

Landscape Influences on Spatial Patterns of White-tailed Deer Herbivory and Condition Indices
in the Central Appalachian Mountains

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Andrew B. Kniewski

Abstract (academic)

White-tailed deer (*Odocoileus virginianus*) are a common and important game species throughout much of the central Appalachian region. The central Appalachian region encompasses a wide variety of habitat conditions and spatial habitat arrangements that may influence deer populations and management as well as deer impacts to ecosystems. Locally to regionally, deer populations have had an increasingly negative effect on forest biodiversity and a growing influence on forest succession. In Virginia, the combination of these factors has prompted establishment of deer population management goals and policies designed to support conservation of biodiversity, forest regeneration, and continued hunting opportunities. However, limited information is available to inform broad-scale assessment of herbivory impacts. Likewise, lack of understanding about the spatial variability of herbivory across and among landscapes impedes consistent application of ecological measures under differing management scenarios and landscape conditions. I evaluated deer herbivory intensity, the predictability of browsing rates, and the relationships and possible interactions between deer body mass and potential food sources, winter severity, and deer population density in the central Appalachian Mountains of Virginia. My results provide support for the inclusion of spatial factors to help partition variation of deer herbivory to allow for improved precision and accuracy in the design of field herbivory impact assessment methods and improve their application across various landscape contexts. Also, effective, broad-scale herbivory impact assessment should include spatially-balanced vegetation monitoring that accounts for regional differences in deer forage preference. Agriculture and other non-forest habitats may provide resources that result in larger deer body mass either directly through food items or indirectly through alteration of the remaining forest habitat such as through increased edge. This suggests that available food sources and habitat are related to deer physiological parameters in the central Appalachian region and vary across landscapes. Likewise, these factors can change or can be affected through management across time. As a

result, spatial approaches for monitoring and analysis are required for effective management and understanding of deer populations and herbivory impacts to biodiversity.

Landscape Influences on Spatial Patterns of White-tailed Deer Herbivory and Condition Indices in the Central Appalachian Mountains

Andrew B. Kniowski

Abstract (public)

White-tailed deer (*Odocoileus virginianus*) are a common and important game species throughout much of the eastern United States including the central Appalachian Mountain region. The central Appalachian region encompasses a wide variety of habitat conditions and habitat arrangements that may influence deer populations and management as well as deer impacts to ecosystems. Deer consume a variety of plants and plant matter and overabundant deer populations have had a negative effect on forest plants and biodiversity. In Virginia, deer population management goals and policies have been designed to support conservation of biodiversity, forest regeneration, and continued hunting opportunities. However, limited information is available to managers to help them improve the assessment of herbivory impacts. Also, lack of understanding of how deer herbivory patterns change across the landscape complicates the use of ecological measures in different areas. I evaluated deer herbivory intensity, the predictability of herbivory rates, and the relationships and possible interactions between deer body condition and potential food sources, winter severity, and deer population density in the central Appalachian Mountains of Virginia. My results suggest that inclusion of spatial factors, such as the movement patterns of deer in the local area, may allow for improved precision and accuracy in the design of field herbivory impact assessment methods. Also, effective, broad-scale herbivory impact assessment should include spatially-balanced vegetation monitoring that accounts for regional differences in deer forage preference. Agriculture and other non-forest habitats may provide resources that result in heavier deer either directly through food items or indirectly through alteration of the remaining forest habitat such as through increased edge. As a result, spatial approaches for monitoring and analysis are required for effective management and understanding of deer populations and herbivory impacts to biodiversity.

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Chapter 1: Introduction

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Deer (Cervidae) have a long and enduring history with humans and their environment. Cave drawings of deer and hunters date back many thousands of years and highlight the interactions and relationships between humans and deer. In North America, white-tailed deer (*Odocoileus virginianus*) (hereafter deer) were hunted by indigenous peoples and used for food, clothing, and tools for millennia (Halls 1984). Likewise, Native Americans directly and indirectly modified habitat and deer populations in ways similar to modern management techniques. Following European settlement, deer continued to be a highly valued natural resource. However, by the early 1900s the combination of a rapidly increasing human population, anthropogenic alterations of habitat, and unrestricted hunting led to a rapid decline and eventual extirpation of deer populations throughout the eastern United States. Through environmental regulations, hunting laws, conservation and restocking efforts, and application of modern wildlife management techniques over the past century, deer populations have rebounded. Due to a lack of natural predators, such as the mountain lion (*Puma concolor*) and gray wolf (*Canis lupus*), many areas now support deer populations that exceed historical densities (McCabe and McCabe 1997).

As deer populations have increased, urbanization and the growth of human populations have led to increased human/deer conflicts and a concern for the impact of deer on other species (Rooney 2001, Côté et al. 2004, McShea 2012). Ungulates are important modifiers in many ecosystems and can alter biodiversity significantly (Hobbs 1996, Rooney and Waller 2003, Royo et al. 2010, Bressette et al. 2012). Deer influence biodiversity in a variety of ways, including directly through their browsing, which changes growth rate, development, survival, and succession of plants and community composition (Russell et al. 2001), and indirectly through a cascade of impacts to other organisms. For example, researchers have related impacts of deer to bird communities, small mammals, and invertebrates (reviewed by Côté et al. 2004). Further, through trampling, grazing, and fecal pellet deposition, deer can influence nutrient

cycling and the soil environment (Hobbs 1996), leading to impacts on less obvious species, such as native earthworms (Rearick et al. 2011).

As a result of their known impact to biodiversity, deer currently are at the forefront of research and discussion of biodiversity (McCabe and McCabe 1997, Rooney 2001, Côté et al. 2004). Biodiversity has become a central focus of conservation effort and research over the past several decades (Redford and Richter 1999, Lévêque and Mounolou 2003). Although the term “biodiversity” can be interpreted in various ways, it generally refers to “the natural variety and variability among living organisms, the ecological complexes in which they naturally occur, and the ways in which they interact with each other and with the physical environment” (Redford and Richter 1999:1247). Over time, biodiversity has become a framework for consideration of a whole range of questions encompassing human societies, sustainable development, ethics, and the natural environment (Lévêque and Mounolou 2003). Because biodiversity plays a primary role in maintaining ecosystem services and productivity (Isbell et al. 2011, Tilman et al. 2012), its conservation provides tangible benefits and incentives to societies and helps provide evaluation of risk, value, and cost (Redford and Richter 1999, Lévêque and Mounolou 2003). To date, research has focused on quantifying economic and biodiversity impacts within limited geographic areas, such as understanding the impact of deer on forest regeneration in specific contexts and deer population densities. However, the impact of deer on biodiversity at broader and less specific scales is less understood (Rooney 2001, Russell et al. 2001, Côté et al. 2004). For example, few data are available regarding biodiversity impacts at the landscape scale, measures of biodiversity impact generally are untested (Rooney and Waller 2003, Frerker et al. 2013), and how deer impact varies spatially is unknown.

Although ecological benchmarks or measures of herbivory impact increasingly have become important metrics to consider in deer population management (deCalesta and Stout 1997, Morellet et al. 2007, Tierney et al. 2009, McShea 2012), current limitations in our understanding impede their application across landscapes. For example, managing deer populations within limits that permit function of a biologically diverse ecosystem was an objective of the Virginia Deer Management Plan (Virginia Department of Game and Inland Fisheries 2015); yet, a lack of data that describe the sensitivity and

consistency of suggested benchmarks across the varied habitats and geology of Virginia has prevented their incorporation in the management decision making processes (N. Lafon, Virginia Department of Game and Inland Fisheries, personal communication). Because landscapes such as the central Appalachian Mountain region often contain high local and regional variation in habitat structure and biodiversity, measures of ecological impact vary in their utility depending on location and habitat configuration, which creates additional challenges for their implementation in management. As a result, understanding how deer herbivory varies spatially is essential to the development of broad-scale assessment methods, to identify areas of high probability of impact, and to develop and apply impact management thresholds at all management scales.

The central Appalachian region is diverse both in its patterns of land use and topography, potentially complicating management of deer and the development of broad-scale deer biodiversity impact assessment methods for the region. Like most regions in the East, widespread clearcutting and exploitation of wildlife occurred throughout the early 1900s. The recovery of habitat and wildlife populations, including deer, occurred similar to that witnessed in other regions albeit over a slower timeframe. Although the region is now predominantly forested, row-crop agriculture and hay production are common in the valleys and the region contains numerous small and moderately sized urban centers. Long mountain ridges with narrow to moderately broad, flat valleys cover much of the region, whereas other areas are more rugged with steep slopes and very narrow valleys. In addition to these landscape features, Appalachian forests are highly diverse ecologically. As a result, managers are faced with managing deer in light of these environmental complexities in addition to the various needs and desires of the hunting public and other stakeholders. Because of this, I studied three aspects of deer herbivory in the central Appalachian Mountains including: 1) the spatial patterns of deer herbivory, 2) the predictability of deer browsing intensity, and 3) the importance of potential food sources to deer populations in the central Appalachian Mountains.

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Chapter 2: Spatial Patterns of White-tailed Deer Herbivory in the Central Appalachian Mountains

Andrew B. Kniewski

Abstract

White-tailed deer (*Odocoileus virginianus*) herbivory can alter biodiversity within ecosystems. Therefore, ecological benchmarks or measures of herbivory impact are needed as assessment tools for deer population management. Lack of understanding regarding the spatial variability of herbivory across and among landscapes impedes consistent application of ecological measures under differing management scenarios and landscape conditions. I evaluated deer herbivory intensity by assessing woody vegetation along 20 transects at each of 30 sites in the central Appalachian Mountains of Virginia, USA, using a spatially-balanced, multi-scale study design. Intra-site browsing intensity variation did not differ among study regions or site diversity categories ($P > 0.15$). Although there was a weak negative relationship between the browsing intensity on an individual transect and the total number of stems therein (pseudo- $r^2_{\text{marginal}} = 0.01$, $\beta = -0.03$ (-0.06, -0.01; 95% CI)), there was a positive relationship between browsing intensity and the total number of stems weighted by deer forage preference (pseudo- $r^2_{\text{marginal}} = 0.07$, $\beta = 0.11$ (0.08, 0.14 95% CI)). Sites with high intensities of browsing were browsed more uniformly ($r^2_{\text{adjusted}} = 0.50$, $F_{1, 28} = 29.5$, $P < 0.001$). Browsing intensity was autocorrelated significantly at separation distances < 1600 m, but was near zero at separation distances ≥ 5 km. Although browsing intensity and stem densities were variable across sites, on average the mean of ≥ 3 transects within a site was within 0.1 of the site mean browsing ratio and 0.5 stems m^{-2} . My results suggest that inclusion of spatial factors to help partition variation of deer herbivory potentially may allow for improved precision and accuracy in the design of field herbivory impact assessment methods and improve their application across various landscape contexts.

Introduction

Ungulates significantly modify ecosystem structure and biodiversity (Hobbs 1996, Rooney and Waller 2003, Royo et al. 2010a, Bressette et al. 2012). Deer (Cervidae) influence biodiversity in a variety of ways, including directly through herbivory, which changes growth rate, development, survival, and succession of plants and resulting community composition (Russell et al. 2001), and indirectly through a cascade of impacts to other organisms. For example, researchers have related impacts of deer to bird communities, small mammals, and invertebrates that respond to change in plant communities (reviewed by Côté et al. 2004). Further, through mechanical action (e.g., trampling and browsing), and fecal pellet deposition, deer can influence nutrient cycling and the soil environment (Hobbs 1996), leading to impacts on litter and below-ground processes and biota (Rearick et al. 2011).

Deer and other ungulates generally live within landscapes that are heterogeneous mosaics of vegetation types and conditions, land forms, and land uses (Urban et al. 1987). Ecologists have long had an interest in spatial patterns resulting from interactions between landscapes and ecological processes (Turner 1989). For example, many ecological factors of importance to plant communities (i.e., moisture, light, nutrients, climate) are correlated with or can be predicted from topographic and geologic attributes of landscapes (Swanson et al. 1988, McNab 1993, Meilleur et al. 1994, Ford et al. 2000, Clinton 2003). White-tailed deer (*Odocoileus virginianus*) (hereafter deer) are the most common and widespread large herbivore in eastern North America. Deer are known to selectively forage based on type and nutritional content of vegetation (Nixon et al. 1970, Vangilder et al. 1982, Berteaux et al. 1998, Dostaler et al. 2011). Furthermore, topographic, climatic, and other variables may influence, or restrict access by deer to landscape areas (Schmitz 1991, Rooney 1997, Comisky et al. 2005, Krueger and Peterson 2006, Chollet et al. 2013). Thus, deer herbivory may vary spatially in relation to landscape characteristics. Although research on deer herbivory has been substantial (Russell et al. 2001, Rooney and Waller 2003, Côté et al. 2004), most studies do not evaluate underlying spatial factors (but see Augustine and Jordan 1998) or how the extent and pattern of observed herbivory impacts occur in landscapes broadly.

Because deer can cause substantial changes to biodiversity, efforts to include ecological benchmarks or measures of herbivory impact in deer population management have increased, particularly in light of real or perceived overabundance in the East (deCalesta and Stout 1997, Morellet et al. 2007, Tierney et al. 2009, McShea 2012). Despite this, our lack of understanding about how herbivory varies spatially across landscapes and among landscape scales impedes effective application of ecological measures in many management scenarios. For example, managing deer populations within limits that permit function of a biologically diverse ecosystem is an objective of the Virginia, USA, state-wide deer management plan (Virginia Department of Game and Inland Fisheries 2007). However, there are few data or established protocols that describe the sampling effort required to measure herbivory impact, the spatial variability of deer herbivory, or the applicability of suggested ecological measures across the varied habitats, landscapes, and geology of Virginia or elsewhere (N. Lafon, Virginia Department of Game and Inland Fisheries, personal communication).

The development of broad-scale herbivory impact assessment methods requires an understanding of how deer browsing intensity or other measures of herbivory vary in relation to habitat productivity, topographic configuration, and other spatial factors. Additionally, understanding the variation of deer herbivory in relation to spatial factors potentially may improve the precision and accuracy of field assessment methods across various landscape contexts. Herein, I use a spatially-balanced, multi-scale study design to examine spatial patterns of deer herbivory, regional and environmental differences in herbivory patterns, and the relationship of deer herbivory to geographical and land use patterns across the central Appalachian Mountains of Virginia, USA. *A priori*, I hypothesized that deer herbivory would vary independently at multiple spatial scales and that patterns of variation would differ among physiographic regions and habitat configurations along predictable gradients. Specifically, I hypothesized that sites with greater land use diversity would have greater variation in herbivory intensity.

Methods

Data collection— My study area was the central Appalachian Mountains region of western Virginia, USA. I divided the study area into six sampling regions following the physiographic divisions of Fenneman (1938) as they occur in Virginia, including the physiographic province Appalachian Plateau, and the physiographic sections Blue Ridge Northern, Blue Ridge Southern, Valley and Ridge Tennessee, and Valley and Ridge Middle. I divided the Valley and Ridge Middle section into two study regions due to its size; the subdivision roughly followed the boundary of the Potomac and James River watersheds, which separate the upper and lower portions of the Shenandoah Valley (Figure 2.1). Elevations range from approximately 200–1700 m. Generally, the Valley and Ridge and, to a lesser extent, the Blue Ridge regions are characterized by long mountain ridges with moderate to steep side slopes and narrow to moderately broad valleys. The Appalachian Plateau is characterized by rugged terrain with steep slopes and very narrow valleys. Landforms in the Appalachian Plateau generally form a dendritic pattern, although relief generally is less than that of the Valley and Ridge or Blue Ridge. Overall, the study area largely is forested (67%), but the valleys display a mix of pasture or hay production (22%) and limited areas of row-crop agriculture, residential, and urban development (Homer et al. 2015). In contrast, the Appalachian plateau is more heavily forested (79%) and has less pasture or hay production (4%) and no row-crop agriculture. Dominant forest types are xeric oak (*Quercus* spp.) and mixed pine (*Pinus* spp.) with scattered, smaller patches of mesic hardwood, cove hardwood, and northern hardwood, depending on region, aspect, and elevation. Forests located >1200 m in elevation frequently are dominated by spruce-fir (*Picea-Abies*) stands.

I selected 30 sites, five sites within each of the six sampling regions. I sampled woody vegetation within forested areas along 20 transects at each site. I distributed sites across a range of habitat and land use configurations using a combination of landscape diversity metrics. I calculated a measure of local forest diversity by creating a 30 × 30 m grid where values were the sum of the number of forest types defined by the Northeastern Terrestrial Wildlife Habitat Classification (Gawler 2008) within a 1 km radius surrounding each grid cell. Forest types were reclassified into 8 major types prior to diversity

calculation to allow better comparability across sampling regions: cove hardwood, xeric oak, floodplain, mesic hardwood, mixed pine, northern hardwood, pine, and spruce-fir (Table A.1). Cove hardwoods were those communities dominated largely by yellow poplar (*Liriodendron tulipifera*), basswood (*Tilia* spp.) and other mesic, mixed mesophytic species; xeric oak communities were dominated by oaks, especially chestnut oak (*Quercus montana*), and occasionally other hardwoods such as hickory (*Carya* spp.), red maple (*Acer rubra*), and blackgum (*Nyssa sylvatica*). Floodplain communities contained American sycamore (*Platanus occidentalis*) and black walnut (*Juglans nigra*) as primary constituents, whereas mesic hardwood communities were dominated by American beech (*Fagus grandifolia*), yellow poplar, and black birch (*Betula lenta*). Mixed pine communities were dominated by various yellow pines and white pine (*Pinus strobus*) and hardwood associates from the xeric oak community; northern hardwoods were those communities dominated by American beech, sugar maple (*Acer saccharum*), and black cherry (*Prunus serotina*). Pine communities were those dominated by various yellow and white pines, whereas spruce-fir communities contained mixtures of red spruce (*Picea rubens*) and Fraser fir (*Abies fraseri*). I ranked locations with forest diversity values ≥ 4 as high forest diversity, locations with a diversity value of 3 as moderate forest diversity, and areas with diversity values of ≤ 2 as low forest diversity.

Similarly, I used the National Land Cover Dataset (Fry et al. 2011) to calculate a measure of land use diversity by creating a 30×30 m grid where values were the number of different land use classes within a 1 km radius surrounding each grid cell. Prior to the diversity calculation, land use classes were reclassified into 7 basic land cover types: water, residential, urban, forest, grassland, pasture, and row-crop. I ranked areas with land use diversity values ≥ 6 as high, areas with diversity values of 4 or 5 as moderate, and areas with diversity values of ≤ 3 as low land use diversity. I identified and categorized possible assessment sites within each region based on their combination of forest and land use diversity values. Within available locations, I selected one site in each of the following combinations of forest and land use diversity: high forest and high land use; high forest and low land use; low forest and high land use; low forest and low land use; and moderate land use, moderate forest diversity. I defined or limited

site boundaries to a circular area $\leq 3 \text{ km}^2$ to limit intra-site variation in browsing intensity due to variations in local deer population density; that is, sites were approximately the size of the home range of an adult deer and an individual deer present on a site could access all areas of the site assuming normal movement patterns (Halls 1984, Tierson et al. 1985, Campbell et al. 2004).

Within each site, I randomly selected 20 transect locations within forested areas using a generalized random-tessellation stratified design (Stevens and Olsen 2004). I stratified locations among 12 topographic and landform criteria representing combinations of slope, topographic exposure, and aspect (Swanson et al. 1988, McNab 1993, Meilleur et al. 1994, Ford et al. 2000, Clinton 2003) (Table 2.1). I defined low to moderate slope as slopes $< 20^\circ$, and high slopes as slopes $> 20^\circ$. I used deviation from mean elevation (DEV) within a 500 m radius (De Reu et al. 2013) as a measure of topographic exposure; positive values indicate the location is relatively higher and negative values indicate the location is relatively lower than the mean elevation of the area (McNab 1993, Wilson and Gallant 2000, De Reu et al. 2013). I defined sheltered landforms as areas with a DEV < -0.7 , and exposed landforms as those with a DEV > 0.7 . I defined areas not strongly exposed or sheltered ($-0.7 < \text{DEV} < 0.7$) as moderate landforms. I defined southeast aspects as aspects between 45° and 225° and northwest aspects as aspects between 0° and 45° or between 225° and 359° . These aspect categories typically split along ridgelines in the study area resulting in an aspect category for each dominant slope face. I oversampled random transect locations within each strata and, as needed, selected alternate random locations within the strata to maintain a minimum distance of 100 m between any two transects. Where strata were not present within a site, I assigned transect locations to an available alternate strata.

I oriented transects perpendicular to the terrain slope to minimize elevation changes along transects or in a random direction if the location had minimal slope. At each transect location, I evaluated the browsing intensity of deer by assessing woody vegetation within 1 m^2 subplots. I only examined and tallied woody stems because these generally leave persistent and conspicuous evidence of browsing, whereas herbaceous vegetation is ephemeral, the whole plant can be consumed, and plants are damaged more easily by non-browsing events (Morellet et al. 2001, Frerker et al. 2013). I distributed subplots

evenly (every 5 m) along 50 m transects (10 per transect). I counted and identified by vegetation species the total number of woody stems between 0.2 m and 1.8 m in height within each subplot and also recorded the number of stems that had been browsed by deer. Although browsing by either Eastern or Appalachian Cottontails (*Sylvilagus* spp.) rarely was encountered, I differentiated browse scars of deer from those of rabbits (Morellet et al. 2001). Additionally, I visually categorized percent cover of grasses (graminoids), ferns (monilophytes), and forbs within each subplot into one of seven categories (0, 0%; 1, 0–5%; 2, 5–25%, 3, 25–50%, 4, 50–75%, 5, 75–95%, 6, 95–100%: Daubenmire 1959, Bureau of Land Management 1996).

Data analysis—I calculated a measure of deer browsing intensity for each transect and site as the proportion of stems browsed by deer (browsed stems/total number of stems; browsing ratio; Castleberry et al. 1999, Frerker et al. 2013). As a measure of deer forage preference, I calculated the browsing ratio of each vegetation species within the study area and each vegetation species by region. I calculated the mean density of woody stems (stems m⁻²) as an estimate of woody forage availability. Because deer browse vegetation preferentially (Nixon et al. 1970, Vangilder et al. 1982, Dostaler et al. 2011), I also calculated browsing ratios and stem densities weighted by deer forage preference. To do so, I multiplied the vegetation stem count by the study-wide or regional browsing ratio for each vegetation species before calculation of the site or transect browsing ratio. This resulted in stems of plant species browsed frequently by deer being more heavily weighted and those of vegetation species rarely browsed being less weighted in totals.

I checked for study-wide vegetation and browsing trends by regressing stem densities and browsing ratios against Universal Transverse Mercator x and y coordinates of each transect. I used linear mixed models with a random factor for site to account for my nested study design (Bolker et al. 2009); coordinates were centered and scaled, stem densities and browsing ratios were square root transformed prior to the analyses. I tested for a difference in forage availability (stems per site) between study regions and between site habitat diversity categories using Kruskal-Wallis rank sum tests (Zar 1984). I used nonparametric tests for all comparisons between regions and habitat diversity categories because there

were few sites per category. I evaluated the relationship between the quantity of forage browsed (stems browsed) and the forage availability (number of stems) on sites using least squares regression (Zar 1984). Number of stems browsed and number of stems available were log transformed to meet assumptions of normality prior to analysis (Zar 1984). I used linear mixed models to evaluate the relationship between the quantity of forage browsed (stems browsed) and forage availability (number of stems) on transects. I included a random factor for site to account for the nested study design and the number of stems available and number browsed were log transformed prior to analysis. Similarly, I evaluated the relationship between the proportion of stems browsed (browsing ratio) and the forage availability (number of stems) on a site using least squares regression. The browsing ratio was square root transformed and the number of stems was log transformed prior to analysis. I used linear mixed models to evaluate the relationship between the proportion of stems browsed (browsing ratio) and the forage availability (number of stems) on transects. I included a random factor for site to account for the nested study design, the browsing ratio was square root transformed, and number of stems was log transformed prior to analysis. I used *R* (Version 3.2.3, www.r-project.org) to calculate statistical tests; packages “lme4” (Version 1.1-10, <https://cran.r-project.org/package=lme4>), “MuMIn” (Version 1.15.6, <https://cran.r-project.org/package=MuMIn>), and “multcomp” (Version 1.4-1, <https://cran.r-project.org/package=multcomp>) were used in mixed model calculations. Pseudo r-squared values were calculated using the methods of Nakagawa and Schielzeth (2013).

To evaluate the influence of sampling effort on site browsing ratio and stem density estimates, I used Monte Carlo simulations to mimic different amounts of sampling effort. For each simulation, I computed the absolute difference of the browsing ratio of a random subset of transects to the browsing ratio of all 20 transects on a site. I varied the number of transects in the subset from 2–19 to simulate different levels of sampling effort resulting in a total of 18 simulations per site. I iterated each simulation 1000 times and recorded the standard deviation and mean difference for each level of sampling effort for all sites study-wide and by region.

I estimated the variability of deer browsing intensity within each site by computing the coefficient of variation (CV; Zar 1984) of the browsing ratio and CV of the weighted browsing ratio. Similarly, I estimated the variability of the woody vegetation density within a site by computing the CV of the number of woody stems and the CV of weighted stem counts. I compared site browsing intensity variation and vegetation density variation between study regions and between site habitat diversity categories using Kruskal-Wallis rank sum tests. I used least squares regression to evaluate the relationship between the variability of browsing intensity and site stem density, stem density variation and site browsing ratio, variability of browsing intensity and site browsing ratio, stem density variation and site stem density, and stem density variation and browsing intensity variation.

I also used Kruskal-Wallis rank sum tests to compare the average percent cover of grasses, ferns, and forbs between study regions and between site habitat diversity categories. Where tests were significant, I used pair-wise Wilcoxon rank sum tests (Zar 1984) to compare between groups using Holm's (1979) correction for multiple comparisons. I used linear mixed models to evaluate the relationship between the browsing ratio and the percent cover of grasses, browsing ratio and percent cover of ferns, and the browsing ratio and percent cover of forbs. Browsing ratios were square root transformed prior to analysis and a random factor for site was included to account for the nested study design.

To evaluate the extent of spatial relatedness of transect stem densities and browsing ratios, I calculated spatial autocorrelation and semi-variance statistics. Autocorrelation is a measure of the degree to which a set of values tend to be clustered together in space, or alternatively, values do not affect one another such that there is independence and spatial randomness (Fortin and Dale 2009). Similarly, semi-variance is a measure of the variability between paired data values within a separation distance class. Data values that are closer together have a smaller semi-variance if there is strong spatial dependence. Models of semi-variance values can be used to evaluate the spatial extent of and spatial contribution to the variation between locations (Isaaks and Srivastava 1989). For example, the y-intercept of the semi-variance model (nugget) can be interpreted as the portion of the sample variance that is not spatially dependent. Likewise, the range is the distance at which paired points no longer are spatially dependent. I

used correlograms and semi-variograms to visualize how autocorrelation and semi-variance change with separation distance. I used package “ncf” (Version 1.1-6, <https://cran.r-project.org/package=ncf>) in *R* to calculate autocorrelation statistics and assess correlation significance in 250 m distance class increments for separation distances 0–2 km and in 10 km distance class increments for separation distances 5–200 km. I used package “gstat” (Version 1.1-0, <https://cran.r-project.org/package=gstat>) in *R* to calculate and fit semi-variance models.

Results

Between 2 June 2014 and 7 August 2014, I tallied 11,137 woody plant stems or 1.86 stems m⁻² of 82 species or species groups. Mean browsing ratio was 0.28, whereas mean study-wide and regionally weighted browsing ratios were 0.41 and 0.46 respectively. Browsing ratios varied considerably among vegetation species study-wide and within species among regions (Table A.2). The mean percent cover categories for ferns and grasses were low across the study area (0.31 and 0.37 respectively); mean forb cover category was 1.12.

Across the study area, I found no geographical trends in stem densities (east to west $\beta = 0.08$ (-0.11, 0.27; 95% confidence interval (CI)); north to south $\beta = 0.07$ (-0.26, 0.12; 95% CI)), or east to west for browsing ratios ($\beta = -0.06$ (-1.51, 0.03; 95% CI)). There was a slight north to south trend in browsing ratio (pseudo- $r^2_{\text{marginal}} = 0.03$, $\beta = 0.09$ (0.00, 0.18; 95% CI)). There were no significant differences between the number of woody stems on sites among regions or diversity categories ($P \geq 0.177$). There was a positive relationship between the number of stems that were browsed on a site and the total number of stems available on the site. The relationship increased in strength as stem weights became more local ($r^2_{\text{adjusted}} = 0.24$, $F_{1, 28} = 10.39$, $P = 0.003$, $\beta = 0.52$; $r^2_{\text{adjusted}} = 0.42$, $F_{1, 28} = 21.99$, $P < 0.001$, $\beta = 0.61$; $r^2_{\text{adjusted}} = 0.64$, $F_{1, 28} = 53.41$, $P < 0.001$, $\beta = 0.87$; for unweighted, study-weighted, and regionally-weighted stem counts respectively). There was a positive relationship between the number of browsed stems on an individual transect and the total number of stems on the transect (pseudo- $r^2_{\text{marginal}} = 0.29$, $\beta = 0.61$ (0.53, 0.69; 95% CI)). The relationship between the number of browsed stems on an individual transect and

weighted stem counts was stronger than unweighted stems (pseudo- $r^2_{\text{marginal}} = 0.50$, $\beta = 0.98$ (0.90, 1.06; 95% CI); pseudo- $r^2_{\text{marginal}} = 0.56$, $\beta = 0.98$ (0.90, 1.05; 95% CI), for study-wide and regionally weighted stem counts respectively). There was a negative relationship between the site browsing ratio and the total number of stems available on a site for unweighted stems ($r^2_{\text{adjusted}} = 0.24$, $F_{1, 28} = 10.24$, $P = 0.003$, $\beta = -0.13$), but no relationship with weighted stem counts ($P \geq 0.108$). Conversely, although there was a weak negative relationship between the browsing ratio on an individual transect and the total number of stems on a transect (pseudo- $r^2_{\text{marginal}} = 0.01$, $\beta = -0.03$ (-0.06, -0.01; 95% CI), there was a positive relationship between the transect browsing ratio and weighted stem counts (pseudo- $r^2_{\text{marginal}} = 0.05$, $\beta = 0.09$ (0.06, 0.13; 95% CI); pseudo- $r^2_{\text{marginal}} = 0.07$, $\beta = 0.11$ (0.08, 0.14 95% CI)), for study-wide and regionally weighted stem counts respectively (Figure 2.2).

Although browsing intensity and stem densities were variable across sites, on average the mean of ≥ 3 transects within a site was within 0.1 of the site mean browsing ratio and 0.5 stems m^{-2} (Figure 2.3). All regions followed a similar sampling effort trend for both browsing ratios and stem densities. Browsing intensity estimates on sites in the Appalachian Plateau and Ridge and Valley regions were less accurate than the Blue Ridge regions and therefore more sampling effort would be required to achieve the same level of estimate accuracy; however, overall study-wide differences were minimal. Similarly, stem density estimate accuracy was similar among regions.

There was no difference in intra-site browsing intensity variation among study regions or site diversity categories ($P > 0.15$). Likewise, there was no difference in study-wide or regionally weighted intra-site browsing variation across study regions or site diversity categories ($P > 0.35$). Intra-site stem density variation and intra-site weighted stem density variation also did not vary among study regions or site diversity categories ($P > 0.08$). There was no relationship between site browsing variation and stem density ($P = 0.683$) or site stem density variation and site browsing ratio ($P = 0.226$). However, there was a negative relationship between site browsing variation and site browsing ratio ($r^2_{\text{adjusted}} = 0.50$, $F_{1, 28} = 29.5$, $P < 0.001$) and site stem density variation and site stem density ($r^2_{\text{adjusted}} = 0.30$, $F_{1, 28} = 14.2$, $P < 0.001$). That is, sites with high intensities of browsing were more uniformly browsed and sites with

higher densities of woody stems had less intra-site variation in woody stem density. There was no relationship between the variation in the number of woody stems and the variation in browsing intensity ($P = 0.970$).

The mean percent cover of grass and forbs vegetation on each site did not differ among regions ($P > 0.43$); however, there was a significant difference in the mean percent cover of ferns among regions ($\chi^2_5 = 15.3$, $P = 0.009$). Subsequent pair-wise comparisons among regions did not confirm which regions differed in fern cover ($P \geq 0.12$); anecdotally, the Appalachian Plateau had a higher mean fern cover category than did other regions (0.72, Appalachian Plateau; 0.22, other regions). The mean percent cover of ferns and forbs on each site did not differ among site diversity categories ($P \geq 0.10$); however, there was a marginally significant difference in the mean percent cover of grass among diversity categories ($\chi^2_5 = 9.52$, $P = 0.049$). Subsequent pair-wise comparisons did not confirm which diversity categories differed in grass cover ($P \geq 0.08$). I found no relationship between transect browsing ratio and percent cover of grass, ferns, or forbs ($P > 0.076$).

Transect stem densities were autocorrelated ($P < 0.05$) at separation distances < 1800 m (Figure 2.4A). I found stem density autocorrelation near zero across separation distances ≥ 5 km, although scattered classes statistically were significant. Similarly, browsing ratios were autocorrelated at separation distances < 1600 m (Figure 2.4B), but were near zero at separation distances ≥ 5 km, although scattered classes statistically were significant. There was little spatial dependence in stem counts or browsing ratios beyond the site scale (Figure 2.5). Large nugget variance for both stem counts and browsing ratios suggested that spatial dependence accounted for only 32% and 21% of the variation at the shortest distance class (approximately 1900 m) respectively (Table 2.2). There was little spatial dependence beyond separation distances of approximately 29 km and 16 km for stem counts and browsing ratios respectively.

Discussion

Spatial patterns of deer herbivory surprisingly were consistent across the study area. Herbivory patterns and the availability of woody forage generally were unchanged among physiographic regions and land use diversity classes. Contrary to my hypothesis, I found no evidence that deer in different physiographic provinces and sub-divisions or habitat conditions use different browsing strategies or display alternate herbivory patterns. Deer are highly adaptable herbivores, yet they browse selectively, choosing some vegetation species preferentially within local areas (Nixon et al. 1970, Vangilder et al. 1982, Dostaler et al. 2011). Although the availability of particular vegetation species and understory communities change substantially across the study area, deer appear to switch among available forage species in their local area to maintain a “consistent” herbivory pattern.

I found several notable spatial herbivory patterns study-wide, including some relationships that change with scale. The total quantity (not proportion) of vegetation browsed on a site and on the transect scale were related positively to the availability of forage. Several forage management strategies have been explored, such as forest harvesting and food plot establishment, that seek to move or concentrate deer herbivory within the landscape by creating patches of available, high density browse in the Appalachians (e.g. Johnson et al. 1995, Campbell et al. 2004, Miller et al. 2009, Crimmins et al. 2010). Optimal foraging theory suggests that deer may consume more vegetation at these locations if it is energetically or nutritionally beneficial (Schoener 1971, Senft et al. 1987). My study supports the idea that deer will consume more vegetation in areas with greater amounts of browse available. Notably, my results suggest this relationship is stronger where the available browse is a type preferred by deer. As a result, managers desiring to shift local browsing intensity of deer should consider carefully the type and amount of browse created via management activities. Likewise, how vegetation in managed areas is expected to develop over time under the anticipated herbivory intensity may provide additional considerations relative to management goals and habitat needs of deer and other wildlife (Johnson et al. 1995, Belote et al. 2012).

The proportion of stems browsed suggests an alternate and scale-dependent relationship with stem density. Although the proportion of stems browsed decreased as stem density increased at both the site and transect scales, this was true only when all stems were considered equally. Where stem densities were weighted for deer preference, the browsing ratio had no relationship with stem density at the site scale and increased with density at the transect scale. This highlights the scale-dependent and selective nature of deer browsing and also the complexity of evaluating herbivory impacts. My data are consistent with the supposition that increasing forage availability would result in a smaller proportion of the vegetation browsed in general. However, when the forage preference of deer also is considered, my data suggest that increasing the density of a preferred browse species would not necessarily reduce the proportion of that species consumed on a site and actually may lead to an increase of the proportion browsed at smaller scales. As a result, attempts to reduce browsing rates on a preferred browse species by increasing its availability may not be viable without careful consideration of the relationship between herbivory of the browse species and the local deer density.

Intra-site spatial browsing uniformity was consistent across the study area. For example, intra-site variation in browsing intensity did not change across land use diversity classes. This is in contrast to my hypothesis that sites with more uniform habitats would be browsed more uniformly than sites with diverse habitats and land use classes. Secondly, I found no relationship between deer browsing intensity variation and stem density variation, suggesting that there may not be a correlation between factors that affect browsing variation and those that affect the variation in stem densities. Because there is a strong relationship between site browsing variation and how intensely the site has been browsed, my data suggest that the spatial pattern of deer herbivory may be associated more directly with the relative deer population density than environmental or vegetative conditions as noted by others (deCalesta and Stout 1997, Augustine et al. 1998, Royo et al. 2010a, Royo et al. 2010b).

Deer herbivory is known to have direct effects on particular vegetation species, forest communities and understories, and indirect effects on many other plants and organisms (Augustine and Frelich 1998, Russell et al. 2001, Rooney and Waller 2003, Côté et al. 2004, Koh et al. 2010). The spatial

patterns of herbivory observed in my study suggest that these effects require consideration of spatial context to be understood fully. Deer are spatially as well as vegetatively selective browsers, but observations are scale-dependent, reflecting in part deer biology in addition to habitat conditions. Koda and Fujita (2011) found that there is a nonlinear relationship between deer density and herbivory of forest vegetation as a result of switching diet and browse species at different population densities. That is, deer may exhibit density-dependent forage selectivity such that less-preferred food is consumed at greater rates due to availability at the moment of consumption or because interactions with conspecifics alter how and where deer forage. Despite these complexities and although my study does not examine causal factors, the spatial uniformity of browsing in areas with low stem densities found in my study posits a mechanism to explain the herbivory pattern whereby areas become steady-state, species depauperate “deer savannas” or “fern parks” (Stromayer and Warren 1997, Augustine et al. 1998, Rooney 2001). Although my data do not indicate a relationship between deer herbivory and fern or grass cover as found in other studies (e.g. Stromayer and Warren 1997, Horsley et al. 2003), my data do suggest that preferred browse species would not escape herbivory by deer even in areas with ample quantities of alternate browse. Likewise, there is ample evidence that vegetation in areas that experience high levels of browsing intensity over long periods of time can be altered significantly, including reduced diversity (Stromayer and Warren 1997, Côté et al. 2004, Royo et al. 2010b). Because of this and because deer are spatially selective browsers, management seeking to preserve biodiversity must address the browsing intensity of the present deer herd regardless of the adequacy of available food sources in maintaining herd health. Vegetative communities shaped by high levels of herbivory can be slow to recover even if herbivory intensity is reduced, resulting in prolonged effects on biodiversity (Stromayer and Warren 1997, Augustine et al. 1998, Baiser et al. 2008, Royo et al. 2010b). As a result, deer management focused solely on maintaining deer health or herd density likely will not address preservation of biodiversity.

My results have several implications for understanding and applying deer herbivory impact assessments to deer management. First, my results provide one of the first examinations of the spatial variability of deer herbivory across landscapes. Particularly, my results reflect a landscape more complex

in topography and associated spatial variability in vegetation communities not present in many other studies of deer herbivory (e.g. Augustine and Frelich 1998, Castleberry et al. 1999, Horsley et al. 2003, Wiegmann and Waller 2006, Goetsch et al. 2011). With improved spatial information, managers have improved capacity to assess the usefulness of available herbivory metrics based on the management scale at question. Additionally, understanding both the management scale and the variability of herbivory can inform decisions on sampling intensity needed to meet management needs and goals. Managers increasingly are called upon to manage holistically for biodiversity and ecosystems rather than one or a few species. By employing an informed, multi-scale approach to the assessment and understanding of deer herbivory and resulting environmental effects, managers will have improved ability to manage for the diverse desires of stakeholders, such as hunters who desire more deer versus foresters or agriculturalists who may want fewer deer.

The management of deer populations in Virginia and elsewhere generally follows political boundaries (e.g., counties) and there is limited ability to alter management scales. Forests and other deer habitat, both publicly and privately owned, regularly are subjected to a variety of manipulative activities including logging, prescribed burning, wildlife opening establishment and maintenance, as well as clearings for homes and other development. Likewise, deer hunting and harvest occur broadly, but are variable over time and space, resulting in highly variable local deer population densities. The combination of mixed management and land use practices, deer harvest, and varying environmental characteristics, can lead to a mosaic pattern of herbivory effects across landscapes (Riley et al. 2003, Walter et al. 2009a, Walter et al. 2009b). To provide information relevant to the needs of managers, the scale of herbivory monitoring should encompass spatial scales applicable to deer management in these contexts. Although there has been a long and extensive effort to understand the effects of deer herbivory (reviewed by Côté et al. 2004), the scales of many studies lack strong connection to the spatial scales that dictate deer management. Although a large and beneficial body of information on deer herbivory exists, I recommend that future research focus on expanding the utility of known herbivory intensity measures while continuing to expand knowledge of deer herbivory patterns and effects.

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Table 2.1. Distribution of transects among topographic and landform criteria on white-tailed deer (*Odocoileus virginianus*) herbivory assessment sites in the central Appalachian Mountains of Virginia, USA, summer 2014. SE, southeast; NW, northwest.

Strata criteria	<i>N</i> transects
Low to moderate slope, exposed landform, SE aspect	2
Low to moderate slope, exposed landform, NW aspect	2
Low to moderate slope, sheltered landform, SE aspect	2
Low to moderate slope, sheltered landform, NW aspect	2
High slope, exposed landform, SE aspect	2
High slope, exposed landform, NW aspect	2
High slope, sheltered landform, SE aspect	2
High slope, sheltered landform, NW aspect	2
Low to moderate slope, average landform, SE aspect	1
Low to moderate slope, average landform, NW aspect	1
High slope, moderate landform, SE aspect	1
High slope, moderate landform, NW aspect	1
<i>Total</i>	<i>20</i>

Table 2.2. Statistics for semivariogram model fits for woody stem density and browsing ratios on white-tailed deer (*Odocoileus virginianus*) herbivory assessment sites in the central Appalachian Mountains of Virginia, USA, summer 2014. The proportion spatially structured (PSS) is the proportion of the sample variance that is explained by spatial structure (Isaaks and Srivastava 1989, Didier and Porter 2003).

Dataset	Model	Nugget	Sill	PSS	Range (m)
Woody density	Spherical	0.156	0.229	0.322	28,913
Browsing ratio	Spherical	0.056	0.071	0.212	16,371

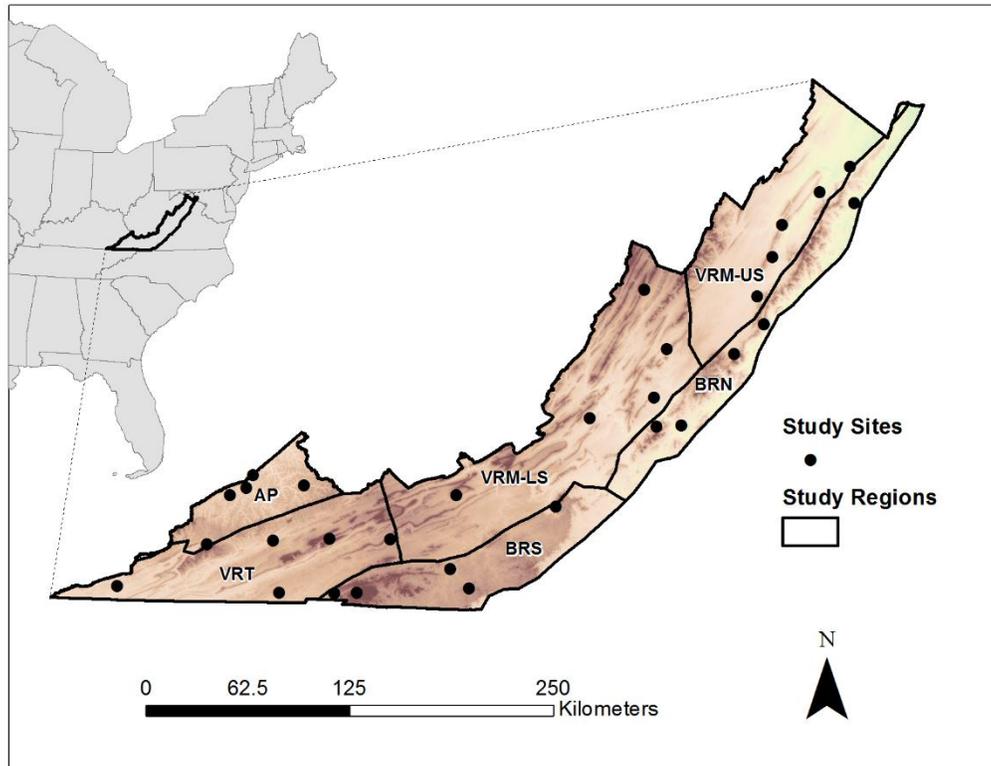


Figure 2.1. White-tailed deer (*Odocoileus virginianus*) herbivory study regions and assessment sites in the central Appalachian Mountains of Virginia, USA, summer 2014. Regions are: Appalachian Plateau, AP; Blue Ridge Northern, BRN; Blue Ridge Southern, BRS; Valley and Ridge Tennessee, VRT; Valley and Ridge Middle - Upper Shenandoah, VRM-US; and Valley and Ridge Middle - Lower Shenandoah, VRM-LS.

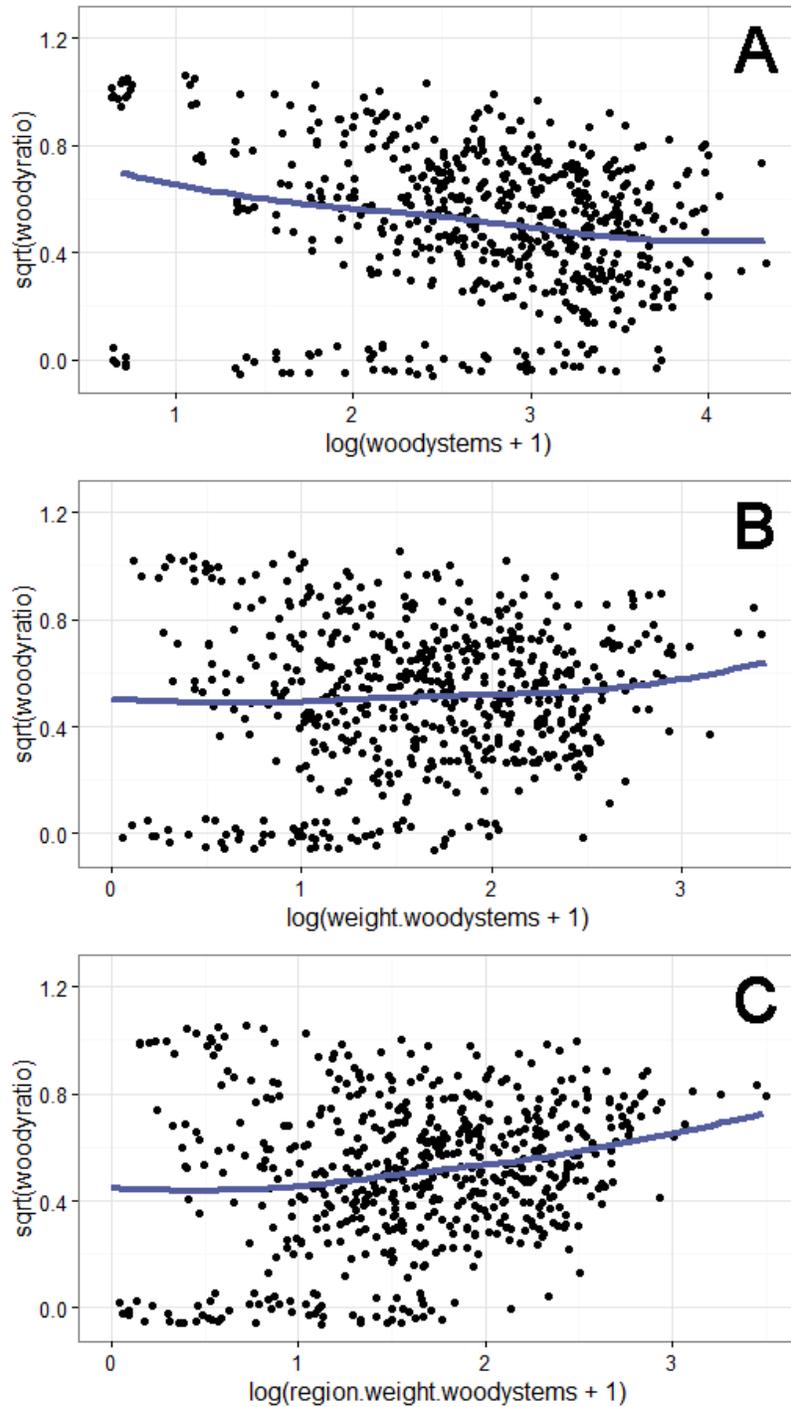


Figure 2.2. The relationship between white-tailed deer (*Odocoileus virginianus*) browsing intensity and the number of woody plant stems (A), study-weighted woody stem counts (B), and regionally weighted stem counts (C) on herbivory assessment sites in the central Appalachian Mountains of Virginia, USA, summer 2014. Trend lines are loess smoothed lines of linear mixed model predicted values; values were jittered up to 0.15 for clarity.

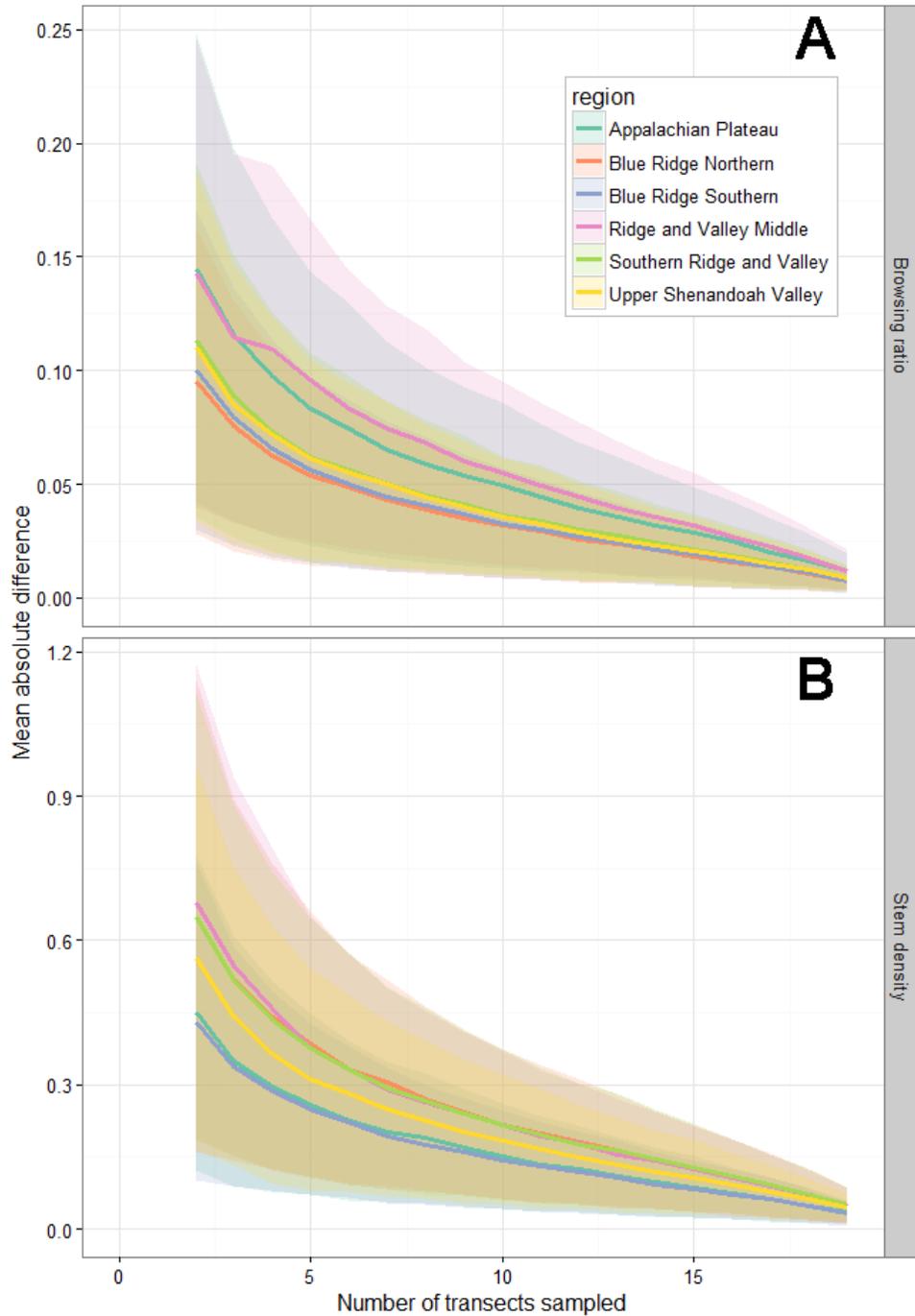


Figure 2.3. Mean absolute difference of woody vegetation browsing ratios (A) or woody vegetation stem densities (B) computed from *Monte Carlo* simulations of reduced sampling on sites compared to the values calculated from sampling 20 transects on white-tailed deer (*Odocoileus virginianus*) herbivory assessment sites in the central Appalachian Mountains, Virginia, USA, summer 2014. Error bars represent ± 1 standard deviation of the mean.

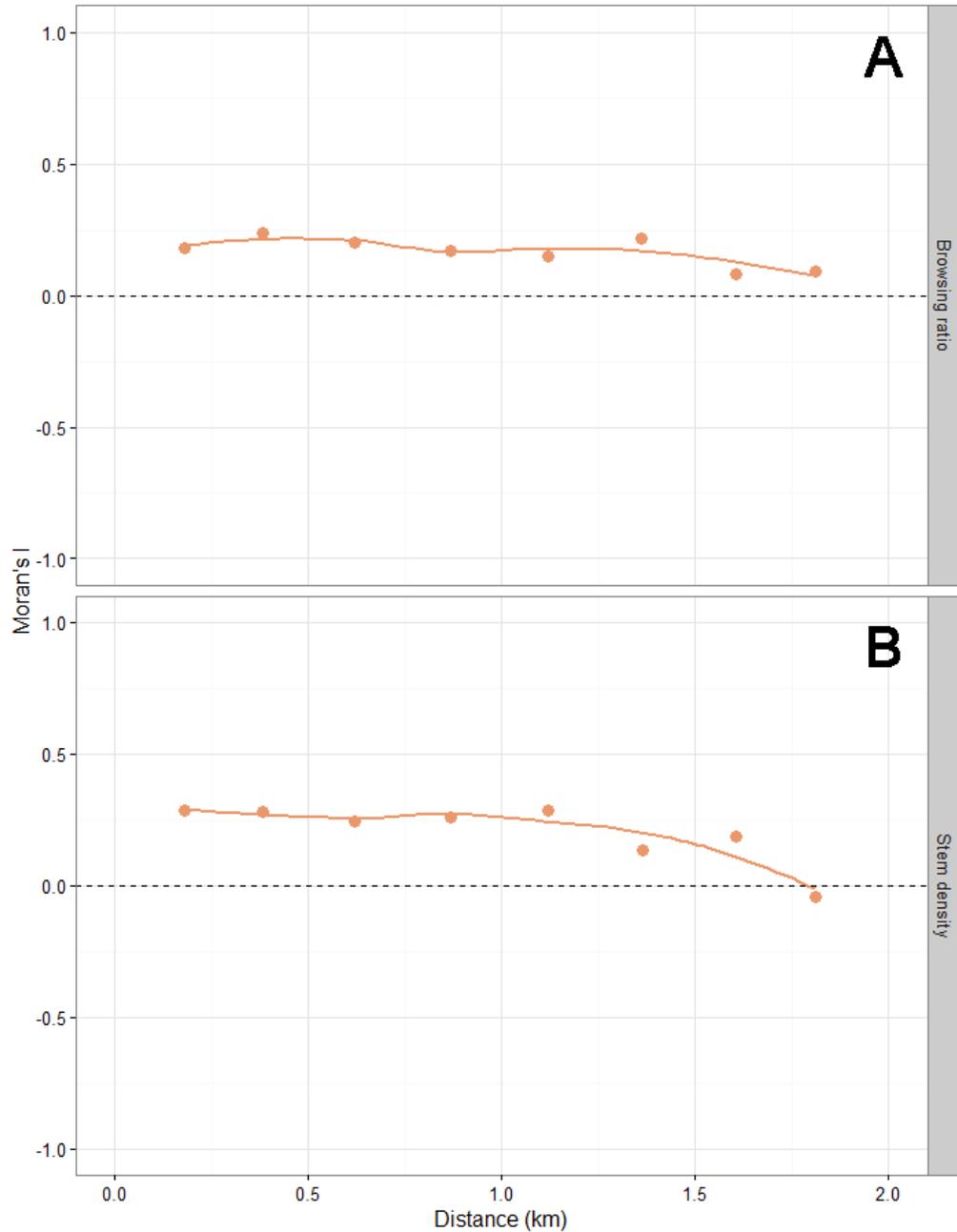


Figure 2.4. Correlograms of woody vegetation browsing ratios (A) and stem densities (B) among transects at white-tailed deer (*Odocoileus virginianus*) herbivory assessment sites in the central Appalachian Mountains of Virginia, USA, summer 2014. Trend lines are loess smoothed fit of the autocorrelation values.

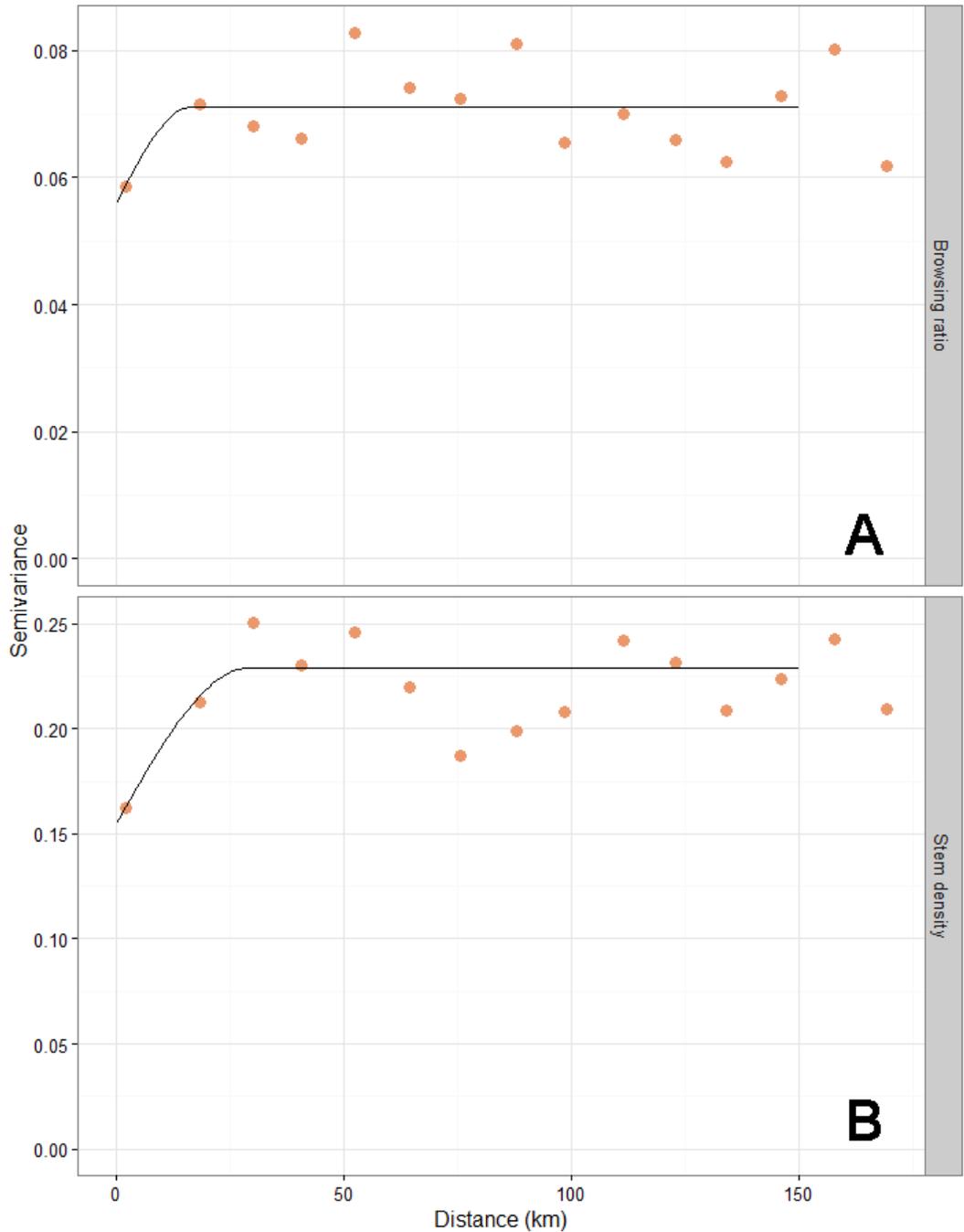


Figure 2.5. Semivariograms for woody vegetation browsing ratios (A) and stem densities (B) among transects at white-tailed deer (*Odocoileus virginianus*) herbivory assessment sites in the central Appalachian Mountains of Virginia, USA, summer 2014.

Appendix A

Table A.1. Forest types and Northeast Terrestrial Wildlife Habitat Classification System (NETWHCS) land cover identifier codes (Gawler 2008) included for white-tailed deer (*Odocoileus virginianus*) herbivory assessment in central Appalachian Mountains, Virginia, USA.

Forest type	NETWHCS identifiers
Cove hardwood	3731, 3732, 3733, 8869
Xeric oak	347, 359, 457, 596, 5920, 5929, 8860
Floodplain	323, 610
Mesic hardwood	887
Mixed pine	24, 339, 591, 600, 602
Northern hardwood	29, 5930, 5939
Pine	331, 332
Spruce-fir	28

Table A.2. Vegetation species browsing ratio (number of stems browsed/available stems) within white-tailed deer (*Odocoileus virginianus*) herbivory assessment study regions, central Appalachian Mountains, Virginia, USA, summer 2014. Species ratios are not reported for regions with ≤ 5 stems recorded in that region; species with ≤ 5 stems in all regions are not reported.

Species	Appalachian Plateau	Blue Ridge Northern	Blue Ridge Southern	Ridge and Valley Middle	Southern Ridge and Valley	Upper Shenandoah Valley
<i>Acer negundo</i>		0.571			0.354	
<i>Acer pensylvanicum</i>	0.312	0.6	0.259	0.25	0.318	
<i>Acer rubrum</i>	0.579	0.406	0.488	0.527	0.471	0.36
<i>Acer saccharum</i>	0.451		0.436		0.235	
<i>Acer spicatum</i>			0.927			
<i>Aesculus flava</i>	0				0	
<i>Ailanthus altissima</i>		0.6		0		0.4
<i>Amelanchier spp.</i>	0.659	0.333	0.563	0.381	0.407	0.375
<i>Asimina triloba</i>	0.029	0.01		0	0	
<i>Berberis canadensis</i>					0.125	
<i>Berberis thunbergii</i>			0.111			0.067
<i>Betula alleghaniensis</i>			0.667			
<i>Betula lenta</i>	0.375	0.381	0.575			0.167
<i>Carpinus caroliniana</i>	0.571	0.419	0.333	0	0.231	
<i>Carya spp.</i>	0.211	0.183	0.24	0.036	0.209	0.226
<i>Castanea dentata</i>	0.625	0.333	0.235	0.3		0.5
<i>Castanea pumila</i>			0.062			0.263
<i>Celastrus orbiculatus</i>		0.065	0.206		0.031	0.231
<i>Celtis occidentalis</i>		0.692		0.143	0.357	0.714

Species	Appalachian Plateau	Blue Ridge Northern	Blue Ridge Southern	Ridge and Valley Middle	Southern Ridge and Valley	Upper Shenandoah Valley
<i>Cercis canadensis</i>	0.167	0.125		0.094	0.231	0.357
<i>Chionanthus virginicus</i>					0.25	
<i>Cornus florida</i>	0.875	0.526	0.619	0.071	0.583	0.476
<i>Corylus americana</i>			0.106		0.088	0.167
<i>Crataegus spp.</i>	1		0.625			
<i>Dirca palustris</i>					0	
<i>Elaeagnus umbellata</i>	0.326	0.083	0.5	0.107	0.171	0.714
<i>Euonymus alatus</i>	1					
<i>Euonymus americanus</i>					0.882	
<i>Fagus grandifolia</i>	0.236	0.064	0.307	0.25	0.122	
<i>Frangula caroliniana</i>					0.2	
<i>Fraxinus americana</i>	0.5	0.471				1
<i>Fraxinus pennsylvanica</i>	0.185	0.308	0.6	0.176	0.365	0.4
<i>Hamamelis virginiana</i>	0.688	0.4	0.44	0.754	0.462	0.229
<i>Hydrangea arborescens</i>	0.375	0.667	0.714			
<i>Ilex opaca</i>	0.364					
<i>Ilex spp. (deciduous)</i>					0.56	0
<i>Juniperus virginiana</i>				0.188	0.333	0.2
<i>Kalmia latifolia</i>	0.206	0.068	0.071	0.121	0.043	0.028
<i>Lindera benzoin</i>	0.561	0.101	0.05	0.344	0.039	0.489
<i>Liriodendron tulipifera</i>	0.333	0.148	0.5		0.167	0.25
<i>Lonicera japonica</i>		0.066	0.122	0.112	0.069	0.047

Species	Appalachian Plateau	Blue Ridge Northern	Blue Ridge Southern	Ridge and Valley Middle	Southern Ridge and Valley	Upper Shenandoah Valley
<i>Lonicera maackii</i>					0.18	0.667
<i>Magnolia acuminata</i>	0.286		0.474			
<i>Magnolia fraseri</i>	0.471		0.273		0	
<i>Menziesia pilosa</i>						0.303
<i>Nyssa sylvatica</i>	0.786	0.698	0.706	0.6	0.714	0.757
<i>Ostrya virginiana</i>	0.474	0.385		0.067	0.174	0.308
<i>Oxydendrum arboreum</i>	0.7	0.312		0.875	0.692	
<i>Parthenocissus quinquefolia</i>	0.16	0.131	0	0.24	0.159	0.077
<i>Pinus strobus</i>		0.469	0.091	0		0.111
<i>Pinus virginiana</i>				0.158		0.167
<i>Prunus avium</i>		0.429				
<i>Prunus serotina</i>	0.714	0.65	0.333		0.286	0.868
<i>Prunus virginiana</i>			0.833			
<i>Quercus alba</i>		0.143	0.074	0	0.077	0.103
<i>Quercus coccinea</i>		0.062				
<i>Quercus ilicifolia</i>						0
<i>Quercus marilandica</i>						0
<i>Quercus montana</i>	0.235	0.12	0.091	0.182	0.125	0.228
<i>Quercus muehlenbergii</i>					0.185	
<i>Quercus rubra</i>	0.462	0.173	0.273	0.391	0.409	0.233
<i>Quercus stellata</i>				0.143		
<i>Quercus velutina</i>	0.4	0.414	0.308	0.328	0.474	0.215

Species	Appalachian Plateau	Blue Ridge Northern	Blue Ridge Southern	Ridge and Valley Middle	Southern Ridge and Valley	Upper Shenandoah Valley
<i>Rhododendron spp.</i> (deciduous)	1	0.864	0.846			0.649
<i>Rhododendron spp.</i> (evergreen)	0.099		0.122	0.075	0.013	
<i>Rhus aromatica</i>					0.062	
<i>Ribes spp.</i>			0.833			
<i>Robinia pseudoacacia</i>						0.5
<i>Rosa spp.</i>	0.857	0.5	0.46	0.532	0.34	0.472
<i>Rubus spp.</i>	0.614	0.108	0.38	0.146	0.164	0.198
<i>Sassafras albidum</i>	0.627	0.278	0.319	0.476	0.412	0.282
<i>Smilax spp.</i>	0.864	0.729	0.709	0.595	0.75	0.502
<i>Symphoricarpos orbiculatus</i>		0.041		0.017	0.1	0
<i>Toxicodendron spp.</i>	0.114	0.148	0.19	0.235	0.055	
<i>Tsuga canadensis</i>	0.1		0	0	0.05	
<i>Ulmus americana</i>				0.333	0.214	
<i>Ulmus rubra</i>	0.333			0.185	0.354	0.421
<i>Vaccinium spp.</i>	0.71	0.258	0.224	0.266	0.445	0.191
<i>Viburnum acerifolium</i>	0.616	0.36	0.567	0.63	0.6	0.246
<i>Viburnum lantanoides</i>			0.75			
<i>Viburnum prunifolium</i>		0.963		0.931	0.875	0.895
<i>Viburnum rufidulum</i>					0.714	
<i>Vitis spp.</i>	0.667	0.5	0.875	0.357	0.632	0.63

Chapter 3: Predicting Intensity of White-tailed Deer Herbivory in the Central Appalachian Mountains

Andrew B. Kniewski

Abstract

White-tailed deer (*Odocoileus virginianus*) play a major role in forested ecosystems, including an increasingly negative effect on forest biodiversity and a magnified role in forest succession. Moderate to high deer populations in the central Appalachians has resulted in lower forest biodiversity and legacy effects in some areas persist even where populations have been reduced. The combination of these factors have prompted the establishment of deer population management goals and policies designed to support conservation of biodiversity and forest regeneration while continuing to support hunting opportunities. However, despite known relationships between herbivory intensity and reduced biodiversity, little information exists regarding the predictability of herbivory intensity across the varied and spatially diverse habitat conditions of the central Appalachians. I examined the predictability of browsing rates across central Appalachian landscapes regarding four aspects of location: vegetative characteristics, physical environment, habitat arrangement, and local demographics. I found that a model fitting the number of stems browsed by local vegetation characteristics received most (62%) of the overall support of all tested models. My data suggest that deer across the varied landscapes and habitat conditions of the central Appalachians responded most predictably to differences in vegetation quantity and type, whereas no other spatial factors consistently affected their browsing intensity. Because herbivory intensity as well as vegetation communities and productivity vary spatially, I suggest that effective broad-scale herbivory impact assessment should include spatially-balanced vegetation monitoring that accounts for regional differences in deer forage preference. Effective monitoring is necessary to avoid biodiversity and community composition changes that progress slowly or are difficult to reverse and may not be detected using traditional deer-density based management goals.

Introduction

Climate change, forest conversion and fragmentation, increases in invasive species, and disruption of historical disturbance regimes all have increased concern about conservation of forest biodiversity. Ungulates play a major role in forested ecosystems (Hobbs 1996, Russell et al. 2001, Rooney and Waller 2003) and, as a result of changes in habitat conditions and decreases in predator populations, ungulates often have had an increasingly negative effect on forest biodiversity and a growing influence on forest succession (Horsley et al. 2003, Côté et al. 2004, McShea 2005, 2012, DiTommaso et al. 2014). In the eastern United States, white-tailed deer (*Odocoileus virginianus*) (hereafter deer) affect forest ecosystems in a variety of ways, including directly through browsing that changes growth rate, development, survival, and succession of plants as well as overall community composition (Russell et al. 2001), and indirectly through a cascade of impacts to other organisms. For example, researchers have related impacts of deer to bird communities, small mammals, and invertebrates (reviewed by Côté et al. 2004).

Similar to other regions in the eastern United States, deer populations in the central Appalachian region have fluctuated significantly over the past century. Following a period of scarcity and then extirpation by 1900, reintroductions, harvest management, and habitat changes since have led to rapidly increasing deer populations and hunter utilization (Halls 1984). Moderate to high deer populations over the past 20–30 years have reduced forest biodiversity and created legacy effects in some areas even where populations have been reduced (Royo et al. 2010, McShea 2012, Tanentzap et al. 2012). Changes in forest management practices also have contributed to changes in deer densities and forage availability (Ford et al. 1993). Forest management changes have been especially influential in the central Appalachians where large areas of land are owned publicly. The combination of these factors have prompted deer population management goals and policies designed to support conservation of biodiversity and forest regeneration while continuing to support hunting opportunities (e.g., Virginia Department of Game and Inland Fisheries 2015b). However, there are few data regarding the

applicability and usefulness of measures of herbivory impact, especially over broad and varied landscapes such as the central Appalachians.

Overall, the effects of deer herbivory have been described well (Rooney 2001, Russell et al. 2001, Rooney and Waller 2003, Côté et al. 2004) and several metrics to assess the intensity of herbivory have been suggested, such as proportion of stems browsed and status of indicator species (Morellet et al. 2001, Morellet et al. 2007, Koh et al. 2010, Frerker et al. 2013). Although these measures of herbivory impact may be valuable within appropriate context, some are difficult for managers to broadly apply across landscapes. For example, indicator species may not be present similarly across different habitat configurations and varied vegetation communities, or metrics may be validated only under certain habitat configurations (Morellet et al. 2007). Within a state or province, deer populations generally are managed on sub-regional or county scales. Yet, the effects of deer herbivory can vary substantially within local areas, such as within parks where hunting is not allowed or conversely within management areas where hunting occurs. Variations in deer harvest, predation, and land use further contribute to local variation in deer herbivory effects. Because of this, predicting the relationship between deer herbivory intensity and spatial factors, such as landscape arrangement and land use, would provide valuable information for managers seeking to assess and monitor herbivory effects across landscapes.

Frerker et al. (2013) reported that a more applicable metric, browsing rate or browsing ratios, provides a reliable indicator of ungulate impact in forest plant communities. Kniowski (Chapter 1) examined the spatial patterns of deer herbivory across Appalachian forested landscapes and found that herbivory patterns remarkably were consistent across varied landscape contexts and across large geographical areas. However, little information exists regarding the predictability of herbivory intensity across landscapes (but see Augustine and Jordan 1998, Campbell et al. 2006). Herein, I examine the predictability of browsing rates across central Appalachian landscapes regarding four distinct aspects of spatial location: vegetative condition, physical environment, habitat arrangement, and local demographics. *A priori*, I hypothesized that vegetative condition would be the strongest predictor of browsing intensity. However, because deer often are most abundant near anthropogenically altered

landscapes (Halls 1984, Augustine and Jordan 1998, Kilpatrick and Spohr 2000), I hypothesized that habitat arrangement factors would be useful in predicting herbivory intensity and that habitat arrangement factors would have a stronger relationship with browsing intensity than physical environment.

Methods

Study area— My study area was located in the central Appalachian Mountains of western Virginia, USA. I divided the study area into six sampling regions following physiographic divisions, including Appalachian Plateau, Blue Ridge Northern, Blue Ridge Southern, Valley and Ridge Tennessee, and Valley and Ridge Middle (Fenneman 1938). I divided the Valley and Ridge Middle section into two study regions due to its size; the subdivision roughly followed the boundary of the Potomac and James River watersheds that separates the upper and lower portions of the Shenandoah Valley (Figure 3.1). Elevations range from approximately 200–1700 m. Generally, Valley and Ridge and, to a lesser extent, the Blue Ridge regions are characterized by long mountain ridges with moderate to steep side slopes and narrow to moderately broad valleys. The Appalachian Plateau is characterized by rugged terrain with steep slopes and very narrow valleys. Landforms in the Appalachian Plateau generally display a dendritic pattern, although local relief generally is less than that of the Valley and Ridge or Blue Ridge. The entire study area predominately is forested (67%), intermixed with pasture or hay production in the valleys (22%), and limited areas of row-crop agriculture, residential, and urban development (Homer et al. 2015). However, the Appalachian Plateau is more forested (79%), has limited pasture or hay production (4%), and no row-crop agriculture. Dominant forest types are xeric oak (*Quercus* spp.) and mixed pine (*Pinus* spp.) with scattered, smaller patches of cove or other mesic hardwoods, and northern hardwoods depending on region, aspect, and elevation. Forests >1200 m in elevation in some locations support red spruce (*Picea rubens*) dominated stands.

Field data collection—I selected five sites within each of the six sampling regions for a total of 30 sites. I sampled woody vegetation within forested areas along 20 transects at each site. I distributed sites across a range of habitat and land use configurations using a combination of landscape diversity

metrics. To facilitate the site distribution, I calculated a measure of local forest diversity by creating a 30 × 30 m grid where values were the sum of the number of forest types defined by the Northeastern Terrestrial Wildlife Habitat Classification System (NETWHCS; Gawler 2008) within a 1 km radius surrounding each grid cell. Forest types were reclassified into 8 types prior to diversity calculation to allow better comparability across sampling regions: cove hardwood, xeric oak, floodplain, mesic hardwood, mixed pine, northern hardwood, pine, and spruce-fir (*Abies* spp.). I ranked locations with forest diversity values ≥ 4 as high forest diversity; locations with a diversity value of 3 as average forest diversity; and areas with diversity values of 1 or 2 as low forest diversity. Similarly, I used the National Land Cover Dataset (NLCD; Fry et al. 2011) to calculate a measure of land use diversity by creating a 30 × 30 m grid where values were the number of different land use classes within a 1 km radius surrounding each grid cell. Land use classes were reclassified prior to diversity calculation into 7 land cover types: water, residential, urban, forest, grass or swampland, pasture, and row-crop. I ranked areas with land use diversity values ≥ 6 as high land use diversity; areas with diversity values of 4 or 5 as average; and areas with diversity values of ≤ 3 as low. I identified and categorized possible assessment sites within each region based on their combination of forest and land use diversity values. Within available locations, I selected one site in each of the following combinations of forest and land use diversity: high forest and high land use; high forest and low land use; low forest and high land use; low forest and low land use; and average land use, average forest diversity. I defined or limited herbivory assessment site boundaries to a ≤ 3 km² circular area to limit intra-site variation in browsing intensity due to variations in local deer population density; sites of this size approximate the home range of an adult deer in the central Appalachians and an individual deer present on a site could access all areas of the site assuming normal movement patterns (Halls 1984, Tierson et al. 1985, Campbell et al. 2004).

Within each site, I selected 20 transect locations randomly within forested areas using a generalized random-tessellation stratified design (Stevens and Olsen 2004). I stratified locations among six topographic and landform criteria; I further subdivided the criteria into two aspect classes for a total of 12 strata classes (Table 3.1). Where strata were not present within a site, I assigned transect locations to

an available alternate strata. I defined low to moderate slope as slopes $\leq 20^\circ$, and high slopes as slopes $> 20^\circ$. I used deviation from mean elevation (DEV) within a 500 m radius (De Reu et al. 2013) as a measure of topographic exposure; positive values indicate the location is higher and negative values indicate the location is lower than the mean elevation of the area (McNab 1993, Wilson and Gallant 2000, De Reu et al. 2013). I defined sheltered landforms as locations with a DEV < -0.7 , and exposed landforms as those with a DEV > 0.7 . I defined average landforms as those not strongly exposed or sheltered ($-0.7 \leq \text{DEV} \leq 0.7$). I defined southeast aspects as aspects between 45° and 225° and northwest aspects as aspects between 0° and 45° or between 225° and 359° . These aspect categories typically split along ridgelines in the study area resulting in an aspect category for each dominant slope face. I oversampled random transect locations within each strata and, as needed, selected alternate random locations within the strata to maintain a minimum distance of 100 m between any two transects.

I oriented transects perpendicular to the terrain slope to minimize elevation changes along the transect or in a random direction if the location had no obvious slope. At each transect location I categorized forest age visually by estimating the average diameter at breast height (dbh) of the largest trees within the stand as young, approximately < 20 cm dbh; intermediate, approximately ≥ 20 cm to ≤ 50 cm dbh; and mature, approximately > 50 cm dbh (DeGraaf et al. 1992). Likewise, I visually classified overstory density at each transect location as: open, moderate, or closed (Young et al. 1967). I recorded recent (within the past year) forest management activities encompassing the transect as burned, harvested, burned and harvested, or none. I categorized forest type at each transect broadly as one of the following types (modified from Braun 1974): spruce-fir, dominated by red spruce and Fraser fir (*Abies fraseri*); northern hardwood, dominated by American beech (*Fagus grandifolia*), sugar maple (*Acer saccharum*) and black cherry (*Prunus serotina*); upland oak or mixed hardwood, dominated by oak species, and other hardwoods such as hickory (*Carya* spp.), red maple (*Acer rubrum*) and blackgum (*Nyssa sylvatica*); cove hardwood dominated by yellow poplar (*Liriodendron tulipifera*), American basswood (*Tilia americana*), and northern red oak (*Q. rubra*); pine-hemlock, dominated by eastern hemlock (*Tsuga canadensis*) and white pine (*Pinus strobus*); mixed pine-hardwood, dominated by various yellow pines and white pine

along with hardwood associates from the upland hardwood community; valley white oak, dominated by white oak (*Q. alba*) but often with other oaks, black walnut (*Juglans nigra*), and blackgum; riparian/floodplain, dominated by American sycamore (*Platanus occidentalis*) and black walnut (*Juglans nigra*).

I evaluated the browsing intensity of deer along each transect by assessing woody vegetation within 1 m² subplots. I only evaluated woody stems because woody stems display persistent and conspicuous evidence of browsing whereas herbaceous vegetation is ephemeral, the whole plant can be consumed, and plants more easily are damaged by non-browsing events (Frerker et al. 2013). I distributed subplots evenly (every 5 m) along 50 m transects (10 per transect). I counted and identified the total number of woody stems between 0.2 m and 1.8 m in height within each subplot by vegetation species and also recorded the number of stems that had been browsed by deer. Although browsing by species other than deer rarely was encountered, I was careful to differentiate between the coarse browse scars resulting from the browsing of deer from clean cut stems resulting from the browsing of rabbits (*Sylvilagus* spp.) or rodents (Morellet et al. 2001).

Spatial data and modeling—I extracted spatial factors for each transect from geographical information system (GIS) layers using *ArcMap* (Version 10.3.1, Environmental Systems Research Institute, Redlands, CA). Physical environment factors, including elevation, DEV, slope (in degrees), and aspect (linearized using the transformation $[1 - \cos(\text{aspect})] + [1 - \sin(\text{aspect})]$), were obtained or derived from the United States Geological Survey (USGS) National Elevation Dataset (<http://nationalmap.gov/>; accessed 9 September 2015) at 1/3 arc-second resolution. I used the Virginia geologic map dataset from the USGS Mineral Resources spatial data repository (<http://mrddata.usgs.gov/geology/state/>; accessed 29 August 2015) to obtain bedrock type. I used *FRAGSTATS* (version 4.2, <http://www.umass.edu/landeco/research/fragstats/fragstats.html>) to calculate landscape and habitat arrangement factors for each transect. I calculated three metrics for land use types, including edge density, mean radius of gyration (a measure of patch extent), and Simpson's diversity index (diversity of land use), and three metrics exclusively for forest land use, including edge density,

mean radius of gyration, and patch cohesion index (a measure of the physical connectedness of patches; patch cohesion increases as the patch type becomes more clumped or aggregated in its distribution) (McGarigal 2015). I calculated all landscape and habitat arrangement factors at two spatial scales, 1 km and 5 km radius circular areas surrounding each transect. Additionally, for each transect, I calculated the distance to the nearest forest edge (defined as any non-forest land use type by the NLCD) for a total of 13 landscape and habitat arrangement factors. Demographic factors included human population density estimates for 2014 by county or city (U.S. Census Bureau 2015) and 2014 deer harvest density by county or city (Virginia Department of Game and Inland Fisheries 2015a). I considered including the decadal average deer harvest density and the coefficient of variation (Zar 1984) of the decadal deer harvest density in my models; however, both factors highly were correlated (>0.82) with either the 2014 human population density or the 2014 harvest density. As a result, I included only the demographic estimates from 2014. In addition to the vegetation characteristics I recorded in the field, I obtained tree canopy cover from the NLCD tree cover dataset (Homer et al. 2015). Because deer browse vegetation preferentially (Nixon et al. 1970, Vangilder et al. 1982, Crimmins et al. 2010, Dostaler et al. 2011), I calculated a measure of average vegetation preference for each transect. To do so, I multiplied stem counts for each vegetation species by the regional browsing ratio for that species. This resulted in stems of plant species browsed frequently by deer being more heavily weighted and those of vegetation species rarely browsed being less weighted in count totals. Using the weighted counts, I calculated the mean stem weight (hereafter forage preference) for each transect.

The proportion of stems browsed, or browsing ratio, has been shown to be a reliable indicator of herbivory intensity and impacts to forest plant communities (Castleberry et al. 1999, Morellet et al. 2001, Frerker et al. 2013). However, modeling ratios directly can be problematic and lead to spurious correlations and difficulty interpreting model coefficients (Kronmal 1993). Because of this, I developed candidate models of herbivory intensity using the number of stems browsed as an independent variable and included the number of stems available and the mean stem preference as dependent variables in all models (Kronmal 1993). I developed candidate models by including additional dependent variables in

groups representing the vegetative condition, physical environment, and demographics as defined above. I included a model for each group of dependent variables separately and all possible pair-wise combinations of the variable groups. I used the same methodology for the factors of landscape and habitat arrangement; because factors were correlated strongly with each other, I created models for each factor individually.

Initially, I fit models with the number of stems browsed as an independent variable and the number of stems available and the mean forage preference as dependent variables in all models as described above. However, I hypothesized that the relationship between the number of stems browsed and the number of stems available would be non-linear; likewise, I hypothesized that the preference of the available stems would influence the proportion of stems browsed and that this relationship may change with forage availability. Accordingly, I included a model with the square of the number of stems available and the interaction between forage preference and stems available as a candidate model. Because the model including the square and interactive terms for the local vegetation characteristics greatly outranked the other candidate models, I used it as a base model and then refit all candidate models including the square and interactive terms and selected spatial factors. I also included a reduced base model that did not include the interaction and squared terms and a null model in the candidate model list for a total of 61 models (Table B.1).

Because transects were nested within sites and sites within sampling regions, I used a linear mixed model approach and included random intercepts for site and region (Snijders 2011). Stems available and stems browsed were $\log + 1$ transformed prior to model fitting. I centered and scaled all other independent continuous variables so that I directly could assess effect sizes (Schielzeth 2010). Because there were multiple transects per county, I included a random intercept for county in each model where demographic factors were present. I ranked models using Akaike's information criterion corrected for small sample size (AIC_c), the difference between the model with the lowest AIC_c and the AIC_c of the i th model (Δ_i), and Akaike's weights (w_i) (Burnham and Anderson 2002). I assessed the variance explained by the top model using marginal and conditional r^2 for linear mixed models as described by

Nakagawa and Schielzeth (2013). To assess the ability of the top model to predict herbivory intensity, I randomly selected 70% of the dataset to use for model fitting and I used the remaining 30% to test the model. I used the top supported model to predict the number of stems browsed on transects for the data retained for model testing. I back transformed the values to the original scale and compared the predicted to the observed values. I predicted values both including and excluding information regarding the random variables to simulate field observations where broader site conditions were and were not known. Predicted values were rounded to the nearest whole number and I evaluated predictive accuracy by calculating mean error, and root mean square error (RMSE) of the predicted values (Chai and Draxler 2014). I used *R* (Version 3.2.3, www.r-project.org) and packages “lme4” (Version 1.1-10, <https://cran.r-project.org/package=lme4>), “MuMIn” (Version 1.15-6, <https://cran.r-project.org/package=MuMIn>), and “multcomp” (Version 1.4-1, <https://cran.r-project.org/package=multcomp>) to fit and rank models.

Results

Between 2 June 2014 and 7 August 2014 I counted and identified 11,137 woody plant stems or 1.86 stems m⁻² of 82 species or species groups across all 30 sites and 600 transects. Mean browsing ratio study-wide was 0.28, whereas mean regionally-weighted browsing ratio was 0.46. Browsing ratios varied considerably among vegetation species study-wide, but ratios were similar among regions (Table B.2). The number of stems per-transect was lowest in the Appalachian Plateau and highest in the Southern Ridge and Valley region (Table 3.2). Conversely, edge density was greater in the Appalachian Plateau and Southern Ridge and Valley regions compared with other regions to the northeast.

The base model fitting the number of stems browsed exclusively by local vegetation characteristics received the most (62%) of the overall support (Table 3.3). Because no other model had $\Delta_i < 2$, I used estimates directly from the best supported model. There was no evidence that models containing factors of the physical environment, habitat arrangement, local demographics, or expanded vegetative conditions were improved over the model containing only the factors relating to the local vegetative conditions. The top model explained 56% of the variation in the number of stems browsed not

accounting for the random factors and 63% of the variation after accounting for random factors. The mean error of predictions by the top model not accounting for random factors was 2.41 stems per transect or 18.0% of the number of available stems; the RMSE was 3.17 stems. The mean error of predictions by the top model accounting for random factors was 2.34 stems per transect or 17.5% of the number of available stems; the RMSE was 3.17 stems.

Discussion

Contrary to my hypothesis, I did not find that spatial factors relating to the physical environment, habitat arrangement, or demographics improved models of deer herbivory intensity. Although deer are known to frequent habitat edges and often are abundant in fragmented landscapes in the Appalachians (Alverson et al. 1988, Ford et al. 1993, Campbell et al. 2006), they also are present in large contiguous forests and highly agricultural areas. Because they adapt well to many habitat types and configurations, demonstrated by their rapid population growth over the last several decades, deer are ubiquitous across the core of their distribution in North America. In the mixed forest and agriculture of southcentral Minnesota, for example, Augustine and Jordan (1998) found that browsing intensity was correlated strongly with the availability of row crops, alfalfa (*Medicago sativa*), and fields within 1.5 km of the sampling location. My study area had only a limited amount of row crops and other agriculture production that may provide supplemental food for deer and, as a result, I was not able to examine the influence of row crops and other potential alternative food sources directly. Lacking strong potential associations between forest edge and alternate, available food resources, edge did not appear to influence browsing intensity in my study. Furthermore, my top supported model suggests that measurements of the type and abundance of available forage were sufficient to predict the intensity of deer herbivory across the variety of landscape characteristics found in the study area.

My predictive herbivory intensity models accounted for both the amount and average preference of the available forage. These factors change substantially across the landscape and in relationship to landscape attributes. For example, McNab (1989, 1993) found strong relationships between tree growth

and landform indices, suggesting a predictable difference in forest productivity and species/community composition across landforms in the Appalachians. In spite of this, I did not find any improvement in models of herbivory intensity by including factors relating to landform or other physical attributes of location. One reason for this lack of relationship may be scale differences between the measurement of physical attributes and how deer browse landscapes or other confounding factors of herbivory.

Landforms vary in size and availability. Also, deer establish relatively stable home range areas that generally encompass different landforms and foraging opportunities. Understory vegetation communities in Appalachian coves are influenced by a suite of factors including cove size, extent of similar habitat in the area, and connectivity to other patches (Ford et al. 2000). Likewise, Ford et al. (1997) examined deer physiological metrics in relation to site productivity and forest types in the southern Appalachians. They found significant correlations between the area of cove hardwood and deer weight; however, there was little absolute correlation with site index. If deer herbivory is influenced to a greater degree by vegetation type than factors such as vegetation quantity, measures of forest productivity, for example, may not necessarily be related directly to browsing intensity. A lack of relationship between landscape attributes and herbivory intensity also could result from very productive areas providing greater amounts of herbaceous forage that may change or mask herbivory pressure on woody species evaluated in my study.

The lack of relationship between spatial factors and deer herbivory intensity highlights both the simplicity of the best supported model and the difficulty of predicting browsing intensity across complex, multi-faceted landscapes. Although my research suggests that herbivory intensity can be predicted with relatively simple models, no physical or demographic attribute or set of attributes were identified that may be useful for identifying landscape areas prone to increased levels of browsing intensity in western Virginia. As a result, without measurement of or obtaining data on local vegetative conditions, broad-scale prediction of herbivory intensity remains difficult. Likewise, understanding forest vegetative condition across landscapes likely will remain a critical component for continued development of herbivory impact assessment methods. New and emerging methods, such as remote sensing of understory conditions (e.g., Latifi et al. 2016), or modifying existing data collection programs, such as the United

States Forest Service, Forest Inventory and Analysis program, that provide more details of understory conditions may provide valuable enhancements to assessing herbivory intensity across landscapes.

Ecosystem change occurs temporarily and spatially. Regular assessment of herbivory intensity would help identify locations at risk and may provide managers both an early warning and sufficient time to implement management changes before substantial or long-term degradations occur. However, landscapes likely already contain areas previously degraded by high levels of deer herbivory. For example, large areas of Pennsylvania currently display substantial reductions in forest biodiversity (Goetsch et al. 2011, Schumacher and Carson 2013) and recovery of these degraded systems can be slow (Royo et al. 2010, Tanentzap et al. 2012). As a result, any broad-scale assessment of herbivory intensity needs to incorporate measures of ecosystem health that encompass current, past, and future conditions and goals to aid in establishing and maintaining healthy and sustainable ecosystems. My results suggest that assessment should include spatially-balanced vegetation monitoring and account for regional differences in deer forage preference. Traditional deer density based management goals may not incorporate ecological factors adequately that affect biodiversity maintenance or recovery (McShea 2012). Because of this, developing effective monitoring of herbivory impacts is essential for the central Appalachian region to prevent negative impacts to biodiversity that are either impossible or would be logistically, temporally, and fiscally expensive to return to a previous, desired state.

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Table 3.1. Distribution of transects among topographic and landform criteria on white-tailed deer (*Odocoileus virginianus*) herbivory assessment sites in the central Appalachian Mountains of Virginia, USA, summer 2014. SE, southeast; NW, northwest.

Strata criteria	<i>N</i> transects
Low to moderate slope, exposed landform, SE aspect	2
Low to moderate slope, exposed landform, NW aspect	2
Low to moderate slope, sheltered landform, SE aspect	2
Low to moderate slope, sheltered landform, NW aspect	2
High slope, exposed landform, SE aspect	2
High slope, exposed landform, NW aspect	2
High slope, sheltered landform, SE aspect	2
High slope, sheltered landform, NW aspect	2
Low to moderate slope, average landform, SE aspect	1
Low to moderate slope, average landform, NW aspect	1
High slope, average landform, SE aspect	1
High slope, average landform, NW aspect	1
<i>Total</i>	<i>20</i>

Table 3.2. Mean \pm standard deviation of model factors for white-tailed deer (*Odocoileus virginianus*) herbivory assessment transects in the central Appalachian Mountains of Virginia, USA, summer 2014. Habitat arrangement metrics were calculated over 1 km and 5 km radius areas as indicated. Deer harvest density and human population density reflect the mean density of the city or county of the transect locations not the mean density for the study region. DEV = Deviation from mean elevation.

	Appalachian Plateau	Blue Ridge Northern	Blue Ridge Southern	Ridge and Valley Middle	Southern Ridge and Valley	Upper Shenandoah Valley
Woody stems (<i>n</i>)	13.47 \pm 8.87	21.23 \pm 13.22	18.19 \pm 9.18	16.84 \pm 13.23	22.94 \pm 13.88	20.21 \pm 13.17
Stems browsed (<i>n</i>)	4.788 \pm 4.415	5.620 \pm 6.665	5.440 \pm 5.008	4.151 \pm 4.265	5.310 \pm 4.603	6.717 \pm 6.641
Stem preference	0.375 \pm 0.144	0.268 \pm 0.105	0.301 \pm 0.146	0.3 \pm 0.191	0.244 \pm 0.123	0.354 \pm 0.141
Browsing ratio	0.395 \pm 0.287	0.253 \pm 0.183	0.321 \pm 0.238	0.352 \pm 0.317	0.274 \pm 0.226	0.395 \pm 0.285
Distance to forest edge (m)	137.5 \pm 100.6	251.9 \pm 212.6	355.7 \pm 330.6	294.5 \pm 304.1	222.1 \pm 318.5	282.9 \pm 231.3
Tree cover (%)	91.7 \pm 15.07	95.88 \pm 8.5	95.76 \pm 7.68	91.28 \pm 14.66	96.92 \pm 5.08	92.12 \pm 11.72
Slope (°)	20.08 \pm 9.98	14.55 \pm 8.05	20.36 \pm 9.25	16.00 \pm 8.68	18.51 \pm 9.31	13.49 \pm 9.78
DEV	-0.026 \pm 1.046	-0.011 \pm 0.914	-0.005 \pm 0.957	0.030 \pm 0.949	0.010 \pm 1.019	-0.126 \pm 0.852
Transformed aspect	1.953 \pm 0.929	1.895 \pm 0.989	2.213 \pm 0.904	2.12 \pm 1.065	2.017 \pm 1.002	1.885 \pm 0.93
Edge density 1 km (m ha ⁻¹)	81.15 \pm 27.77	52.38 \pm 30.83	41.54 \pm 29.36	50.5 \pm 43.12	69.74 \pm 37.58	36.28 \pm 26.71
Radius of gyration 1km (m)	110.5 \pm 36.9	142.8 \pm 57.6	188.8 \pm 161.3	182.9 \pm 136.7	139.7 \pm 143.5	222.2 \pm 139.6
Simpson's diversity index 1 km	0.331 \pm 0.156	0.246 \pm 0.164	0.201 \pm 0.162	0.219 \pm 0.201	0.384 \pm 0.224	0.22 \pm 0.217
Edge density 5 km (m ha ⁻¹)	83 \pm 18.62	47.66 \pm 17.62	59.66 \pm 25.42	49.44 \pm 14.63	89.32 \pm 39.46	59.53 \pm 14.3
Radius of gyration 5km (m)	92.3 \pm 7.66	142.6 \pm 16.9	99.16 \pm 12.59	130.2 \pm 12.2	97.24 \pm 8.07	129.7 \pm 13.5
Simpson's diversity index 5 km	0.365 \pm 0.092	0.276 \pm 0.143	0.31 \pm 0.141	0.321 \pm 0.104	0.527 \pm 0.171	0.468 \pm 0.094
Forest edge density 1 km (m ha ⁻¹)	64.73 \pm 18.8	46.16 \pm 27.86	31.13 \pm 22.62	42.64 \pm 33.2	51.35 \pm 27.55	28 \pm 17.95
Forest radius of gyration 1km (m)	257 \pm 188.7	341.1 \pm 195	467.8 \pm 206.9	446.1 \pm 244.5	308 \pm 203.6	446.7 \pm 248
Forest patch cohesion index 1 km	99.07 \pm 0.86	99.62 \pm 0.36	99.75 \pm 0.33	99.72 \pm 0.43	99.42 \pm 0.47	99.44 \pm 0.85
Forest edge density 5 km (m ha ⁻¹)	65.18 \pm 12.08	39.85 \pm 12.47	45.72 \pm 17.72	39.03 \pm 11.06	52.61 \pm 15.49	40.46 \pm 12.24

	Appalachian Plateau	Blue Ridge Northern	Blue Ridge Southern	Ridge and Valley Middle	Southern Ridge and Valley	Upper Shenandoah Valley
Forest radius of gyration 5km (m)	169.5 ± 47.3	266.8 ± 109.4	161.8 ± 43.4	171.3 ± 40.4	112.6 ± 16.7	121.2 ± 13.3
Forest patch cohesion index 5 km	99.87 ± 0.08	99.75 ± 0.18	99.86 ± 0.1	99.83 ± 0.13	98.66 ± 1.39	99.42 ± 0.4
Deer harvest density (<i>n</i> km ⁻²)	0.824 ± 0.207	1.792 ± 0.357	1.736 ± 0.474	1.669 ± 0.326	1.152 ± 0.496	1.797 ± 0.368
Human population density (<i>n</i> km ⁻²)	26.74 ± 32.92	27.17 ± 15.88	40.59 ± 28.74	14.56 ± 6.97	115.4 ± 189.4	47.76 ± 17.82

Table 3.3. Three best supported linear mixed models of number of woody plant stems browsed by white-tailed deer (*Odocoileus virginianus*) on herbivory assessment transects in the central Appalachian Mountains, Virginia, USA, summer 2014. Model parameters are given as well as the degrees of freedom (df), log likelihoods (logLik), Akaike's information criterion corrected for small sample size (AIC_c), difference in AIC_c value between top model and i th model (Δ_i), and model support (w_i). All models contained a random intercept for site and study region; the base model included the number of available stems, the square of the number of available stems, forage preference, and the interaction between the number of stems available and forage preference.

Model	df	logLik	AIC_c	Δ_i	w_i
Base model	8	-340.89	698.1	0	0.618
Base model + Simpson's diversity index 5 km	9	-342.39	703.2	5.10	0.048
Base model + Forest edge density 5 km	9	-342.47	703.4	5.24	0.045

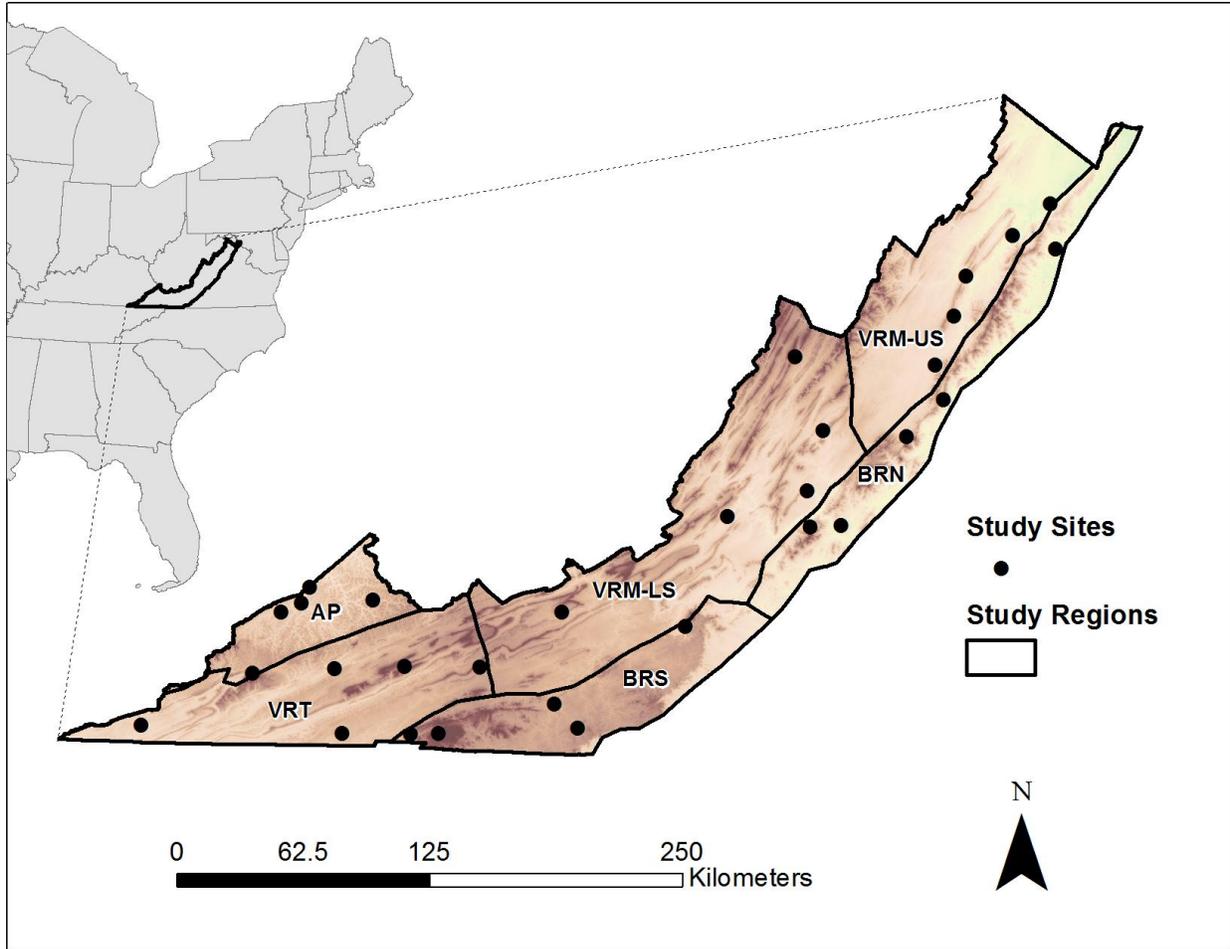


Figure 3.1. White-tailed deer (*Odocoileus virginianus*) herbivory study regions and assessment sites in the central Appalachian Mountains, Virginia, USA, summer 2014. Regions are: Appalachian plateau, AP; Blue Ridge Northern, BRN; Blue Ridge Southern, BRS; Valley and Ridge Tennessee, VRT; Valley and Ridge Middle - Upper Shenandoah, VRM-US; and Valley and Ridge Middle - Lower Shenandoah, VRM-LS.

Appendix B

Table B.1. Dependent fixed effects of linear mixed models fitted and ranked with the number of woody vegetation stems browsed by deer on assessment transects in the central Appalachian Mountains, Virginia, USA as the dependent variable. All models included random intercept terms for site and study region; those including deer harvest density and human population density also included a random intercept for county. The base model included the number of available woody stems, the square of the number of available stems, forage preference, and the interaction between forage preference and available stems. DEV = Deviation from mean elevation.

Model	Dependent fixed effects
1	1 (<i>null</i>)
2	stems + preference
3	stems + stems ² + preference + preference:stems (<i>base model</i>)
4	base model + slope + DEV + aspect + bedrock
5	base model + forest type + forest age + overstory + recent management + tree cover
6	base model + distance to edge
7	base model + edge density 1km
8	base model + radius of gyration 1km
9	base model + Simpson's diversity index 1km
10	base model + forest edge density 1 km
11	base model + forest radius of gyration 1km
12	base model + forest patch cohesion index 1km
13	base model + edge density 5km
14	base model + radius of gyration 5km
15	base model + Simpson's diversity index 5km
16	base model + forest edge density 5km
17	base model + forest radius of gyration 5km
18	base model + forest patch cohesion index 5km
19	base model + deer harvest density + human population density
20	base model + forest type + forest age + overstory + recent management + tree cover + slope + DEV + aspect
21	base model + slope + DEV + aspect + bedrock + distance to edge
22	base model + slope + DEV + aspect + bedrock + edge density 1km
23	base model + slope + DEV + aspect + bedrock + radius of gyration 1km
24	base model + slope + DEV + aspect + bedrock + Simpson's diversity index 1km

Model	Dependent fixed effects
25	base model + slope + DEV + aspect + bedrock + forest edge density 1 km
26	base model + slope + DEV + aspect + bedrock + forest radius of gyration 1km
27	base model + slope + DEV + aspect + bedrock + forest patch cohesion index 1km
28	base model + slope + DEV + aspect + bedrock + edge density 5km
29	base model + slope + DEV + aspect + bedrock + radius of gyration 5km
30	base model + slope + DEV + aspect + bedrock + Simpson's diversity index 5km
31	base model + slope + DEV + aspect + bedrock + forest edge density 5km
32	base model + slope + DEV + aspect + bedrock + forest radius of gyration 5km
33	base model + slope + DEV + aspect + bedrock + forest patch cohesion index 5km
34	base model + slope + DEV + aspect + bedrock + deer harvest density + human population density
35	base model + forest type + forest age + overstory + recent management + tree cover + distance to edge
36	base model + forest type + forest age + overstory + recent management + tree cover + edge density 1km
37	base model + forest type + forest age + overstory + recent management + tree cover + radius of gyration 1km
38	base model + forest type + forest age + overstory + recent management + tree cover + Simpson's diversity index 1km
39	base model + forest type + forest age + overstory + recent management + tree cover + forest edge density 1 km
40	base model + forest type + forest age + overstory + recent management + tree cover + forest radius of gyration 1km
41	base model + forest type + forest age + overstory + recent management + tree cover + forest patch cohesion index 1km
42	base model + forest type + forest age + overstory + recent management + tree cover + edge density 5km
43	base model + forest type + forest age + overstory + recent management + tree cover + radius of gyration 5km
44	base model + forest type + forest age + overstory + recent management + tree cover + Simpson's diversity index 5km
45	base model + forest type + forest age + overstory + recent management + tree cover + forest edge density 5km

Model	Dependent fixed effects
46	base model + forest type + forest age + overstory + recent management + tree cover + forest radius of gyration 5km
47	base model + forest type + forest age + overstory + recent management + tree cover + forest patch cohesion index 5km
48	base model + forest type + forest age + overstory + recent management + tree cover + deer harvest density + human population density
49	base model + deer harvest density + human population density + distance to edge
50	base model + deer harvest density + human population density + edge density 1km
51	base model + deer harvest density + human population density + radius of gyration 1km
52	base model + deer harvest density + human population density + Simpson's diversity index 1km
53	base model + deer harvest density + human population density + forest edge density 1 km
54	base model + deer harvest density + human population density + forest radius of gyration 1km
55	base model + deer harvest density + human population density + forest patch cohesion index 1km
56	base model + deer harvest density + human population density + edge density 5km
57	base model + deer harvest density + human population density + radius of gyration 5km
58	base model + deer harvest density + human population density + Simpson's diversity index 5km
59	base model + deer harvest density + human population density + forest edge density 5km
60	base model + deer harvest density + human population density + forest radius of gyration 5km
61	base model + deer harvest density + human population density + forest patch cohesion index 5km

Table B.2 Vegetation species browsing ratio (number of stems browsed/available stems) within white-tailed deer (*Odocoileus virginianus*) herbivory assessment study regions, central Appalachian Mountains, Virginia, USA, summer 2014. Species ratios are not reported for regions with ≤ 5 stems recorded in that region; species with ≤ 5 stems in all regions are not reported.

Species	Appalachian Plateau	Blue Ridge Northern	Blue Ridge Southern	Ridge and Valley Middle	Southern Ridge and Valley	Upper Shenandoah Valley
<i>Acer negundo</i>		0.571			0.354	
<i>Acer pensylvanicum</i>	0.312	0.6	0.259	0.25	0.318	
<i>Acer rubrum</i>	0.579	0.406	0.488	0.527	0.471	0.36
<i>Acer saccharum</i>	0.451		0.436		0.235	
<i>Acer spicatum</i>			0.927			
<i>Aesculus flava</i>	0				0	
<i>Ailanthus altissima</i>		0.6		0		0.4
<i>Amelanchier spp.</i>	0.659	0.333	0.563	0.381	0.407	0.375
<i>Asimina triloba</i>	0.029	0.01		0	0	
<i>Berberis canadensis</i>					0.125	
<i>Berberis thunbergii</i>			0.111			0.067
<i>Betula alleghaniensis</i>			0.667			
<i>Betula lenta</i>	0.375	0.381	0.575			0.167
<i>Carpinus caroliniana</i>	0.571	0.419	0.333	0	0.231	
<i>Carya spp.</i>	0.211	0.183	0.24	0.036	0.209	0.226
<i>Castanea dentata</i>	0.625	0.333	0.235	0.3		0.5
<i>Castanea pumila</i>			0.062			0.263
<i>Celastrus orbiculatus</i>		0.065	0.206		0.031	0.231
<i>Celtis occidentalis</i>		0.692		0.143	0.357	0.714

Species	Appalachian Plateau	Blue Ridge Northern	Blue Ridge Southern	Ridge and Valley Middle	Southern Ridge and Valley	Upper Shenandoah Valley
<i>Cercis canadensis</i>	0.167	0.125		0.094	0.231	0.357
<i>Chionanthus virginicus</i>					0.25	
<i>Cornus florida</i>	0.875	0.526	0.619	0.071	0.583	0.476
<i>Corylus americana</i>			0.106		0.088	0.167
<i>Crataegus spp.</i>	1		0.625			
<i>Dirca palustris</i>					0	
<i>Elaeagnus umbellata</i>	0.326	0.083	0.5	0.107	0.171	0.714
<i>Euonymus alatus</i>	1					
<i>Euonymus americanus</i>					0.882	
<i>Fagus grandifolia</i>	0.236	0.064	0.307	0.25	0.122	
<i>Frangula caroliniana</i>					0.2	
<i>Fraxinus americana</i>	0.5	0.471				1
<i>Fraxinus pennsylvanica</i>	0.185	0.308	0.6	0.176	0.365	0.4
<i>Hamamelis virginiana</i>	0.688	0.4	0.44	0.754	0.462	0.229
<i>Hydrangea arborescens</i>	0.375	0.667	0.714			
<i>Ilex opaca</i>	0.364					
<i>Ilex spp. (deciduous)</i>					0.56	0
<i>Juniperus virginiana</i>				0.188	0.333	0.2
<i>Kalmia latifolia</i>	0.206	0.068	0.071	0.121	0.043	0.028
<i>Lindera benzoin</i>	0.561	0.101	0.05	0.344	0.039	0.489
<i>Liriodendron tulipifera</i>	0.333	0.148	0.5		0.167	0.25
<i>Lonicera japonica</i>		0.066	0.122	0.112	0.069	0.047

Species	Appalachian Plateau	Blue Ridge Northern	Blue Ridge Southern	Ridge and Valley Middle	Southern Ridge and Valley	Upper Shenandoah Valley
<i>Lonicera maackii</i>					0.18	0.667
<i>Magnolia acuminata</i>	0.286		0.474			
<i>Magnolia fraseri</i>	0.471		0.273		0	
<i>Menziesia pilosa</i>						0.303
<i>Nyssa sylvatica</i>	0.786	0.698	0.706	0.6	0.714	0.757
<i>Ostrya virginiana</i>	0.474	0.385		0.067	0.174	0.308
<i>Oxydendrum arboreum</i>	0.7	0.312		0.875	0.692	
<i>Parthenocissus quinquefolia</i>	0.16	0.131	0	0.24	0.159	0.077
<i>Pinus strobus</i>		0.469	0.091	0		0.111
<i>Pinus virginiana</i>				0.158		0.167
<i>Prunus avium</i>		0.429				
<i>Prunus serotina</i>	0.714	0.65	0.333		0.286	0.868
<i>Prunus virginiana</i>			0.833			
<i>Quercus alba</i>		0.143	0.074	0	0.077	0.103
<i>Quercus coccinea</i>		0.062				
<i>Quercus ilicifolia</i>						0
<i>Quercus marilandica</i>						0
<i>Quercus montana</i>	0.235	0.12	0.091	0.182	0.125	0.228
<i>Quercus muehlenbergii</i>					0.185	
<i>Quercus rubra</i>	0.462	0.173	0.273	0.391	0.409	0.233
<i>Quercus stellata</i>				0.143		
<i>Quercus velutina</i>	0.4	0.414	0.308	0.328	0.474	0.215

Species	Appalachian Plateau	Blue Ridge Northern	Blue Ridge Southern	Ridge and Valley Middle	Southern Ridge and Valley	Upper Shenandoah Valley
<i>Rhododendron spp.</i> (deciduous)	1	0.864	0.846			0.649
<i>Rhododendron spp.</i> (evergreen)	0.099		0.122	0.075	0.013	
<i>Rhus aromatica</i>					0.062	
<i>Ribes spp.</i>			0.833			
<i>Robinia pseudoacacia</i>						0.5
<i>Rosa spp.</i>	0.857	0.5	0.46	0.532	0.34	0.472
<i>Rubus spp.</i>	0.614	0.108	0.38	0.146	0.164	0.198
<i>Sassafras albidum</i>	0.627	0.278	0.319	0.476	0.412	0.282
<i>Smilax spp.</i>	0.864	0.729	0.709	0.595	0.75	0.502
<i>Symphoricarpos orbiculatus</i>		0.041		0.017	0.1	0
<i>Toxicodendron spp.</i>	0.114	0.148	0.19	0.235	0.055	
<i>Tsuga canadensis</i>	0.1		0	0	0.05	
<i>Ulmus americana</i>				0.333	0.214	
<i>Ulmus rubra</i>	0.333			0.185	0.354	0.421
<i>Vaccinium spp.</i>	0.71	0.258	0.224	0.266	0.445	0.191
<i>Viburnum acerifolium</i>	0.616	0.36	0.567	0.63	0.6	0.246
<i>Viburnum lantanoides</i>			0.75			
<i>Viburnum prunifolium</i>		0.963		0.931	0.875	0.895
<i>Viburnum rufidulum</i>					0.714	
<i>Vitis spp.</i>	0.667	0.5	0.875	0.357	0.632	0.63

Chapter 4: Relationship of Potential Food Sources and Winter Severity on White-tailed Deer Body Mass in the Central Appalachian Mountains

Andrew B. Kniewski

Abstract

Body mass of white-tailed deer (*Odocoileus virginianus*) at fall harvest in the Appalachian Mountains is influenced by hard mast production, population density, habitat condition, and severity of the previous winter's weather. Although mast production and winter weather vary temporally, the relationships between alternate food sources or habitat condition and deer body mass are less well understood. Other food sources potentially could complement or mediate temporally variable factors. However, because many factors can influence body mass in deer and may interact in complex ways, comprehensive evaluation can be difficult and many potential interactions remain largely untested. I evaluated the relationships and possible interactions between deer body mass and potential food sources, winter severity, and deer population density in the central Appalachian region using historical deer harvest data. Using data collected annually in 24 counties from 1991–2000, I fit linear mixed models to test specific hypotheses. A model that included proportion forest and mast abundance for the fawn and yearling years was the best supported model, receiving 77% of the overall model support. Agriculture and other non-forest habitats may provide resources that result in larger body mass either directly through food items or indirectly through alteration of the remaining forest habitat such as through increased edge. My results suggest that, regardless of mast crop, areas with more habitat diversity will support larger body mass in deer. However, because of the possible masked relationship between body mass and inherent productivity, evaluation of site quality and productivity may be valuable for wildlife managers seeking to enhance the quality and quantity of alternate food sources.

Introduction

Physiological measures, such as body mass at fall harvest of white-tailed deer (*Odocoileus virginianus*) (hereafter deer) and other cervid species, can be influenced by static and temporally variable attributes, such as hard mast production (Wentworth et al. 1992), population density (Keyser et al. 2005), and habitat condition and quality (Ford et al. 1997). Deer consume a variety of foods that vary considerably seasonally and year-to-year. These variations can impact body mass among cohorts (Mech et al. 1991) and effects may persist through life (Albon et al. 1992). Additionally, the severity of winter weather varies widely year-to-year and can influence deer survival and reproduction (Mech et al. 1987, DelGiudice et al. 2002, Garroway and Broders 2007).

Hard mast is important for numerous wildlife species, including deer (Van Dersal 1940). Indeed, the availability of acorns affects the survival and reproductive success of many wildlife species including black bears (*Ursus americanus*) (Elowe and Dodge 1989), wild turkeys (*Meleagris galapavo*) (Steffen et al. 2002), and many small mammals (Wolff 1996, McShea 2000). In deer, hard mast availability affects reproduction, fawn survival, body mass, and antler development (Feldhamer et al. 1989, Wentworth et al. 1992). Although the importance of hard mast crops has been documented, the relationship of alternate food sources or habitats (e.g., agriculture production or mixed forest/residential areas) to deer body mass is less well understood. Deer frequently are found in mixed habitat areas (Halls 1984, Augustine and Jordan 1998, Kilpatrick and Spohr 2000) and food sources found there could potentially complement or mediate mast production. However, many factors influence body mass in deer and may interact in complex ways. As a result, comprehensive evaluation can be difficult and many potential interactions remain largely untested.

Deer populations in the central Appalachian region occupy a wide variety of habitat conditions and spatial habitat arrangements. Large portions of the central Appalachian region are forested with limited alternate and edge habitats. Likewise, mountainous areas frequently have shallow, rocky soils with reduced soil fertility when compared to areas with fewer mountains and the bordering piedmont province. Typically, deer densities in these mountainous forested areas have been lower than those

portions of the landscape with more mixed habitat compositions. This often is hypothesized to be a result of dependence on density-independent drivers, such as weather and mast production, that vary greatly from year-to-year (Wentworth et al. 1992, Ford et al. 1997, Patterson and Power 2002). Because of this, understanding the influence of and interactions among potential food sources, deer population density, and winter severity would allow for more precision in the management of deer under various landscape scenarios.

My objective was to elucidate the relationships and possible interactions between deer body mass and potential food sources, winter severity, and deer population density in the central Appalachian region. Although winters in the Appalachian region generally are less severe than those in northern portions of the deer's distribution and rarely impart negative effects on body condition, weather can vary substantially across local topographic conditions (e.g., high elevations) and may pose an interactive effect in years with poor mast production and/or high population densities. In turn, the effects of low mast production may be moderated by alternate food sources such as agriculture habitat where available.

Methods

My study area was located in the central Appalachian region of western Virginia, USA, and encompassed all counties in Virginia that intersect the Blue Ridge and Valley and Ridge provinces (Fenneman 1938) (Figure 4.1). Elevations range from approximately 200–1700 m. Generally, the Valley and Ridge and, to a lesser extent, the Blue Ridge provinces are characterized by long mountain ridges with moderate to steep side slopes and narrow to moderately broad valleys. The entire study area predominantly was forested (58%), intermixed with pasture or hay production in the valleys (17%), shrub dominated areas (10%), and limited areas of row-crop agriculture, residential, and urban development (Homer et al. 2004). Dominant forest types are moderate to xeric oak (*Quercus* spp.) and mixed pine (*Pinus* spp.) with scattered, smaller patches of mesic hardwood, cove hardwood, and northern hardwood, depending on region, aspect, and elevation (Simon 2011). On average, 1.3 male deer km⁻² year⁻¹ (range

1.2–1.4 km² year⁻¹ study wide, 0–2.7 km² year⁻¹ for individual counties) were harvested in the study area 1991–2000. Approximately 17% of the study area is publicly owned.

I obtained deer harvest records and associated data, originating from technical game check stations, from the Virginia Department of Game and Inland Fisheries (VDGIF). Technical check station data was available for the years 1988–2001 for deer harvested on public and private land. However, these records did not include deer taken as part of deer management assistance programs administered on private land. I used dressed weights of yearling male deer (approximate age, 1.5 years) as an index of deer condition believed most reflective of habitat quality and population density (Ford et al. 1997, Keyser et al. 2005). I extracted yearling male dressed weights for the years 1991–2000 for all counties in the study area as this was the period that had the largest number of counties with continuous data; only counties with data in each year were included in the analysis. I calculated mean weight of yearling males by county and year. I used the 3-year running average of male deer harvested per km² in each county as an index of deer population density. I used the density index at year of conception as it was the year that had the greatest relation to body mass in other studies in the East (Keyser et al. 2005). I calculated the percent forest in each county as classified by the National Land Cover Dataset (Homer et al. 2004). As a measure of mast abundance, I obtained acorn production estimates for the study area from the VDGIF. Details on the collection and estimation of acorn production each year can be found in Fearer et al. (2008). I used acorn production measured at all acorn sampling locations located in the study area and natural neighbor spatial interpolation (Sibson 1981) to estimate acorn production for each county and year. Log-transformed estimates of acorns per tree were used in models. Similarly, to obtain an estimate of winter severity, I used the number of days with ≥ 2.5 cm accumulated snow between 1 October and 30 April each year at National Oceanic and Atmospheric Administration weather stations in the study area. Because average snowfall varies widely across the study area and among weather stations, I used standard scores (Zar 1984) of the number of snow days at each station and natural neighbor spatial interpolation to estimate winter severity for each county and year.

I built candidate models reflecting specific hypotheses regarding potential food sources (mast production and proportion forest habitat as the surrogate), deer density, and weather in relation to deer condition (Table 4.1). Hypotheses tested were 1) body mass is best predicted by deer density, 2) body mass is best predicted by conditions occurring during the pre-natal gestation period, 3) body mass is best predicted by conditions during the fawn year following parturition, 4) body mass is best predicted by conditions during the yearling year, 5) body mass is best predicted by mast production, 6) body mass is best predicted by winter severity, 7) body mass is best predicted by proportion of forest habitat, 8) body mass is best predicted by forest habitat and mast production including during gestation, and 9) body mass is best predicted by forest habitat and mast production excluding gestation. I also included null and all parameters (global) models in my candidate set. I hypothesized that the effect of winter severity may interact with mast productivity of the same year. Therefore, I included the interaction of mast and winter severity of the same year in models where those factors were included concurrently. Likewise, I hypothesized that the effect of mast production may vary with forest habitat and included the interaction of forest habitat and mast in all models where those factors are included concurrently. I built linear mixed models following the process recommended by Zuur et al. (2009) and ranked candidate models using Akaike's information criterion corrected for small sample size (AIC_c), the difference between the model with the lowest AIC_c and the AIC_c of the i th model (Δ_i), and Akaike's weights (w_i) (Burnham and Anderson 2002). I assessed the variance explained by the top model using marginal and conditional r^2 for linear mixed models as described by Nakagawa and Schielzeth (2013). Because data were nested by county, all candidate models included a random factor for county; likewise, because data were a time series, I fit models with an auto-regressive order 3 structure to account for the correlation across time (Zuur et al. 2009). I used partial effects plots to visualize the relationship and interactions between factors of the best supported model. I used *R* (Version 3.3.1, www.r-project.org) and packages "nlme" (Version 3.1-128, <https://cran.r-project.org/package=nlme>) and "MuMIn" (Version 1.15-6, <https://cran.r-project.org/package=MuMIn>) to fit and rank models.

Results

I retained 24 counties in the study area with data for each year from 1991–2000. Counties had a mean of 50 (range 1–200) yearling buck harvest records per year. My model including proportion forest habitat and mast abundance exclusively for the fawn and yearling years was the best supported model receiving 77% of the overall model support (Table 4.2). All other models had $\Delta_i > 2$. My best supported model explained a moderate amount of the variation in the data (pseudo- $r^2_{\text{marginal}} = 0.191$) and graphical evaluation of predicted values under different proportions of forest habitat and mast production scenarios suggests a strong interactive effect of forest and mast production (Figure 4.2).

Discussion

My best supported model of yearling buck body mass included factors for the proportion of forest and mast production in both the fawn and yearling year. The support for the top model greatly exceeded that for models focused solely on particular age periods, deer density, winter severity, or proportion of forest cover, suggesting strong additive or interactive affects between factors or age periods. Other studies have noted relationships between deer body mass and various factors simultaneously (Feldhamer et al. 1989, Wentworth et al. 1992, Ford et al. 1997). My results suggest that, early in development, conditions during multiple years and across multiple factors are influential and it is beneficial to examine them concurrently. Notably, these factors can be additive and/or interact affecting outcomes dramatically. For example, my best supported model suggests that the effect of forest habitat on body mass where both the fawn and yearling years have low mast production is opposite to that when both years have high mast production.

Several studies found relationships between deer condition and winter severity or maternal condition (Mech et al. 1987, Feldhamer et al. 1989, Mech et al. 1991, DelGiudice et al. 2002). In my study, models including winter severity were not supported strongly, possibly for three reasons. First, winters during the study period were too mild to have a significant impact on body mass at the time of harvest. Secondly, winter weather in the central Appalachian region affects, at most, survival and not

body mass (DelGiudice et al. 2002). Finally, the metric or scale of measurement may not have been related to the data. High winter severity scores (max 3.92, unpublished data) suggest that severe winter weather occurred on at least a portion of the study area periodically over the years assessed. Also, the winter severity metric used is similar to that used in other studies (Mech et al. 1987). Few studies have examined the effect of winter severity on deer body mass in the Appalachians; however, in the southern Appalachians, winter severity was not correlated with body mass (Ford et al. 1997) suggesting that winter weather may play a more limited role than in northern areas. Although studies in northern portions of the deer's distribution found relationships between body mass and maternal condition (Mech et al. 1987, Mech et al. 1991), the inclusion of mast production during gestation did not improve model support in my study. It is possible that maternal condition affects offspring most directly in relation to winter severity. However, Feldhamer et al. (1989) found that the effects of winter weather and mast can be cumulative and affect populations over several years beyond what I examined in this study. Regardless, in this study, I did not identify any relationships between deer condition and winter severity or maternal condition.

Overall, my best supported model suggests a negative relationship between deer body mass and the proportion of forest habitat. That is, deer in heavily forested areas generally have a smaller body mass than those from areas with a greater proportion of non-forest habitat. Miller et al. (2009) found that maintaining about 14% of an area in well-distributed early successional or recently regenerated forests substantially reduced herbivory rates by providing abundant food resources. Although I did not evaluate the type of non-forest habitats in my study, I suspect they significantly impact the resources provided. Notably, the area of agriculture crops planted in each county was strongly correlated negatively with the proportion of forest (-0.77, unpublished data). This suggests that the presence of non-forest habitat may provide resources that result in larger body mass either directly through food items other than hard mast or indirectly through alteration of the remaining forest habitat such as through increased edge (Alverson et al. 1988, Johnson et al. 1995, Ford et al. 1997). Alternately, the proportion of forest also is correlated with topography in my study area. Typically, mountainous areas are heavily forested and have shallower, less fertile soils, possibly impacting the quality and quantity of forage available. Because of the

relationship between inherent productivity and agriculture production in my study area, it is difficult to fully understand the relationships and interaction between body mass, forest cover, and inherent productivity.

Deer population density can influence body mass in certain deer populations in the southeast USA (Sams et al. 1998, Keyser et al. 2005). However, in Florida, USA, Shea et al. (1992) was unable to detect a relationship likely due to abundant, but nutritionally poor, forage. In my study, I used a harvest index as a coarse estimate of population density and density was not included among my best supported models. However, due to the unknown reliability of the metric used to track population density, I suggest caution in interpreting these results. Deer are expected to have a lower body mass at high population density due to increased competition for food resources and other interactions (Sams et al. 1998). It is possible that deer populations in my study area have adequate food resources at current densities and therefore do not display a body mass-density relationship. Also, any body mass-density relationship could be masked if population densities are limited by density-independent factors such as mast crops (Wentworth et al. 1992, Ford et al. 1997). If density-independent factors are largely at play, deer populations may only display density-body mass relationships in particular areas, time periods, or in certain combinations of density and environmental conditions. Finally, if differences in land ownership, management, and habitat configurations result in deer populations varying rapidly across the landscape, it is possible that the analysis scale used in this study is too large to detect relationships occurring at smaller spatial scales.

Because of the importance of hard mast (Van Dersal 1940, Wentworth et al. 1992), oaks have been a focus of management activities across the Appalachian region (Dey 2002). In my study, the strong interactive effect of mast production in consecutive years and in relation to proportion of forest habitat supports the idea that mast production is a density-independent factor in deer condition in the central Appalachians. Oak trees take many years to reach mast producing age and mast crops vary substantially year-to-year, making it difficult for wildlife managers to significantly alter mast production even over many years (Fearer et al. 2008, Lashley et al. 2009). My results suggest that regardless of mast crop,

areas with more diversity of habitats will support larger body mass in deer. However, because of the possible masked relationship between body mass and inherent productivity, evaluation of site quality and productivity may be valuable for wildlife managers seeking to enhance the quality and quantity of alternate food sources (Johnson et al. 1995, Ford et al. 1997). Wildlife openings and other breaks in habitat are more easily managed on a short-term basis and may provide alternate sources of food for wildlife in poor mast years; however, providing ample hard mast should remain a focus of long-term management goals. Although mast production varies cyclically on many factors (Feldhamer et al. 1989, Wentworth et al. 1992, Fearer et al. 2008), my results suggest that maintaining or increasing oak forest is critical to maintaining deer condition in heavily forested areas. Management goals targeting well-distributed, hard mast producing forests with interspersed alternate habitats, where possible, will be best suited to support body mass in deer over time in the central Appalachian region.

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Table 4.1. Hypotheses and associated models tested for fitting body mass of yearling male white-tailed deer (*Odocoileus virginianus*) in central Appalachian Mountains, Virginia, USA, 1991–2000. Number subscripts indicate associated year lag from year of harvest and factors are winter severity (winter), mast production (mast), proportion of forest habitat (forest), and deer population density index (density).

Hypothesis	Model
null	~1
global, all parameters and interactions	winter ₁ + winter ₂ + mast ₀ + mast ₁ + mast ₂ + density + forest + forest:mast ₀ + forest:mast ₁ + forest:mast ₂ + winter ₁ :mast ₁ + winter ₂ :mast ₂
global, no interactions	winter ₁ + winter ₂ + mast ₀ + mast ₁ + mast ₂ + density + forest
deer density	density
gestation year	winter ₂ + mast ₂ + density + forest + forest:mast ₂ + winter ₂ :mast ₂
fawn year	winter ₁ + mast ₁ + density + forest + forest:mast ₁ + winter ₁ :mast ₁
yearling year	mast ₀ + density + forest + forest:mast ₀
mast abundance	mast ₀ + mast ₁ + mast ₂
winter severity	winter ₁ + winter ₂
proportion forest	forest
proportion forest and mast abundance including gestation	forest + mast ₀ + mast ₁ + mast ₂ + forest:mast ₀ + forest:mast ₁ + forest:mast ₂
proportion forest and mast abundance excluding gestation	forest + mast ₀ + mast ₁ + forest:mast ₀ + forest:mast ₁

Table 4.2. Best supported linear mixed models fitting body mass of yearling male white-tailed deer (*Odocoileus virginianus*) and winter severity (winter), mast production (mast), proportion of forest habitat (forest), and deer population density index (density) in central Appalachian Mountains, Virginia, USA, 1991–2000. Number subscripts indicate associated year lag from year of harvest and model parameters are given as well as the effective degrees of freedom (df), log likelihoods (logLik), Akaike’s information criterion corrected for small sample size (AIC_c), difference in AIC_c value between top model and *i*th model (Δ_i), and model support (w_i).

Model	df	logLik	AIC_c	Δ_i	w_i
forest + mast ₀ + mast ₁ + forest:mast ₀ + forest:mast ₁	11	-744.3	1511.8	0	0.77
forest + mast ₀ + mast ₁ + mast ₂ + forest:mast ₀ + forest:mast ₁ + forest:mast ₂	13	-743.34	1514.3	2.52	0.218
winter ₁ + winter ₂ + mast ₀ + mast ₁ + mast ₂ + density + forest + forest:mast ₀ + forest:mast ₁ + forest:mast ₂ + winter ₁ :mast ₁ + winter ₂ :mast ₂	12	-748.31	1522	10.24	0.005
winter ₁ + mast ₁ + density + forest + forest:mast ₁ + winter ₁ :mast ₁	18	-742.3	1523.7	11.93	0.002

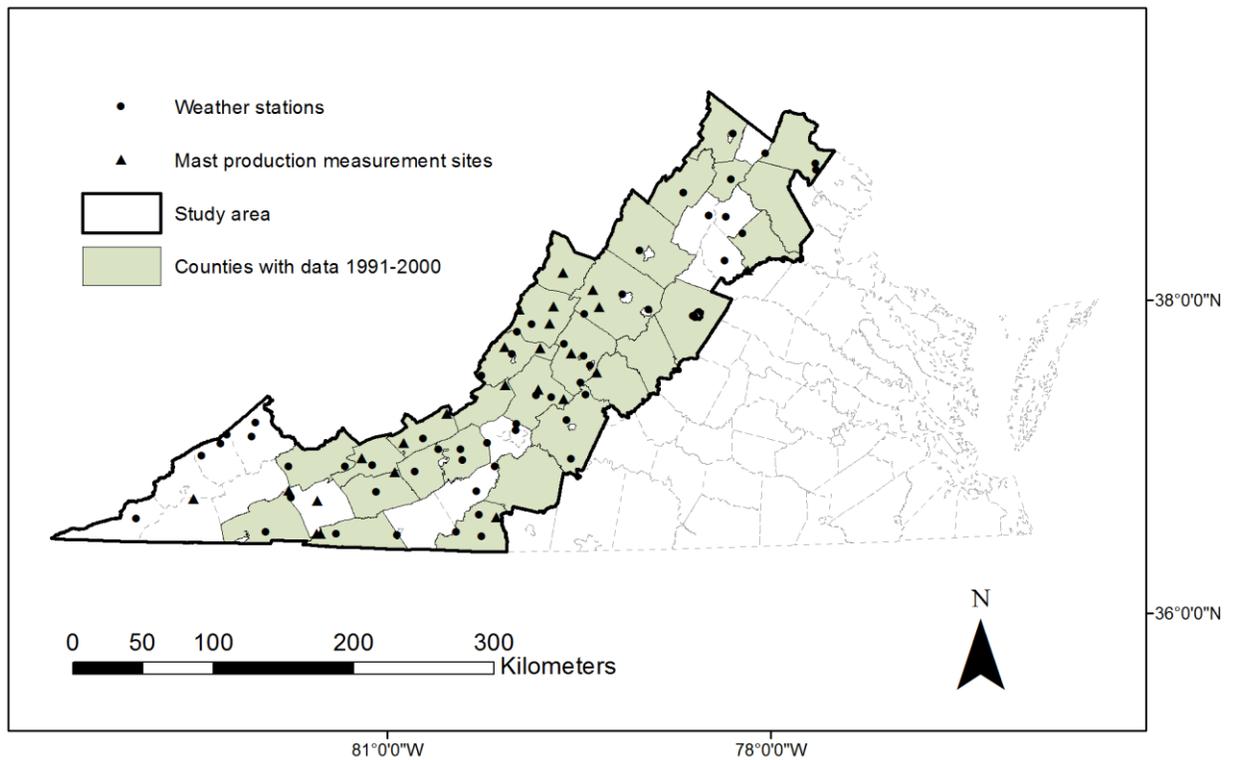


Figure 4.1. White-tailed deer (*Odocoileus virginianus*) body mass study area, weather station locations, and mast production measurement sites in the central Appalachian Mountains of Virginia, USA, 1991–2000.

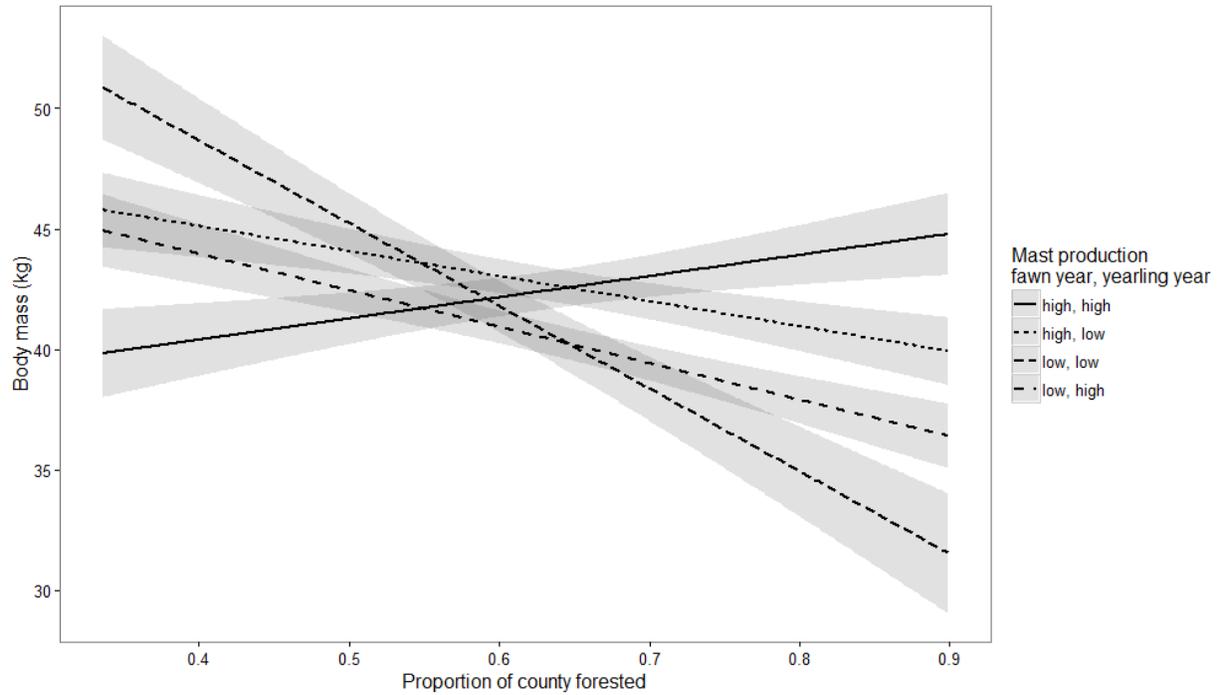


Figure 4.2. Body mass (\pm standard error) of yearling male white-tailed deer (*Odocoileus virginianus*) by proportion of county forested under different mast production scenarios as predicted by the best supported model for the central Appalachian Mountains of Virginia, USA, 1991–2000.

Chapter 5: Conclusion

Andrew B. Kniewski

A great deal of research has been conducted delineating how and to what extent white-tailed deer (*Odocoileus virginianus*) (hereafter deer) herbivory affects plants and plant communities in a variety of field conditions and settings in North America (Russell et al. 2001). Likewise, the impact of deer on many organisms beyond direct impacts to plants also has been evaluated (DeGraaf et al. 1991, deCalesta 1994, McShea and Rappole 2000, Côté et al. 2004, Rearick et al. 2011). There is little question that deer, especially at high densities, influence forest succession, alter forest composition, and can reduce biodiversity substantially at multiple trophic levels.

Deer are found throughout the central Appalachian region and densities in many areas currently are or within the recent past have been high. Because of this, concern is increasing regarding the management of deer in the context of sustaining forest biodiversity, both generally and for particular rare or declining species. Several metrics to assess the intensity of herbivory have been suggested, such as proportion of stems browsed and status of indicator species potentially impacted by deer (Morellet et al. 2001, Morellet et al. 2007, Koh et al. 2010, Freker et al. 2013). Yet, previous to my research and regardless of the usefulness of the various metrics, little information existed on spatial variability of deer browsing or other relevant spatial factors to inform the application of herbivory assessment metrics across broad landscapes.

The central Appalachian region contains a broad range of landscape and topographic configurations, land use patterns, and inherent landscape productivities—all of which inherently are spatial in nature. Likewise, deer biology and behavior are linked intricately to space use. For example, deer, and all other animals, need food, water, and cover, elements that must be met by and within their environment. Deer establish and maintain relatively stable home range areas that supply these needs and they often use areas within their home range repeatedly, depending on the need and availability of resources (Halls 1984, Campbell et al. 2004). Management of deer also is defined and executed spatially,

often by political boundaries that may or may not relate well to spatial scales relevant to deer and landscape diversity patterns. This spatial diversity increases the difficulty of applying deer management strategies or assessment protocols broadly. My research directly addressed some of these concerns by providing information regarding spatial patterns of deer herbivory, the predictability of and factors influencing herbivory intensity, and relationships between land use diversity, temporally variable food sources, and deer physiological factors.

My research suggests that spatial patterns of deer browsing broadly are consistent within the central Appalachian region, possibly reducing the need for spatially complex herbivory assessment methods. However, I found that the woody plant species preferred by deer (Nixon et al. 1970, Vangilder et al. 1982, Berteaux et al. 1998, Dostaler et al. 2011) vary considerably among my study regions and are selected even where overall browsing intensity is low. My research specifically examined woody vegetation. However, forbs and other herbaceous vegetation compose a large portion of forest biodiversity and herbivory impacts on herbaceous plant biodiversity may or may not be reflected in the status of woody vegetation. Research by Frerker et al. (2013) in the Great Lakes region of the United States suggests that browsing rates and ratios provide reliable indicators of herbivory impacts on biodiversity, including herbaceous vegetation, even across broad landscapes. However, in the central Appalachian region, my results provide an incomplete assessment of browsing rates in relation to long-term and broadly inclusive biodiversity impacts. Because many of the plants of the highest conservation concern in the central Appalachian region are herbaceous, it is important to not extend the results of my study to all plants until relationships between impact on woody species and other species groups in the region are firmly established. Likewise, many herbaceous plant communities in the study area likely have been impacted by high levels of herbivory through overabundant deer or livestock grazing in the past and, as a result, currently display reduced biodiversity. Because of this, I suggest formal evaluation of the relationship between herbaceous biodiversity and woody browsing rates in the central Appalachian's before it is accepted broadly as an indicator of herbivory impact. Where indicator species are used

(Morellet et al. 2007, Koh et al. 2010), I suggest they should be selected only after thorough evaluation of deer forage preference in the desired management area.

Although the uniformity of deer browsing can vary substantially from site to site, my results suggest it is related most strongly to the overall intensity of browsing on a site and not to topographic position or distribution of available forage. Because sites with higher intensities of browsing were browsed more uniformly, herbivory assessments are less likely to misclassify highly impacted areas due to inadequate sampling intensity. However, because deer maintain relatively stable home ranges, the scale of assessment protocols needs to relate to deer biology in addition to management context. Because of this, the spatial distribution of herbivory assessments should be of key importance in the design of herbivory impact sampling protocols. Likewise, the scale-dependence in understanding assessment results cannot be overlooked.

My results suggest that deer browse vegetation predictably based on the type and quantity of vegetation available, but I did not find any overarching topographic or landscape factors that influenced browsing intensity. Although this potentially reduces the complexity of herbivory assessment protocols, it impedes delineation of areas that may be more prone to herbivory impacts without field assessment. This result highlights the ubiquity of deer in the study area and their mobility—where food preferred by deer is available, they predictably find and consume it without regard to its location. As a result, regular field assessment of herbivory intensity or vegetation characteristics is needed to identify and monitor areas at risk of biodiversity impacts due to excessive herbivory (Rooney 2001, Côté et al. 2004, McShea 2012).

Lastly, I found that yearling buck body mass was best fit with a model that included proportion of forest and mast production in both the yearling and fawn years. My analysis of spatial herbivory patterns supports the generalistic and mobile nature of deer across habitat configurations and regions. However, deer consume a variety of seasonally available foods, such as hard mast, in addition to woody vegetation (Wentworth et al. 1992) and these food sources are distributed unevenly, spatially, and temporally. Although deer live in a variety of habitats, they often are associated with edge or mixed habitat areas

throughout most of the eastern United States (Halls 1984, Augustine and Jordan 1998, Kilpatrick and Spohr 2000). My results suggest that, although access to areas that produce abundant mast may benefit deer body mass, and, by extension, fitness, due to the temporal variability in mast production and availability, deer benefit from including habitats that provide alternate food sources in their home range. For example, agriculture production, improved pasture, soft mast, and abundant browse in early successional areas often are used by deer (Alverson et al. 1988, Ford et al. 1993). These interacting factors suggest that areas with mixed habitat often favored by deer may provide resources leading to the most consistent and highest fitness over time. Likewise, my results suggest that large areas of contiguous forest found throughout the central Appalachian region likely provide sub-optimal habitat for deer and may support fewer deer or deer in poorer physiological status than areas with mixed habitats. I suggest that managers seeking to support deer in central Appalachian forests maintain or increase diverse, mixed-species oak forest and, where possible, maintain or increase the diversity of forest age classes and alternate habitats such as early successional areas. Mixed oak communities may help to buffer years of low mast production for a particular oak species or group as failures between groups are not always synchronous (Fearer et al. 2008). Due to reductions in fire frequency and past forest management practices, many forests in the central Appalachians are composed mainly of uniform, even-aged stands (Nowacki and Abrams 2015). Returning fire and management practices that encourage heterogeneous and mixed forest age classes will increase the amount and diversity of available forages (Ford et al. 1993, Crimmins et al. 2010). However, due to the cyclic nature of hard mast production (Fearer et al. 2008), highly forested areas with large portions of mature oak forest still may provide inconsistent benefits to deer over time. Deer populations in oak-dominated forests inflated by abundant mast may contribute to high levels of browsing and herbivory impacts due to lack of alternate food sources when mast is not in season or in years of poor mast production.

Regardless of current conditions, managers should evaluate whether management actions that support deer in a given area are desirable from a biodiversity perspective or are in the best interest of stakeholders. For example, converting mature forest to early successional habitat through timber harvest

to benefit deer and upland game birds may conflict directly with management for species that require large core areas of mature forest, which may be more limited in the region. My results indicate maintaining deer populations and biodiversity in the central Appalachian region requires knowledge of deer spatial patterns and habitat relationships in addition to regular evaluation of herbivory impacts within a spatially balanced framework. Because of this, data on spatial patterns of deer movement, specifically in the different landscape configurations found in the central Appalachians, will be key to the design of field herbivory assessment protocols. Recent advances in global positioning collars for deer allow for high temporal and spatial resolution of deer locations (Kolodzinski et al. 2010, Webb et al. 2010). Movement information from even a few individuals in several landscape configurations would aid the development and precision of herbivory assessment protocols. This is especially true if the collection of the movement data was designed specifically to inform herbivory assessment protocols. Because the needs of landowners and other stakeholders as well as their management goals and ecological conditions substantially vary across the landscape, assessment thresholds and possibly assessment protocols likely also will have to vary. The development of assessment protocols and thresholds should allow for a range of ecological conditions and management goals. Localized data and understanding of deer movements, herbivory patterns, and management goals across the landscape will provide a foundation and structure for development of a spatially balanced framework essential for long-term herbivory impact assessment and management in the central Appalachian region.

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