forage and cover characteristics in Cataloochee Valley, GSMNP

used to measure forest forage availability. Ground cover variables were measured using 1 m^2 subplots located in the center of each of the larger overstory plots and included percent cover by life form, measured by visually estimating the areal coverage of grasses, forbs, ferns, sedges/rushes, seedlings, shrubs, and total vegetative cover. Seedlings were also counted by species to determine density and species richness. Litter and soil variables were measured to determine if there were changes related to compaction resulting from differing elk use. Four litter depth measurements and four 5 x 5 cm (diameter x depth) soil core samples were collected in each of the larger overstory plots in the four cardinal directions at 10 m from the center of the plot.

The 47 plot locations used for measuring habitat variables were revisited in April-May 2013 to assess woody browse availability and use by elk. Two 1.8 m width parallel line transects each 5 meters long and 5 meters apart were used to survey the proportion of stems browsed to stems available at each plot location. On each transect, woody species were identified to genus and the number of woody stems available for browsing (< 2.0 m from the ground) and the number of stems browsed was counted by species using the methods described by Ford et al. (1993). Percent of available twigs browsed, relative abundance, and relative use for each species were calculated from these data (Table 6) (Strole and Anderson 1992). It is important to note that white-tail deer browse and elk browse are not distinguishable and although some deer do inhabit the Cataloochee Valley, the population is very small (personal communication, Joe Yarkovich, GSMNP Wildlife Biologist). This was confirmed by the lack of deer sightings and presence of sign during the duration of field work. Therefore, this study assumes that the browse data collected is elk browse.

Variable	Calculation	
Percent of available twigs browsed	# twigs browsed of a spp. # twigs available of a spp.	x 100
Relative abundance	# of twigs available of a spp.# of twigs available of all spp.	x 100
Relative use	<pre>#of twigs browsed of a spp. total # of twigs browsed of all spp.</pre>	x 100

Table 6. Browse survey calculations for each plant species identified during an elk browse survey, GSMNP.

Data Analyses

The 161 transect locations with pellet group counts and GIS data layers representing forest type, understory density class, and anthropogenic disturbance use history were used to analyze landscape scale elk forest selection. The distances of each transect location to nonforested areas (open fields and human disturbance) was analyzed in R (R Development Core Team 2011) using logistic and simple linear regression. The proportions of each forest type, understory class, and disturbance history class within the study area were calculated using GIS. The total number of observed pellet groups were counted for each specific habitat category within forest type, understory density, and disturbance history and the expected number of elk pellet groups were calculated by multiplying the proportion of the area for each category (category $m^2/study$ area m^2) by the number of total pellets counted (n=154). The observed occurrence of elk pellet groups was compared to the expected occurrence of elk pellet groups for each habitat category within each forest type, understory density, and disturbance history using Chi-squared Goodness of Fit analyses to test if elk were selecting these forest type, understory density, or disturbance history categories in proportion to their occurrence within the study area (Neu et al. 1974, Beyers and Steinhorst 1984). A Bonferroni Z-statistic (Beyers and Steinhorst 1984) was used to construct Bonferroni confidence intervals to identify whether the frequency of habitat category use was more than, less than, or equal to the frequency expected.

Non-metric multidimensional scaling (NMDS) ordinations were performed collectively on the 47 plot-based habitat variables to visualize possible patterns among the three varying habitat selection categories where varying selection was indicated by 0, 1-2, > 2 pellet groups representing low, moderate and high selection, respectively by elk. The NMDS ordinations were calculated using the program PC-ORD (McCune and Mefford 1995) and were based on Bray-Curtis dissimilarities. A multiresponse permutation procedure (MRPP; McCune and Mefford 1995) was used to verify ordination results and to determine if habitat variables differed among plots of varying selection.

A single-factor ANOVA on each habitat variable measured in the four strata (forest canopy structure, understory, ground cover, and litter-soil) was used to evaluate differences among plots of varying elk pellet group frequencies (0, 1-2, >2). Percentage and proportional data were arcsine transformed and count data was log-transformed to meet ANOVA assumptions. If the ANOVA suggested a difference (p < 0.05), a Tukey's multiple comparisons procedure was used to determine which of the three pellet-frequency selection categories differed. A Spearman's rank correlation matrix was created in R was used to test colinearity between the number of elk pellet groups counted at each plot and all measured plot variables and general site characteristics (slope, aspect), to identify and test the strength of a relationship between pellet group counts and measured habitat data.

The relative abundance (RA) and relative use (RU) of each woody browse species and across all woody browse species were compared using Chi-squared analysis and the Bonferroni Z statistic to test if elk were browsing species in proportion to their occurrence in the study area. The Bonferroni Z statistic was also used to test if elk were using browse species in proportions to their occurrence among plots of the three pellet group selection categories and among plots of the four forest cover types. Plant species were assigned as browsed at rates greater than, less than, or equal to availability if relative use values were higher, lower, or statistically equal to relative abundance values, respectively (p > 0.10) (Crimmins et al. 2010).

Results

In total, 88 km of elk trails were mapped; 45 km were designated high use trails, 30 km were designated moderate use, and 13 km low use (Figure 1). Trails occurred in all of the eight forest cover types listed in Table 1. Elk trails both followed and branched from established park trails, roads, and open fields. High use trails often led to areas with evidence of previous human settlement such as chimney falls, wooden foundational structures, and piled rock fencing. Elk were often spotted on trails and evidence of antler rubbing, bedding, and browse were apparent in some locations based on visual observation.

Fecal pellet groups detected on 15m transects ranged between 0 and 8 (Table 7). Zero elk fecal pellets were detected on 60% of the 161 transects, 28% had between 1-2 pellet groups detected, and 12% of the transects had greater than 2 pellet groups detected. Logistic regression analysis of presence and absence of pellets revealed a 60 % chance of detecting an elk pellet group within 5 meters of nonforested areas (open fields and human disturbances) but as this distance increased to 3000 m, the probability of detecting an elk pellet group declined to 10 % (p < 0.01) (Figure 2). In addition, simple linear regression revealed that although the amount of variation explained was small (7%), the number of elk pellet groups in forested areas was significantly greater as the distance to nonforest areas decreased (p < 0.01) (Figure 3).

# Pellet Groups	# Transects
0	96
1	25
2	20
3	8
4	4
5	4
6	1
7	1
8	2
Total	161

Table 7. Number of 15m transects with pellet group counts ranging from 0 to 8

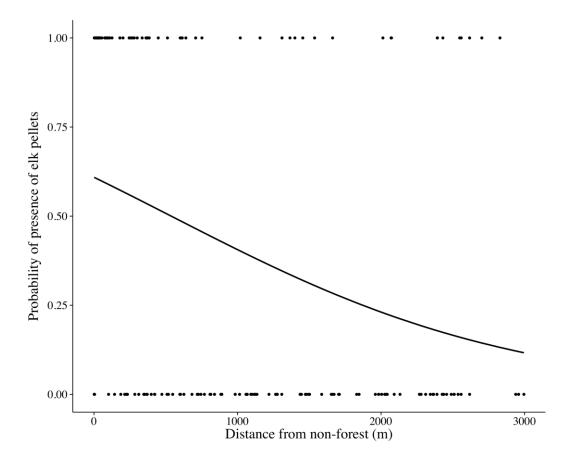


Figure 2. Probability of detecting elk fecal pellets near nonforested areas in Cataloochee Valley, GSMNP

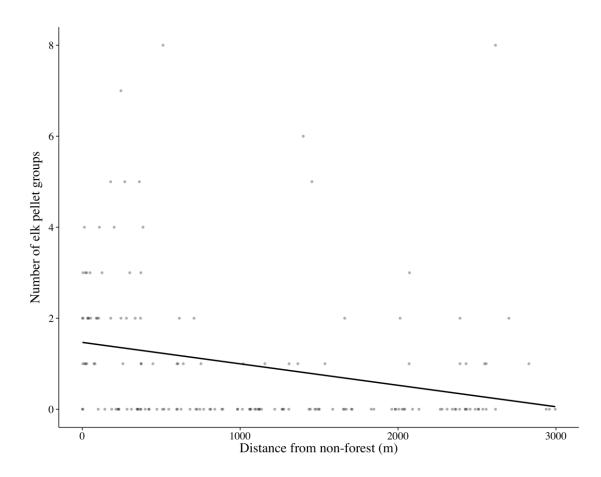


Figure 3. Relationship of elk fecal pellet frequency to distance to nonforested areas in Cataloochee Valley, GSMNP

Of the 154 observations of elk fecal pellet groups, Goodness-of-Fit comparisons showed the expected number of elk pellet groups in forest cover types differed significantly from their occurrence within the study area (7 df, p < 0.001). Successional and floodplain forest types were selected in greater proportion to their availability (p < p(0.05), while northern hardwood, high elevation oak, and montane-cove forests were selected less than their available area (p < 0.05). Elk selected hemlock, oak-hickory, and pine forest types in proportion to their availability (Table 8). Goodness-of-Fit comparisons also showed the expected number of elk pellets in the understory density classes differed significantly from the proportion of their availability (5 df, p < 0.001). Herbaceous/deciduous and rhododendron (light/medium density) understory classes were selected in proportion to their availability, but heavy densities of *Rhododendron* and Kalmia understory were selected less (p < 0.05). Kalmia (light/medium density) was the only understory class variable in the study area selected in greater proportion than its availability (p < 0.05) (Table 8). In addition, Goodness-of-Fit comparisons showed the expected number of elk pellets in the disturbance use history classes differed significantly from the proportion of their availability (5 df, p < 0.001). Areas with diffuse disturbance were selected less than their availability (p < 0.05), while concentrated settlement was selected in greater proportion (p < 0.05). Historic use histories of corporate logging and primary forest were selected in proportion to their availability (Table 8). Overall means for each variable measured in the plots is summarized by forest type in Tables 9 and 10. Means revealed that successional plots tended to have the highest percentage of vegetation ground cover and grass cover. Average basal area

areaTotalGroupsof Pellet(Confident Interval) Habitat Type (km²)AreaObsExpof Pellet(Confident Interval)Forest TypeOak-Hickory23.70.25729410.1920.106 \leq P1 \leq 0.106P1 \leq 0.106Floodplain0.50.0051120.066*0.011 \leq P2 \leq 0.101P2 \leq 0.100P3P3P3P3P3High Elevation Oak10.00.1098170.046*0.000 \leq P4 \leq 0.000 \leq P5 \leq 0.000 \leq P4 \leq 0.000 \leq P5 \leq 0.000 \leq P4 \leq 0.000	n of	Proportion							
Habitat Type(km²)AreaObsExpGroups1Interval)Forest TypeOak-Hickory23.70.25729410.1920.106 \leq P1 \leq 0.106Floodplain0.50.0051120.066*0.011 \leq P2 \leq 0.101Hemlock9.20.10025150.1660.084 \leq P3 \leq 0.102High Elevation Oak10.00.1098170.046*0.000 \leq P4 \leq 0.000 \leq P4 \leq 0.000Montane-Cove22.20.24121370.139*0.063 \leq P5 \leq 0.0160.016 \leq P6 \leq 0.000P4 \leq 0.073*0.016 \leq P6 \leq 0.016Northern Hardwood13.90.15211240.073*0.016 \leq P6 \leq 0.024P7 \leq 0.139 \leq P7 \leq 0.141P1 \leq 0.07113110.0860.024 \leq P8 \leq 0.024 \leq P8 \leq 0.028*0.201 \leq P2 \leq 0.241154Understory Density Class ² 22.90.24942390.2780.183 \leq P1 \leq 0.201 \leq P2 \leq 0.201 \leq P2 \leq 0.201 \leq P3 \leq 0.201 \leq P4 \leq 0.201 \leq P2 \leq 0.201 \leq P4 \leq 0.201 \leq P4 \leq 0.201 \leq P2 \leq 0.201 \leq P4 \leq 0.201 \leq P4 \leq 0.201 \leq P4 \leq 0.201 \leq P2 \leq 0.201 \leq P4 \leq 0.201 \leq P2 \leq 0.201 \leq P4 \leq		Occurrenc		-	ellet	# P	%	Total	
Forest TypeOak-Hickory23.70.25729410.1920.106 \leq P ₁ \leq 0Floodplain0.50.0051120.066*0.011 \leq P ₂ \leq 0Hemlock9.20.10025150.1660.084 \leq P ₃ \leq 0High Elevation Oak10.00.1098170.046*0.000 \leq P ₄ \leq 0Montane-Cove22.20.24121370.139*0.063 \leq P ₅ \leq 0Northern Hardwood13.90.15211240.073*0.016 \leq P ₆ \leq 0Successional3.50.0383670.232*0.139 \leq P ₇ \leq 0Pine6.60.07113110.0860.024 \leq P ₈ \leq 0Total Pellet Groups154154154154Understory Density Class²Herbaceous/Deciduous22.90.24942390.2780.183 \leq P ₁ \leq 0Kalmia (L,M)15.50.16846260.298*0.201 \leq P ₂ \leq 0Kalmia (L,M)29.90.32554490.3510.250 \leq P ₄ \leq 0Rhododendron (L,M)29.90.32554490.3510.250 \leq P ₄ \leq 0Other3.40.037860.0460.000 \leq P ₆ \leq 0Total Pellet Groups154154154154Disturbance HistoryConcentrated settlement14.30.1671240.461 </td <td></td> <td>(Confidence</td> <td></td> <td></td> <td>oups</td> <td>Gro</td> <td>Total</td> <td>area</td> <td></td>		(Confidence			oups	Gro	Total	area	
Oak-Hickory Floodplain23.70.25729410.1920.106 $\leq P_1 \leq 0$ Floodplain0.50.0051120.066*0.011 $\leq P_2 \leq 0$ Hemlock9.20.10025150.166 $0.084 \leq P_3 \leq 0$ High Elevation Oak10.00.109817 0.046 * $0.000 \leq P_4 \leq 0$ Montane-Cove22.20.2412137 0.139 * $0.063 \leq P_5 \leq 0$ Northern Hardwood13.90.1521124 0.073 * $0.016 \leq P_6 \leq 0$ Successional3.50.038367 0.232 * $0.139 \leq P_7 \leq 0$ Pine6.60.0711311 0.086 $0.024 \leq P_8 \leq 0$ Total Pellet Groups154154154154Understory Density Class ² Herbaceous/Deciduous22.9 0.249 4239 0.278 $0.183 \leq P_1 \leq 0$ Kalmia (L,M)15.5 0.168 4626 0.298 * $0.201 \leq P_2 \leq 0$ Kalmia (L,M)29.9 0.325 5449 0.351 $0.250 \leq P_4 \leq 0$ Rhododendron (L,M)29.9 0.325 5449 0.000 * $0.000 \leq P_5 \leq 0$ Other3.4 0.037 86 0.046 $0.002 \leq P_6 \leq 0$ Disturbance History154154154154Concentrated settlement14.3 0.16 7124 0.461 * $0.419 \leq P_1 \leq 0$ <td>l)</td> <td>Interval)</td> <td>3¹</td> <td>Groups</td> <td>Exp</td> <td>Obs</td> <td>Area</td> <td>(km²)</td> <td>Habitat Type</td>	l)	Interval)	3 ¹	Groups	Exp	Obs	Area	(km²)	Habitat Type
Floodplain0.50.0051120.066* $0.011 \le P_2 \le P_1$ Hemlock9.20.10025150.166 $0.084 \le P_3 \le P_1$ High Elevation Oak10.00.1098170.046* $0.000 \le P_4 \le P_1$ Montane-Cove22.20.24121370.139* $0.063 \le P_5 \le P_1$ Northern Hardwood13.90.15211240.073* $0.016 \le P_6 \le P_1$ Successional3.50.0383670.232* $0.139 \le P_7 \le P_1 \le P_1$ Pine6.60.07113110.086 $0.024 \le P_8 \le P_1 \le P$									Forest Type
Hemlock9.20.10025150.166 $0.084 \le P_3 \le 0$ High Elevation Oak10.00.1098170.046* $0.000 \le P_4 \le 0$ Montane-Cove22.20.24121370.139* $0.063 \le P_5 \le 0$ Northern Hardwood13.90.15211240.073* $0.016 \le P_6 \le 0$ Successional3.50.0383670.232* $0.139 \le P_7 \le 0$ Pine6.60.07113110.086 $0.024 \le P_8 \le 0$ Total Pellet Groups154154154154Understory Density Class²Herbaceous/Deciduous22.90.24942390.278 $0.183 \le P_1 \le 0$ Kalmia (L,M)15.50.16846260.298* $0.201 \le P_2 \le 0$ Kalmia (H)9.20.1004160.026* $0.000 \le P_3 \le 0$ Rhododendron (L,M)29.90.32554490.351 $0.250 \le P_4 \le 0$ Rhododendron (H)11.00.120018 $0.000 \le 0.000 \le P_5 \le 0$ Other3.40.03786 0.046 $0.002 \le P_6 \le 0$ Disturbance History154154154154	0.279	$0.106 \le P_1 \le 0$							
High Elevation Oak Montane-Cove10.00.1098170.046*0.000 $\leq P_4 \leq 0$ Montane-Cove22.20.24121370.139*0.063 $\leq P_5 \leq 0$ Northern Hardwood13.90.15211240.073*0.016 $\leq P_6 \leq 0$ Successional3.50.0383670.232*0.139 $\leq P_7 \leq 0$ Pine6.60.07113110.0860.024 $\leq P_8 \leq 0$ Total Pellet Groups154154154Understory Density Class²Herbaceous/Deciduous22.90.24942390.2780.183 $\leq P_1 \leq 0$ Kalmia (L,M)15.50.16846260.298*0.201 $\leq P_2 \leq 0$ Kalmia (H)9.20.1004160.026*0.000 $\leq P_3 \leq 0$ Rhododendron (L,M)29.90.32554490.3510.250 $\leq P_4 \leq 0$ Other3.40.037860.0460.002 $\leq P_6 \leq 0$ Disturbance History154154154154	-	$0.011 \le P_2 \le 0$	*						1
Montane-Cove22.20.24121370.139*0.063 $\leq P_5 \leq P_5$ Northern Hardwood13.90.15211240.073*0.016 $\leq P_6 \leq P_6$ Successional3.50.0383670.232*0.139 $\leq P_7 \leq P_7 \leq P_7$ Pine6.60.07113110.0860.024 $\leq P_8 \leq P_7$ Total Pellet Groups154154154154Understory Density Class²Herbaceous/Deciduous22.90.24942390.2780.183 $\leq P_1 \leq P_2 \leq P_1$ Kalmia (L,M)15.50.16846260.298*0.201 $\leq P_2 \leq P_2$ Kalmia (H)9.20.1004160.026*0.000 $\leq P_3 \leq P_2$ Rhododendron (L,M)29.90.32554490.3510.250 $\leq P_4 \leq P_2$ Other3.40.037860.0460.002 $\leq P_6 \leq P_2$ Disturbance History154154154	0.248	$0.084 \le P_3 \le 0$		0.166	15		0.100	9.2	
Northern Hardwood13.9 0.152 11 24 0.073 $*$ $0.016 \le P_6 \le 0$ Successional 3.5 0.038 36 7 0.232 $*$ $0.139 \le P_7 \le 0$ Pine 6.6 0.071 13 11 0.086 $0.024 \le P_8 \le 0$ Total Pellet Groups 154 154 154 $0.016 \le P_6 \le 0$ Understory Density Class ² Herbaceous/Deciduous 22.9 0.249 42 39 0.278 $0.183 \le P_1 \le 0$ Kalmia (L,M) 15.5 0.168 46 26 0.298 $*$ $0.201 \le P_2 \le 0$ Kalmia (H) 9.2 0.100 4 16 0.026 $*$ $0.000 \le P_3 \le 0$ Rhododendron (L,M) 29.9 0.325 54 49 0.351 $0.250 \le P_4 \le 0$ Other 3.4 0.037 8 6 0.046 $0.002 \le P_6 \le 0$ Disturbance HistoryConcentrated settlement 14.3 0.16 71 24 0.461 $*$ $0.419 \le P_1 \le 0$	0.092	$0.000 \le P_4 \le 0$	*						
Successional Pine3.50.0383670.232* $0.139 \le P_7 \le 0$ Pine6.60.07113110.086 $0.024 \le P_8 \le 0$ Total Pellet Groups154154154154Understory Density Class²Herbaceous/Deciduous22.90.24942390.278 $0.183 \le P_1 \le 0$ Kalmia (L,M)15.50.16846260.298* $0.201 \le P_2 \le 0$ Kalmia (H)9.20.1004160.026* $0.000 \le P_3 \le 0$ Rhododendron (L,M)29.90.32554490.351 $0.250 \le P_4 \le 0$ Rhododendron (H)11.00.120018 0.000 * $0.000 \le P_5 \le 0$ Other3.40.03786 0.046 $0.002 \le P_6 \le 0$ Total Pellet GroupsTotal Pellet Groups									

Table 8. Elk habitat selection versus available habitat in Cataloochee Valley, GSMNP. Selection is based on fecal pellet group counts at 161 transect locations. Habitat types are described in Tables 1, 2, and 3

¹ * = significant at p < 0.05

² L, M, H = light, medium, high density

	<u>Forest Type</u>				
	Cove	Hemlock	Montane oak-	Successional	
Variable	(n=10)	(n=9)	hickory (n=11)	(n=17)	
Avg. Basal Area (m ² /plot)	23.6 (17.1)	19.4 (7.63)	26.0 (11.1)	18.6 (9.27)	
Tree species richness	6.50 (1.27)	7.00 (1.32)	8.75 (1.60)	6.88 (2.29)	
Canopy Cover	0.79 (0.13)	0.72 (0.17)	0.69 (0.17)	0.76 (0.09)	
Proportion Midstory trees	0.45 (0.19)	0.55 (0.18)	0.46 (0.15)	0.50 (0.15)	
Proportion Overstory trees	0.35 (0.14)	0.26 (0.16)	0.35 (0.12)	0.28 (0.13)	
Proportion Superstory trees	0.20 (0.09)	0.19 (0.10)	0.19 (0.12)	0.22 (0.12)	
Midstory Exposure Class	0.85 (0.50)	1.43 (0.62)	1.14 (0.61)	1.41 (0.56)	
% vegetation cover	0.58 (0.21)	0.43 (0.27)	0.44 (0.26)	0.63 (0.18)	
% grass cover	0.01 (0.02)	0.01 (0.01)	0.01 (0.01)	0.03 (0.06)	
% forb cover	0.26 (0.21)	0.21 (0.28)	0.20 (0.23)	0.31 (0.21)	
% fern cover	0.05 (0.06)	0.06 (0.07)	0.04 (0.11)	0.10 (0.16)	
% sedge/rush cover	0.04 (0.10)	0.01 (0.02)	0.01 (0.02)	0.03 (0.05)	
% shrub cover	0.13 (0.23)	0.05 (0.13)	0.09 (0.17)	0.01 (0.02)	
% understory foliage	0.39 (0.14)	0.36 (0.13)	0.33 (0.15)	0.32 (0.13)	
% seedling cover	0.09 (0.05)	0.09 (0.07)	0.10 (0.06)	0.15 (0.14)	
Seedling species density	16.3 (12.7)	18.9 (13.6)	18.4 (18.0)	9.12 (8.31)	
Seedling species richness	3.33 (0.87)	3.56 (1.33)	3.42 (1.31)	2.65 (2.03)	
Litter depth	3.20 (1.43)	2.81 (1.54)	2.38 (0.83)	2.07 (1.51)	
Soil-bulk density	55.2 (16.9)	73.6 (60.9)	56.3 (18.1)	60.8 (16.8)	

Table 9. Means (S.E.) values for habitat variables measured in 315m² plots in four forest types of varying elk selection in Cataloochee Valley, GSMNP

Table 10. Mean size and density of dominant woody species in 315m² plots in four forest types of varying elk selection in Cataloochee Valley,GSMNP

Forest Type	Dominant Tree spp.	Avg # trees/ha	Avg DBH (cm)	Avg BA/ha	Avg # seedlings/ha
Hemlock	Tsuga spp.	370.4	14.9	6.5	0
	Acer rubrum, Acer saccharum	116.4	14.9	4.6	447.9
	Rhododendron spp.	109.4	7.5	0.5	14.1
	Other (n=17)	373.9	25.4	19.0	199.9
Montane oak-					
hickory	Acer rubrum, Acer saccharum	225.4	17.5	5.4	228.6
	Tsuga spp.	177.8	14.5	2.9	0
	Oxydendrum arboreum	98.4	16.4	2.1	5
	Other (n=21)	343.8	19.3	18.9	168.27
Successional	Liriodendron tulipifera	183.0	27.1	10.5	5.6
	Acer rubrum, Acer saccharum	130.7	18.6	3.5	37.4
	Hamamelis	61.6	15.1	1.1	0
	Other (n=24)	418.4	16.4	11.0	158.8
Cove	Betula spp.	146.5	24.6	6.9	12.7
	Tsuga spp.	146.1	13.6	2.1	0
	Rhododendron spp.	88.9	6.9	0.3	22.2
	Other (n=24)	466.7	25.4	31.5	130.2

tended to be greater in montane oak-hickory stands, and smaller in successional forests. The canopy cover among forest types was similar, ranging between 69% to 79% canopy closure (Table 9). For the three selection categories of pellet group frequencies, NMDS and MRPP revealed no significant dissimilarities in forest canopy variables (average basal area (m²/plot), tree species richness, canopy cover, proportion midstory trees, proportion of overstory trees, proportion superstory trees, midstory light exposure) (Figure 4) or percent understory foliage, ground cover (percent total vegetation cover, percent cover by life form, seedling species density, seedling species richness), and littersoil variables (Litter depth, soil-bulk density) (Figure 5) and MRPP showed no significant differences (p < 0.178) among these groups. Further investigation using ANOVA revealed that none of the habitat variables (forest canopy, understory foliage density, ground cover, litter-soil variables) differed significantly (p < 0.05) among the plots with the three varying elk pellet group frequencies (Table 11). However, there was a trend of greater average tree basal areas (m²/plot), tree species richness, and seedling species richness in plots with 0 pellet groups and plots with pellet groups > 2 (p = 0.073, 0.090, and 0.09 respectively). Spearman rank correlation coefficients between the number of pellet groups counted at each plot and the 21 measured plot variables revealed that none of the variables had significant correlations with the number of pellet groups detected (p > 0.05).

A total of 27 woody species were identified among plots during the browse survey. Species with the greatest relative abundance (RA) were Carolina silverbell, mountain laurel, and striped maple. Flowering dogwood, eastern white pine, sassafras tulip-poplar, American strawberry-bush blackberry, American beech, and American

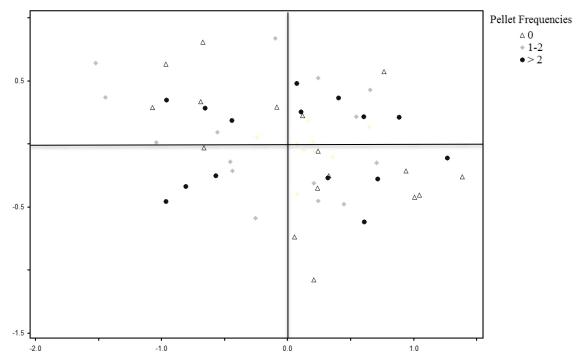


Figure 4. NMDS ordination of forest structure variables among plots of varying elk fecal pellet group selection categories (0, 1-2, >2)

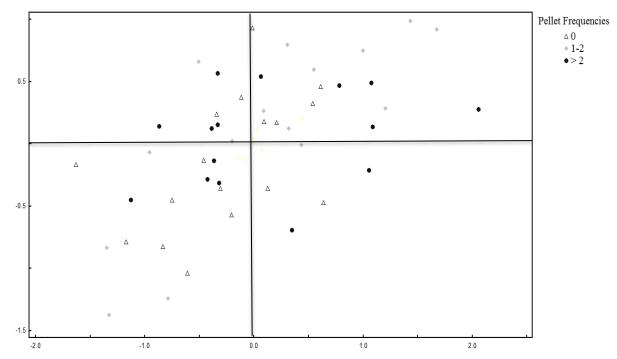


Figure 5. NMDS ordination of ground cover, understory foliage density, and litter-soil habitat variables among plots of varying elk pellet group selection categories (0. 1-2, >2)

Pellet Group Frequency						
Variable	0	1-2	>2			
	(n=17)	(n=15)	(n=15)	P-value		
Avg. Basal Area (m ² /plot)	24.8 (15.7)	16.9 (6.59)	22.6 (8.19)	0.07		
Tree species richness (#)	7.78 (1.80)	6.73 (2.15)	7.27 (1.83)	0.09		
Canopy Cover (%)	0.75 (0.13)	0.74 (0.13)	0.73 (0.16)	0.97		
Proportion Midstory trees	0.47 (0.15)	0.46 (0.17)	0.53 (0.18)	0.35		
Proportion Overstory trees	0.30 (0.14)	0.33 (0.14)	0.30 (0.14)	0.84		
Proportion Superstory trees	0.23 (0.14)	0.21 (0.08)	0.17 (0.10)	0.44		
Midstory Exposure Class (#)	1.33 (0.63)	1.18 (0.64)	1.17 (0.54)	0.91		
% vegetation cover	0.59 (0.26)	0.45 (0.21)	0.55 (0.22)	0.97		
% grass cover	0.00 (0.01)	0.02 (0.06)	0.01 (0.02)	0.35		
% forb cover	0.30 (0.27)	0.21 (0.16)	0.24 (0.22)	0.84		
% fern cover	0.09 (0.17)	0.05 (0.06)	0.06 (0.09)	0.44		
% sedge/rush cover	0.01 (0.02)	0.05 (0.09)	0.02 (0.04)	0.91		
% seedling cover	0.10 (0.07)	0.11 (0.09)	0.13 (0.13)	0.97		
% shrub cover	0.08 (0.18)	0.01 (0.03)	0.09 (0.17)	0.84		
% understory foliage	0.37 (0.11)	0.30 (0.15)	0.37 (0.15)	0.48		
Seedling Species Density (#)	18.4 (17.8)	9.53 (9.87)	15.6 (8.34)	0.16		
Seedling Species Richness (#)	3.39 (1.58)	2.40 (1.55)	3.64 (1.34)	0.09		
Litter depth (cm)	2.70 (1.78)	2.70 (1.14)	2.13 (1.04)	0.91		
Soil Bulk Density (g/cm ³)	49.1 (16.8)	65.6 (14.5)	70.3 (46.7)	0.97		

Table 11. Analyses of variance comparing forest canopy structure, ground cover, understory foliage density, and litter-soil variables among plots with varying elk pellet group selection categories (0, 1-2, >2) in Cataloochee Valley, GSMNP

Variable	r	Relationship	P-value
Slope (%)	0.18	-	0.24
Aspect (degrees)	0.03	+	0.82
Basal Area (m ² /plot)	0.05	+	0.19
Tree species richness (#)	0.20	+	0.18
proportion midstory trees	0.16	+	0.29
proportion overstory trees	0.05	-	0.76
proportion superstory trees	0.16	-	0.28
midstory light exposure (#)	0.10	-	0.52
Canopy Cover (%)	0.01	-	0.31
understory foliage density	0.09	-	0.56
% vegetative ground cover	0.03	-	0.93
% grass cover	0.02	+	0.22
% forb cover	0.06	-	0.83
% fern	0.11	-	0.72
% sedges-rushes	0.00	0	0.33
% shrub	0.01	+	0.63
% seedling	0.10	+	0.91
seedling density (#)	0.09	+	0.94
seedling species richness (#)	0.11	+	0.89
Litter depth (cm)	0.15	+	0.91
Soil bulk density (g/cm ³)	0.13	+	0.40

Table 12. Spearman rank correlation coefficients (r) between measured plot variables and pellet group frequencies from 47 plots in Cataloochee Valley, GSMNP

hornbeam were browsed at rates higher than their respective availabilities (p < 0.05) while witch-hazel, birch, maple, blueberry, eastern hemlock, mountain laurel, Carolina silverbell, rhododendron, mountain doghobble, and basswood were browsed at rates lower than their respective availabilities (p < 0.05). The relative abundance of woody browse was highest in successional and hemlock forests but only successional forests had browse rates higher than browse available (p < 0.05) (Table 14). The relative abundance of browse available also differed among plots of different fecal pellet group frequencies (0, 1-2 and > 2 pellet groups). Plots with pellet groups selection categories ranging from 1-2 groups and > 2 groups were browsed at rates higher than the respective browse availability (p < 0.05) (Table 14).

Species	PATB ¹	RA	RU	Use ²
Cherry (Prunus spp.)	21.74	0.35	0.48	Equal
Oak (<i>Quercus</i> spp.)	14.29	0.53	0.48	Equal
Greenbriar (Smilax spp.)	11.05	2.86	2.03	Equal
Chestnut oak (Quercus prinus)	0.00	0.51	0.00	Equal
Yellow buckeye (Aesculus flava)	0.00	0.33	0.00	Equal
Hickory (Carya spp.)	0.00	0.30	0.00	Equal
American holly (<i>Ilex opaca</i>)	0.00	0.23	0.00	Equal
Flowering dogwood (Cornus florida)	55.04	5.52	19.54	Greater
Eastern White Pine (Pinus strobus)	41.84	2.12	5.71	Greater
Sassafras (Sassafras albidum)	36.60	3.53	8.32	Greater
Tulip-poplar (<i>Liriodendron tulipifera</i>)	36.17	0.71	1.64	Greater
American strawberry-bush (Euonymus				
americanus)	35.29	3.32	7.54	Greater
Blackberry (Rubus spp.)	33.66	3.08	6.67	Greater
American beech (Fagus grandifolia)	26.33	5.65	9.57	Greater
American hornbeam (Carpinus caroliniana)	23.68	3.43	5.22	Greater
Striped maple (Acer pennsylvanicum)	23.49	9.73	14.70	Greater
Sourwood (Oxydendrum arboreum)	18.66	6.04	7.25	Greater
Witch-hazel (Hamamelis virginiana)	10.98	2.47	1.74	Less
Birch (Betula spp.)	7.61	4.15	2.03	Less
Maple (Acer rubrum, Acer saccharum)	7.24	6.65	3.09	Less
Blueberry (Vaccinium spp.)	5.26	1.43	0.48	Less
Eastern hemlock (Tsuga canadensis)	5.18	3.77	1.26	Less
Mtn. Laural (Kalmia latifolia)	2.34	10.30	1.55	Less
Carolina silver bell (Halesia tetraptera)	0.72	14.64	0.68	Less
Rhododendron (Rhododendron maximum)	0.00	6.86	0.00	Less
Mountain doghobble (Leucothoe fontanesiana)	0.00	1.28	0.00	Less
Basswood (Tilia americana)	0.00	0.23	0.00	Less
$^{1}PATB = percent of available twigs browsed, RA = 100000000000000000000000000000000000$	= relative ab	undance	RU = rela	ative use

Table 13. Woody browse availability and use by elk in the Cataloochee Valley, GSMNP

 $^{1}PATB = percent of available twigs browsed, RA = relative abundance, RU = relative use <math>^{2}Use = less or greater use than available (p < 0.05)$

Forest Type	PATB ¹	RA	RU	Use ²
Successional	26.9	34.6	59.9	Greater
Montane-cove	9.85	18.2	11.5	Less
Oak-Hickory	12.1	20.4	15.9	Less
Hemlock	7.39	26.9	12.8	Less
Pellet Group Frequenc	су У			
0	10.9	38.8	27.5	Less
1-2	19.2	34.7	42.7	Greater
> 2	17.6	26.5	29.9	Greater

Table 14. Browse variation among forest types and pellet group selection categories in the Cataloochee Valley, GSMNP

 $^{1}PATB =$ percent of available twigs browsed, RA = relative abundance, RU = relative use $^{2}Use =$ less or greater use than available (p < 0.05)

Discussion

In GSMNP elk are selecting successional and floodplain forests in greater proportions than the available proportions of these forest types in the study area based on elk pellet group counts and browse survey results. Since the arrangement of food and cover relate closely to how elk distribute themselves (Thomas et al. 1988, Leckenby 1984, Cook 2002, Kigima and Fairbanks 2013), the preferential selection of these forest types suggest they are providing desirable food and cover habitat components. In contrast, results from GPS collar locations in the five years after the initial introduction indicated elk preferred open grazing land with interspersed cover (Murrow et al. 2009). With limited grassland habitat in the Cataloochee Valley, it appears elk are now selecting forest types that have desired forage biomass. Data from 72 studies that quantified elk diet selection in western North America between 1938 and 2002 revealed that although elk consistently selected for graminoids in all habitat types, they would also forage in disturbed forested areas where the availability of graminoids was low (Christianson and Creel 2007). Forest structures with more open canopies maintained by disturbance provide greater light to the forest floor which can increase primary production of herbaceous forage species (Perryman et al. 2002; Van Dyke and Darragh 2006, Lashley et al. 2011). Disturbance is characteristic of both successional and floodplain forest types in GSMNP (Jenkins 2007) and thus they are more likely to have greater availability of graminoids and herbaceous species. In Idaho, forests in the early stages of succession produced more forage and were selected more by elk (Irwin and Peek 1983). Of the four forest types evaluated for habitat variables, successional plots in GSMNP contained the highest percentages of total vegetative ground cover and the highest percentage of

graminoids (grasses, sedges-rushes) (Table 9). In addition, the trend in average basal area (m²/per plot) suggests that elk are selecting areas with less basal area. In the Blue Mountains of Oregon basal area was used to estimate crown closure to index cover for elk. The selection of areas with less basal area in GSMNP suggests that elk are selecting more open forests (Dealy 1985). Although, floodplain forests were not evaluated for habitat variables in GSMNP, they are described as containing a dense and species rich herbaceous layer that can contain abundant availability of sedges-rushes (graminoids) (Madden et al. 2004, Jenkins 2007).

Throughout their range elk in forested ecosystems choose forest stands in earlier successional stages with less dense canopies that produce ground cover for forage (Basile 1979, Singer 1979, Metlen et al. 2004, Van Dyke and Darragh 2006), suggesting that forests with older forest characteristics are not being selected by elk for forage. In GSMNP older forests such as northern hardwood and high elevation oak forests were selected less than their availability. Although plot variables were not measured in these forest types, both are characterized by closed canopies where tree reproduction only occurs in gaps (Madden et al. 2004). Furthermore, the full shading of the forest floor promotes shade-tolerant species and only 2 of the 10 species/species groups browsed in greater proportions to their availability were shade tolerant. Ungulate browsing preferences vary with tree species, and preferential selection has been documented to alter the growth and survival of the understory in high-light environments but not low-light environments, suggesting a preference for shade intolerant species for browse (Runkle 1982, Tripler et al. 2005, Long et al. 2008).

Montane-cove forests which were also selected less than their availability had similar average percent of vegetative ground cover as successional forests but only 2% of cover was grass and less than 10% was of composed of sedge-rush cover (Table 9). Hemlock and montane-oak hickory forests selected in equal proportions to their availability had dominant tree species and basal areas consistent with forests in the intermediate stage of succession (Williams 2010) (Table 10). These older forests with their dense canopies produce less understory and ground vegetation for forage. The current intermediate successional stage of hemlock and oak-hickory forests in the study area where light to the forest floor is limited was reflected in habitat variables where both forest types had the lowest percent of vegetative ground cover.

In addition to selection of forest types maintained by disturbance, elk selected areas with different anthropogenic disturbance histories. Elk were selecting habitat with concentrated settlement disturbance history in greater proportions than available in the study area suggesting this disturbance history has resulted in younger forests where greater ground vegetation is available for food and cover (Irwin and Peek 1983). Settlement areas were cleared to bare ground and remained as treeless home sites, fields, and pastures (Pyle 1988). Ecological succession did not move these areas back toward forest until GSMNP was established in 1934. In comparison to the other three disturbance use histories, forests in old settlement are the youngest, and likely have more open canopies and greater vegetation biomass for forage. Primary forests selected in proportion to their availability are older forests with closed canopies and little understory biomass (Williams 2010). Areas of corporate logging were also selected in proportion to their availability despite the fact they were heavily disturbed. These areas in GSMNP can

quickly return to mature forest due to stump sprouting and were likely closed canopied forests despite the previous logging disturbance (Williams 2010). Diffuse disturbance history areas that were selected less than their availability contained large trees at the time of disturbance and would, therefore, now be older more closed forests, suggesting why their selection was less than availability.

In addition to gramminoid biomass, woody browse was also important forage and a habitat selection factor for elk in GSMNP. Pellet group density correlated positively with woody browse use and plots with one or more pellet groups had relative browse use in greater proportions to browse available, while browse in plots with zero pellet groups had less. Plots containing zero pellet groups had the highest abundance of available browse but only 11% of the browse available of the species/species groups that were browsed, in greater proportion to their availability. Therefore, species specific aspects of browse appear to be more important than abundance. In plots where pellet groups were detected, the availability of browse species/species groups used in greater proportions then their availability was higher (1-2 pellet groups (26%), > 2 pellets groups (15%)),also suggesting species specific components of the browse available are more important than the abundance of browse for habitat selection. Although their diets show great plasticity, elk will select diets of similar nutritional value in a variety of habitats by being selective about species browsed (Baker and Hobbs 1982). This appears to be occurring in GSMNP where despite high flora diversity, only ten species/species groups were browsed in greater proportion than their availability.

Species specific selection for browse also appears to be a driver for forest type selection. Available browse species in hemlock and montane-oak hickory forests that

were selected in proportion to their availability and montane cove forests selected less consisted of only 12-13% of the species/species groups browsed in greater proportions. In contrast, successional plots not only had the greatest amount of available browse but the browse contained 42% of the species/species groups selected in greater proportions. Because elk can switch from a diet composed primarily of grasses to one of browse (Jenkins and Starkey 1993, Cook 2002, Schneider et al. 2006) forest habitat types with both forms of forage such as successional forests (and likely floodplain forests) likely provide better habitat for forage and, therefore, influence selection.

Analyses detected no significant differences in any variables measured among plots of varying pellet group selection categories for any of the four forest types suggesting that at their current population size in the Cataloochee Valley, elk habitat selection is not causing measurable differences in vegetation composition and structure, or litter-soil layers. Despite differences in the tree species and the successional state of the forest types examined, canopy cover data indicated 73% of the 47 plots had canopies 75-95% closed suggesting these four forest types (even successional) are relatively mature and would have less quantity and species diversity (Hanley 1980, Huot 1974, Johnson et al. 2000) for elk forage.

The close proximity of greater quantity and quality of forage plants to cover is an important component of elk habitat throughout their range (Frank and McNaughton 1993, Schoenecker et al. 2004). In GSMNP elk selected forested areas closer to open fields and areas of human disturbance. Forests adjacent to grassland communities have been documented as high elk use areas with use decreasing with increased distance from the interface of forest and nonforest communities (Reynolds 1966, Coop 1971) such as

observed in GSMNP. This relationship is likely due to the ecotones between forests and open fields having a higher diversity and quantity of forage which is shown to be an important aspect of elk habitat selection in GSMNP (Murrow et al. 2009) while the shorter distance to forest provides quicker access to cover (Wisdom et al. 2006, Skovlin et al. 2002).

For elk, open habitat is important for forage, but older forests with high percent canopy closure (75-100%) are important for cover (Starkey et al. 1982, Witmer and deCalesta1983, Kamler et al. 2008). Elk in western Oregon manage heat stress by sheltering in old growth forests during midday and throughout late spring to early fall (Witmer and deCalesta 1983) and elk in the old growth rainforests of Oregon and Washington had larger group sizes than would be expected in the closed canopied forests (Jenkins and Starkey 1996). Forested areas with dense canopies are not limited in the Cataloochee Valley; instead they compose a majority of the area in GSMNP. Therefore, the understory composition and density within these stands is likely driving habitat selection in respect to cover for protection from weather and predators (Mysterud and Ostbye 1999, Skovlin et al. 2002, Strohmeyer et al. 1999, Seward 2003, White et al. 2010). Although, forested areas are important for cover (Mysterud 1999), overly dense areas make travel difficult and, therefore, are selected less. Elk in GSMNP are using forested areas with understory classes of light/medium densities of Kalmia in greater proportion than their availability, suggesting that this understory class provides adequate cover and the light to medium density might allow easier movement and ground cover for forage. Heavy density Rhododendron and Kalmia understory classes were used less than their availability and these dense thickets are described by Jenkins (2007) as nearly

impossible to traverse and with a sparse herbaceous layer and low species richness, thus make relatively poor elk habitat. The differential selection of understory density types by elk in GSMNP is likely related to size and spacing of cover and forage (Leckenby 1984). In the Canadian Rocky Mountains, elk selected areas with less dense understory where movement costs were lower (Frair et al. 2005) and in north-central Idaho elk calf recruitment was negatively correlated with high percent understory cover because newborn calves had difficulty negotiating dense shrub fields and were more vulnerable to predation (White et al. 2010).

In summary, elk in GSMNP are not selecting forest types with the highest percent of canopy closure because with the full shade of the forest floor these forest types do not provide adequate biomass for forage or preferred ungulate browse. Instead, elk in GSMNP are selecting forests that contain preferred forage produced by stands with more open canopies in close proximity to open fields and areas of human disturbance that lack overly dense understories that impede travel. The elk in GSMNP are following a similar pattern to elk throughout their range by selecting areas that have more open forest canopies maintained by disturbances, and selecting undisturbed continuous forests less because they do not contain preferred or abundant forage (Basile 1979, Singer 1979, Van Dyke and Darragh 2006).

Management Implications

Elk are utilizing GSMNP vegetation for food, cover, and traveling. Since native ungulates can exert considerable influence on the composition and structure of vegetation (Frank and McNaughton 1993, Schoenecker et al. 2004), density dependent processes associated with population structure of large mammals may interact with ecosystem functioning to increase or decrease biodiversity depending on the size of the herbivore population and the carrying capacity of the ecosystem inhabited (Stewart et al. 2009). The lack of measurable differences in habitat composition and structure or litter-soil layers among pellet group frequencies suggests that at their current population size in the Cataloochee Valley, elk habitat selection is not having negative impacts on park resources. However, the high availability of high quality forage may be the factor driving this lack of negative impacts by elk. GSMNP is renowned as a center of biodiversity within North America due to the complex ecological gradients that combine to create a highly diverse mosaic of biological communities (Jenkins 2007). This abundance and diversity appears to be providing sufficient preferred food resources for elk in GSMNP. Populations below carrying capacity can grow into larger herds with high levels of reproductive success (Cook 2002). The growing population of elk in GSMNP shows positive recruitment (Yarkovich et al. 2011) indicating that this population is currently below carrying capacity and that the habitat available is providing abundant food with high nutritional value.

Understanding that elk select successional and floodplain forests, moderate understories of *Kalmia*, areas of historic concentrated settlements, and forested areas close to open fields/human disturbance in GSMNP suggests monitoring of sensitive park resources should be focused in these areas. In the surrounding forests around Cades Cove, GSMNP, white-tailed deer altered the cover, diversity, and population demographics of forest herbs (Webster et al. 2005) and suppressed tree regeneration (Griggs et al. 2006). Knowing that elk prefer floodplain and early successional forests that are relatively uncommon in the Southern Appalachians suggests large elk densitites could alter these ecosystems. Since floodplain covers only approximately 1% of GSMNP, it is a conservation priority (Madden et al. 2004) and monitoring sensitive park resources in floodplain forests in the Park is particularly important, especially near open fields or human disturbance areas.

Using elk pellet group counts to indicate elk presence and absence on the landscape paired with GIS raster layers that helped describe habitat available was both a cost effective and time efficient method for determining elk habitat selection and use, and could be used for long term monitoring. Direct methods (observation, capture, radiotelemetry) to monitor wildlife habitat selection can be difficult when animals are elusive, capture invasive, or topography is difficult to transverse (Buckland et al. 2001). Indirect methods that survey evidence of sign such as feces, tracks, or nests are practical, efficient and relatively inexpensive ways to monitor wildlife distributions (Neff 1968, Buckland et al. 1993, Buckland et al. 2001). For example, in this study the 161 transects surveyed for fecal pellets took one individual approximately 120 hours and led to an understanding of elk habitat selection.

In GSMNP the pairing of pellet group counts with GIS layers can inform the development of long-term vegetation monitoring needed for elk habitat management. Given that elk in GSMNP appear to be selecting forest habitat with more open canopies where understory vegetation for forage and browse is preferred, future monitoring that detects pellet groups in forest types currently selected less by elk could indicate the population is nearing carrying capacity for preferred habitat. Elk selection of areas with low quality forage could indicate depletion of food sources in preferred younger forests (Langvatn and Hanley 1993). High pellet counts in areas not currently preferred by elk in

GSMNP will indicate more intensive habitat management strategies should be considered. For example, throughout GSMNP, fire suppression has allowed the succession of closed canopy forests, where quality forage for elk is limited (Canon et al. 1987, Romme et al. 1995, Van Dyke and Darragh 2006). Habitat improvement practices such as burning could be undertaken to improve elk forage (Lashley et al. 2011).

LITERATURE CITED

- Allen, E.O. 1972. Elk and timber-a public land jigsaw. Montana Outdoors. February 1971: 38-40.
- Anderson, R. C., and A. J. Katz. 1993. Recovery of browse- sensitive tree species following release from white- tailed deer (*Odocoileus virginianus*) browsing pressure. Biological Conservation 63:203-208.
- Augustine, D. J., and S. J. McNaughton. 1998. Ungulate effects on the functional species composition of plant communities: herbivore selectivity and plant tolerance. Journal of Wildlife Management 62:1165–1183.
- Baker, D. L., and N. T. Hobbs. 1982. Composition and quality of elk summer diets in Colorado. The Journal of Wildlife Management 46(3):694-703.
- Basile, Joseph V. 1979. Elk-aspen relationships on a prescribed burn. U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station,Ogden, Utah, USA. INT-271.
- Bechtold, W. A. 2003. Crown-diameter prediction models for 87 species of stand-grown trees in the eastern United States. Southern Journal of Applied Forestry 27:269-278.
- Beck, J. L., and J. M. Peek. 2005. Great Basin summer range forage quality: do plant nutrients meet elk requirements? Western North American Naturalist 65(4):516-527.
- Bender, L. C., and J. B. Haufler. 1999. Relationships between social group size of elk (*Cervus elaphus*) and habitat cover in Michigan. The American Midland Naturalist 135(2): 261-265.
- Beyers, C. R., and R. K. Steinhorst. 1984. Clarification of a technique for analysis of utilization-availability data. Journal of Wildlife Management 48:1050-1053.
- Binkley, D., F. J. Singer, M. Kaye, and R. Rochelle. 2003. Influence of elk grazing on soil and nutrients in Rocky Mountain National Park. Forest Ecology and Management 185:239–247.
- Bryant, L. D., and C. Maser. 1982. Classification and distribution. Pages 1-59 *in* D. E.
 Toweill and J. W. Thomas, editors. North American elk: ecology and management.
 Smithsonian Institution Press, Washington, D. C., USA.
- Buckland, S. T., D. A. Anderson, K. P. Burnham, and J. L. Laake. 1993. Distance Sampling: Estimating Abundance of Biological Populations. Chapman & Hall, London, UK.
- Buckland, S. T., D. R. Anderson, K. P. Burnham, J. L. Laake, D. L. Borchers, and L. Thomas. 2001. Introduction to distance sampling: Estimating abundance of biological populations. Oxford University Press, Oxford, UK.

- Canon, S. K., P. J. Urness, and N. V. DeByle. 1987. Habitat selection, foraging behavior, and dietary nutrition of elk in burned aspen forest. Journal of Range Management 40(5): 443-438
- Carl, G. R., and C. T. Robbins. 1988. The energetic cost of predator avoidance in ungulates: hiding versus following. Canadian Journal of Zoology 66: 239-246.
- Carpenter, J., and N. Silvy. 1991. Movements and habitat relations of a small elk population in West Texas. Pages 64-68 *in* Proceedings of the elk vulnerability symposium. A. G. Christensen, L. J. Lyon, and T. N. Lonner, compilers. Montana State University, Bozeman, Montana, USA.
- Christianson, D. A., and S. Creel. 2007. Review of environmental factors affecting elk winter diets. Journal of Wildlife Management. 71(1): 164-176.
- Conard, J. M., and P. S. Gipson. 2012 Foraging ecology of elk (*Cervus elaphus*) in a Tallgrass Prairie. Southwestern Naturalist 57(1):92-96.
- Cook, J. G. 2002. Nutrition and food. Pages 259-350 *in* D. E. Toweill and J. W. Thomas, editors. North American elk: ecology and management. Smithsonian Institution Press, Washington, D. C., USA.
- Coop K. J. 1971. Habitat use, distribution, movement and associated behavior of elk, Little Belt, Montana. Thesis, University of Idaho, Moscow, USA.
- Cox, J.J. 2010. Tales of a repatriated megaherbivore: challenges and opportunities for management of reintroduced elk in Appalachia. Pages 632-642 in Proceedings of the 17th Central Hardwood Forest Conference. General Technical Report P-78. United States Department of Agriculture, Forest Service, Northern Research Station.
- Creel, S., and J. A.Winnie, Jr. 2005. Responses of elk herd size to fine-scale spatial and temporal variation in the risk of predation by wolves. Animal Behavior 69: 1181-1189.
- Crimmins, S. M., J. W. Edwards, W. M. Ford, P. D. Keyser, and J. M. Crum. 2010. Browsing patterns of white-tailed deer following increased timber harvest and a decline in population density. International Journal of Forestry Research 592034, 7 pages. doi: 10.1155/9384
- Danell, K., R. Bergstrom, L. Edenius, and G. Ericsson. 2003. Ungulates as drivers of tree population dynamics at module and genet levels. Forest Ecology and Management 181:67-76
- Dealy, J. E. 1985. Tree basal area as an index of thermal cover for elk. United States Department of Agriculture, Forest Service, Pacific Northwest Research Station, Portland, Oregon, USA.

- Elliot, K. J., L. R. Boring, and W. T. Swank. 1998. Changes in vegetation structure and diversity after grass-to-forest succession in a southern Appalachian watershed. The American Midland Naturalist 140: 219-232.
- Feranec, R., and S. Stable. 2007. Carbon isotope values reveal evidence of resource partitioning among ungulates from modern C3-dominated ecosystems in North America. Palaeogeography, Palaeoclimatology, Palaeoecology 252: 575-586.
- Flerov, K. K. 1952. Musk deer and deer: Fauna of the USSR. Volume 2. Mammals. The Academy of Sciences, Moscow, USSR.
- Ford, W. M., A. S. Johnson, P. E. Hale, and J. M. Wentworth. 1993. Availability and use of spring and summer woody browse by deer in clear-cut and uncut forests of the southern Appalachians. Southern Journal of Applied Forestry 17:116–119.
- Frair J. L., E. H. Merrill, H. L. Beyer, J. M. Morales, D. R. Visscher, and D. Fortin. 2005. Scales of movement by elk (*Cervus elaphus*) in response to heterogeneity in forage resources and predation risk. Landscape Ecology 20: 253-287.
- Frank, D. A., and S. J. McNaughton. 1993. Evidence for the promotion of above ground grassland production by native large herbivores in Yellowstone National Park. Oecologia 96:157-161.
- Geist, V. 1998. Red deer. Pages 170-222 *in* Deer of the World: Their Evolution, Behavior, and ecology. Stackpole, Mechanicsburg, Pennsylvania, USA.
- Geist, Valerius. 2002. Adapative Behavioral Strategies. Pages 389-43 in D. E. Toweill and J. W. Thomas, editors. North American elk: ecology and management. Smithsonian Institution Press, Washington, D. C., USA.
- Gordon, I. J., A. J. Hester, and M. Festa-Bianchet. 2004. The management of wild large herbivores to meet economic, conservation and environmental objectives. Journal of Applied Ecology 41(6):1021-1031.
- Griggs, J. A., J. H. Rock, C. R. Webster, and M. A. Jenkins. 2006. Vegetative legacy of a protected deer herd in Cades Cove, Great Smoky Mountains National Park. Natural Areas Journal 26:126-136.
- Grogan, P., T. D. Bruns, and F. S. Chapin III. 2000. Fire effects on ecosystem nitrogen cycling in a Californian bishop pine forest. Oecologia 122: 537-544.

- Grover, K. E., and M. J. Thompson. 1986. Factors influencing spring feeding site selection by elk in the Elkhorn Mountains, Montana. Journal of Wildlife Management 50(3): 466-470.
- GSMNP-EA. 2011. Environmental assessment for the establishment of elk (*Cervus elaphus*) in Great Smoky Mountain National Park: Elk Status and Management. United States Department of the Interior, National Park Service.
- Guthrie, R D. 1966. The extinct wapiti of Alaska and Yukon Territory. Canadian Journal of Zoology 44(1): 47-57.
- Hanley T. A. 1980. Nutritional Constraints on Food and Habitat Selection by Sympatric Ungulates. Thesis, University of Washington, Seattle, USA.
- Hanley, T. A., C. T. Robbins, and D. E. Spalinger. 1989. Forest habitats and the nutritional ecology of Sitka black-tailed deer: a research synthesis with implications for forest management. United States Department of Agriculture, Forest Service, Pacific Northwest Research Station, Portland, Oregon, USA. PNW-G7R-230
- Harper, J. A., J. H. Harn, W. W. Bentley, and C. F. Yocom. 1967. The status and ecology of the Roosevelt elk in California. Wildlife Monographs 16: 3-49
- Hayes, R. L., C. Summers, and W. Seitz. 1981. Estimating wildlife habitat variables. United States Department of the Interior, Fish and Wildlife Service. FWS/OBS-81/47.
- Holthausen, R.S., M.J. Wisdom, J. Pierce, D.K. Edwards and M. M. Rowland. 1994. Using expert opinion to evaluate a habitat effectiveness model for elk in western Oregon and Washington. Res. Pap. PNW-RP-479. United States Department of Agriculture, Forest Service, Portland, Oregon. PNW-RP-479
- Hudson, R. J. H., and A. Bubenik. 2002. Physical and physiological adaptations. Pages 199-257 in D. E. Toweill and J. W. Thomas, editors. North American Elk: ecology and management. Mithsonian Institution Press, Washington D.C., USA
- Huot, J. 1974. Winter habitat of white-tailed deer at Thirty-one Mile Lake, Quebec. Canadian Field Naturalist 8:293-301.
- Irwin, L. L., and J. M. Peek. 1983. Elk habitat use relative to forest succession in Idaho. Journal of Wildlife Management 47(3): 664-672.
- Jenkins, M. A. 2007. Vegetation Communities of Great Smoky Mountains National Park. The Great Smoky Mountains National Park All Taxa Biodiversity Inventory: A Search for Species in Our Own Backyard. Southeastern Naturalist 261:35-56.

- Jenkins, K. J. and E. E. Starkey 1991. Food habits of Roosevelt elk. Rangelands 13(6): 261-265.
- Jenkins, K. J., and E. E. Starkey. 1993. Winter forages and diets of elk in old-growth and regenerating coniferous forests in western Washington. The American Midland Naturalist 130(2): 299-313.
- Jenkins, K. J., and R. G. Wright. 1986. Dietary niche relationships among cervids relative to winter snowpack in northwestern Montana. Canadian Journal of Zoology 65:1397-1401.
- Johnson, B. K., J. W. Kern, M. J. Wisdom, S. L. Findholt, and J. G. Kie. 2000. Resource selection and spatial separation of elk and mule deer in spring. Journal of Wildlife Management 64: 685-697.
- Jones, P. F., and R. J. Hudson. 2002. Winter habitat selection at three spatial scales by American elk, *Cervus elaphus*, in west-central Alberta. The Canadian Field-Naturalist 116(2): 183-191.
- Kamler, J. F., W. Jedrzejewski, and B. Jedrzejewska. 2008. Home ranges of red deer in a european old-growth forest. The American Midland Naturalist 159(1):75-82.
- Kufeld, R. C. 1973. Foods eaten by the Rocky Mountain elk. Journal of Range Management 26(2): 106-113.
- Langvatn, R., and T. A. Hanley 1993. Feeding-patch choice by red deer in relation to foraging efficiency. Oecologia 95(2): 164-170.
- Larkin, J. L., J. J. Cox, M. W. Wichrowski, M. R. Dzialak, and D. S. Maehr. 2004. Influences on release-site fidelity of translocated elk. Restoration Ecology 12(1): 97-105.
- Lashley, M. A., C. A. Harper, G. E. Bates, and P. D. Keyser. 2011. Forage availability for white-tailed deer following silvicultural treatments in hardwood forests. Journal of Wildlife Management 75(6):1467–1476.
- Leblond, M., J. Frair, D., Fortin, C. Dussault, J. P. Ouellet, and R. Courtois, R. 2011. Assessing the influence of resource covariates at multiple spatial scales: an application to forest-dwelling caribou faced with intensive human activity. Landscape Ecology 26:1433–1446.
- Leckenby, D. A. 1984. Elk use and availability of cover and forage habitat components in Blue Mountains, northeastern Oregon, 1976-1982. Oregon Department of Fish and Wildlife, Research Development, Portland, Oregon, USA.

- Leege, T. A., and G. Godbolt. 1985. Herbaceous response following prescribed burning and seeding of elk range in Idaho. Northwest Science 59(2): 134-143.
- Lepardus, J. L., L. I. Muller, and J. L. Kindall. 2011. Seasonal forage availability and diet for reintroduced elk in the Cumberland Mountains, Tennessee. Southeastern Naturalist. 2011. 10(1):53-74.
- Lister, A. M. 1987. Diversity and evolution of antler form in Quaternary deer. Pages 81-89 in C. M. Wemmer, editor. Biology and Management of the Cervidae. Smithsonian Institute Press, Washington, D.C., USA.
- Long, R. A., J. L. Rachlow, and J. G. Kie. 2008. Effects of season and scale on response of elk and mule deer to habitat manipulation. Journal of Wildlife Management 72(5): 1133-1142.
- Lundelius, E. L. Jr., C. S. Churcher, T. Downs, C. R. Harington, E. H. Lindsay, G. E. Schultz, H. A. Semken, S. D. Webb, and R. J. Zakrzewski. 1987. The North American Quaternary sequence. Pages 211-235 in M.O. Woodburne, editor. Cenozoic mammals of North America: geochronology and biostratigraphy. University of California Press, Berkley, USA.
- Madden, M. R., T. Welch, P. Jordan, R. Jackson, R. Seavey, and J. Seavey. 2004. Digital vegetation maps for the Great Smoky Mountains National Park. Final Report to the United States Department of Interior National Park Service, 1443-CA-5460-98-019. Center for Remote Sensing and Mapping Science, University of Georgia. Athens, GA.
- Marcum, C. L., and M. D. Scott. 1985. Influences of weather on elk use of springsummer habitat. Journal of Wildlife Management 49(1): 73-76.
- Marques, F. F. C., S. T. Buckland, D. Goffin, C. E. Dixon, D. L. Borchers, B. A. Mayle, and A. J. Peace. 2001. Estimating deer abundance from line transect surveys of dung: Sika deer in southern Scotland. Journal of Applied Ecology 38(2): 349-363.
- McCune, B., and M.J. Mefford. 1995. PC-ORD. Multivariate Analysis of Ecological Data, Version 2.0. MjM Software Design, Gleneden Beach, Oregon, USA.
- McNaughton, S. J. 1979. Grazing as an optimization process grass ungulate relationships in the Serengeti. The American Naturalist 113:691-703.
- Metlen, K. L., C. E. Fiedler, and A. Youngblood. 2004. Understory response to fuel reduction treatments in the Blue Mountains of northeastern Oregon. Northwest Science 78: 175-185.

- Merrill, E. H., A. Callahan-Olson, K. J. Raedeke, R. D. Taber, and R. J. Anderson. 1995. Elk (*Cervus elaphus roosevelti*) dietary composition and quality in the Mount St. Helens blast zone. Northwest Science 69:9 -18.
- Miller, G.R., R. P. Cummins, and A. J. Hester. 1999. Red deer and woodland regeneration in the Cairngorms. Scottish Forestry 52:14–20.
- Murie, O. L. 1951. The elk of North America. Stackpole, Harrisburg, Pennsylvania, USA.
- Murrow, J. L. 2007. An experimental release of elk into Great Smoky Mountains National Park. Dissertation, University of Tennessee, Knoxville, USA.
- Murrow, J. L., J.D. Clark, and E. K. Delozier. 2009. Demographics of an experimentally released population of elk in Great Smoky Mountains National Park. Journal of Wildlife Management 73:1261–1268.
- Mysterud, A. 1999. Seasonal migration pattern and home range of roe deer (*Capreolus*) *capreolus*) in an altitudinal gradient in southern Norway. Journal of Zoology 247: 479–486.
- Mysterud, A., and E. Østbye. 1999. Cover as a habitat element for temperate ungulates: effects on habitat selection and demography. Wildlife Society Bulletin 27(2): 385-394.
- Neff, D. J. 1968. The pellet-group count technique for big game trend, census, and distribution: a review. Journal of Wildlife Management 32:597-614.
- Nelson, J. R., and D. G. Burnell. 1975. Elk-cattle competition in central Washington. Pages 71-83 in B. F. Roche, editor. Range multiple use management. University of Idaho, Moscow, USA.
- Neu, C. W., C. R. Byers, and J. M. Peek. 1974. A technique for analysis of utilization availability data. Journal of Wildlife Management 38:541-545.
- Nudds, Thomas D. 1977. Quantifying the vegetation structure of wildlife cover. Wildlife Society Bulletin 5:113-117.
- O'Gara, B. and R. Dundas. 2002. Distribution: Past and Present. Pages 67-119 *in* D. E. Toweill and J. W. Thomas, editors. North American elk: ecology and management. Smithsonian Institution Press, Washington, D.C., USA.
- Packer, P. E. 1963. Soil stability requirements for the Gallatin elk winter range. Journal of Wildlife Management 27:401-410.

- Palmer S. C. F., A. J. Hester, D. A. Elston, and I. J. Gordon. 2003. The perils of having tasty neighbors: grazing impacts of large herbivores at vegetation boundaries. Ecology 84:2877–2890.
- Pastor, J., B. Dewey, R. Moen, D. Mladenoff, M. White, and Y. Cohen. 1998. Spatial patterns in the moose-forest-soil ecosystem on Isle Royale, Michigan, USA. Ecological Applications 8(2): 411-424.
- Peek, J. M. 2003. Wapiti (*Cervus elaphus*). Pages 877–888 in Wild Mammals of North America. Feldhamer, G.A., B. C. Thompson, and J. A. Chapman, editors. The Johns Hopkins University Press, Baltimore, Maryland, USA.
- Perryman, B. L., R. A. Olson, S. Petersburg, and T. Nauman. 2002. Vegetation response to prescribed fire in Dinosaur National Monument. Western North Amercian Naturalist 62:414-422.
- Provenza, F. D. 1995. Postingestive feedback as an elementary determinant of food preference and intake in ruminants. Journal of Range Management 48:2-17.
- Pyle, C. 1985. Vegetation disturbance of the Great Smoky Mountains National Park: An analysis of archival maps and records. United States Department of the Interior, National Park Service, Southeast Region, Atlanta, GA, USA.
- Pyle, C. 1988. The Type and Extent of Anthropogenic Vegetation Disturbance in the Great Smoky Mountains before National Park Service Acquisition. Southern Appalachian Botanical Society 53 (3):183-196.
- R Development Core Team (2011). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN3-900051-07-0, URL http://www.R-project.org/
- Raedeke, K. J., J. J. Millspaugh, and P. E. Clark. 2002. Population characteristics. Pages 449–491 in D. E. Toweill and J. W. Thomas, editors. North American elk: ecology and management. Smithsonian Institution Press, Washington, D.C., USA.
- Reynolds, H. G. 1966. Use of openings in spruce-fir forests of Arizona by elk, deer, and cattle. United States Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colorado, USA.
- Romme, W. H., M. G. Turner, L. L. Wallace, and J. S. Walker. 1995. Aspen, elk, and fire in northern Yellowstone National Park. Ecology 76(7): 2097-2106.
- Rooney, T. P. and D. M. Waller. 2003. Direct and indirect effects of white-tailed deer in forest ecosystems. Forest Ecology and Management 181:165-176.

- Runkle, J. R. 1982. Patterns of disturbance in some old-growth mesic forests of eastern North America. Ecology 63:1533-1546.
- Sachro, L. L., W. L. Strong, and C. C. Gates. 2005. Prescribed burning effects on summer elk forage availability in the subalpine zone, Banff National Park, Canada. Journal of Environmental Management 77: 183-193.
- Sawyer, H., R. M. Nielson, F. G. Lindzey, L. Keith, J. H. Powell, and A. Abraham. 2007. Habitat selection of Rocky Mountain elk in a nonforested environment. Journal of Wildlife Management 71(3): 868-874.
- Schneider, J., D. Maehr, K. Alexy, J. Cox, J. Larkin, and B. C. Reeder. 2006. Food habits of reintroduced elk in southeastern Kentucky. Southeastern Naturalist 5(3):535-546
- Schoenecker, K. A., F. J. Singer, L. C. Zeigenfuss, D. Binkley, and S. C. Romulo. 2004. Effects of elk herbivory on vegetation and nitrogen processes. Journal of Wildlife Management 68(4): 837-849.
- Schroer, G. L., K. J. Jenkins, and B. B. Moorhead. 1993. Roosevelt elk selection of temperate rain forest seral stages in western Washington. Northwest Science 67(1): 23-29
- Schäublin, S., and K. Bollmann . 2011. Winter habitat selection and conservation of hazel grouse(*Bonasa bonasia*) in mountain forests. Journal of Ornithology152(1):179-192.
- Seward, N. W. 2003. Elk calf survival, mortality, and neonatal habitat use in eastern Kentucky. Thesis, University of Kentucky, Lexington, USA.
- Shaw, C. E., C. A. Harper, M. W. Black, and A. E. Houston. 2010. Initial effects of prescribed burning and understory fertilization on browse production in closedcanopy hardwood stands. Journal of Fish and Wildlife Management 1:64-72.
- Short, H. L., W. Evans, and E. L. Boeker. 1977. The use of natural and modified pinyon pine-juniper woodlands by deer and elk. Journal of Wildlife Mangement 41(3): 543-559.
- Skovlin, J. M., P. J. Edgerton, and B. R. McConnell. 1983. Elk use of winter range as affected by cattle grazing, fertilizing, and burning in southeastern Washington. Journal of Range Management 36(2): 184-189.
- Skovlin, J. M, P. Zager, and B. K. Johnson. 2002. Habitat requirement evaluations. Pages 531–556 in D. E. Toweill and J. W. Thomas, editors. North American elk: ecology and management. Smithsonian Institution Press, Washington, D.C., USA.

- Singer, F. J. 1979. Habitat partitioning and wildfire relationships of cervids in Glacier National Park, Montana. Journal of Wildlife Management 43(2): 437-444
- Smith, B. L., and S. H. Anderson. 2001. Does dispersal help regulate the Jackson elk herd? Wildlife Society Bulletin 29(1): 331-341.
- Starkey, E. E., D. S. deCalesta, and G. W. Witmer. 1982. Management of Roosevelt Elk: Habitat and Harvest. Pages 353-362 in Transactions of the 47th North American Wildlife and Natural Resources Conference, Portland, Oregon
- Stewart, K., R. Bowyer, R. W. Ruess, B. L. Dick, and J. G. Kie. 2006. Herbivore optimization by North American elk: Consequences for theory and management.Wildlife Monographs 167: 1-24.
- Stewart, K., R. Bowyer, J. Kie, B. Dick, and R. Ruess. 2009. Population density of North American elk: effects on plant diversity. Oecologia 161(2):303-312.
- Strohmeyer, D. C., and J. M. Peek. 1996. Wapiti home range and movement patterns in a sagebrush desert. Northwest Science 70(2): 79-87.
- Strohmeyer, D. C., J. M. Peek, and T. R. Bowlin. 1999. Wapiti bed sites in Idaho sagebrush steppe. Wildlife Society Bulletin 27:547–551.
- Strole, T.A. and R.C. Anderson. 1992. White-tailed deer browsing: Species preferences and implications for central Illinois forests. Natural Areas Journal 12:139-144.
- Telesco, R. L., F. T. Van Manen, J. D. Clark, and M. E. Cartwright. 2007. Identifying site for elk restoration in Arkansas. Journal of Wildlife Management 71:1393–1403.
- Thomas, J. W., D. A. Leckenby, M. Henjum, R. J. Pedersen, and L. D. Bryant. 1988. Habitat-effectiveness index for elk on Blue Mountain Winter Ranges. United States Department of Agriculture, Forest Service, Pacific Northwest Research Station, Portland, Oregon, USA. PNW-GTR-218
- Toweill, D. E., and J. W. Thomas., editors 2002. The future of elk and elk management.
 Pages 793-841 *in* North American elk: ecology and management. Washington,
 DC: Smithsonian Institution Press, Washington, DC, USA.
- Tripler, C.E., C. D. Canham, R. S. Inouye, and J. L. Schnurr. 2005. Competitive hierarchies of temperate tree species: Interactions between resource availability and white-tailed deer. Ecoscience 12(4): 494-505.
- Van Dyke, F., and J. A. Darragh. 2006. Short- and longer-term effects of fire and herbivory on sagebrush communities in south-central Montana. Environmental Management 38(3): 365-376.

- Van Etten, R. C. 1959. Development and evaluation of new deer census techniques. Michigan Department of Conservation, Job Completion Report, Project W-70-R;Sub-job A-1-6.
- Walter, W. D., D. M. Leslie, Jr., and J. A. Jenks. 2006. Response of Rocky Mountain elk (*Cervus elaphus*) to wind-power development. American Midland Naturalist 156:363–375.
- Webster, C. R., M. A. Jenkins, and J. H. Rock. 2005. Long-term response of spring flora to chronic herbivory and deer exclusion in Great Smoky Mountains National Park, USA. Biological Conservation 125(3): 297-307.
- White, P. J.; K. M. Proffitt, D. L. Mech, S. B. Evans, J. A. Cunningham, and K. L. Hamlin. 2010. Migration of northern Yellowstone elk: implications of spatial structuring. Journal of Mammalogy 91(4): 827-837.
- Williams, D. D. 2010. The Forests of Great Smoky Mountains National Park: A Naturalist's Guide to Understanding and Identifying Southern Appalachian Forest Types. Possum Publications, Athens, Georgia, USA.
- Wisdom, M. J., M. Vavra, J. M. Boyd, M. A. Hemstrom, A. A. Ager, and B. K. Johnson.
 2006. Understanding ungulate herbivory-episodic disturbance effects on vegetation dynamics: knowledge gaps and management needs. Wildlife Society Bulletin 34(2): 283-292
- Witmer, G. W., and D. S. deCalesta. 1983. Habitat use by female Roosevelt elk in the Oregon Coast Range. Journal of Wildlife Management 47(4): 933-939.
- Yarkovich, J., J. Clark, and J. Murrow. 2011. Effects of black bear relocation on elk calf recruitment at Great Smoky Mountains National Park. Journal of Wildlife Management 75(5): 1145-1154.
- Zeigenfuss, L.C., F.J. Singer, and D. Bowden. 2002. Vegetation responses to natural regulation of elk in Rocky Mountain National Park. Biological Science Report USGS/BRD/BSR-1999-0003. United States Government Printing Office, Denver, Colorado.