EVALUATING THE EFFECTS OF FORAGE AVAILABILITY AND LANDSCAPE COMPOSITON ON WHTE-TAILED DEER MORPHOMETRICS ACROSS THE EASTERN U.S.

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ABSTRACT

White-tailed deer (*Odocoileus virginianus*) management often focuses on improving nutrition to increase deer morphometrics, and many landowners use harvest data to track management progress. Better understanding the relationship among deer morphology, nutrition, landscape characteristics, and climate should inform deer management throughout much of the eastern US. I collected deer forage data in 2021–2023 from 43 sites in 25 states across the eastern US and worked with cooperating landowners and managers to collect harvest data from 35 of those sites. Adult female body mass explained 64% of the variation in mature male antler size on sites across the eastern US, and a 4.4-cm increase in male antler size was predicted for every 1-kg increase in female body mass. I detected a similar relationship from harvest data collected in Mississippi, which confirmed this relationship occurs at multiple spatial scales, and managers can use female body mass to track changes in herd health towards their objectives. Among the 87 species/genera I collected as deer forage, forbs contained the greatest average nutritional content, followed by semiwoody and woody plants. Crude protein and phosphorus concentrations correlated within an individual plant, but the number of plants meeting lactation-level phosphorus requirements was limited, which indicates phosphorus likely is the most limiting nutrient for deer across the eastern US. Site-specific forage availability across most sites was far less than forage availability reported in studies that implemented experimental treatments to improve forage availability. Climate and landscape composition had the strongest influence on male and female morphology across the eastern US. Females were 1.4 kg heavier and male antler size was 4.9 cm greater with every 1˚C decrease in average annual temperature. Females were 1.6 kg heavier and male antler size was 7.1 cm greater with every 10% increase in landscape crop coverage. Site-specific forage availability influenced female body and male antler size after controlling for landscape effects.

Specifically, female mass increased by 0.15 kg and male antler size increased by 0.7 cm for every 1 deer day/ha increase in NCC with a phosphorus constraint. Managers interested in increasing deer morphology should consider increasing forage availability within the context of their climate and landscape to help develop realistic management expectations.

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INTRODUCTION

Morphometric variation within a wildlife species often is a response to different selective pressures occurring across their distribution (Gould and Johnston 1972). Investigating morphometric variation has long been a source of inquiry for ecologists, especially in reference to delineation of species and subspecies (Galtier 2018). Although taxonomic questions may seem trivial, conservation of endangered and threatened species often requires consideration of morphometrics and their role in speciation (Mace 2004, Johnson et al. 2018, Tyler et al. 2020). Morphological variation may be great within a widely-distributed species, and investigations into such variation have been conducted on numerous species (e.g. Clavijo-Baquet et al. 2010, Berthouly-Salazar et al. 2012, Warwick et al. 2015, Cox et al. 2020).

Morphological variation may develop from a variety of environmental factors. The importance of climate in animal morphology was likely first documented by Bergmann, and both inter- and intra- species morphology is influenced by temperature, precipitation, and other climatic variables (Bergmann 1847, Gay and Best 1996, Hellberg et al. 2001, Ficetola et al. 2016). Factors such as prey base, dispersal ability, and forage availability also may result in morphological variation across the distribution of a species (Greve et al. 2008, Hinton et al. 2019). Of these factors, forage availability during the growing season may be most important in explaining morphology, as differences in forage availability during periods of growth may better explain size distribution in animals than hypotheses related directly to climate (Geist 1986, Wolverton et al. 2009, Huston and Wolverton 2011).

Response to variations in forage availability is strongly influenced by epigenetic processes. Epigenetic mechanisms include several processes that can activate, reduce, or disable particular genes which influence phenotype (Bossdorf et al. 2008). These mechanisms can act on

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both current and future generations, and the inheritance between generations may play a role in ensuring phenotype matches the environment without losing genetic diversity in an individual or population (Geist 1978, Rakyan et al. 2003, Blewitt et al. 2006). Nutrition often is considered when investigating epigenetics in mammals, as phenotypic changes may occur based on the nutrition of females in previous generations (Wolff et al. 1998, Cooney et al. 2002, Cropley et al. 2006). These maternal effects may influence body size, survival, and the development of secondary sexual traits (Mech et al. 1991, Monteith et al. 2009).

Body size and condition often are evaluated when considering nutritional effects, as they influence multiple life history traits. For example, survival is strongly influenced by nutritional condition and body size (Hurley et al. 2014, Sergeyev et al. 2021). Reproductive success and productivity also are influenced by nutritional condition (Keech et al. 2000, Rodriguez-Hidalgo et al. 2010, Milner et al. 2013, Ronget et al. 2017, Hilderbrand et al. 2019). Nutritional availability during periods of reproduction are especially impactful on survival and reproductive success (Parker et al. 2009, Tollefson et al. 2010, Bender et al. 2013, Proffitt et al. 2021). Thus, demography is regulated in part by the nutritional status of individuals in a population (Bishop et al. 2010, Couturier et al. 2010, Ozgul et al. 2010, Taillon et al. 2012). Additional information on nutritional condition may be derived from examination of secondary sexual characteristics for species in which they are present.

Secondary sexual characteristics are costly for individuals to produce, and thus can provide insight into animal condition. These traits typically are produced by males, and include both behavioral and physical characteristics used to increase reproductive success (Byers et al. 2010). Many of the physical secondary sexual characteristics focus on ornamentation, which includes traits such as plumage, pigmentation, horns, and antlers (Møller et al. 1998, Pryke et al.

2001, Rosenthal and Hebets 2015). Although some of these traits may serve as both armaments and ornaments, females of many species select to breed with males that have larger or more elaborate structures (Clutton-Brock 2009, Morina et al. 2018). Although these traits may increase reproductive success, individuals must balance production of costly traits with the need to acquire sufficient nutrition to survive (Berglund et al. 1996, Birkhead et al. 1999, Sentinella et al. 2013, Wilson et al. 2019). Thus, they may serve as an "honest signal" of phenotypic quality for females selecting mates (Ditchkoff et al. 2001, Vanpé et al. 2007, Ezenwa and Jolles 2008, Ciuti and Apollonio 2010).

White-tailed deer nutritional ecology

The white-tailed deer (*Odocoileus virginianus*; hereafter, deer) is a species of great economic, ecological, and social interest throughout their distribution. In the U.S., 8.1 million hunters pursue deer annually, resulting in billions of dollars of economic impact. (U.S. Department of Interior 2017). Additionally, 356 million acres of land is owned or leased for hunting in the U.S., and the management of these lands provides benefits to both game and nongame wildlife species (Macaulay 2016).

Deer are concentrate selectors that select to consume the highest-quality parts of nutrient-rich forages based on their needs throughout the year (Hofmann 1989). Concentrate selectors are able to select forages that provide either greater availability of limiting nutrients or lower concentrations of overabundant nutrients that may be toxic (Moser et al. 2006, Lashley and Harper 2012, Dykes et al. 2020). Woody browse, forbs, and mast are forages most commonly consumed by deer, but their use and availability differ throughout the year. For example, deer require forages higher in energy during winter, and tend to select forages with greater fat and carbohydrate contents. Conversely, deer tend to select forages with greater concentrations of

protein and higher digestibility during spring and summer (Hewitt 2011). Forbs and browse comprise approximately 70% of the annual diet of deer, but other food sources such as hard and soft mast may be seasonally important (Feldhammer et al. 1989, Wentworth et al. 1992, Hewitt 2011).

Changes in diet selection may occur because of differences in availability as well as changes in nutritional requirements at different times of the year. Gestation, lactation, and antler growth are the three most costly life history processes for deer that require elevated nutritional levels. Lactation requires 6.7 times the energy of basal metabolic rate, as well as a diet that is 14–16 percent crude protein (National Research Council 2007). Antler growth requires 1.49 times the energy of basal metabolic rate, and a diet that is a minimum of 9–10% crude protein (Aleson et al. 1996, National Research Council 2007). Other nutrients also may be limiting at times, and phosphorus especially has been considered a limiting nutrient that influences diet selection and morphometrics (Jacobson 1984, Horrell et al. 2015, Dykes et al. 2018). Females require approximately 0.3% phosphorus and 0.34% of calcium in their diet to support lactation (National Research Council 2007). Adult males require approximately 0.12–0.14 % phosphorus and 0.15–0.17% calcium in their diet while growing antlers (National Research Council 2007).

Minimum nutritional requirements are based on captive diet studies, and it is possible that nutrient values above these requirements may allow for increased morphometrics. Regardless, they provide a useful metric to evaluate forage quality based on plant type and tissue age. Forbs tend to provide the greatest nutrient content, followed by semiwoody and woody plants (Mixon et al. 2010, Lashley et al. 2011, Nanney et al. 2018). Younger plant parts are more digestible and have greater concentrations of most nutrients compared to older plant parts (Lashley et al. 2014, Vera-Velez and Lamb 2021). Deer must balance their various nutritional demands while making

foraging decisions, as they must simultaneously meet multiple nutritional constraints while avoiding toxicity. Several studies have considered the correlation within deer forages (Short et al. 1966, Vangilder et al. 1982), but there is limited information correlating important nutrients within individual plants across a large geographic range. Phosphorus is commonly considered among the most limiting nutrient for deer in the eastern US (Jacobson 1984, Barnes et al. 1990, Lashley et al. 2015, Dykes et al. 2018), yet crude protein often is used to estimate nutritional carrying capacity (Lashley et al. 2011, Nanney et al. 2018, Harper et al. 2021, Turner et al. 2024). Thus, comparing nutrient availability could help discern which tends to be the most limiting, and understanding which plants meet the minimum nutritional requirements from the literature could inform management to increase growing-season forage availability.

Nutritional effects on morphology

Body and antler size of deer are influenced by nutritional quality and quantity. Deer fed low-quality diets have both lower body mass and antler size (French et al. 1956, Verme 1969, Harmel et al. 1988). Body and antler size also are influenced by other factors, such as deer density and land use, which affect forage abundance and quality (Simard et al. 2008, Hefley et al. 2013). The effects of nutrition on antler size is of particular interest, as antlers serve as a signal of phenotypic quality to females during mate selection (Morina et al. 2018). The production of costly ornamentation requires male deer to balance reproductive success with nutrient acquisition, so antler production may be especially sensitive to nutritional constraints (Jones et al. 2018).

The relationship between body mass and antler growth also is influenced by forage availability, as males may allocate surplus nutrition to antler production. For example, red deer (*Cervus elaphus*) in a region with greater forage availability had proportionately larger antlers

than red deer in a region with lower forage availability (Mattioli et al. 2021). Antler investment is influenced by both age and body mass in moose (*Alces alces*) and red deer (Stewart et al. 2000, Gómez et al. 2012). When considering the relationship between antler size and body mass in several cervid species, Lemaítre et al. (2014) noted that beyond the threshold of 110 kg, antler allocation did not increase linearly with body mass. Antler allocation also may be influenced by large-scale climatic conditions, as over half the annual variation in age-specific antler mass in Mississippi was explained by climate models (Strickland et al. 2020). Finally, cervids may invest more of their resources into reducing breakage once they reach an optimal size, as antler mass tends to increase at a greater rate than frame characteristics in older males (Michel et al. 2016, Jones et al. 2018).

Body condition and nutritional availability also regulate deer population dynamics. For example, females provided a lower-quality diet produced fewer fawns than those provided a higher-quality diet (Verme 1969). Density-dependent responses to increasing populations are commonly documented in deer, and can result in lower female productivity (McCullough 1979). Although several factors may play a role in density-dependent population dynamics, forage availability likely is the most important for large ungulates (Stewart et al. 2011, Bowyer et al. 2014).

Managers often collect and use harvest data from male and female deer to evaluate management progress. Many landowners are interested in producing larger-antlered males and collect antler measurements from harvested males, such as gross Boone and Crockett antler score (Nesbitt et al. 2009). Harvest data from adult males often is relatively limited and many properties harvest a greater number of females than males, which would allow for a faster detection to morphological changes if female data can be used (Turner et al. 2021). Thus,

managers often use female body mass to evaluate overall herd health, but we are unaware of any

data correlating female body mass to male antler size. Given the frequent use of these metrics by

managers, determining whether these metrics correlate within a site would be helpful for

managers trying to improve forage availability to increase morphology.

Factors influencing available nutrition

Although there are multiple factors that influence the phenology of costly life history processes,

costly life history processes for deer likely are timed to take advantage of high-quality forage

availability (Clutton-Brock et al. 1989). Indeed, phenology of both antler growth and parturition

in other cervid species vary based on environmental conditions that influence forage availability

(Clements et al. 2010, Bonnet et al. 2019). The timing of these life history traits also conforms to

the "ecologically and evolutionarily relevant net primary productivity" hypothesis, which states

that forage production during the growing season likely is the driver for variation in species

distributions and morphometrics throughout the world (Huston and Wolverton 2009). Given the

potential importance of growing-season forage on deer nutrition and morphometrics, it is

necessary to consider factors that influence nutrition for deer.

Numerous factors influence nutrient availability for deer, but among the most important

are the vegetation types present within their home range. For example, closed-canopy hardwood

forest may provide only 18 to 193 kg/ha of available forage, whereas a soybean field may

provide in excess of 3,500 kg/ha of available forage during the same time (Lashley et al. 2011,

Turner et al. 2020). These differences can lead to great variation in observed morphometrics

across the distribution of deer. In Mississippi, average eviscerated body mass of mature males

from a region with widespread agriculture was approximately 13 kg heavier than deer from a

region dominated by pine forests (Strickland and Demarais 2000). Antler size also was

influenced by vegetation cover, as 3.5-year-old males produced antlers with approximately 60 cm greater Boone and Crockett scores on average in the agricultural region compared to the pine forest region (Michel et al. 2016). In Missouri, deer from the forested Ozark region had smaller antlers than deer from regions with more agriculture (Kissel et al. 2002). The influence of landscape composition also may influence the number of large males produced per county across the Midwestern U.S. (Cain et al. 2019).

Climatic conditions such as precipitation, temperature, and season length influence deer forage availability and demographics. For example, drought conditions decrease the production and quality of deer forage plants (Lashley and Harper 2012). The negative effects of drought on cervid productivity, morphometrics, and forage availability has been documented in mule deer (*Odocoileus hemionus*) and white-tailed deer populations in the western and southwestern U.S. (Lawrence et al. 2010, Foley et al. 2012, DeYoung et al. 2019, Peterson et al. 2019). Flooding also may negatively influence deer by decreasing forage availability, body mass, and survival (MacDonald-Beyers and Labisky 2005, Strickland et al. 2012, Jones et al. 2019). Length of the growing season has multiple effects on forage availability, both positive and negative. In regions with longer growing seasons, forage production is not impacted as early by frost and cold weather. However, forage quality declines during the late growing season in these regions may create a stress period for deer (Short 1975). This interaction between season length and forage quality results in complications when interpreting differences in deer morphometrics across their distribution.

Habitat management also can influence nutritional condition of deer. Canopy reduction and prescribed fire can increase forage production by approximately 500 to 700% in hardwood forests (Lashley et al. 2011, Turner et al. 2020). These same tools also may be applied in

softwood forests, and are commonly used in those dominated by pine (Iglay et al. 2010, Mixon et al. 2010, Keene et al. 2020). In open vegetation types, fire and the removal of nonnative grasses via herbicide application increases forage production (Harper 2017, Harper et al. 2021). Managers also may shift vegetation types completely, as forage production may be increased by approximately 800% when forests are shifted to early successional plant communities using timber harvest, fire, and herbicide treatments (Nanney et al. 2018). Many managers use agronomic plantings, which can provide high-quality forage during nutritionally stressful periods of the year (Lashley et al. 2011, Glow and Ditchkoff 2017, Harper 2019). However, the response of plant communities to management are partially dependent on abiotic conditions, such as climate and soil.

OBJECTIVES

Understanding the relationship among landscape characteristics, forage availability, climate, and animal morphometrics is an important question in the fields of ecology and wildlife management. The ecology and distribution of species may be based largely on these factors, but most previous studies on these topics are limited in either scope or range. The white-tailed deer provides an opportunity to further understand these relationships, as deer are distributed across a vast geographic area with great variation in body and antler size. Furthermore, deer hunting is enjoyed by millions annually, and many hunters and managers are interested in increasing deer body and antler size.

I worked with my major professor and graduate committee to develop a study that would evaluate factors influencing deer nutrition and morphology across the eastern U.S. to provide useful information to managers. I partnered with landowners and managers at 43 sites across 25 states to collect deer forage and harvest data. My specific objectives were to: (1) correlate male

and female morphology, (2) determine nutrient limitations in deer forage samples, and (3)

evaluate the influence of climate, landscape coverage, and forage availability on male and female

morphology.

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CHAPTER 1. CORRELATING MALE WHITE-TAILED DEER ANTLER SIZE WITH FEMALE BODY MASS ACROSS MULTIPLE SPATIAL SCALES

ABSTRACT

Managers use morphometric data collected from harvested animals as indicators of nutritional condition. Antler or horn size often are considered in ungulates, but there are problems associated with biased and limited harvest data available from male animals in many populations. Adult female body mass also may be collected, but little information exists on how male antler size scales with female body mass. We evaluated the relationship between property-specific mature male white-tailed deer (*Odocoileus virginianus*) antler size and adult female body mass from harvest data collected at 2 spatial scales. Regression predicted a 4.4-cm increase in average mature male antler size for every 1-kg increase in female body mass from 31 properties across the eastern United States, 2015–2023. Adult female mass explained 64% of the variation in mature antler size, and including latitude as a covariate did not improve model fit. When we considered data from 174 properties in Mississippi, USA, 1991–1994, we predicted a 4.7-cm increase in average mature male antler size for every 1-kg increase in adult female body mass. Including soil resource region in the Mississippi model explained 48% of the variation in mature male antler size by accounting for differences in average sizes across regions. Our results indicate average female body mass correlates with mature male antler size at multiple spatial scales. We recommend managers collect body mass and age from harvested female deer, as female mass represents a useful metric to track management progress and predict changes in antler size.

INTRODUCTION

Morphometric data often are evaluated when assessing nutritional condition of wildlife

populations. These data can provide insight into population response to management and may

help predict demographic changes that are regulated by nutrition (e.g., mule deer [*Odocoileus*

hemionus], Bishop et al. 2010; caribou [*Rangifer tarandus*], Couturier et al. 2010, Taillon et al.

2012; yellow-bellied marmots [*Marmota flaviventris*], Ozgul et al. 2010). For example,

nutritional condition and body size strongly influence survival of elk (*Cervus canadensis*) and

mule deer (Hurley et al. 2014, Sergeyev et al. 2021). Reproductive success and productivity also

are influenced by nutritional condition of moose (*Alces alces*), red deer (*Cervus elaphus*), brown

bear (*Ursus arctos*), and a variety of other birds and mammals (Keech et al. 2000, Rodriguez-

Hidalgo et al. 2010, Milner et al. 2013, Ronget et al. 2017, Hilderbrand et al. 2019). Body mass

may vary based on regional differences in forage availability, latitudinal gradients, or both

(Bergmann 1847, Strickland and Demarais 2000). Female body size may be a better measure of

condition than male size in some species, as depletion of male body mass during the breeding

season adds considerable variation to harvest data (Apollonio et al. 2020, Strickland et al. 2017).

Thus, indices other than male body mass that are easily collected by managers may be needed to

evaluate nutritional condition.

Secondary sexual characteristics can provide insight into male nutritional condition.

These traits are costly to produce and include both behavioral and physical characteristics used to

increase reproductive success (Byers et al. 2010). Many of the physical secondary sexual

characteristics focus on ornamentation, which includes traits such as plumage, pigmentation,

horns, and antlers (Møller et al. 1998, Pryke et al. 2001, Rosenthal and Hebets 2015). Although

some of these traits may serve as armaments and ornaments, females of many species select to

breed with males that have larger or more elaborate structures (Clutton-Brock 2009, Morina et al. 2018). These traits may increase reproductive success, but individuals must balance production of costly traits with the need to acquire sufficient nutrition to survive (Berglund et al. 1996, Birkhead et al. 1999, Sentinella et al. 2013, Wilson et al. 2019). Thus, they may serve as an honest signal of phenotypic quality for females selecting mates (Ditchkoff et al. 2001, Vanpé et al. 2007, Ezenwa and Jolles 2008, Ciuti and Apollonio 2010). Given how costly these traits are to produce, physical secondary sexual characteristics may be evaluated to indicate nutritional status of a population in response to management.

Producing larger-antlered males is an objective for many white-tailed deer (*Odocoileus virginianus*; deer) managers, but there may be problems associated with using male harvest data to evaluate antler qualities of a population. For example, many properties have a limited male harvest relative to female harvest if they are engaging in quality or trophy deer management (Hamilton et al. 2007, Shaw and Harper 2008, Harper et al. 2012, Mitterling et al. 2021). The issue of small sample size is further compounded when we consider the need to stratify male antler size by age, as many males are harvested before they reach their maximum antler size at approximately 5.5 years of age (Demarais and Strickland 2011, Hewitt et al. 2014). Male harvest strategies also may result in skewed antler data, such as when males harvested at younger age classes have larger than average antlers (Demarais and Strickland 2017). Biased harvest, commonly referred to as high-grading, of males before maturity by antler size may be common, and may result in younger age classes of harvested animals skewed towards individuals with larger antlers than the population average (Strickland et al. 2001). Antler growth curves by age exist, which allow managers to project ages at maturity to reduce the issue of high-grading (Demarais and Strickland 2011, Hewitt et al. 2014). Although these harvesting strategies have

minimal genetic effects given the mating system of deer (Webb et al. 2012), they result in data that may not reflect the actual population-level morphometrics.

Body mass of female deer may serve as a better indicator of herd condition and health than antler size. Harvest of female deer typically is greater than that of males on most properties, and larger sample sizes may result in faster detection of changes in morphometrics (Turner et al. 2021). Additionally, female body mass peaks at an earlier age than male antler size, and many consider females as adults when they reach 2.5 or 3.5 years old, which allows for analysis as a group (Strickland et al. 2008, Turner et al. 2019). Finally, harvest data of adult females likely are less skewed by hunter selection than antler size (Langvatn and Loison 1999). Female body mass may be used by managers to track nutritional status (Strickland et al. 2017), yet little information exists relating female body mass to antler size on a given site.

The relationship between mature male antler size and adult female body mass is unclear. Also, any relationship between female mass and antler size may vary with latitude or soil resource region. Therefore, we analyzed harvest data at 2 spatial scales to evaluate whether site-specific female body mass correlated with antler size. We predicted larger female body mass would correlate to larger average antler size. We also predicted including soil resource region would improve fit of models by accounting for differences in average morphometrics between regions, as there may be slight differences in the relationship between body and antler size based on forage availability related to land use, such as agriculture.

STUDY AREA

We analyzed morphometric data at 2 spatial scales to consider the relationship between female body mass and male antler size. We used harvest data from 31 properties across 19 states in the eastern United States to represent our eastern dataset (Figure 1.1). All figures and tables are

located at in an appendix at the end of the chapter. These properties were primarily privately owned, and landscape composition and management varied widely across sites. We selected sites based on harvest data collection history and differences in average deer size, as we wanted to create a model based on a large gradient of deer size across the eastern United States. Harvest data on these sites were collected 2015–2023. Latitude ranged from 28.10 to 44.24˚N, and we used the latitude at the center of each site as a model covariate. Average site elevation ranged from approximately 15–750 m above sea level. Average temperature was 13.2˚C (range = 4.7– 22.2 ˚C; National Oceanic and Atmospheric Administration 2024).

We also used data from 174 hunting clubs and state wildlife management areas across Mississippi, USA, to evaluate whether we could correlate average antler and female body size with more fine-scale data. Harvest data used for analysis were collected 1991–1994. We grouped these sites into 3 regions based on differences in landscape composition and deer size by grouping similar soil resource regions described by Pettry (1977; Figure 1.2). Our goal with these groupings was to capture some variation in body and antler size, which may be present based on changes in forage availability related to land use. The Delta region included the Delta soil resource area and all properties within the Mississippi River Batture. The Delta region featured agricultural production as a primary land use and produced the largest average deer in Mississippi. The Lower Coastal Plain region included the Lower Coastal Plain and Coastal Flatwoods soil resource areas, where forest was the primary land cover and average deer were the smallest within the state. The Loess-Upper Coastal Plain region included the Loess, Upper Coastal Plain, Blackland Prairie, and Interior Flatwoods soil resource areas. The Loess-Upper Coastal Plain region featured a mixture of agricultural and forestland, and deer were intermediate in size between the other 2 regions (Strickland and Demarais 2000). Average site elevation

ranged from approximately 20–200 m above sea level. Average temperature was 17.6 ˚C

(National Oceanic and Atmospheric Administration 2024).

Geology, vegetation types, climate, land uses, and harvest management across our study

sites that spanned 19 states were diverse and highly variable. This wide range of conditions and

geographic area of study provided a strong inference space for our analysis and potential

management applications.

METHODS

Morphometric data collection

Managers at each site collected morphometric data from harvested male and female deer. Female

deer mass was measured to the nearest kilogram. Most sites collected entire carcass mass, but we

used a conversion factor of 1.3 to convert eviscerated to entire carcass body mass on sites that

only collected eviscerated mass. We derived this factor from the average conversion factor on

sites collecting eviscerated and entire carcass mass from the same deer; it is similar to the

conversion factor estimated by Klinger et al. (1985).

Managers removed the lower jawbone and aged deer using tooth replacement and wear

(Severinghaus 1949). Although we acknowledge there is error associated with age estimation

using this technique (Gee et al. 2002, Storm et al. 2014, Foley et al. 2021), error in aging should

not influence our results beyond a possible reduction in model fit. Given tooth replacement and

wear is commonly used by managers to estimate ages, our model fit should indicate whether the

relationship between female body mass and male antler size are robust to aging errors. Some

sites in the eastern dataset removed lower incisors for aging with cementum annuli, and we used

these age estimates when available (Low and Cowan 1963, Gilbert 1966). In both datasets, we

included only female deer ≥2.5 years old, as we were interested in considering adult females

rather than subadults or fawns (Gee et al. 2014). Additionally, we included only males ≥3.5 years

old, and grouped these males into 3 categories: 3.5 years old, 4.5 years old, and ≥5.5 years old.

We were interested in quantifying average gross antler score at maturity (≥5.5 years old),

and antler data collection varied among sites in both the eastern and state datasets. On sites

where possible, managers collected gross Boone and Crockett (B&C) antler score, which is a

standardized antler measuring system (Nesbitt et al. 2009). Several of the eastern sites and all the

Mississippi sites collected main beam lengths and the number of points from each male, but we

were able to use a predictive formula developed by Strickland et al. (2013) to estimate gross

B&C score from each male. This approach provided us with either a measured or estimated gross

B&C score for each male ≥3.5 years old for each site.

We then estimated average antler size at maturity for each site using all 3.5-, 4.5-, and

≥5.5-year-old males. Thus, we were able to evaluate each site using a single metric for antler

size, while also controlling for potential harvest bias at younger age classes, which may be

occurring on many sites. Many of our sites were harvesting 3.5- and 4.5-year-old males, which

had equal or larger antlers than ≥5.5-year-old males at the same site. On these sites, we would

likely underestimate the average antler size at maturity, as older males in the harvest did not

represent a true random sample in the population (Demarais and Strickland 2017). Males ≥3.5

years old were predominant in the male harvest at most of our sites, which allowed us to include

nearly all males harvested from each site in analysis.

We multiplied the gross B&C score of 3.5-year-old males by 1.28 and the gross B&C

score of 4.5-year-old males by 1.09 to project their score at maturity (Demarais and Strickland

2011). After projecting the mature scores for 3.5- and 4.5-year-old males, we combined these

with the actual collected score of males ≥5.5 years old on each site and calculated the average projected score at maturity for each site.

Analysis

We were interested in modeling the relationship between adult female body mass and projected gross B&C score at maturity for each site at the eastern and state scales. Therefore, we created linear regression models in Program R version 4.2.2 (R Core Team 2022) and compared them using Akaike's Information Criterion corrected for small sample size (AIC$_c$; Burnham and Anderson 1998). We considered the model with the lowest AIC$_c$ value to be best fit but considered other models within 2 ΔAIC$_c$ as competing models.

For the eastern dataset, we set average site-level projected gross B&C score at maturity as our dependent variable and created 3 models to consider. The first included only average adult female body mass as an explanatory variable. The second included average adult female body mass and latitude as explanatory variables, as we wanted to determine whether including latitude would improve model fit given the wide range of deer sizes and states we were considering. The third included average adult body female body mass, latitude, and an interaction between female mass and latitude to determine whether the slope of the relationship between female body and male antler size changed with latitude.

We set average site-level projected gross B&C score at maturity as our dependent variable for the state model and created 3 competing models. The first included only average adult female body mass as an explanatory variable, and the second included soil resource region with average adult female body mass as explanatory variables. The third included average adult female body mass, soil resource region, and an interaction between female mass and soil region to determine whether the relationship between female mass and male antler size differed between

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regions. We included the sample size of male antler scores from each property as a weighted term in all models to account for differences in sample size among sites and used α = 0.05 as our level of significance for each model.

RESULTS

Eastern model

Our eastern dataset from 31 sites across 19 states included 869 male antler scores and 2,042 female body mass measurements, for an average of 28 males (range = 4–161) and 65.9 females (range = 6–205) per site. The model with adult female mass alone was the best model, and the model including adult female mass and latitude was competing (Table 1). Latitude was not a significant variable in the competing model, so we selected the model with adult female mass alone as the best model (Table 2). The model including an interaction between female mass and latitude was not competing, indicating the relationship between female mass and male antler size does not change across the latitudinal gradient we studied. Adult female body mass explained 64.4% of the variation in mature male antler score, with average mature male antler size increasing by 4.4 cm (SE ± 0.59) for every 1-kg increase in adult female body mass ($P < 0.001$; Figure 1.3).

State model

Our state dataset from 174 sites in Mississippi included 13,365 male antler scores and 72,380 female body mass measurements, for an average of 76.8 males (range = 15–123) and 416 females (range = 11–1159) per site. The top model included adult female body mass and soil region as a factor (Table 1). The model without soil region was not a competing model ($\Delta AIC_c =$ 6.36), but the beta value for adult female mass was similar in both models (Table 3). The model including an interaction between female mass and soil region also was not competing ($\Delta AIC_c =$

2.85), and none of the model covariates were significant (Table 3). For the top model, every 1-kg increase in adult female body mass correlated with a 4.7-cm (SE ± 0.59) increase in mature male antler size. The model also predicted antlers from the Delta soil region would be 36.7 cm and 16.9 cm larger than deer from the Lower Coastal Plain and Loess-Upper Coastal Plain regions, respectively (Figure 1.4). The model including adult female mass and soil region as covariates explained 48% of the variation in mature male antler size in Mississippi.

DISCUSSION

Our data correlate female size and a male secondary sexual trait in white-tailed deer. It appears the relationship between male antler size and female body mass is relatively fixed across spatial scales, as our eastern model beta value of 4.4 (95% CI = 3.2–5.6) closely resembled that of the Mississippi model beta value of 4.7 (95% CI = 3.5–5.8). The close correlation between these morphometrics would suggest fine-scale variation in factors such as deer density and forage availability are influencing male and female morphometrics similarly across sites (Mattioli et al. 2021). The inclusion of region in the Mississippi model supports this hypothesis, as male antler and female body size are correlated even when regional differences in morphometrics were considered (Strickland and Demarais 2000). Conversely, latitude was not included in our top eastern model as either an intercept or slope effect, suggesting other factors have a stronger role in morphometrics and allometry (Wolverton et al. 2009). Additional work is needed to separate various effects of forage availability and environmental conditions on morphometrics, and either male or female morphometric data may be used to evaluate this relationship.

Nutrition, deer density, climate, and genetics influence morphology, and our analysis demonstrated morphological traits arising from these conditions correlated between sexes. Our analysis was not designed to evaluate factors changing body or antler size but rather to determine

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whether male and female morphology correlated across a variety of environmental conditions across the landscape. For example, changes in forage availability or quality strongly influence both antler and body size (French et al. 1956, Harmel et al. 1988). Differences in density also may influence morphology (Klein and Strandgaard 1972, Simard et al. 2008, Hefley et al. 2013), as an increased number of deer would reduce forage available to the entire population. Thus, either nutritional or density-dependent changes in body and antler size should act on both sexes simultaneously. Correlation between male and female morphology suggests the mechanisms acting on male and female size are similar, validating either as an appropriate metric to monitor conditions at a site.

Increasing male antler size at maturity may be an objective of some management programs, but harvest data for males are limited on many sites, and female harvest data typically are more readily available. Under strategies such as Quality Deer Management or Trophy Deer Management, adult female harvest often is greater than adult male harvest to reduce density, balance the sex ratio, or both (Ditchkoff et al. 1997, Turner et al. 2022). Detecting significant changes in morphometrics based on management is likely to be delayed and may not be possible if only male harvest data are considered. This issue is exacerbated when age structure of harvest is considered, as male antler size generally is maximized at an older age than female body size (Strickland et al. 2008, Hewitt et al. 2014). Although there is error associated with age estimation from harvested animals, our model fit demonstrates female body size correlates with male antler size despite this error. Therefore, harvest data from females may provide a more robust and timelier dataset to evaluate the influence of management.

Male antler size data may be skewed towards individuals with larger antlers on some properties, such as those where certain antler-size criteria are used to determine availability for

harvest (Hewitt et al. 2014). Male antler size from high-graded populations is difficult to accurately evaluate, as harvested animals may not represent averages in the population. Applying average antler growth curves to predict score at maturity is an approach to account for high-grading in populations where most harvested males are ≥3.5 years of age and some mature (i.e., ≥5.5 yr) males are not harvested because of relatively low antler scores. All our sites meet these requirements, but high grading otherwise can strongly skew harvest data. Although several have hypothesized possible negative genetic effects of high-grading in other ungulate populations (Mysterud 2011, Festa-Bianchet et al. 2014, Pozo et al. 2016), few have considered the possible effects of skewed harvest data. These shortcomings of antler size data highlight the use of female data to track herd health and management progress, especially given the correlation between male antler size and female body mass.

Allometry in male cervids has been demonstrated across species, yet few have considered allometry between males and females from the same population. For example, allometry between male antler and body size has been demonstrated in Irish elk (*Megaloceros giganteus*; Gould 1973), red deer (Gómez et al. 2012, Mattioli et al. 2021), roe deer (*Capreolus capreolus*; Vanpé et al. 2007), and white-tailed deer (Jones et al. 2018). Positive nonlinear allometry also has been documented across cervid species, suggesting a maximum threshold above which we would not expect as strong a correlation between body and antler size (Lemaître et al. 2014, Ceacero 2016, Lopez and Stankowich 2023). Lemaître et al. (2014) estimated this threshold at approximately 110 kg, which is larger than the average mature male white-tailed deer across most of their distribution (Ditchkoff 2011). The correlation between male antler and body size would indicate male body mass could be used instead of antler size to evaluate herd health, but males lose approximately 14% of body mass during breeding (Strickland et al. 2017). Female body size also

may change slightly through the hunting season (Strickland et al. 2017) and correcting for this change could improve model fit. Even without including a correction for harvest date, however, our results demonstrate adult female body mass serves as a consistent metric to track herd health that correlates with male antler size.

MANAGEMENT IMPLICATIONS

Managers interested in influencing deer morphometrics should collect body mass and age from all harvested deer and antler scores from harvested males. Adult female mass may be used to track changes in nutrition based on habitat management or changes to deer density on sites with limited male harvest data. Managers can use female body mass data and our regression results to project antler size at maturity, which may be particularly useful in areas where a large percentage of males are harvested at younger age classes. We also recommend managers consider our approach of projecting antler size to maturity, as high-grading on many sites reduces the use of male harvest data when larger-antlered males are harvested at younger ages.

ACKNOWLEDGMENTS

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APPENDIX

Table 1.1. Akaike's Information Criterion corrected for small sample size (AIC$_c$) scores for models correlating projected white-tailed deer mature male Boone and Crockett antler score and adult female mass for deer in the eastern United States (eastern dataset) and in Mississippi, USA (state dataset). Data for the eastern models were collected 2015–2023, and data for the state model were collected 1991–1994. Latitude was considered as a covariate in the eastern model set, and soil resource region as a factor in the state model set. An interaction term also was considered between female mass and latitude or region. Weight represents the likelihood of a model relative to other candidate models.

Model	AIC$_c$	ΔAIC$_c$	Weight
Eastern dataset			
Female mass	315.25	0.00	0.55
Female mass + latitude	316.64	1.39	0.27
Female mass + latitude + female mass × latitude	317.44	2.19	0.18
State dataset			
Female mass + region	1,689.47	0.00	0.78
Female mass + region + female mass × region	1,692.33	2.85	0.19
Female mass	1,695.84	6.36	0.03

Table 1.2. Beta-values (β), standard error (SE), and *P*-values for candidate models regressing white-tailed deer average mature male Boone and Crockett antler score and adult female mass across 31 sites in 19 states in the United States collected 2015–2023. Latitude for each site is included as a covariate, along with an interaction between latitude and adult female mass.

Models and covariates	β	SE	*P*
Female mass			
Intercept	112.32	34.12	0.003
Female mass	4.39	0.59	<0.001
Female mass + latitude			
Intercept	77.19	47.16	0.113
Female mass	3.47	1.04	0.002
Latitude	2.39	2.22	0.291
Female mass+ latitude + female mass × latitude			
Intercept	-528.28	446.68	0.247
Female mass	13.55	7.47	0.081
Latitude	20.01	13.11	0.139
Female mass × latitude	-0.29	0.21	0.184

Table 1.3. Beta-values (β), standard error (SE), and *P*-values for candidate models regressing white-tailed deer average mature male Boone and Crockett antler score and adult female mass across 174 sites in Mississippi, USA, collected 1991–1994. Soil region for each site was included as a factor: Delta, Lower Coastal Plain (LCP), and Loess-Upper Coastal Plain (Loess-UCP). An interaction term between soil region and female mass was also included in 1 candidate model. The intercept of the model including soil region uses the Delta region as the intercept.

Models and covariates	β	SE	*P*
Female mass + region			
Intercept	115.30	33.75	<0.001
Female mass	4.65	0.59	<0.001
LCP	-36.70	11.47	0.002
Loess-UCP	-16.92	6.81	0.014
Female mass + region+ female mass × region			
Intercept	229.50	110.18	0.039
Female mass	2.62	1.95	0.181
LCP	-124.78	135.46	0.358
Loess-UCP	-147.39	115.22	0.203
Female mass × LCP	1.46	2.60	0.577
Female mass × Loess-UCP	2.35	2.07	0.257
Female mass			
Intercept	41.98	24.92	0.094
Female mass	5.79	0.48	<0.001
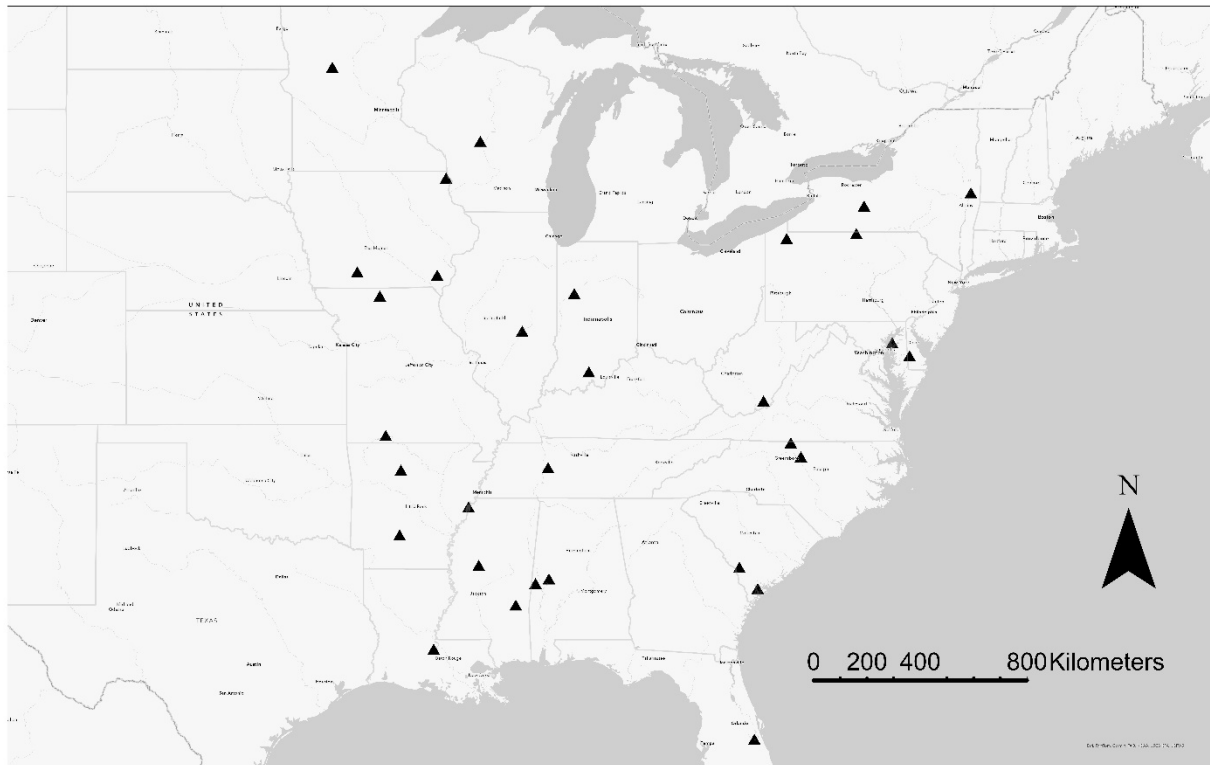
Figure 1.1. Study sites where white-tailed deer male antler size and adult female body mass were collected from harvest data, 2015–2023, to evaluate correlation between measurements of harvested deer across the eastern United States.
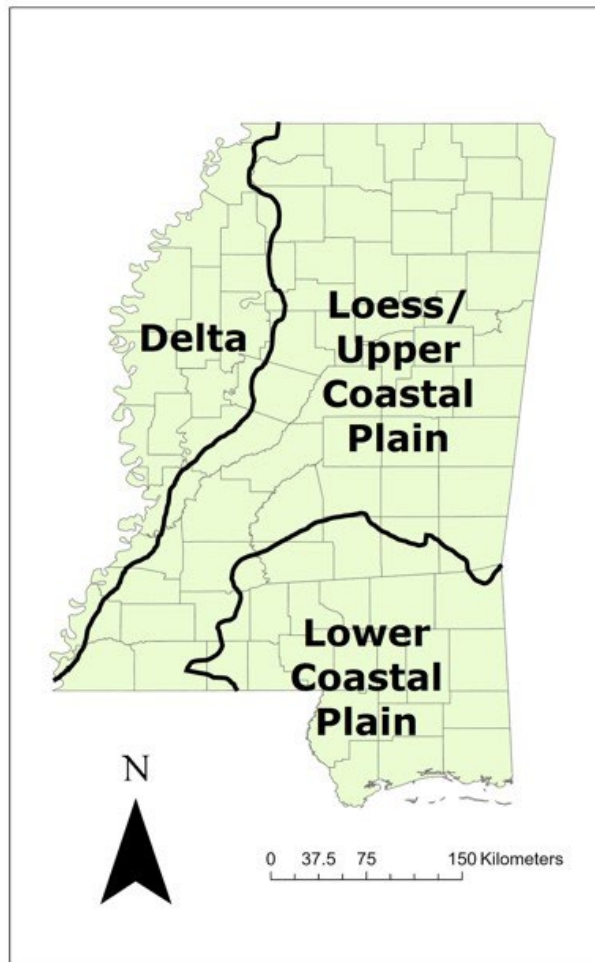
Figure 1.2. Soil resource regions in Mississippi, USA, used as covariates in a model considering the relationship between property-specific average mature white-tailed deer male antler size and adult female body mass, 1991–1994.
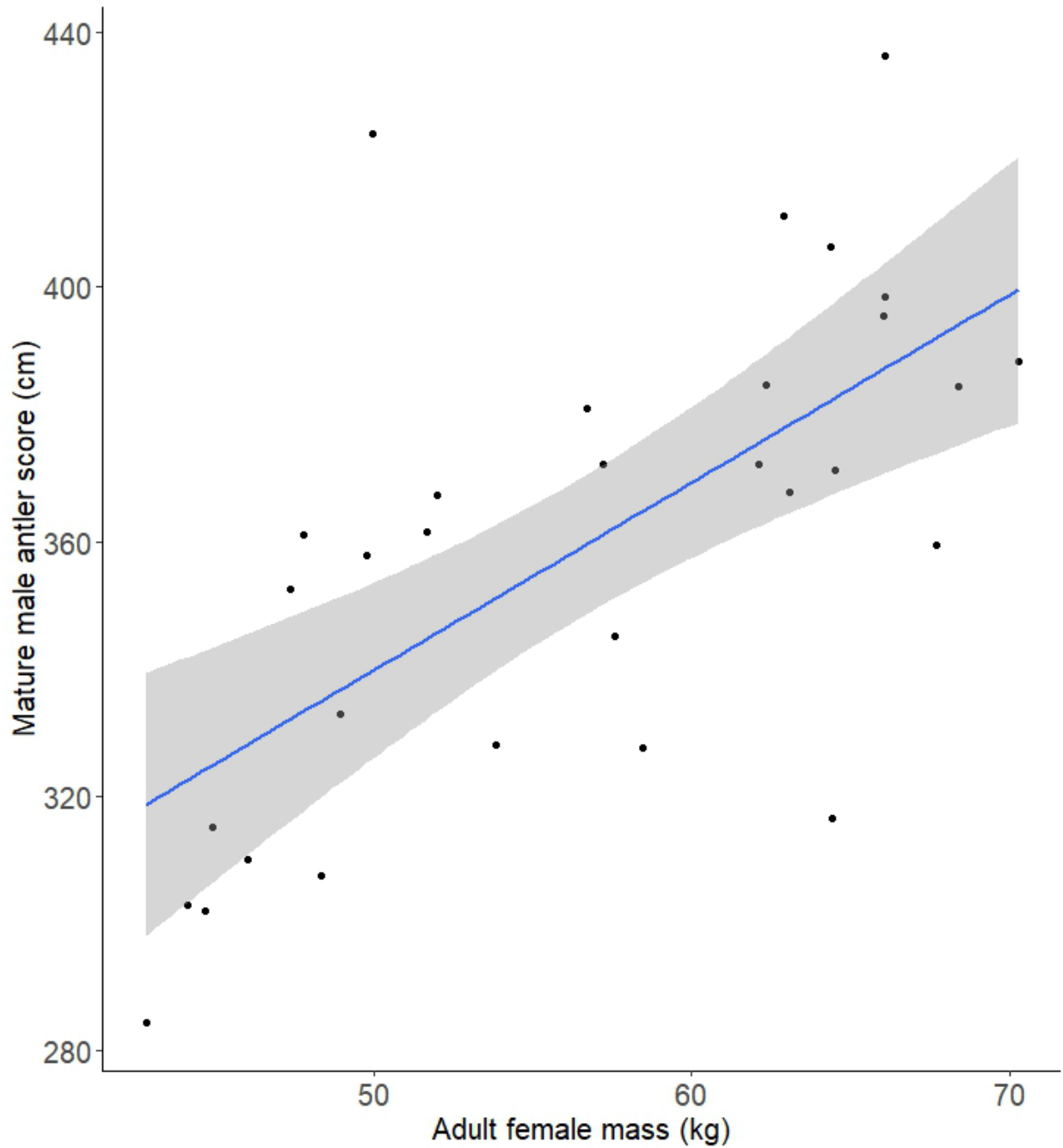
Figure 1.3. Relationship between property-specific average mature white-tailed deer male antler size and adult female body mass collected on 31 sites across 19 states in the eastern United States, 2015–2023 ($R^2 = 64.4\%$). Each point represents a property average, and the bands represent a 95% confidence interval.
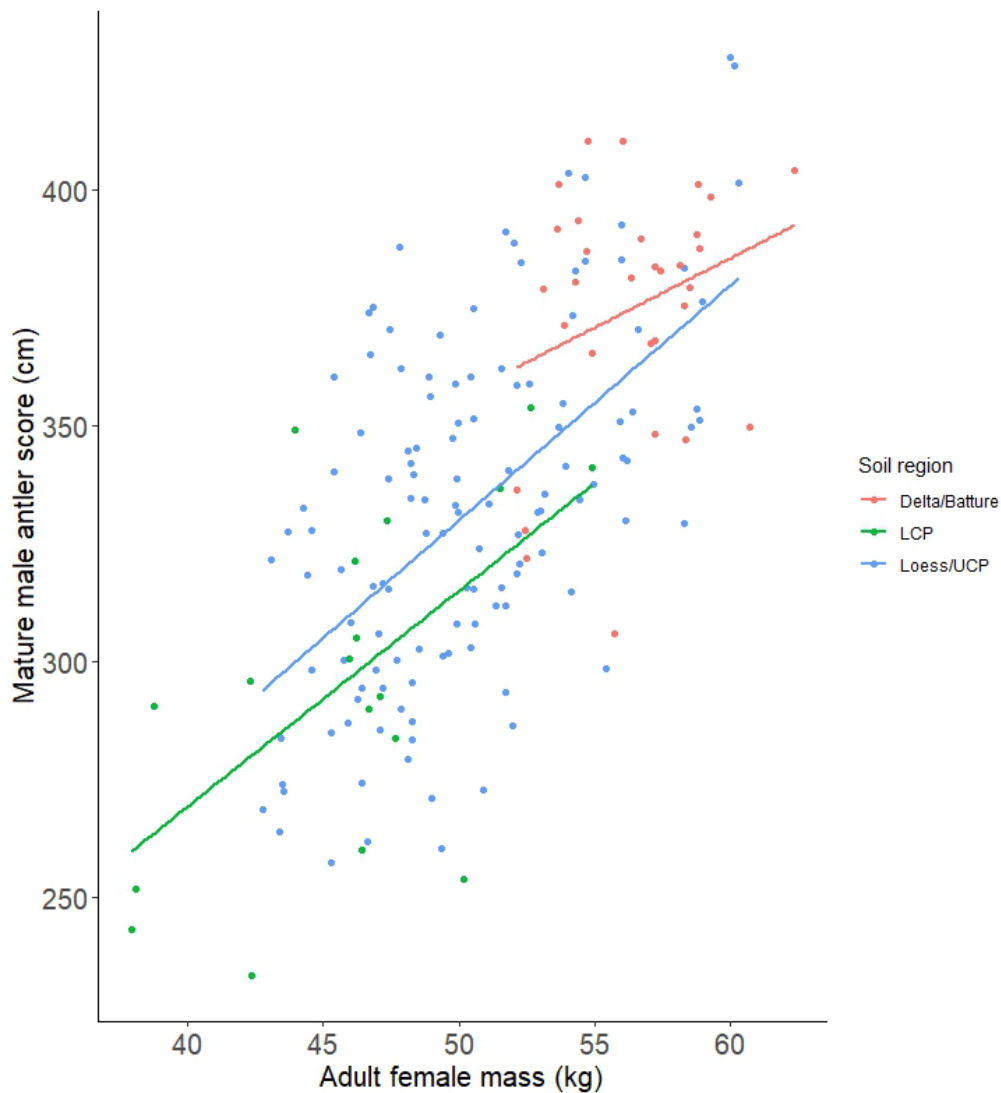
Figure1. 4. Relationship between property-specific average mature white-tailed deer male antler size and adult female body mass across 3 soil resource regions of Mississippi, USA, 1991–1994 ($R^2 = 48\%$). The red points are properties in the Delta region or inside the Mississippi River Batture (Delta/Batture), the green points are properties in the Lower Coastal Plain (LCP), and the blue points are properties in the Loess and Upper Coastal Plain (Loess-UCP). Lines represent regression results for each region with the corresponding color

CHAPTER 2. PLANT NUTRIENT CONCENTRATIONS INFORM HERBIVORE DIET CONSTRAINTS

ABSTRACT

Management of large herbivores often involves improving availability of forages sufficient in nutrient density to allow animals to meet dietary demands. Nutritional carrying capacity (NCC) models commonly are used to compare plant communities and management strategies, but failure to use the most limiting nutrient in models could result in overestimating NCC. Moreover, the relationship between limiting nutrients often is not considered, which may influence the utility of NCC models based on a single nutrient, especially when herbivores must simultaneously meet multiple constraints. We examined crude protein and phosphorus concentrations in 87 plant genera and species commonly eaten by white-tailed deer (*Odocoileus virginianus*) to determine whether they would meet a minimum 14% crude protein and 0.3% phosphorus constraint for a lactating female. We used these nutrients because they are the two most used nutrients in NCC studies related to deer. Crude protein and phosphorus demands were met in 43.9% and 18.8% of sampled forages, respectively. Concentrations of crude protein and phosphorus were greatest in young forbs, with an average of 18.6% crude protein and 0.28% phosphorus. We found a correlation between protein and phosphorus concentrations, but not all plants which met protein requirements simultaneously provided sufficient phosphorus. We created NCC models using crude protein and phosphorus and documented phosphorus tended to be more limiting, but variation existed among sites, indicating either nutrient may be more limiting in a particular area. Thus, conservation efforts for deer should focus on managing for a diversity of plants, particularly those forbs which simultaneously meet multiple nutritional demands, given nutrient concentrations may vary widely across plant species.

INTRODUCTION

Nutrient availability strongly influences diet selection by herbivores. Forages dense in limiting nutrients, such as crude protein (CP), phosphorus (P), sodium, cobalt, or soluble sugars, are selected by herbivores (Verheyden-Tixier et al. 2008, Ceacero et al. 2009, Lashley et al. 2015, Dykes et al. 2018, Dykes et al. 2020). Diet balancing occurs as animals attempt to meet their nutritional constraints while avoiding potentially toxic concentrations of particular nutrients (Belovsky 1978, Langvatn and Hanley 1993, Weckerly 1994, Provenza et al. 2003, Ginane and Petit 2005, Ceacero et al. 2015, Dykes et al. 2020). Thus, concentrations of multiple nutrients play a role in foraging decisions, and herbivores must optimize forage intake to simultaneously meet multiple nutritional demands (Westoby 1974, Hanley 1997).

Life history processes determine nutritional requirements in large herbivores. Lactation is the costliest nutritional process for mammals, and diet quality during lactation often is used as a minimum benchmark when evaluating forage availability. White-tailed deer (Odocoileus virginianus; hereafter, deer) lactation with twin fawns requires 4.7 times greater energy and 1.4 times greater CP intake than maintenance (Hewitt 2011). Males also require elevated energy and CP intake for antler growth (National Research Council 2007, Hewitt 2011). Forage quality and availability during costly life history processes strongly influence morphology and demography (Pettorelli et al. 2001, Jones et al. 2010). Given nutritional requirements peak in May–July September for both sexes during lactation and active antler growth, and management often focuses on providing high-quality forages during this time.

Nutrient availability differs among plant species, age of plant tissue, season of year, and climatic conditions (Lashley and Harper 2012, Lashley et al. 2014, Lashley et al. 2022). Forbs tend to have greater nutrient concentrations than woody plants, but wide variation exists among

different species (Mixon et al. 2010, Lashley et al. 2011, Nanney et al. 2018). Younger plant parts tend to have greater concentrations of most nutrients, and thus are selected by most herbivores (Lashley et al. 2014, Vera-Velez and Lamb 2021). Across the landscape, seasonal differences in forage quality and availability may strongly influence both selection and diet quality (Short 1975, Ben-Shahar and Coe 1992, Verheyden-Tixier et al. 2008, Lashley et al. 2022). Climatic conditions, especially drought events, and disturbance such as fire, also influence nutrient availability (Lashley and Harper 2012, Sittler et al. 2018, Lashley et al. 2022).

Nutritional carrying capacity (NCC) models are used to estimate forage availability for large herbivores. NCC models were proposed by Hobbs and Swift (1985), and they provide an estimate of forage quantity meeting a minimum nutritional constraint. Most deer research has used CP when evaluating nutrition during the growing season (Edwards et al. 2004, Lashley et al. 2011, Nanney et al. 2018, Nichols et al. 2021, Turner et al. 2024). CP likely is more limiting for white-tailed deer during spring and summer than digestible energy, given most selected forages meet minimum energy requirements during that time (Lashley et al. 2015). Previous research has indicated P also may limit morphometrics in many areas of the southeastern U.S. (Jacobson 1984), and deer often select plants with high P concentrations, indicating P is an important nutrient for diet selection and may be limiting on the landscape (Grasman and Hellgren 1993, Lashley et al. 2015, Dykes et al. 2018, Nichols et al. 2021, Lashley et al. 2022). In reality, CP, P, and many other nutrients, must be met simultaneously through selective foraging, and nutrients may cooccur at high levels within selected plants (Vangilder et al. 1982, Langvatn and Hanley 1993). Thus, evaluating the relationship between these nutrients and determining which is most limiting would improve our understanding of diet selection and nutritional limitations.

Despite the scope of research on herbivore forage availability and selection, we found there is limited information that directly quantifies nutrient concentrations among young and old tissue of various forbs, semiwoody, and woody plants across a wide geographic range. We evaluated which forages provide limiting nutrients, which should aid managers when managing vegetation communities to increase NCC. Additionally, we created NCC models using CP and P to determine which nutrient represented the most-limiting constraint on a variety of sites across the distribution of a large herbivore. We developed three hypotheses related to forage nutrients. First, we hypothesized there would be differences in nutrition among plant types, and predicted young forb tissue would provide the greatest average nutrient levels. This prediction was based on how strongly forbs influence NCC estimates, though few studies have considered average quality by plant class across a broad geographic range (Nanney et al. 2018, Harper et al. 2021, Nichols et al. 2021). Second, we hypothesized CP and P would by be positively correlated by plant species, allowing foraging decisions to balance intake of both nutrients simultaneously. Finally, we hypothesized CP and P NCC estimates using CP or P as the constraint would be positively correlated, and predicted P would be more limiting at most sites than CP as suggested in Lashley et al. (2015).

METHODS

Study area

We collected forages at 43 sites across 25 states (Figure 1) to test for nutrient concentrations. All figures and tables are located at in an appendix at the end of the chapter. We attempted to distribute sites across a wide geographic area to assess variation in forage availability and quality. Site size averaged 567 ha (range: 53–4553 ha) and latitude ranged from 28.10 to 44.24˚N. Most sites were selected through collaboration with the National Deer Association

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(NDA) to identify cooperating members who would allow us to collect forage samples on their private property. We also added several sites managed by state agencies when we were unable to locate a site within a particular area.

Data collection

We collected forages at 43 sites across 25 states (Figure 2.1) to test for nutrient concentrations. We attempted to distribute sites across a wide geographic area to assess variation in forage availability and quality. Site size averaged 567 ha (range: 53–4553 ha) and latitude ranged from 28.10 to 44.24˚N. Most sites were selected through collaboration with the National Deer Association (NDA) to identify cooperating members who would allow us to collect forage samples on their private property. We also added several sites managed by state agencies when we were unable to locate a site within a particular area.

We collected selected deer forage plants at each site late May–early August, 2021–2023 to assess forage availability across each property. We collected forages at ≥100 sample points at each site during a single visit lasting 1–2 days using a stratified sampling design. First, we delineated the following vegetation types based on management history and aerial images on each site: closed-canopy hardwood forest, closed-canopy softwood forest, open-canopy hardwood forest, open-canopy softwood forest, early succession, food plot, row crop, pasture/hay, and shrubland. Forested areas were assigned based on dominant tree coverage, and whether they were closed (<30% canopy openness) or open (≥30% canopy openness). Early succession were areas dominated primarily by native, herbaceous plants. Food plots were areas planted with agronomic crops to provide forage and/or attraction for viewing and hunting. Pasture/hay included all areas dominated by grass which was regularly mowed, hayed, or grazed, and areas dominated by shrubs were considered shrubland. We assigned one random sampling

point within a vegetation type for each percentage point that vegetation type comprised on a site. For vegetation types with <20% coverage, we would assign 20 random points to ensure adequate sampling intensity. For example, if a site had 70% coverage of row crop, 23% coverage of pasture, and 7% coverage of early succession, we would collect 70 random points in the row crop, 23 random points in the pasture, and 20 random points in the early succession.

We collected all forages inside a 0.5 m^2 frame placed at each random sampling point that were moderately to highly selected by deer based on the literature (Miller and Miller 2005, Harper 2019) and/or commonly browsed across a site (Appendices 1, 2, 3). We collected young and relatively old leaves separately to determine nutrient concentration by age of plant part. We considered young leaves those closest to the tips of twigs that tend to be more digestible and higher in concentration of several nutrients (Lashley et al. 2014). Older leaves were fully formed leaves on the plant occurring below the youngest leaves nearest the tip of a stem or twig. We did not collect the oldest leaves near the bottom of stems or twigs that had begun to turn yellow or otherwise discolored.

We mixed subsamples collected across frames to produce a single sample for each plant species and age from each site to analyze nutrient concentrations. We classified forage samples into the following forage classes: young forb, old forb, young semiwoody, old semiwoody, young woody, and old woody. Semiwoody plants included brambles and vines, and woody plants included trees and shrubs. We dried forage samples to constant mass at 50°C, weighed them, and sent them to either Custom Laboratory or the Clemson University Agriculture Service Laboratory for wet chemistry nutritional analysis of CP and P concentrations. In cases where we did not have sufficient biomass (>5 g dried) to submit a sample of both young and old tissue of a species for a site, we combined them into a composite sample. Composite samples were only

used in NCC estimation and were not included in analysis related to nutritional comparisons by plant class or tissue age.

Following nutrient analysis, we created NCC estimates for each site based on CP and P. We calculated mixed-diet NCC estimates based on CP and P constraints for each vegetation type at each site based on Hobbs and Swift (1985) using a 14% CP constraint, 0.3% P constraint, and 2.3 kg/day intake of a lactating female with twin fawns. We then calculated an NCC estimate for CP and P at each site by multiplying the NCC of each vegetation type by the proportion of a site in the vegetation type. These weighted estimates for each nutrient allowed us to compare whether CP or P tended to be more limiting across a variety of sites in the eastern U.S.

Analysis

We compared concentrations of CP and P between our forage classes using ANOVA in Program R (R Core Team 2021). Upon detecting significant differences between forage classes for a particular nutrient, we used Tukey's HSD multiple comparison test to determine which forage classes differed. Additionally, we considered forage values relative to the nutritional requirements of a lactating female to determine the proportion of forages within each class that would meet those requirements and used a chi-squared test to determine whether these proportions differed among forage classes.

We also created a generalized least squares (GLS) model to evaluate correlation between CP and P concentrations. GLS modeling allows for nonconstant variance by weighing each observation based on a variance function, and we used the power of the variance covariate (VarPower) in package nlme (Pinheiro et al. 2023). We also regressed mixed-diet CP and P NCC estimates against each other to evaluate whether these estimates correlated. We square-root transformed NCC estimates based on both CP and P to meet normality assumptions. Neither of

these models were designed to imply causation, but rather to evaluate relationships among forage nutrients and NCC estimates that may influence diet selection and nutrient availability.

RESULTS

We collected 918 forage samples for nutritional analysis, representing 88 plant genera/species. We collected a total of 45 genera/species of forbs (Table 2.3), 11 genera/species of semiwoody plants (Table 2.4), and 32 genera/species of woody plants (Table 2.5). Of our samples, 497 were forbs, 202 were semiwoody, and 219 were woody plants. Young forbs provided the greatest nutrient concentrations, with an average of 18.6% CP and 0.28% P. Old forbs had the second-greatest nutrient concentrations, with an average of 16% CP and 0.23% P. Young and old parts of semiwoody and woody plants provided similar, reduced nutrient concentrations, averaging from 11.6–12.5% CP and 0.15–0.17% P (Table 2.1).

The proportion of forages meeting CP (x^2=230.1, df= 5, p<0.001), P (x^2=143.3, df= 5, p<0.001), and both constraints simultaneously (x^2=151.2, df= 5, p<0.001) varied among forage plant classes. Only 43.9% and 18.8% of all forages met the CP and P constraints, respectively. Only 29.2% of forbs met both the CP and P constraint, and only 2% of semiwoody and 0.9% of woody plants simultaneously met both constraints (Table 2.2). Of the plants that met the CP constraint, only 37.5% also met the P constraint. Conversely, 87.3% of plants that met the P constraint simultaneously met the CP constraint. Our GLS model detected a positive relationship between CP and P levels in deer forage plants, with CP concentration increasing by 3.6% (p<0.001) for every 0.1% increase in P concentration.

Sitewide NCC estimates based on a 14% CP constraint averaged 33.5 (±13.2) deer days/ha, and NCC estimates based on a 0.3% P constraint averaged 9.7 (±2.2) deer days/ha. CP estimates were greater than P at 38 sites, whereas P estimates were greater than CP at 5 sites. Six

of the sites did not have any sampled forages that met the minimum P requirement, whereas all sites had ≥1 sampled forage that met the minimum CP requirement. We found a positive correlation between site-specific NCC for CP and P, with CP NCC increasing by 0.29 (±0.1) deer days/ha for every 1 deer day/ha increase in P NCC (p=0.039; Figure 2.2).

DISCUSSION

Nutrient concentrations varied by plant class, with forbs having greater CP and P concentrations than semiwoody or woody plants. Our data support the separate collection and categorization of young and old plant parts for forbs when estimating deer carrying capacity, as nutrient concentrations differed based on tissue age. We found positive correlation between CP and P concentrations within forages, but most plants did not meet both nutritional constraints simultaneously. Plants meeting the P constraint tended to also meet the CP constraint, whereas many plants which provided adequate CP concentrations did not simultaneously meet P constraints. Although we also found correlation between NCC estimates derived from CP and P, we generally found lower NCC estimates based on P compared to CP, and some sites had no plants meeting the minimum P requirements for a lactating female with twin fawns.

Forbs provided the greatest nutrient concentrations in our study, consistent with previous research (Mixon et al. 2010, Nanney et al. 2018). Young forb tissue provided the greatest levels of CP and P of any forage class, followed by old forb tissue. Deer generally select forbs over other plant classes when they are available (Vangilder et al. 1982, Henke et al. 1988, Nanney et al. 2018), but not all forbs met both CP and P requirements. Even if deer were to consume only plants meeting a minimum CP constraint, it is possible they would fail to meet P demands as less than a third of forbs met both nutrient constraints simultaneously. Diet selection must involve multiple nutrients to ensure herbivores fulfill their nutritional requirements, and consideration

should be given to how selection for a particular nutrient may influence intake of another nutrient (Dykes et al. 2020). Thus, meeting nutritional demands that allow for maximum productivity or body size depends upon providing plant communities with forbaceous species able to simultaneously meet both CP and P requirements.

Collecting and analyzing young and old plant tissue separately is most important when working with higher-quality forages. Several previous studies have collected and analyzed all leaves together when evaluating forage quality and availability (Edwards et al. 2004, Jones et al. 2009, Glow et al. 2019), which may result in less precise NCC estimates when forbs comprise a large proportion of forages. As concentrate selectors, deer selectively forage on younger plant tissue of specific species when available (Lashley et al. 2014), which would tend to increase their diet quality compared to a whole-plant forage sample. Although we did not find support for differences in forage quality based on the age of woody and semiwoody samples, others have found such differences, especially among young tissue collected soon after a disturbance (Schindler et al. 2004, Nichols et al. 2021, Lashley et al. 2022). Future work should collect young and old tissue separately for forbs, and also for semiwoody and woody plants when disturbance, such as fire, stimulates resprouting young plant tissue.

Although there has been considerable work conducted over the past several decades investigating nutritional requirements for deer, we believe additional work is needed to refine estimates of NCC. Previous studies investigating nutritional demands have had relatively small sample sizes, and many involved only fawns/yearlings or a mixture of age classes, which may be a problem as nutritional requirements may vary with age (French et al. 1956, Holter et al. 1979, Grasman and Hellgren 1993, Asleson et al. 1996). Given the great amount of individual variation in nutrient use and requirements (Provenza 2018), it is difficult to determine nutritional demands

without a robust sample. Changes in nutrient absorption rates, retention, and resorption from bone during stress periods may allow deer to meet nutrient requirements without dietary changes (Grasman and Hellgren 1993, Hewitt et al. 2011), further complicating the development of accurate nutritional constraints. Minimum P requirements for cervids are especially lacking in the literature (Shin et al. 2000), which may partially explain CP being a more commonly used constraint in NCC models. Future research should develop accurate estimates for multiple nutrients as required for maximum growth, milk production, and antler size to better understand the role of plant nutrients in deer morphology.

Other nutrients beyond CP and P also may influence diet selection and nutritional ecology of deer. Energy requirements for deer are well-established in the literature, but most herbaceous forages meet minimum nutritional requirements (Lashley et al. 2015, Turner 2024). Calcium and potassium also are required for maintenance and growth, but these minerals are unlikely to be limiting given most forages meet or exceed estimated requirements (Barnes et al. 1990, Turner et al. 2021). Toxicity also plays a role in diet selection, as nutrient balancing requires avoidance of toxicity in addition to maximizing limiting nutrients. Sulfur may be particularly important, as several have documented strong avoidance of plants with high sulfur concentrations (Ceacero et al. 2015, Dykes et al. 2020). Incorporating toxicity thresholds into NCC models would improve our estimates of nutrient availability, but we currently lack toxicity estimates for deer (Dykes et al. 2020). Developing toxicity constraints would benefit management of large herbivores, but providing a diversity of plants meeting minimum requirements of limited nutrients likely is the best approach to allow animals to meet nutritional demands while avoiding toxicity given our current understanding of diet balancing.

Correlation between CP and P in selected deer forages should allow deer to concomitantly select plants with greater concentrations of both nutrients. Our results build on the results of Vangilder et al. (1982), who found correlation among nutrients within 34 selected forages in the Missouri Ozarks. Similarly, Short et al. (1966) reported that P was correlated with CP among nine mule deer (*Odocoileus hemionus*) forages. Although nutrient cooccurrence allows deer to select plants with great concentrations of both nutrients, they may particularly select for plants with more P given fewer forages meet P requirements. Plants providing adequate P generally also met CP constraints, so diet selection for P likely would result in adequate CP intake. Strong selection of P has been documented in multiple systems (Lashley et al. 2015, Dykes et al. 2018), and several studies have noted P as a limiting mineral in deer forages (Blair et al. 1977, Barnes et al. 1990, Ramírez et al. 1996).

Consideration should be given to using NCC models with explicit nutritional constraints to not only estimate forage availability, but also to determine which nutrients may be most limiting. Our data indicate nutrient limitations vary among sites. Other research has noted P as a major nutrient limitation that influences populations and diet selection (Jacobson 1984, Lashley et al. 2015, Dykes et al. 2018), and our results indicate CP is unlikely the most-limiting nutrient across the eastern U.S. It is important to note that estimated nutritional constraints, especially for P, vary by sex, age, and study design (French et al. 1956, Ullrey et al. 1975, Grasman and Hellgren 1993). Actual P requirements for lactation may differ from our constraint of 0.3% (Shin et al. 2000), but NCC is still a valuable measure of relative forage quality and availability. Although the literature suggests P may be more limiting than CP in some areas, few have made direct comparisons of NCC estimates derived using P and CP constraints. NCC may respond differently to habitat management treatments based on the nutritional constraint used (Jones et al.

2009), and, it may be appropriate to use the nutrient which results in the lowest NCC estimate for each site to provide the most-suitable measure of forage available to meet nutritional demands. Therefore, competing models of NCC based on multiple nutritional constraints could be developed with the lowest estimate used to represent forage availability when comparing treatments or sites to best represent nutritional availability capable of supporting a particular life-history process.

CONCLUSIONS

We present data on average nutritional concentrations of young and old leaves of forbaceous, semiwoody, and woody deer forage species. We considered both the average nutrient levels, as well as whether various forages would meet the nutritional requirements for lactating females. We also considered whether NCC models using CP or P would result in different estimates of carrying capacity. Our findings indicate forbs provided the highest average nutritional quality, with young forb tissue having greater nutritional quality than older forb tissue. However, not all forbs met both the CP or P constraint simultaneously, indicating deer need to balance their diet with foraging selection. We also found correlation between CP and P in selected deer forages. Finally, NCC estimates tended to be lower when considering a nutritional constraint based on P versus CP, but this was not the case for all sites. Given variation in individual requirements and some uncertainty around nutritional constraints, managers should promote a diversity of forbs to provide deer sufficient availability of dietary CP and P.

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APPENDIX

Table 2.1. Mean and standard error (SE) for percent crude protein (CP) and phosphorus (P) for various forage classes collected across the eastern U.S., late May–early August, 2021–2023. Different letters within a nutrient column represent significant differences in nutrient concentration among plant types.

	CP	SE	P	SE
Y Forbs	18.6 C	0.37	0.28 C	0.01
O Forbs	16.0 B	0.38	0.23 B	0.01
Y Semiwoody	12.5 A	0.32	0.17 A	0.01
O Semiwoody	12.2 A	0.19	0.15 A	0.004
Y Woody	11.7 A	0.41	0.15 A	0.01
O Woody	11.6 A	0.24	0.15 A	0.01

Table 2.2. Total sample size (N) and proportion of forages meeting crude protein (CP), phosphorus (P), and simultaneously meeting CP and P across various forage classes collected across the eastern U.S., late May–early August, 2021–2023. Constraints are based on the minimum requirements of a lactating female, with a 14% CP minimum and 0.3% P minimum.

	N	CP	P	CP and P
Y Forbs	282	73%	39.7%	36.2%
O Forbs	215	56.7%	20.9%	20%
Y Semiwoody	55	25.5%	3.6%	3.6%
O Semiwoody	147	17.7%	3.4%	1.4%
Y Woody	51	11.8%	3.9%	0%
O Woody	168	17.3%	4.2%	1.2%

Table 2.3. List of forbs collected on sites across the eastern U.S. during late May–early August, 2021–2023 to evaluate deer forage availability and quality.

Common name	Scientific name	Common name	Scientific name
Alfalfa	*Medicago sativa*	Hog peanut	*Amphicarpaea bracteata*
Alyceclover	*Alysicarpus vaginalis*	Horseweed	*Erigeron canadensis*
Am. jointvetch	*Aeshynomene americana*	Ironweed	*Vernonia* spp.
Asiatic dayflower	*Commelina communis*	Jewelweed	*Impatiens capensis*
Aster	*Aster* spp.	Joe-pye weed	*Eutrochium purpureum*
Beggars-lice	*Desmoidum* spp.	Lespedeza	*Lespedeza* spp.
Beggarticks	*Bidens* spp.	Manyflowered pennywort	*Hydrocotyle umellata*
Birdsfoot trefoil	*Lotus corniculatus*	Mountain mint	*Pycnanthemum* spp.
Black-eyed susan	*Rudbeckia* spp.	Partridge pea	*Chamaecrista fasciculata*
Boneset	*Eupatorium* spp.	Pigeonwings	*Clitoria mariana*
Buckwheat	*Fagopyrum esculentum*	Pokeweed	*Phytolacca americana*
Butterfly pea	*Centrosema virginianum*	Prickly lettuce	*Lactuca serriola*
Chicory	*Cichorium intybus*	Ragweed	*Ambrosia* spp.
Cinquefoil	*Potentilla simplex*	Rosinweed	*Silphium* spp.

Table 2.3. Continued

C. lambsquarters	*Chenopodium album*	Snakeroot	*Sanicula* spp.
Coneflower	*Echinacea* spp.	Stinging nettle	*Laportea canadensis*
Cowpea	*Vigna unguiculata*	Sunflower	*Helianthus* spp.
Croton	*Croton capitatus*	Swamp agrimony	*Agrimonia parviflora*
Daisy fleabane	*Erigeron annuus*	Vervain	*Verbena* spp.
Florida pusley	*Richardia scabra*	Violet	*Viola* spp.
Goldenrod	*Solidago* spp.	Virginia meadowbeauty	*Rhexia virginica*

Table 2.4. List of semiwoody plants collected on sites across the eastern U.S. during late May–early August, 2021–2023 to evaluate deer forage availability and quality.

Common name	Scientific name
Alabama supplejack	*Berchemia scandens*
Blackberry	*Rubus* spp.
Crossvine	*Bignonia capreolata*
Grape	*Vitis* spp.
Greenbriar	*Smilax* spp.
Japanese honeysuckle	*Lonicera japonica*
Multiflora rose	*Rosa multiflora*
Peppervine	*Ampelopsis arborea*
Trumpet creeper	*Campsis radicans*
Virginia creeper	*Parthenocissus quinquefolia*
Yellow jessamine	*Gelsemium sempervirens*

Table 2.5. List of woody plants collected on sites across the eastern U.S. during late May–early
August, 2021–2023 to evaluate deer forage availability and quality.

Common name	Scientific name	Common name	Scientific name
American beautyberry	*Callicarpa americana*	Gallberry	*Ilex glabra*
Ash	*Fraxinus* spp.	Hackberry	*Celtis* spp.
Autumn olive	*Elaeagnus umbellata*	Hickory	*Carya* spp.
Black cherry	*Prunus serotina*	Honeylocust	*Gleditsia triacanthos*
Black locust	*Robinia pseudoacacia*	Maple	*Acer* spp.
Blackgum	*Nyssa sylvatica*	Mulberry	*Morus* spp.
Blueberry	*Vaccinium* spp.	Oak	*Quercus* spp.
Bush honeysuckle	*Lonicera tatarica*	Sassafras	*Sassafras albidum*
Carolina buckthorn	*Rhamnus caroliniana*	Serviceberry	*Amelanchier arborea*
Chinese privet	*Ligustrum sinense*	Staggerbush	*Lyonia* spp.
Common persimmon	*Diospyros virginiana*	St. Johnswort	*Hypericum* spp.
Coralberry	*Symphoricarpos orbiculatus*	Sumac	*Rhus* spp.
Devil's walking stick	*Aralia spinosa*	Sweetleaf	*Symplocos tinctoria*
Dogwood	*Cornus* spp.	Viburnum	*Viburnum* spp.
Eastern redbud	*Cercis canadensis*	Yaupon	*Ilex vomitoria*
Elm	*Ulmus* spp.	Yellow poplar	*Liriodendron tulipifera*
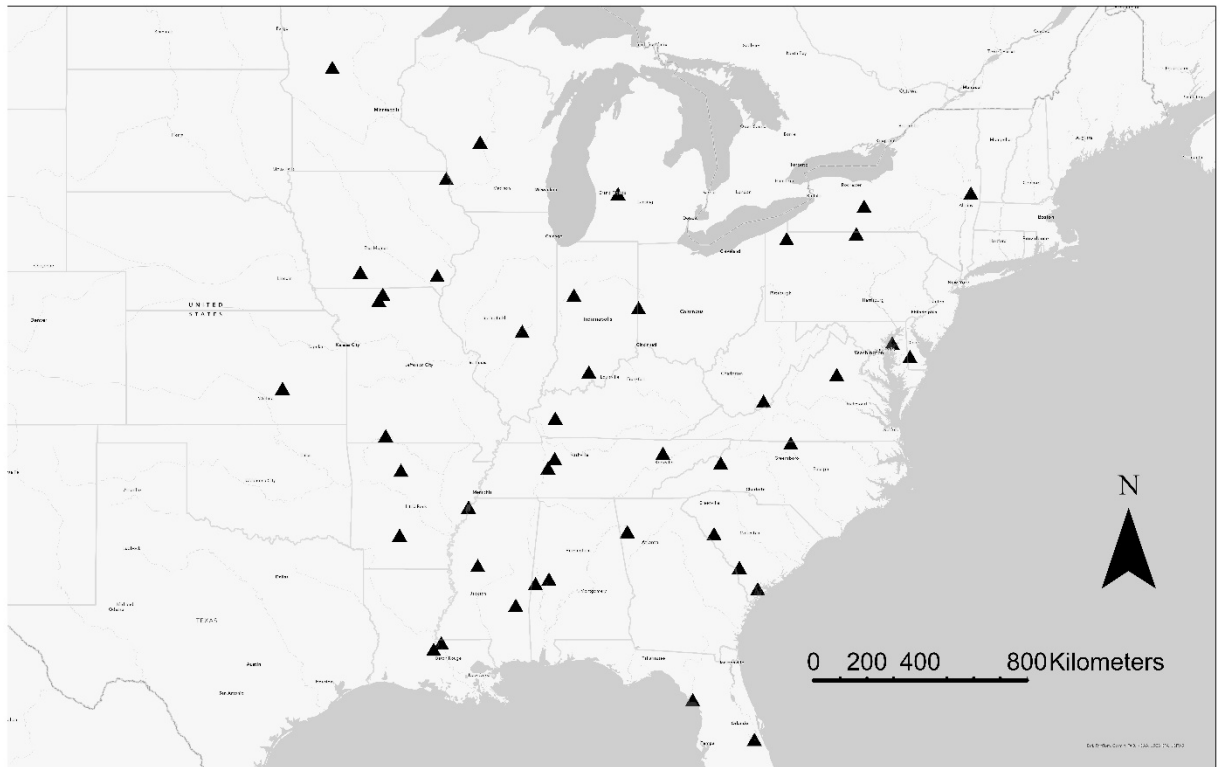
Figure 2.1. Locations of sites across the eastern U.S. where deer forage samples were collected late May–early August, 2021–2023.
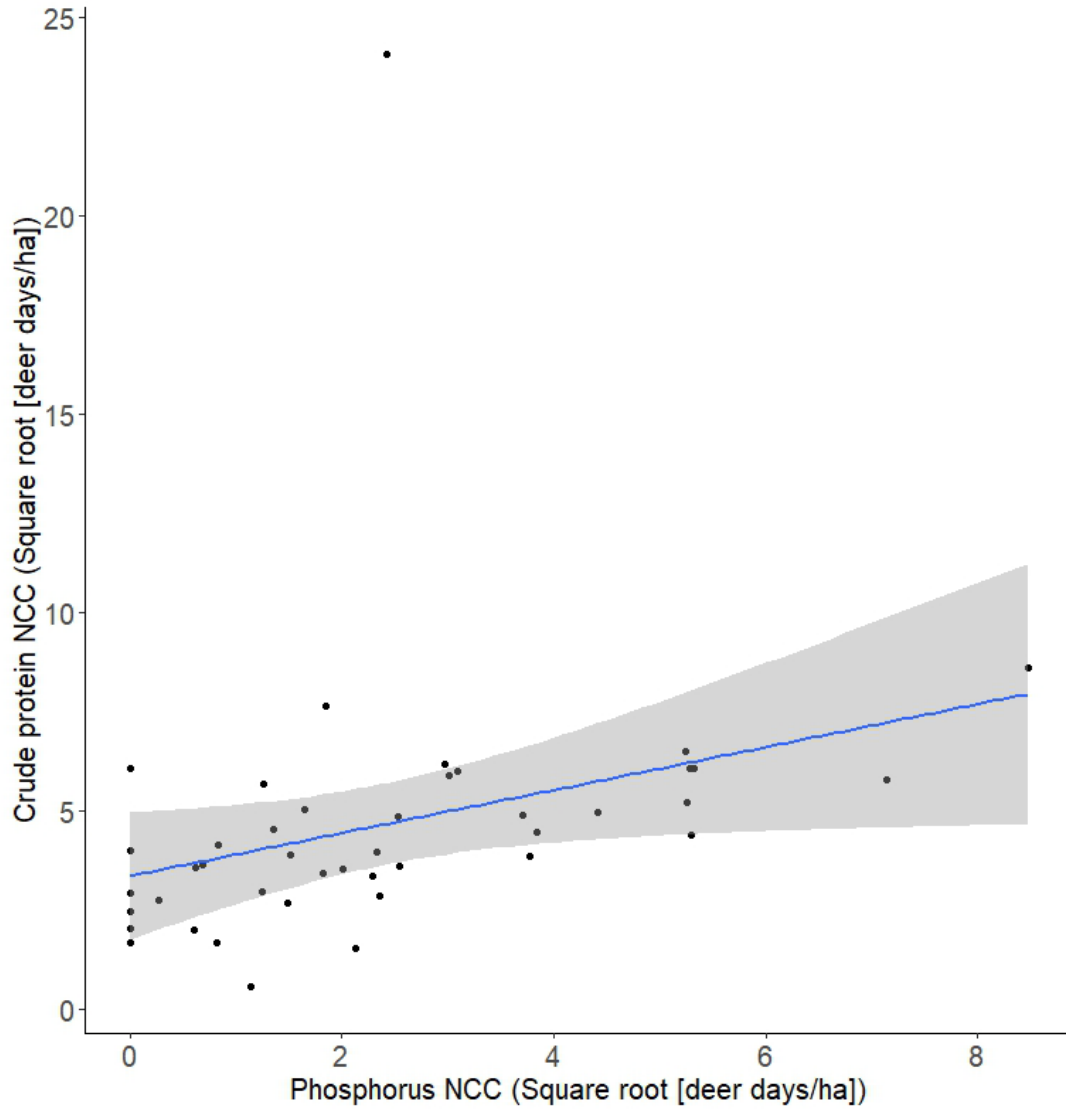
Figure 2.2. Relationship between site-specific lactation-level nutritional carrying capacity (NCC) estimates derived based on crude protein (CP) and phosphorus (P) from 43 sites across the eastern U.S., late May–early August, 2021–2023. NCC is given in deer days/ha, and square-root transformations were performed on data prior to analysis. CP estimates are based on 14% CP constraint and P estimates based on 0.3% P constraint. Bands represent a 95% confidence interval.

CHAPTER 3. INFLUENCE OF CLIMATE, LANDSCAPE COMPOSITION, AND FORAGE AVAILABILITY ON WHITE-TAILED DEER MORPHOMETRICS

ABSTRACT

Environmental factors such as climate and forage availability strongly influence morphological variation in wildlife. White-tailed deer (*Odocoileus virginianus*) body and antler size vary widely across their geographic distribution, and managers want to better understand factors associated with larger morphometrics. Large deer often are associated with landscapes providing greater forage availability, but there is limited information on the influence of temperature, landscape, and site-specific forage availability in changing deer morphology across a wide geographic area. We collected body mass, antler size, and site-specific growing-season forage availability from 35 properties across 21 eastern U.S. states. Average annual temperature and row crop coverage were included in models for females and males, with cooler sites and those having greater row crop coverage producing larger deer. Average female body mass increased by 1.4 kg for every 1˚C decrease in average annual temperature and increased by 1.6 kg for every 10% increase in landscape crop coverage. Mature male antler size also correlated with temperature and crop coverage, with antler size increasing by 4.9 cm for every 1˚C decrease in average annual temperature and increasing by 7.1 cm for every 10% increase in landscape crop coverage. After controlling for landscape effects, adult female mass correlated with site-specific nutritional carrying capacity based on a 0.3% phosphorus constraint (P NCC), with average female body mass increasing by 0.15 kg for every 1 deer day/ha increase in P NCC. Male antler size was marginally correlated with P NCC as well, with antler size increasing by 0.7 cm for every 1 deer day/ha increase in P NCC. Our results indicate climate and landscape variables have a consistent influence on deer morphology, and we found support for site-specific growing-season forage availability influencing female body and male antler size. Given the limited forage availably we recorded, management intensity required to increase P NCC and influence antler and body size

may be greater than what is occurring at most sites throughout the eastern US. We recommend managers increase site-specific nutritional availability within the context of landscape-level nutrition to help shape expectations if increasing deer morphometrics is an objective.

INTRODUCTION

Morphological variation in wildlife may develop from a variety of environmental factors. The association between climate and animal morphology likely was first documented by Bergmann, and both inter- and intra- species morphology are influenced by temperature, precipitation, and other climatic variables (Bergmann 1847, Gay and Best 1996, Hellberg et al. 2001, Ficetola et al. 2016). Factors such as forage, prey base, and dispersal ability also may result in morphological variation within a species (Greve et al. 2008, Hinton et al. 2019). Species with a large geographic distribution, such as white-tailed deer (*Odocoileus virginianus*; hereafter, deer) often exhibit great differences in morphology based on environmental differences across their range (Hopkins and Thurman 2010, Heffelfinger 2011). Forage availability during the growing season has been suggested as an important factor explaining morphology, as differences in forage availability during periods of growth may better explain size distribution in animals than hypotheses related directly to climate (Geist 1986, Wolverton et al. 2009, Huston and Wolverton 2011).

Deer body and antler size are influenced by nutritional quality and quantity. Nutritional carrying capacity (NCC) often is used to measure the availability of forages meeting a particular nutritional threshold, such as crude protein (CP), phosphorus (P), or digestible energy (DE; Hobbs and Swift 1985, Nanney et al. 2018, Nichols et al. 2021, Turner et al. 2024). Deer fed low-quality diets have both smaller body mass and antler size than those on a greater nutritional plane (French et al. 1956, Verme 1969, Harmel et al. 1988). Similarly, body and antler size are influenced by factors such as deer density and land use that affect forage abundance and quality (Kie et al. 1983, Simard et al. 2008, Hefley et al. 2013). The effect of nutrition on antler size is of particular interest, as antlers serve as a signal of phenotypic quality to females during mate selection (Morina et al. 2018). Epigenetic effects act on both body and antler size, which results

in some generational lag from changes to nutrition (Monteith et al. 2009, Michel et al. 2016). Thus, morphology may be relatively fixed within an area for some time after changes in forage availability occur.

Forage availability can vary widely based on landscape composition, which strongly influences deer morphology. For example, closed-canopy hardwood forests may provide only 20–200 kg/ha of available forage, whereas an agricultural field may provide in excess of 3,500 kg/ha of available forage during the same time (Lashley et al. 2011, Nanney et al. 2018, Turner et al. 2020). Differences in forage availability can lead to great variation in observed morphometrics across the distribution of deer, as both body and antler sizes tend to be larger in agricultural-dominated regions compared to those dominated by closed-canopy forests (Strickland and Demarais 2000, Kissel et al. 2002, Strickland and Demarais 2008, Hefley et al. 2013, Michel et al. 2016). Within agricultural-dominated regions, however, greater numbers of large-antlered males are harvested in counties with interspersion of forest and agriculture because of the cover provided by forested areas (Cain et al. 2019). Dispersal may mask some nutritional effects if data are considered at a smaller scale, as epigenetic effects strongly regulate morphology (Monteith et al. 2009, Michel et al. 2016). Although correlation between landscape composition and morphology has been established across multiple regions, management practices to influence forage availability often are applied at a smaller scale.

Habitat management practices can significantly increase deer NCC, but changes in morphology related directly to NCC are difficult to quantify. Canopy reduction in forests increases understory deer forage production, and disturbance such as prescribed fire can promote nutrient-dense forbs and stump sprouts (Nanney et al. 2018, Nichols 2020, Nichols et al. 2021, Turner et al. 2024). Herbicide applications also may be used in forests and fields to control

undesirable species and release selected forages (Edwards et al. 2004, Harper et al. 2021). Food plots are a common management practice used to promote deer forage, and typically represent a small percentage of properties planted in highly-selected and productive forages (Lashley et al. 2011, Harper 2019, Turner et al. 2024c). Deer use and attraction to these treatments is well-established, but few have directly linked morphology to forage availability resulting from various management regimes.

Given the interest in nutritional effects on deer morphology, we evaluated the influence of temperature, landscape composition, and NCC on body and antler size across the eastern US. We were specifically interested in evaluating variation in morphology at 2 spatial scales. At the landscape scale, we hypothesized average annual temperature would influence morphology and predicted larger body and antler sizes at colder sites. We also predicted larger body and antler sizes with greater row crop coverage. At the property scale, we hypothesized NCC would change body and antler size, and predicted a positive correlation between morphology and NCC.

STUDY AREA

We evaluated nutritional effects on deer morphometrics on 35 properties across 21 states where managers collected harvest data from 2017–2023 (Figure 3.1). All figures and tables are located in an appendix at the end of the chapter. Most of these properties were privately-owned and were selected from the National Deer Association Deer Steward II graduate list. The Deer Steward program trains hunters, landowners, and managers on harvest data collection, and we selected a geographic representation of sites within our study area of program attendees who responded to a questionnaire indicating they would like their property included in our study. In areas without previous Deer Steward program attendees, we coordinated with state wildlife agency staff to locate suitable properties engaged in Deer Management Assistance programs. All sites had deer

management as an objective, but many were managed primarily for revenue from agricultural or forest products. We also included two Wildlife Management Areas where harvest data were collected during special quota hunts. Although our sites may not be representative of every area within the eastern U.S., they represent a diversity in land use, landscape composition, climate, landowner objectives, management regimes, and deer morphology. Average property size was 646.7 ha (SE ±131.6) ranging from 52.6–4552.7 ha.

METHODS

Morphometric data collection

Morphometric data were collected from harvested deer by managers at each site, including body mass of females and antler size of males. Tooth wear and replacement was used by most managers to estimate age of harvested male and female deer (Severinghaus 1949). Although some error is associated with age estimation using tooth wear (Gee et al. 2002, Storm et al. 2014, Foley et al. 2021), this technique commonly is used by managers and errors in aging should only potentially reduce our model fit. Some sites used cementum annuli analysis on lower incisors, and we included these age estimates when available (Low and Cowan 1963, Gilbert 1966). We primarily were interested in adult female body mass and mature male antler size, as male body mass varies widely throughout the breeding season (Strickland et al. 2017, Apollonio et al. 2020). For our analysis, we considered all females ≥2.5-years old as adult females (Gee et al. 2014) and included males ≥3.5-years old into our antler size at maturity estimation.

Managers at all 35 sites collected body mass data from harvested female deer. Most collected whole carcass mass, but some sites collected body mass from eviscerated carcasses. On those sites, we multiplied eviscerated mass by 1.3 to estimate whole body mass from eviscerated carcasses. We derived this conversion factor from sites collecting both whole and eviscerated

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mass from the same deer, and it was similar to a conversion factor from the literature (Klinger et al. 1985).

Harvest data from males were collected at 30 of the sites. We were especially interested in quantifying antler size at maturity (≥5.5-years old), as many managers are interested in increasing antler size for harvest. When possible, managers measured antlers using the Boone and Crockett (hereafter, B&C) scoring system, which includes measurements for mass, main beam length, tine length, and inside spread (Nesbitt et al. 2009). The B&C scoring system is a standardized technique to measure antler size, and we used gross antler score without deductions to quantify antler size for harvested males. On some sites, managers did not collect B&C scores from all deer, and we used a predictive formula developed by Strickland et al. (2013b) to estimate gross B&C score using main beam length and total number of points. Although we were most interested in antler size at maturity, many sites harvested males 3.5 and 4.5 years old. Additionally, selective harvest may have resulted in mature male antler size in the harvest data that did not represent a true random sample from the populations (Demarais and Strickland 2017). To increase our male sample and account for possible high-grading, we estimated mature antler size from 3.5- and 4.5-year-old males based on average antler growth curves. We multiplied gross B&C score by 1.28 for 3.5-year-old males and by 1.09 for 4.5-year-old males to project their score at maturity (Demarais and Strickland 2011). We added these score estimates with the actual gross scores of 5.5-year-old males to calculate the average estimated mature antler score for each site.

Landscape-level covariates

We used the 2019 National Landcover Database Version 3.0 (Dewitz 2021; hereafter, NLCD) to evaluate the influence of landscape characteristics on morphology. We placed a 10-km buffer

around each property boundary, then calculated the percentage of each landcover type within the buffer for each site. We selected this buffer distance to include areas where males may have been born before dispersing onto the site and being harvested (Kammermeyer and Marchington 1976, Long et al. 2005, Shaw et al. 2006), given maternal nutritional effects on morphology (Michel et al. 2016). We then categorized NLCD landcover types into three classes for our analysis: forest, herbaceous/shrubland, and row crop. NLCD deciduous forest, evergreen forest, and mixed forested were included in the forest classification. Herbaceous/shrubland represented open areas not planted in row crops, and included NLCD pasture/hay, grassland/herbaceous, and shrub/scrub categories. Finally, the NLCD cultivated crops category was included as our row crop landscape covariate. These vegetation types comprised the majority of landcover on/around our sites and were selected based on our hypothesis related to landcover. Finally, we were interested in the effects of climate related to heat regulation and recorded the average annual temperature at each site from the Climate at a Glance County Time Series (NOAA 2024).

Property-level covariates

We wanted to control for the potential influence of landscape-level covariates to determine the influence of forage availability at the property level. Thus, we grouped properties based on their landscape-level row crop percentage and along latitudinal gradients. Average landscape row crop percentage was 15.2%, so we assigned properties into low (<15.2% row crop; N=13) and high (>15.2% row crop; N=22) row crop coverage. We also wanted to control for the influence of regional variation in morphology related to climate and other factors, so we grouped properties into 3 latitudinal groups. The South ranged from 25.5–34° N (N=12), the Middle ranged from 34.5–39.5° N (N=12), and the North ranged from 40–44.5° (N=11). These groups were included

in subsequent property-level analysis to control for landscape effects on morphology at the property level. Finally, we included total property size in hectares as a model covariate.

We sampled forage on each site once during 2021–2023 between late May and early August. Landowner records, aerial images, and site visits were used to manually delineate ArcGIS Pro (ESRI 2020) shapefiles of the following vegetation types on each site prior to sampling: closed-canopy hardwoods, closed-canopy softwoods, open-canopy hardwoods, open-canopy softwoods, pasture/hay, row-crop agriculture, food plots, and early succession. We assigned stand type based on which tree type comprised >50% of each stand. Open-canopy stands were defined as those with ≥30% sunlight reaching the ground, whereas closed-canopy stands were those with <30% sunlight reaching the ground (McCord et al. 2014. Pasture/hay included frequently mowed, hayed, or grazed openings dominated by native or nonnative grasses. Row-crop agriculture included any crop that was harvested and was predominately soybeans (*Glycine max*), corn (*Zea mays*), and cereal grains (e.g., *Triticum aestivum, Avena sativa, Secale cereale*). Food plot included all areas planted with annual or perennial plantings to attract and/or provide forage for wildlife. Early succession included areas dominated by shade-intolerant plants in seral stages 1–3, as well as pine stands <6 years old (Harper 2017). Developed areas and water were excluded from sampling.

We collected vegetation samples at multiple random points within every vegetation type on each property. For every 1% of the property in each vegetation type, we assigned a random sampling point to that vegetation type. We collected 20 random samples within any vegetation type with <20% coverage to ensure adequate sampling intensity. We collected forage within a 0.5-m frame we placed at each random point and collected young and old plant parts separately

from species identified as selected by deer in previous literature (Miller and Miller 2005, Lashley et al. 2014, Harper 2019).

We dried forage samples at 50°C for 72 hours and weighed to the nearest 1/10th g on a digital scale. Following weighing, we mixed samples across vegetation types to measure average nutrient content of every forage species/age we collected at each site. In 2021 and 2022, we sent ≥5 g from the combined subsamples to Custom Laboratory for grinding and analysis. In 2023, we ground all samples to a homogenous powder, and sent ≥5 g from the combined subsamples to the Agricultural Service Laboratory at Clemson University. Both forage labs calculated percent P, nitrogen, and neutral detergent fiber using wet chemistry analysis. We multiplied nitrogen content by 6.25 to estimate CP (Robbins et al. 1987). We calculated a conservative digestible energy (DE) estimate using a technique outlined by Lashley et al. (2015) by first estimating dry matter digestibility of each sample from equations developed by Robbins et al. (1987) using neutral detergent fiber. We then multiplied dry matter digestibility by an estimated gross energy of 3.7 kcal g^{-1} to calculate DE for each plant sample. We used CP, P, and DE results in conjunction with forage biomass calculations to determine deer days/ha of available forage on each property using an explicit mixed-diet nutritional constraint model (Hobbs and Swift 1985).

We first calculated total forage biomass without any nutritional constraints for each site by multiplying the average kg/ha of forage for each vegetation type by the percentage of a site in each vegetation type and summing those estimates. We used CP, P, and DE constraints based on the requirements of a 45-kg lactating female with a single fawn to estimate forage availability. We used a 14% CP, 0.3% P, and 1.96 kcal g^{-1} DE constraints (National Research Council 2007, Hewitt 2011), and estimated NCC for each constraint separately. We calculated NCC estimates for each vegetation type at a site, then calculated an average site-level NCC for CP and P by

multiplying the NCC estimate of a vegetation type by the percentage of a site in each vegetation type and summing those estimates. Thus, we calculated separate total site-level estimates for NCC based on CP (hereafter, CP NCC), P (hereafter, P NCC), and DE (hereafter, DE NCC).

Analysis

We primarily were interested in determining which variables were most correlated with larger body and antler size at 2 spatial scales. Thus, we created sets of candidate linear regression models in Program R version 4.3.3 (R Core Team 2024). At both scales, we created separate sets of models for our response variables of average adult female body mass and projected mature antler size and compared models using Akaike Information Criterion corrected for small sample size (AICc; Burnham and Anderson 1998). The model with the lowest AICc score was the top model, and we considered models within 2 ΔAICc as competing models. At the landscape scale, we included models with climate and landscape coverage effects. Our climate covariate was average annual temperature, and models with and without average annual temperature were included. Landscape covariates included row crop, herbaceous/shrubland, and forest coverage within the 10-km buffer around each site.

Our property-level analysis included estimates of NCC, property size, and groups based on landscape crop coverage and region. The NCC covariates included CP NCC, P NCC, and DE NCC. We did not include forage biomass as a covariate, as it correlated closely with DE NCC (R^2=0.995). We included only one NCC covariate within a given model, as correlation was present between NCC estimates and we wanted to determine which specific covariate had the strongest effect on morphology. We created models including combinations of NCC, region, crop group, and property size. At both spatial scales we used α=0.05 as our level of significance for

covariates within the top and competing models that we considered. We checked model assumptions related to independence, normality, and variance prior to analysis.

RESULTS

Landscape composition and climate

Forest was the most common landcover class within the 10-km buffer on our sites, comprising an average of 39.2% coverage (SE = 4.0; Range = 0.1–77.3). Herbaceous/shrubland averaged 20.4% of the landscape around our sites (SE = 2.3; Range = 0.2–58.7), and row crop was 15.2% of the 10-km buffer on average (SE = 3.3; Range = 0–76.7). Annual temperature averaged 13.2 ˚C (SE = 0.7), and ranged from 4.7–22.2 ˚C.

Property-level nutritional carrying capacity estimates

Vegetation types and NCC estimates varied widely across the properties we sampled. Closed-canopy hardwood forests averaged 48.4% coverage (SE = 4.7 Range = 0–99.3) and provided 43.7 kg/ha biomass (SE = 6.2; Range = 5.1–147), 4.5 deer days/ha CP NCC (SE=1.0; Range = 0–25.9), 1.4 deer days/ha P NCC (SE = 0.4; Range = 0–7.9), and 18.4 deer days/ha DE NCC (SE = 2.7; Range = 2.2–63.9) on sites where they were present. Closed-canopy softwood forests averaged 13.6% coverage (SE = 3.6; Range = 0–75.5) and provided 67.8 kg/ha biomass (SE = 22.7; Range = 9.2–600), 7.2 deer days/ha CP NCC (SE = 2.7; Range = 0–69.0), 2.9 deer days/ha P NCC (SE = 1.6; Range = 0–39.6), and 29.1 deer days/ha DE NCC (SE = 9.9; Range = 4–260.8) on sites where they were present. Open-canopy hardwood forests averaged 2.7% coverage (SE = 1.4; Range = 0–75.5) and provided 91.9 kg/ha biomass (SE = 16.4; Range = 8.2–327.9), 9.9 deer days/ha CP NCC (SE = 2.2; Range = 0–39.5), 3.6 deer days/ha P NCC (SE = 0.7; Range = 0–12.2), and 40.2 deer days/ha DE NCC (SE = 6.8; Range = 3.6–142.5) on sites where they were present. Open-canopy softwood forests averaged 8.3% coverage (SE = 2.8; Range = 0–

53.7) and provided 90 kg/ha biomass (SE = 6.3; Range = 29–160.1), 6.3 deer days/ha CP NCC (SE = 0.7; Range = 0–12.8) , 1.2 deer days/ha P NCC (SE = 0.4; Range = 0–6.7) , and 44.9 deer days/ha DE NCC (SE = 3.6; Range = 22.7–91.2) on sites where they were present.

Food plots averaged 3.8% coverage (SE = 0.5; Range = 0–10.7) and provided 123.3 kg/ha biomass (SE = 26.4; Range = 5.2–884.3), 20.5 deer days/ha CP NCC (SE = 4.7; Range = 0–155.6), 20.0 deer days/ha P NCC (SE = 5.1; Range = 0–155.6), and 57.5 deer days/ha DE NCC (SE = 11.5; Range = 2.9–384.4) on sites where they were present. Row crop averaged 6.7% coverage (SE = 2.6; Range = 0–64.1) and provided 410.6 kg/ha biomass (SE = 137.7; Range = 0–2692.6), 72.3 deer days/ha CP NCC (SE = 24.2; Range = 0–473.8), 19.6 deer days/ha P NCC (SE = 3.6; Range = 0–69.8), and 178.5 deer days/ha DE NCC (SE = 59.9; Range = 0–1170.4) on sites where it was present. Early succession averaged 14.6% coverage (SE = 2.6; Range = 0–72.9) and provided 228.1 kg/ha biomass (SE = 28; Range = 14.2–660.3), 21.6 deer days/ha CP NCC (SE = 2.7; Range = 0–62.3), 9.5 deer days/ha P NCC (SE = 2.2; Range = 0–54.2), and 91 deer days/ha DE NCC (SE = 10.6; Range = 6.2–219.6) on sites where it was present. Pasture/hay averaged 2.5% coverage (SE = 1.3; Range = 0–72.9) and provided 14.8 kg/ha biomass (SE = 3.3; Range = 0–53.4), 2.1 deer days/ha CP NCC (SE = 0.6; Range = 0–8.6), 0.8 deer days/ha P NCC (SE = 0.1; Range = 0–1.4), and 6.1 deer days/ha DE NCC (SE = 1.5; Range = 0–23.2) on sites where it was present. Site-wide biomass averaged 122.9 kg/ha (SE = 36.7; Range = 9.3–1334.7). Average site-wide NCC estimates at our sites tended to be greatest for DE, followed by CP and P. Site-wide DE NCC averaged 51.3 deer days/ha (SE = 15.9; Range = 3–580.4), CP NCC averaged 35.9 deer days/ha (SE = 15.9; Range = 0.3–580.0), and P NCC averaged 9.3 deer days/ha (SE = 2.0; Range = 0–51.0).

Our dataset included body mass from 2371 adult females, with an average of 67.7 samples per site. Adult female body mass averaged 55.8 kg and site averages ranged from 42.9–70.3 kg. Our dataset included projected mature antler size from 861 males, with an average of 28.7 samples per site. Sitewide gross antler score of mature males averaged 346.4 cm and site averages ranged from 273.1–436.4 cm.

Landscape-level analysis

The top model for adult female body mass included average temperature and crop coverage (Table 3.1). For every 1˚C decrease in average annual temperature, female body mass increased by 1.4 kg ($p<0.001$; Table 3.2). For every 10% increase in crop coverage within the 10-km buffer around each site, female body mass increased by 1.6 kg ($p = 0.001$). Within our dataset, 70.7% of the variation in female body mass was explained by the model including temperature and crop coverage (Figure 3.2).

The top model for mature male gross antler score included average temperature and crop coverage (Table 3.3). Average mature antler score increased by 4.9cm ($p = 0.001$) for every 1˚C decrease in average annual temperature (Table 3.2). For every 10% increase in crop coverage within the 10-km buffer around each site, average male antler size increased by 7.1 cm ($p = 0.025$). The top model explained 41.0% of the variation in mature male antler size (Figure 3.3).

Property-level analysis

The top model for female mass at the property-level included P NCC, Region, Crop group, and property size (Table 3.4), and a competing model included P NCC, Region, and Crop group. In the top model, females were 0.15 kg heavier for every 1 deer day/ha increase in P NCC ($p = 0.024$; Table 3.5, Figure 3.4). Females were 9 kg heavier in the North ($p <0.001$) and 4.2 kg lighter in the South ($p = 0.020$) compared to the Middle Region. Females were 4.5 kg heavier on

properties with >15% landscape-level row crop coverage ($p = 0.008$). There was a marginally significant influence of property size ($p = 0.091$), but the effect size was limited. The top model including property size explained 78.8% of the variation in female body mass, whereas the competing model without property size explained 77.3% of the variation.

The top model for male antler size included an effect of P NCC and Region (Table 3.5). Competing models included combinations of Region, Crop group, and CP NCC, but Crop group and CP NCC were not significant in any competing models (Table 3.7). In the top model, males were 60.4 cm larger in the Middle Region compared to the South ($p<0.001$), but did not differ between the Middle and North ($p=0.707$). There was a marginally significant influence of P NCC on antler size, with mature male antler size increasing by 0.7 cm for every 1 deer day/ha increase in P NCC ($p=0.0998$; Figure 3.5). The model including P NCC and Region explained 58.2% of the variation in male antler size.

DISCUSSION

Adult female body mass and mature male antler size both were consistently influenced by average annual temperature and coverage of row crops, with larger body and antler sizes associated with cooler temperatures and greater row crop coverage at the landscape level. At the property-level, P NCC had a positive influence on female body mass when we accounted for the influences of region and landscape crop coverage. P NCC had a marginal, positive influence on male antler size at the property level when we accounted for the effect of region. Our results demonstrate climate, landscape, and site-specific forage availability influence deer morphology across the eastern US.

Average annual temperature was included among top models for landscape-level female body mass and male antler size. We hypothesized deer across our study region would conform to

the heat regulation hypothesis, which previously has been documented in several cervids (Levengood et al. 1994, Sand et al. 1995, Flajšman et al. 2018). Average temperature may act in concert with other factors, such as landscape forage availability, to cause variation in deer morphology across a wide spatial scale (Kubo and Takatsuki 2015). For example, variation in red deer (*Cervus elaphus*) body size, which conformed to expected patterns based on Bergmann's rule, was interpreted as related to nutrition more than climate (Langvatn and Albon 1986). Wolverton et al. (2009) reported differences in white-tailed deer morphology related to nutrition and population density despite deer size following expected latitudinal trends. Conversely, moose (*Alces alces*) body size in Sweden may be related more closely with climate than forage availability (Sand et al. 1995), but their populations were exposed to colder temperatures at more northernly latitudes than most deer in the eastern U.S. Ecologically and evolutionary relevant net primary productivity may explain this discrepancy, as Huston and Wolverton (2011) determined growing-season forage availability generally increases at sites farther from the equator within a mid-latitudinal gradient. Net primary productivity reaches a maximum at temperate latitudes between 30° and 50°, which includes our entire study area (Huston and Wolverton 2009). Geist (1987) considered that deer appear to conform to Bergmann's rule because they fall within this latitude and suggested that changes in morphology are actually related to the availability of high-quality forages during the growing season. Although our results indicate temperature correlates closely with morphology, other factors such as landscape-level forage availability may act as a mechanism behind this correlation.

Row crop coverage also positively correlated with female body mass and male antler size, highlighting the importance of landscape-scale nutritional availability. Larger deer commonly are associated with agricultural landscapes (Strickland and Demarais 2008, Hefley et

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al. 2013, Quebedeaux et al. 2019), as crops such as soybeans and alfalfa provide large amounts of nutritious and selected food resources during the growing season (Harper 2019). Greater numbers of large-antlered males across the Midwestern U.S. are associated with interspersion of forest and cropland (Cain et al. 2019), as cover may be a limiting factor in some areas with extensive crop coverage. The greatest row crop coverage in the landscape surrounding our sites was 77%, so it is unlikely cover limited populations or morphometrics at our sites. Therefore, increased coverage of row crops (or large amounts of other nutritious forages) within the range we examined should promote greater forage availability and larger deer. Epigenetics play a key role in the importance of landscape-level nutrition, as changes to nutrition often take multiple generations to influence body and antler size (Monteith et al. 2009, Michel et al. 2016). Epigenetic effects may swamp some nutritional improvements conducted on a property, but we still observed a positive correlation between forage availability and morphology at the property level.

Nutritional carrying capacity using a P constraint positively influenced morphology on a property after we accounted for landscape variables. Forage resources are a key factor in morphology across multiple cervid species (Geist 1986, Harmel et al. 1989, Terada et al. 2012, Ramanzin and Sturaro 2014), but few have related morphology with forage availability at the property level . Rankins et al. (2023) considered the influence of forage quantity and quality on deer morphology at four sites in South Texas, but was unable to link morphology with forage availability. We used NCC, which simultaneously accounts for both forage quantity and quality, which may have contributed to our ability to correlate morphology with forage. Although we considered P, CP, and DE constraints, only P NCC correlated with morphology. Several have noted P as being a limiting nutrient across the eastern US (Jacobson 1984, Lashley et al. 2015,

Dykes et al. 2018, Turner 2024), which our results support. After accounting for landscape covariates influencing forage, our results suggest managers may observe a positive influence on morphology following management which improves P NCC.

Property-level forage availability had a stronger influence on female body mass compared to male antler size. Body size has a positive influence on female survival and productivity (Keech et al. 2000, Rodriguez-Hidalgo et al. 2010, Milner et al. 2013, Hilderbrand et al. 2019, Sergeyev et al. 2021). Male reproductive success may increase with larger antlers (Morina et al. 2018), but we would expect a diminished response to site-specific forage availability of males at the scale we studied based on their life history. Males use larger home ranges than females (Stewart et al. 2011), and are thus more likely to spend a greater amount of time foraging at locations outside of our sampled sites. Some males also may have been harvested during an excursion outside of their home range (Karns et al. 2011), and their home range may have had different forage availability than our study sites. Differential dispersal rates also may be important, as more males than females were likely born to mothers living off the properties we sampled (Kilgo et al. 1996, Long et al. 2005, Stewart et al. 2011). Given the influence of epigenetics on lifelong antler and body size (Monteith et al. 2009, Michel et al. 2016), greater rates of dispersal could increase the importance of the landscape relative to site-specific nutrition for males. Finally, male harvest data may less accurately reflect population average size relative to females, as harvest bias in males is common (Strickland et al. 2001, Turner et al. 2024d). Our data indicated managers could expect a positive influence of P NCC on morphology of both sexes, but the observed effects may be diminished in males.

Other factors we did not measure also may influence morphology. Deer density is strongly correlated to morphology, with greater density generally decreasing antler and body size

(Ashley et al. 1998, Zannése et al. 2006, Hefley et al. 2013, Smolko et al. 2022). However, deer density primarily affects populations by reducing per-capita forage availability (Barr and Wolverton 2014, Lashley et al. 2015), so our estimates of NCC should have accounted for most density-dependent effects. Specifically, if deer density was greater on a site, we would have expected to measure reduced NCC because of increase herbivory of available forage. Timing of harvest influences female body mass (Strickland et al. 2017), but these changes are relatively limited and would be difficult to account for across varying hunting season structures and breeding chronologies. Finally, it is possible morphology varied based on environmental factors within a given year (Strickland et al. 2013a, Strickland et al. 2020), but all our sites collected harvest data for ≥3 years. Therefore, our samples likely represent site-level averages which were suitable for our analysis without accounting for additional covariates.

The NCC estimates we calculated generally are lower than what others have reported in the literature (Edwards et al. 2004, Lashley et al. 2011, Harper et al. 2021, Powell et al. 2022), especially for unforested and open-canopy forest vegetation types. Estimates of NCC are meant to serve as an index for comparison between sites or treatments (Hobbs and Swift 1985) and should not be used as an absolute measure of carrying capacity. In general, pasture/hay and closed-canopy forests provided the least forage availability, whereas food plots, early succession, and row crop provided the greatest, which is similar to what others have reported (Lashley et al. 2011, Nanney et al. 2018, Powell et al. 2022). Estimates in pasture/hay were low because perennial grasses dominated those sites with few forbs available. Closed-canopy forests on our sites provided limited forage availability which were similar to Control units in manipulative studies investigating forest management for deer (Edwards et al. 2004, Turner et al. 2020, Turner et al. 2024a, Turner and Harper 2024). Conversely, several studies have documented greater

NCC estimates in early succession, food plots, and open-canopy forests managed for deer forage than we measured (Edwards et al. 2004, Lashley et al. 2011, Powell et al. 2022, Turner et al. 2024a). Our study was designed to estimate relative forage availability across a variety of sites rather than determine treatment effects, and these differences in NCC suggest most properties are not managed at similar intensity as studies designed to increase forage availability. For example, our average food plot NCC estimate is less than that reported in some studies (Lashley et al. 2011) partially because many sites only had fallow annual cool-season plantings, which provided limited forage availability when we sampled because planted species had already produced seed and died. Early successional plant communities at several sites were dominated by grasses, which reduced NCC estimates (Harper et al. 2021, Powell et al. 2022), and many open-canopy forests we sampled were dominated by low-quality woody plants that did not meet minimum nutritional requirements (Turner and Harper 2024). We believe it is important to stress that the NCC estimates we calculated represent average forage availability across most properties, but do not reflect forage availability following management to specifically improve deer nutrition.

Forage availability and composition at each site likely are responsible for our reduced NCC estimates rather than reduced nutrient concentrations in selected species at some sites. For example, common ragweed (*Ambrosia artemisiifolia*) was present on 23 of our sites and averaged 18.9% CP and 0.3% P. Horseweed (*Conyza canadensis*) was present on 16 of our sites and averaged 18.2% CP and 0.41% P. Soybeans were present on 22 of our sites and averaged 28% CP and 0.36% P. Thus, plant species were present at most sites which met or exceeded minimum CP and P requirements, but relatively intensive management is required to increase their availability across a property. Increased coverage of forbs is necessary on many properties, as most semiwoody and woody plants failed to meet minimum nutritional requirements (Nanney

et al. 2018, Harper et al. 2021). Blackberry (*Rubus* spp.) was present on all of our sites and averaged 11.8% CP and 0.14% P. Virginia creeper (*Parthenocissus quinquefolia*) was present on 25 of our sites and averaged 12.8% CP and 0.24% P. Understory oaks (*Quercus* spp.) were present at 21 of our sites and averaged 10.5% CP and 0.11% P. Despite most of our sites listing deer as a focal species for management, the majority had relatively limited availability of high-quality forages. Our results indicate improving forage availability on a property at a scale to sufficiently raise P NCC likely would increase average body and antler size over time.

CONCLUSION

Climate, landscape, and site-specific forage availability influence deer morphology across the eastern U.S. Deer body and antler size were negatively correlated with temperature, which could be related to conformation to heat regulation or factors associated with net primary productivity at a different scale than we measured. Landscape-level nutritional availability also influenced morphometrics, as row crop coverage positively affected body and antler size. Site-specific measures of P NCC were correlated with larger female body and male antler size when we accounted for landscape effects, but the effect size was larger for females. Managers interested in producing larger deer should consider both site-specific and landscape-level nutritional availability while acknowledging temperature-related gradients in size may be relatively fixed.

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APPENDIX

Table 3.1. Akaike Information Criterion corrected for small sample size (AICc) scores predicting whole body mass of female white-tailed deer (*Odocoileus virginianus*) at 35 sites across the eastern U.S, 2021–2023. Average temperature is the annual average temperature at each site. Crop, Forest, and Herbaceous/shrub represent the percentage of each landcover type within a 10-km buffer of each site. Weight represents the likelihood of a model relative to other candidate models.

Model	AICc	ΔAICc	Weight
Average temp + Crop	211.82	0	0.76
Average temp + Forest	214.22	2.39	0.23
Average temp	222.68	10.86	0
Average temp + Herbaceous/shrub	225.24	13.42	0
Crop	244.13	32.31	0
Forested	249.79	37.96	0
Herbaceous/shrub	252.63	40.81	0

Table 3.2. Beta-values (β), standard error (SE) and p-values for covariates in top model predicting whole body mass of female and average mature antler size of male white-tailed deer (*Odocoileus virginianus*) in kilograms at sites across the eastern U.S., 2021–2023. Average temperature is the annual average temperature at each site and Crop represents the percentage of row crop within a 10-km buffer of each site.

	β	SE	*p-value*
Female body mass			
Intercept	71.65	2.77	<0.001
Average temperature	-1.38	0.18	<0.001
Crop	0.16	0.04	0.001
Male antler size			
Intercept	398.05	20.05	<0.001
Average temperature	-4.92	1.35	0.001
Crop	0.71	0.30	0.025

Table 3.3. Akaike Information Criterion corrected for small sample size (AICc) scores predicting

average antler size of mature male white-tailed deer (*Odocoileus virginianus*) at 30 sites across

the eastern U.S., 2021–2023. Average temperature is the annual average temperature at each site.

Crop, Forest, and Herbaceous/shrub represent the percentage of each landcover type within a 10-

km buffer of each site. Weight represents the likelihood of a model relative to other candidate

models.

Model	AICc	ΔAICc	Weight
Average temp + Crop	300.91	0	0.70
Average temp	303.92	3.00	0.16
Average temp + Herbaceous/shrub	305.15	4.24	0.08
Average temp + Forest	306.00	5.09	0.05
Crop	310.19	9.28	0.01
Herbaceous/shrub	312.59	11.68	0
Forest	315.99	15.08	0

Table 3.4. Akaike Information Criterion corrected for small sample size (AICc) scores predicting whole body mass of female white-tailed deer (*Odocoileus virginianus*) at the property-level. Properties were grouped into 3 Region groups based on latitude, and 2 Crop groups based on the percentage of the landscape in row-crop. Size represents the property size in hectares. CP NCC, P NCC, and DE NCC are nutritional carrying capacity estimates using a 14% crude protein, 0.3% phosphorus, and 1.96 kcal g^{-1} DE constraint, respectively. Weight represents the likelihood of a model relative to other candidate models.

Model	AICc	ΔAICc	Weight
P NCC + Region + Crop + Size	205.86	0	0.40
P NCC + Region + Crop	206.22	0.36	0.33
Region + Crop + Size	208.97	3.11	0.08
Region + Crop	209.61	3.76	0.06
P NCC + Region	209.84	3.99	0.05
DE NCC + Region + Crop + Size	212.07	6.22	0.02
CP NCC + Region + Crop + Size	212.11	6.25	0.02
DE NCC + Region + Crop	212.47	6.61	0.01
CP NCC + Region + Crop	212.53	6.67	0.01
DE NCC + Region	220.22	14.36	0
CP NCC + Region	220.67	14.81	0

Table 3.5. Beta-values (β), standard error (SE) and p-values for covariates in top and competing models predicting whole body mass of female white-tailed deer (*Odocoileus virginianus*) at the property-level at 35 sites across the eastern U.S., 2021–2023. Properties were grouped into 3 Region groups (South, Middle, North) based on latitude, and 2 Crop groups (Low, High) based on the percentage of the landscape in row-crop. Size represents the property size in hectares. P NCC is a nutritional carrying capacity estimate using a 0.3% phosphorus constraint. The Middle Region and High Crop serve as the references which are included in the intercept calculation.

	β	SE	*p-value*
P NCC + Region + Crop + Size			
Intercept	56.88	2.05	<0.001
P NCC	0.15	0.06	0.024
North region	8.98	1.43	<0.001
South region	-4.18	1.70	0.020
Low crop	-4.46	1.56	0.008
Size	-0.002	0.001	0.091
P NCC + Region + Crop			
Intercept	55.42	1.94	<0.001
P NCC	0.16	0.06	0.021
North region	9.74	1.73	<0.001
South region	-5.01	1.69	0.006
Low crop	-3.93	1.58	0.019

Table 3.6. Akaike Information Criterion corrected for small sample size (AICc) scores predicting

average antler size of mature male white-tailed deer (*Odocoileus virginianus*) at the property-

level at 30 sites across the eastern U.S., 2021–2023. Properties were grouped into 3 Region

groups based on latitude, and 2 Crop groups based on the percentage of the landscape in row-

crop. Size represents the property size in hectares. CP NCC, P NCC, and DE NCC are nutritional

carrying capacity estimates using a 14% crude protein, 0.3% phosphorus, and 1.96 kcal g^{-1} DE

constraint, respectively. Weight represents the likelihood of a model relative to other candidate

models.

Model	AICc	ΔAICc	Weight
P NCC + Region	292.36	0	0.28
Region + Crop	293.42	1.06	0.17
CP NCC + Region	294.28	1.92	0.11
CP NCC + Region + Crop	294.30	1.94	0.11
P NCC + Region + Crop	294.66	2.30	0.09
DE NCC + Region	295.19	2.83	0.07
DE NCC + Region + Crop	295.47	3.11	0.06
Region + Crop + Size	295.75	3.39	0.05
CP NCC + Region + Crop + Size	296.78	4.42	0.03
P NCC + Region + Crop + Size	297.45	5.09	0.02
DE NCC + Region + Crop + Size	298.01	5.65	0.02

Table 3.7. Beta-values (β), standard error (SE) and p-values for covariates in top and competing models predicting average antler size of mature male white-tailed deer (*Odocoileus virginianus*) at the property-level at 30 sites across the eastern U.S., 2021–2023. Properties were grouped into 3 Region groups (South, Middle, North) based on latitude, and 2 Crop groups (Low, High) based on the percentage of the landscape in row-crop. Size represents the property size in hectares. CP NCC, P NCC, and DE NCC are nutritional carrying capacity estimates using a 14% crude protein, 0.3% phosphorus, and 1.96 kcal g^{-1} DE constraint, respectively. The Middle Region and High Crop serve as the references which are included in the intercept calculation.

|	β	SE	*p-value*
P NCC + Region			
Intercept	357.39	11.24	<0.001
P NCC	0.72	0.42	0.0998
North region	4.78	12.58	0.707
South region	-60.41	13.30	<0.001
Region + Crop			
Intercept	376.52	11.05	<0.001
North region	-0.37	12.66	0.977
South region	-65.21	12.99	<0.001
Crop	-14.59	10.57	0.179
CP NCC + Region			
Intercept	369.68	9.57	<0.001
CP NCC	-0.06	0.05	0.301
North region	4.00	13.09	0.762
South region	-67.73	13.09	<0.001
CP NCC + Region + Crop			
Intercept	379.85	11.10	<0.001
CP NCC	-0.07	0.05	0.173
North region	3.13	12.68	0.807
South region	-65.32	12.75	<0.001
Low crop	-17.59	10.60	0.109
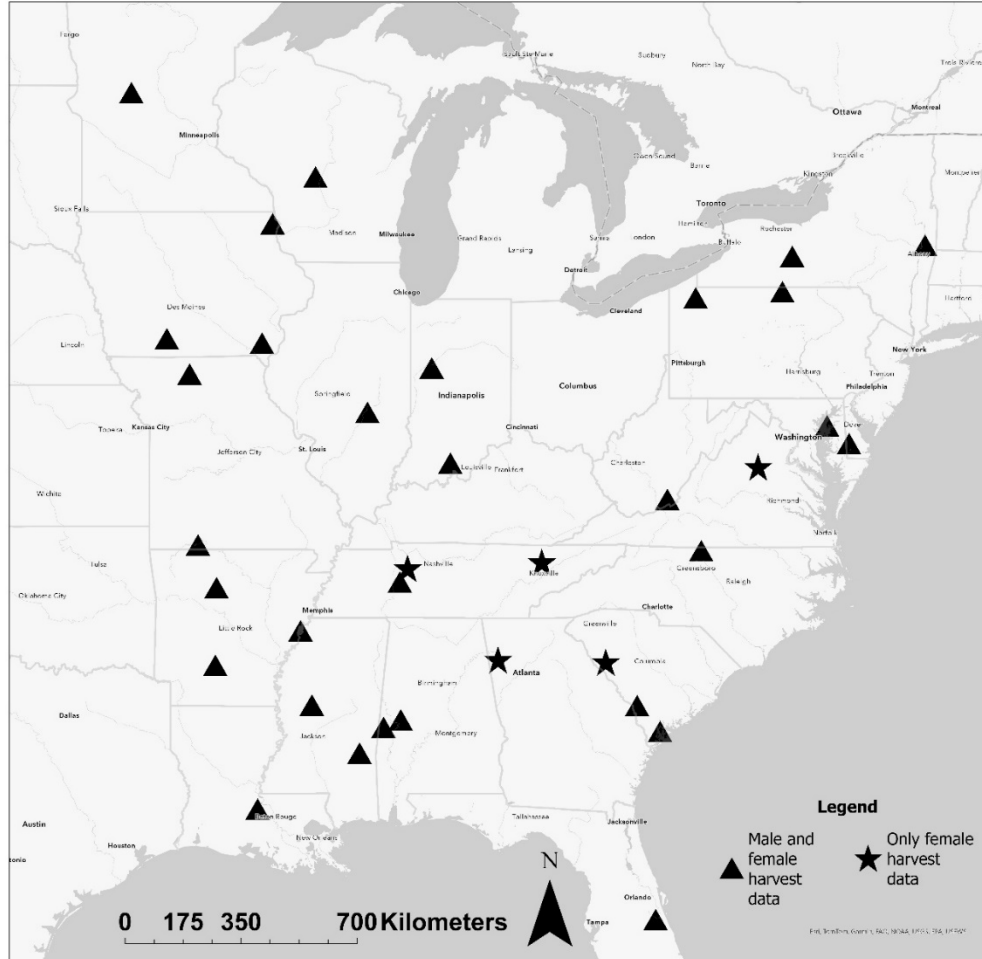
Figure 3.1. Study sites where white-tailed deer (*Odocoileus virginianus*) harvest and forage data were collected. Triangles represent sites where harvest data were collected from both males and females, whereas stars represent sites where only female harvest data were collected and analyzed.
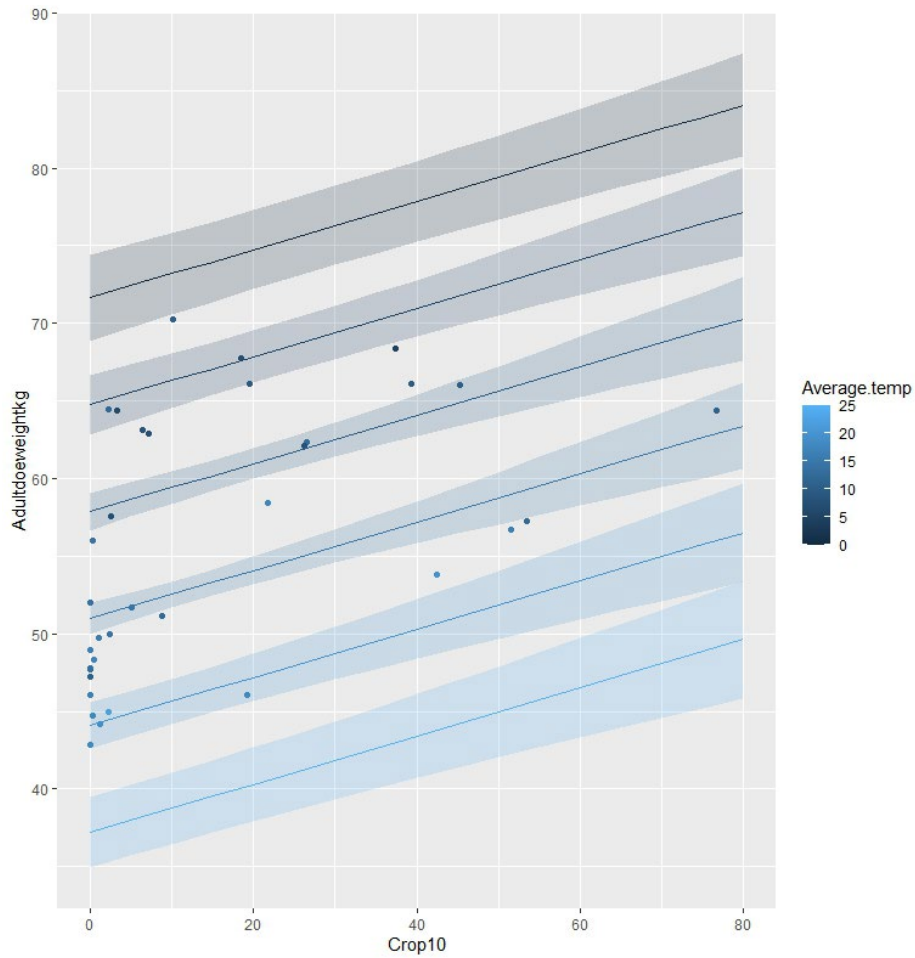
Figure 3.2. Effects plot predicting the relationship between property-specific average annual temperature (˚C) and percent coverage of row crop within a 10-km buffer on average adult female white-tailed deer (*Odocoileus virginianus*) whole body mass (kg). Bands represent 95% confidence intervals around regression lines.
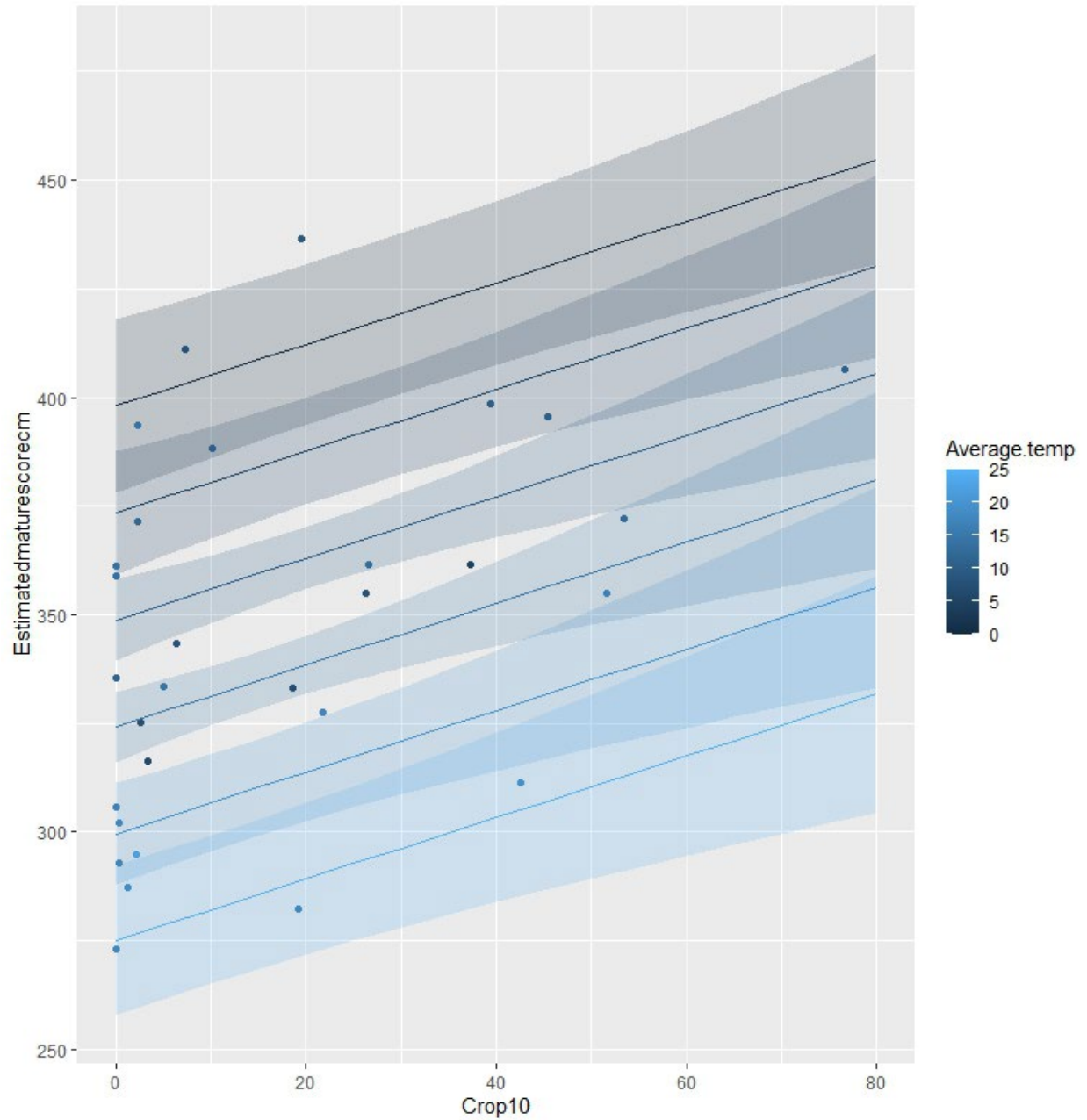
Figure 3.3. Effects plot predicting the relationship between property-specific average annual temperature (°C) and percent coverage of row crop within a 10-km buffer on average mature male (*Odocoileus virginianus*) antler size (cm). Bands represent 95% confidence intervals around regression lines.
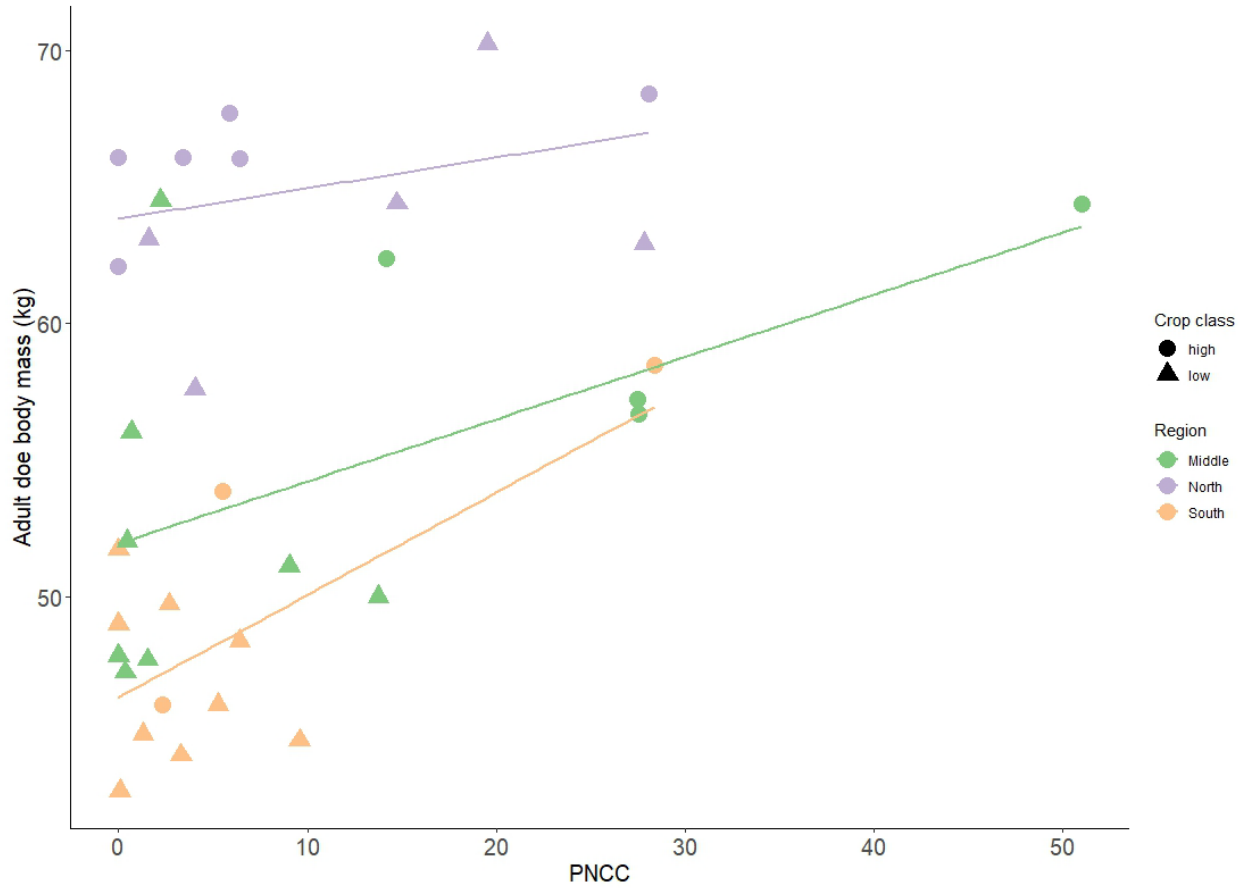
Figure 3.4. Effects plot predicting the relationship between nutritional carrying capacity using a 0.3% phosphorus constraint (PNCC) and average adult female white-tailed deer (*Odocoileus virginianus*) body mass (kg) by region and crop classification.
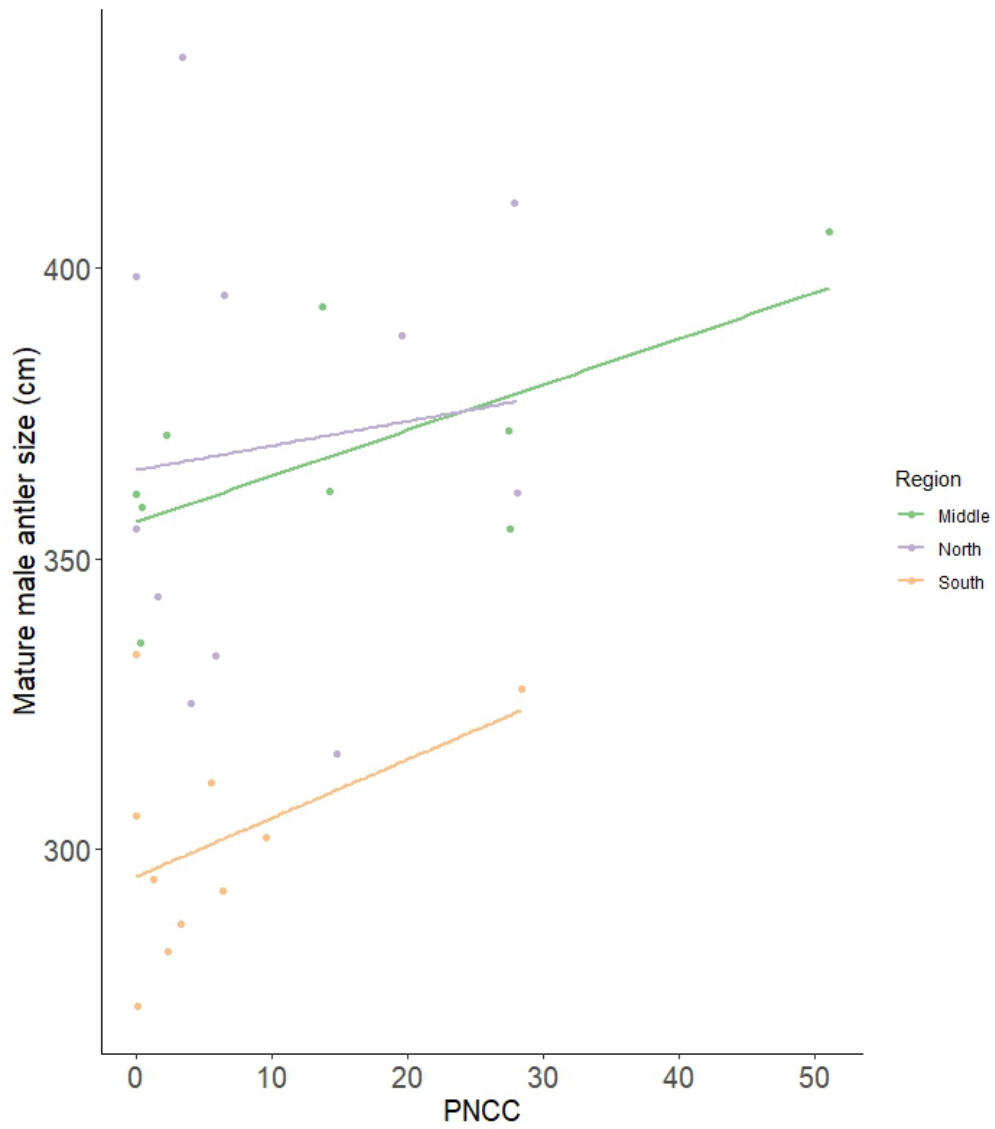
Figure 3.5. Effects plot predicting the relationship between nutritional carrying capacity using a 0.3% phosphorus constraint (PNCC) and average mature male white-tailed deer (*Odocoileus virginianus*) antler size (cm) across 3 geographic regions.

CONCLUSION

Many wildlife agency personnel and private landowners across the eastern US are interested in management to increase morphometrics of harvested white-tailed deer. Increasing antler size of mature males often is a primary management objective, and harvest data can be a useful tool to track progress. Data should be collected from all harvested deer, and our study validates the use of female body mass to predict changes in mature male harvest data. Sites with limited male harvest and/or harvest data from a high-graded sample may use our results to determine expected male antler size based on female body mass.

Properties working to increase deer body and antler size often manage for improved nutritional availability, which can vary based on plant composition. Forbs provided the greatest average nutrient concentrations, whereas the majority of semiwoody and woody forages failed to meet lactation-level requirements of crude protein or phosphorus. Concentrations of protein and phosphorus correlated within plant species and genera but more plants met lactation-level protein requirements than phosphorus. Our results indicate phosphorus likely is the most limiting nutrient for deer across the eastern US, and researchers quantifying nutritional carrying capacity should consider using phosphorus constraints in addition to protein. Our results indicate increasing nutritional carrying capacity requires providing a diversity of forbs capable of meeting multiple nutritional constraints.

Larger deer across the eastern US are strongly associated with properties having cooler annual temperatures and greater landscape coverage of agriculture, and managers should shape body and antler size expectations based on these factors.. Site-specific forage availability based on a phosphorus constraint was correlated with increased female body and male antler size, so management to increase coverage of high-quality forages on a property may help meet

landowner objectives related to increasing morphology. However, forage availability across our sites was relatively poor compared forage availability reported in various studies that implemented experimental treatments to increase forage. Thus, managers should consider more intensive treatments than they currently apply to increase forb coverage and nutrient availability across their properties. Habitat management treatments may include conversion of forest to early succession, herbicide applications to reduce grass coverage in fields, reducing canopy cover in forests to promote woodlands and savannas, and application of fire during different times throughout the year. Such treatments would not only increase deer forage availability, but also provide resources for many nongame wildlife species that are in decline.

VITA

Mark A. Turner grew up in North Carolina. Hunting, fishing, and helping manage his family farm inspired a passion for the outdoors which led him to pursue wildlife management as a career. He received a Bachelor of Science in Fisheries, Wildlife, and Conservation Biology from North Carolina State University and a Master of Science in Wildlife Sciences from Auburn University. His Ph.D. at the University of Tennessee investigated factors influencing deer morphology across the eastern US.