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ARTICLE
Animal Ecology

Influence of temperature, landscape, and fine-scale forage availability on ungulate morphometrics

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Abstract

Abiotic and biotic variables strongly influence morphological variation in wildlife, but there is disagreement on the relative importance of various factors. Primary competing hypotheses regarding drivers of interpopulation animal morphology include those related to heat regulation and those related to forage availability. Despite data to support both hypotheses in various systems, few have considered fine-scale forage availability data across a large geographic area. White-tailed deer (*Odocoileus virginianus*) body and antler size vary widely across their geographic distribution, with larger deer often associated with landscapes providing large amounts of high-quality forage. However, there is limited information on the influence of temperature, landscape, and site-specific forage availability on deer morphology across a wide geographic area. We collected body mass, antler size, and site-specific growing-season forage availability from 35 locations across 21 eastern US states. 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 4.9 cm for every 1°C decrease in average annual temperature and increasing 7.1 cm for every 10% increase in landscape crop coverage. After controlling for landscape effects, adult female mass was correlated with site-specific nutritional carrying capacity based on a 0.3% phosphorus constraint (P NCC), with average female body mass increasing 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 0.7 cm for every 1 deer day/ha increase in P NCC. Our results support the Resource Rule at the local scale, but temperature and landscape factors contribute to interpopulation variation in morphology across broad spatial scales.

KEYWORDS
antler size, Bergmann's rule, body size, harvest data, *Odocoileus virginianus*, white-tailed deer

INTRODUCTION

Morphological variation in wildlife may develop from several environmental factors. The association between climate and animal morphology likely was first documented by Bergmann, and both interspecies morphology and intraspecies morphology are influenced by temperature, precipitation, and other climatic variables (Bergmann, 1847; Ficetola et al., 2016; Gay & Best, 1996; Hellberg et al., 2001). In addition to potentially changing morphology through heat conservation and dispersal mechanisms (Blackburn & Hawkins, 2004; Speakman & Król, 2010), climate affects primary productivity and prey availability, which also may result in morphological variation within a species (Greve et al., 2008; Hinton et al., 2019). There is considerable debate about mechanisms causing intraspecies morphological variation related to latitude and climate, and hypotheses including those related to resource availability, starvation resistance, heat regulation, migration ability, and phylogenetics have been proposed (Blackburn et al., 1999).

Two of the primary hypotheses considered to explain morphological variation are related to heat regulation and forage availability. Animal morphology related to heat conservation may be considered the original hypothesis provided by Bergmann (1847), whereby larger animals generally are found in colder climates because of a reduced surface area to volume ratio. Across species, the relationship between latitude and body size generally has been validated (Blackburn & Gaston, 1996; Clauss et al., 2013) with several studies specifically finding support for the heat conservation hypothesis (Blackburn & Hawkins, 2004; Rodríguez et al., 2008). Others have suggested that heat dissipation actually may be more important than heat conservation (Speakman & Król, 2010), but both conservation and dissipation result in a negative relationship between body size and temperature. In contrast, others have suggested forage availability may be a more 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 temperature (Geist, 1986; Huston & Wolverton, 2011; Wolverton et al., 2009). This hypothesis was termed the Resource Rule by McNab (2010), who reported the distribution of resources could be used to account for morphological variation in many species. Similarly, landscape factors that promote greater and/or higher quality forage availability result in larger mammals (Hewison et al., 2009; Mysterud et al., 2001). There still is disagreement on these hypotheses and evaluating them with a species that exhibits great differences in morphology across their distribution, such as white-tailed deer (*Odocoileus virginianus*; hereafter, deer), would help disentangle the effects of temperature and forage on morphology (Heffelfinger, 2011; Hopkins & Thurman, 2010). Average body mass can vary more than two times in deer with adult male mass ranging from approximately 40 kg for the Key deer subspecies (*O. virginianus clavium*) to >100 kg for deer in the midwestern and northern United States (Ditchkoff, 2011). Additionally, deer antlers are a unique secondary sexual characteristic that generally correlate in size with body mass but likely are not directly influenced by temperature (Demarais & Strickland, 2011). Thus, deer are an ideal species to simultaneously consider the influences of temperature and forage availability on morphology.

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 & Swift, 1985; Nanney et al., 2018; Nichols et al., 2021; Turner & Harper, 2024; Turner, Bones, 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; Harmel et al., 1989; Verme, 1969). Nutritional effects are apparent when considering deer size between areas with different landscape-level forage availability (Hefley et al., 2013; Quebedeaux et al., 2019; Strickland & Demarais, 2008). Similarly, deer body and antler size correlate negatively with deer density, as greater deer density reduces forage abundance and quality (Hefley et al., 2013; Kie et al., 1983; McCullough, 1985; Simard et al., 2008). 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; Vanpé et al., 2007), which should result in males producing larger antlers until resources to maintain survival and antler growth are limiting. Despite the general pattern of greater nutrition leading to larger morphology, the scale at which nutrition acts on morphology warrants further consideration.

Forage availability varies widely with 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 3500 kg/ha of available forage during the same time (Harper, 2019; Lashley et al., 2011; Nanney et al., 2018; Turner et al., 2020). Differences in forage availability can lead to great variation in observed morphology across the distribution of deer, as both body and antler size tend to be larger in agricultural-dominated regions than in those dominated by closed-canopy forests (Hefley et al., 2013; Kissell et al., 2002; Michel et al., 2016;

Strickland & Demarais, 2000, 2008). Dispersal may moderate some nutritional effects if data are considered at a smaller scale, as epigenetic effects regulate morphology at a larger scale than most properties where deer management occurs (Michel et al., 2016; Monteith et al., 2009). Although correlation between landscape composition and morphology has been established across multiple regions, there are few data considering the effects of fine-scale forage availability across a large geographic area.

Factors influencing mammal morphology are broadly considered in ecology, yet studies designed to simultaneously evaluate broad landscape features with fine-scale, site-specific plant community effects on size are lacking. In an effort to reconcile hypotheses related to heat regulation and forage availability, we evaluated the influence of temperature, landscape composition, and NCC on body and antler size across the eastern United States. Given the broad geographic distribution of our sample sites, we expected to find some support for both hypotheses, and we were specifically interested in evaluating variation in morphology at two spatial scales. At the broad scale, we hypothesized average annual temperature would influence morphology, and we predicted larger body and antler sizes at colder sites. We also predicted larger body and antler sizes with greater nutrient availability, which is largely represented by row crop coverage at the broad scale. At the fine scale, we hypothesized NCC would change body and antler size, and we predicted a positive correlation between morphology and NCC.

METHODS

Study area

We evaluated nutritional effects on deer morphometrics on 35 properties across 21 states where managers collected harvest data from 2017 to 2023 (Figure 1). 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 program attendees who represented a broad geographic scale and responded to a questionnaire indicating they were willing to include their property 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. Quality deer management was an objective at all sites, but many were managed primarily for revenue from agricultural or forest products. We also included two Wildlife Management Areas managed by state wildlife agencies where harvest data were collected during special quota hunts. Our study sites represented a diversity in land use, landscape composition, climate, landowner objectives, management regimes, and deer morphology across the eastern United States. Although a few of the properties used bait (i.e., corn) during the hunting season (where legal), none had a supplemental feeding program or otherwise distributed feed other than bait at limited times during the deer hunting season. Average property size ranged from 53 to 4553 ha and averaged 647 ± 132 ha (mean ± SE).

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 rather than bias our estimates. Some sites used cementum annuli analysis on lower incisors, and we included these age estimates when available (Low & 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 mass from the same deer, and it was similar to the conversion factor reported by Klinger et al. (1985).

Harvest data from males were collected at 30 of the sites. 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 asymmetry deductions to quantify

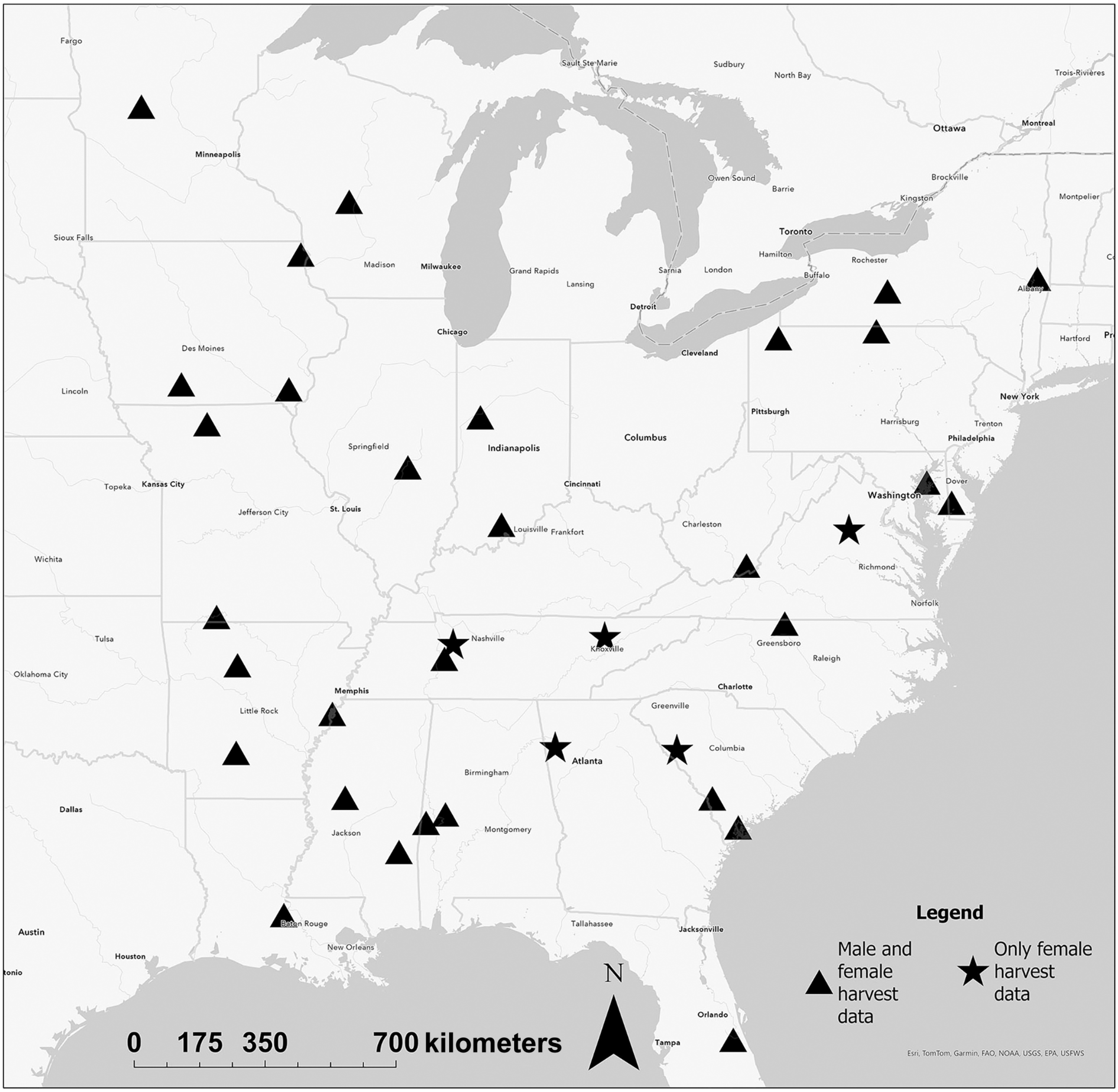

FIGURE 1 Study sites where white-tailed deer (*Odocoileus virginianus*) harvest and forage data were collected. Triangles represent sites where harvest data were collected from both males and females, whereas stars represent sites where only female harvest data were collected and analyzed.

antler size for harvested males. On some sites, managers did not collect the B&C score from all deer. For those, we used a predictive formula developed by Strickland, Jones, et al. (2013) 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, males that were only 3.5 and 4.5 years old were harvested at some sites. 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 & Strickland, 2017). To increase our male sample and account for possible high-grading (i.e., harvest skewed toward above-average males at younger age classes), 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 & Strickland, 2011). We included 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.

Broad-scale covariates

We used the 2019 National Land Cover 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 and 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 & Marchinton, 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. Primary row crops within the site buffers were soybeans (*Glycine max*), corn (*Zea mays*), and cereal grains (e.g., *Triticum aestivum*, *Avena sativa*, *Secale cereale*). 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 (National Oceanic and Atmospheric Administration, 2024).

Fine-scale 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 three latitudinal groups. The South ranged from 25.5 to 34° N ($N = 12$ for females, $N = 10$ for males), the Middle ranged from 34.5 to 39.5° N ($N = 12$ for females, $N = 9$ for males), and the North ranged from 40 to 44.5° ($N = 11$ for females and males). 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 at each site once between late May and early August, 2021–2023. 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 forest 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, corn, and cereal grains. Food plots 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 herbaceous plants (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 & Miller, 2005; Lashley et al., 2014; Harper, 2019) or those commonly browsed on a site (see Turner et al., 2025 for a full list of species collected).

We dried forage samples at 50°C for 72 h and weighed to the nearest 1/10th gram 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 (3068 State Highway 37, Monett, MO) for grinding and analysis. In 2023, we ground all samples to a homogeneous 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 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 & Swift, 1985).

We first calculated total forage biomass without any nutritional constraints for each site by multiplying the average kilograms per hectare 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 twin fawns to estimate forage availability. We used a 14% CP, 0.3% P, and 1.96 kcal g^{-1} DE constraint (National Research Council, 2007; Hewitt, 2011), and we estimated NCC for each constraint separately. We chose to use a lactation-based NCC model for both males and females given the importance of long-term nutrition during development (Monteith et al., 2009; Michel et al., 2016) and because lactation requirements meet or exceed those for antler growth (National Research Council, 2007, Hewitt, 2011). We calculated NCC estimates for each vegetation type at a site, then calculated an average site-level NCC for CP, P, and DE 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 two 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 corrected Akaike information criterion (AIC_c) for small sample size (Burnham & Anderson, 1998). The model with the lowest AIC_c score was the top model, and we considered models within 2 ΔAIC_c as competing models. At the broad 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 fine-scale 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 various 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 followed the recommendations of Muff et al. (2022) to conclude strong evidence when $p < 0.01$, moderate evidence when $p < 0.05$, and weak evidence when $p < 0.1$. We checked model assumptions related to independence, normality, and variance prior to analysis.

TABLE 1 Corrected Akaike information criterion (AIC_c) for small sample size scores predicting whole body mass of female white-tailed deer (*Odocoileus virginianus*) at 35 sites across the eastern United States, 2021–2023.

Model	AIC_c	ΔAIC_c	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

Note: Average temp 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.

TABLE 2 Beta values (β), 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 United States, 2021–2023.

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

Note: Average temp is the annual average temperature at each site and crop represents the percentage of row crop within a 10-km buffer of each site.

RESULTS

Landscape composition and climate

Forest was the most common landcover class within the 10-km buffer on our sites, comprising 39.2% ± 4.0% coverage (mean ± SE; range = 0.1%–77.3%). Herbaceous/shrubland averaged 20.4% ± 2.3% of the landscape around our sites (range = 0.2%–58.7%), and row crop was 15.2% ± 3.3% of the 10-km buffer (range = 0%–76.7%). Annual temperature averaged 13.2 ± 0.7°C and ranged from 4.7 to 22.2°C. Annual temperature averaged 8.3°C (range = 4.7–10.7°C) in the North region, 13.3°C (range = 11.0–16.7°C) in the Middle region, and 17.8°C (range = 14.6–22.2°C) in the South region.

Fine-scale NCC estimates

Site-wide biomass averaged 122.9 ± 36.7 kg/ha (range = 9.3–1334.7 kg/ha). Average site-wide NCC estimates at our sites tended to be greatest for DE, followed by CP

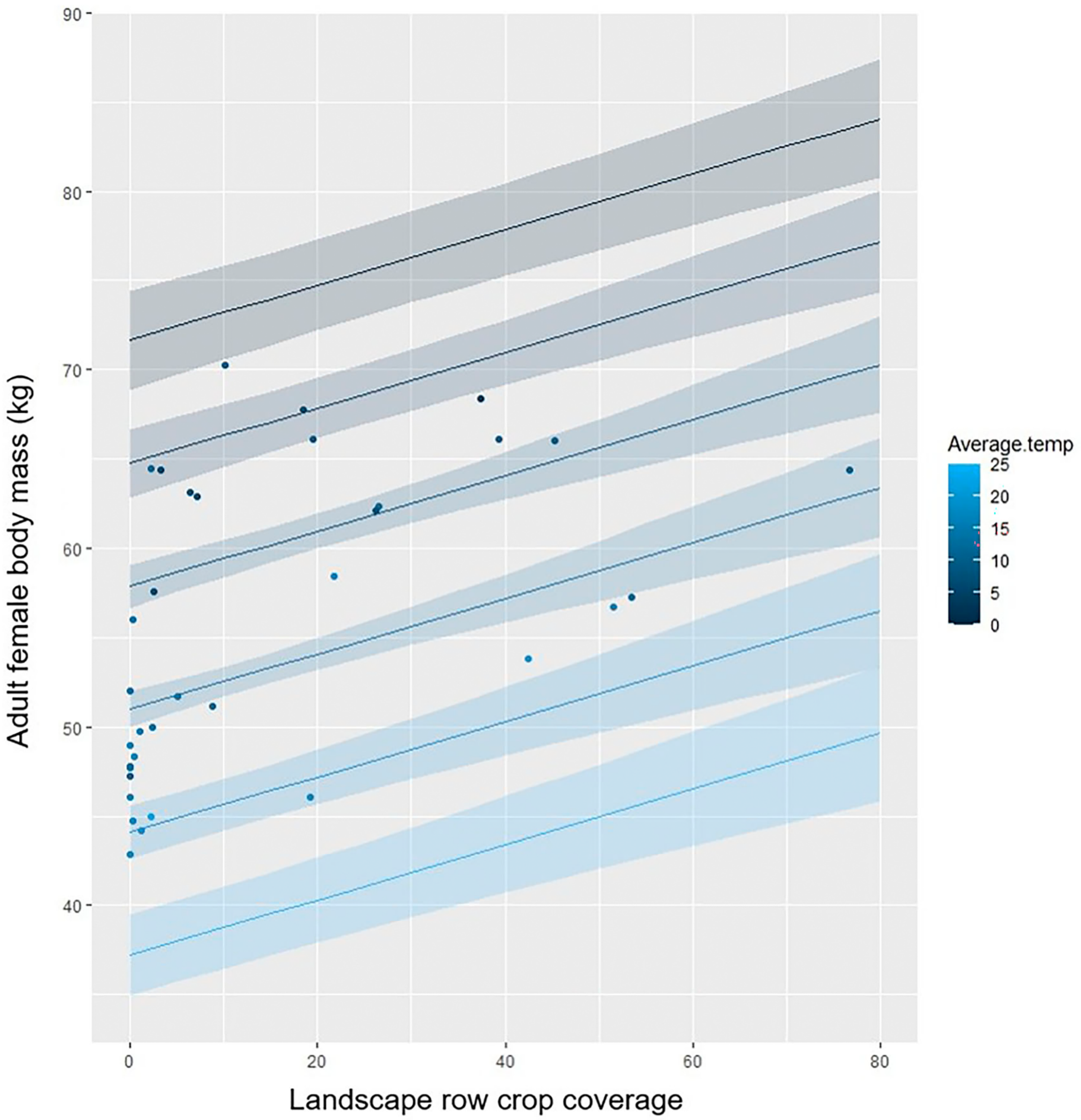

FIGURE 2 Effects plot predicting the relationship between site-specific average annual temperature (in degrees Celsius) and percent coverage of row crop within a 10-km buffer on average adult female white-tailed deer (*Odocoileus virginianus*) whole body mass. Bands represent 95% CIs around regression lines.

and P. Site-wide DE NCC averaged 51.3 ± 15.9 deer days/ha (range = 3–580.4 deer days/ha), CP NCC averaged 35.9 ± 15.9 deer days/ha (range = 0.3–580.0 deer days/ha), and P NCC averaged 9.3 ± 2.0 deer days/ha (range = 0–51.0 deer days/ha).

Deer morphology

Our dataset included body mass from 2371 adult females, with an average of 67.7 animals/site (range: 6–205 animals/site). Adult female body mass averaged 55.8 kg and site averages ranged from 42.9 to 70.3 kg. Our dataset included projected mature antler size from 861 males, with an average of 28.7 animals/site (range: 4–161). Site-wide gross antler score of mature males averaged 346.4 cm and site averages ranged from 273.1 to 436.4 cm.

Broad-scale analysis

The top model for adult female body mass included average temperature and landscape crop coverage (Table 1). For every 1°C decrease in average annual temperature, there was strong evidence that female body mass increased by 1.4 kg ($p < 0.001$; Table 2). For every 10% increase in landscape crop coverage within the 10-km buffer around each site, there was strong evidence that 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 2).

The top model for mature male gross antler score included average temperature and landscape crop coverage (Table 3). There was strong evidence that average mature antler score increased by 4.9 cm ($p = 0.001$) for every 1°C decrease in average annual temperature (Table 2). For every 10% increase in landscape crop coverage within the 10-km buffer around each site, we found moderate evidence that 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).

Fine-scale analysis

The top model for female mass at the fine scale included P NCC, region, crop group, and property size (Table 4), and a competing model included P NCC, region, and crop group. In the top model, there was moderate evidence that females were 0.15 kg heavier for every 1 deer day/ha increase in P NCC ($p = 0.024$; Table 5, Figure 4). Females were 9 kg heavier in the North ($p < 0.001$) and 4.2 kg lighter in the South ($p = 0.020$) than in the Middle region. There was strong evidence that females were 4.5 kg heavier on properties in the high (>15%) crop group ($p = 0.008$). There was weak evidence for an 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 6). 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 7). In the top model, there was strong evidence that 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 weak evidence for a positive 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 5). The model including P NCC and region explained 58.2% of the variation in male antler size.

DISCUSSION

Our results demonstrate temperature, landscape, and site-specific forage availability influence deer morphology across a broad geographic range in the eastern United States, and we found support for morphology

TABLE 3 Corrected Akaike information criterion (AIC_c) for small sample size scores predicting average antler size of mature male white-tailed deer (*Odocoileus virginianus*) at 30 sites across the eastern United States, 2021–2023.

Model	AIC_c	ΔAIC_c	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

Note: Average temp 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.

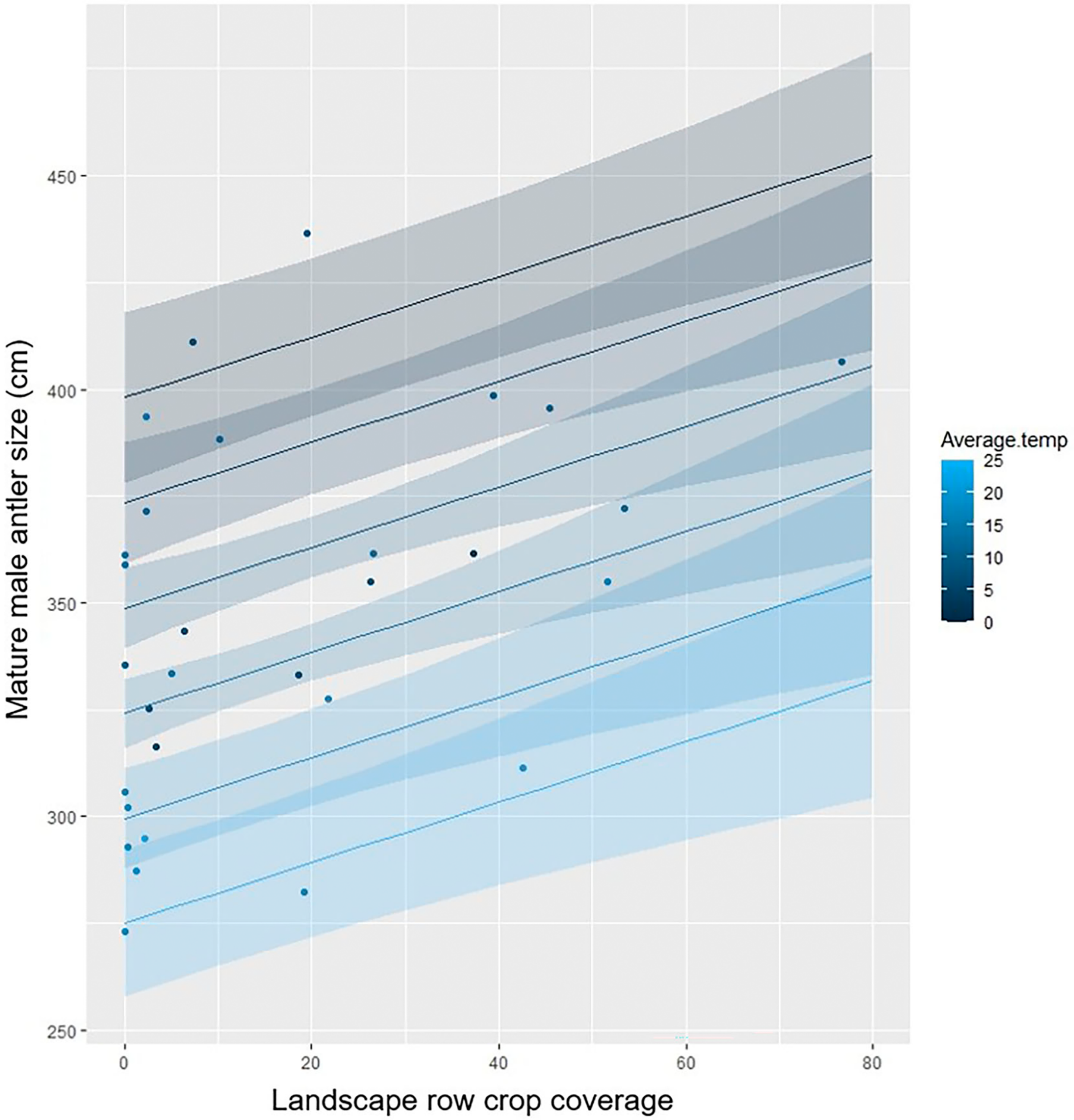

FIGURE 3 Effects plot predicting the relationship between site-specific average annual temperature (in degrees Celsius) and percent coverage of row crop within a 10-km buffer on average mature male (*Odocoileus virginianus*) antler size. Bands represent 95% CIs around regression lines.

being simultaneously modulated by heat regulation and food resources. Adult female body mass and mature male antler size both were consistently influenced by average annual temperature and landscape coverage of row crops, with larger body and antler sizes associated with cooler temperatures and greater row crop coverage. At the fine scale, P NCC had a positive influence on female body mass when we accounted for the influence of region and landscape crop coverage. P NCC had a weak, positive influence on male antler size at the fine scale when we accounted for the effect of region.

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). However, there is some disagreement about the mechanisms behind correlation between temperature

TABLE 4 Corrected Akaike information criterion (AIC_c) for small sample size scores predicting whole body mass of female white-tailed deer (*Odocoileus virginianus*) at the fine scale.

Model	AIC_c	ΔAIC_c	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

Note: Properties were grouped into three region groups (South, Middle, and North) based on latitude, and two 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} digestible energy constraint, respectively. Weight represents the likelihood of a model relative to other candidate models.

TABLE 5 Beta values (β), SE, and *p* values for covariates in top and competing models predicting whole body mass of female white-tailed deer (*Odocoileus virginianus*) at the fine scale at 35 sites across the eastern United States, 2021–2023.

Model	β	SE	*p*
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

Note: Properties were grouped into three region groups (South, Middle, and North) based on latitude, and two 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.

and size, as 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 & Takatsuki, 2015). For example, variation in red deer (*Cervus elaphus*) body size, which conformed to expected patterns based on Bergmann's rule, was interpreted to be related more to nutrition than to climate (Langvatn & 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 to climate than to forage availability (Sand et al., 1995), but their populations were exposed to colder temperatures at more northerly latitudes than most deer in the eastern United States. Ecologically and evolutionarily relevant net primary productivity may partially 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. Ecologically relevant productivity, which they contended should focus on the growing season, reaches a maximum at temperate latitudes between 30° and 50° (Huston & Wolverton, 2009), which includes our entire study area. 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. Nonetheless, we found strong correlation between temperature and morphology after considering landscape-level forage availability, so our data suggest it is likely that heat regulation (either conservation or dissipation) plays some role in observed morphology.

Effects of temperature on antler size likely relate to allometry, as we would not expect temperature to directly influence antler size. Rather, males with larger body sizes produce larger antlers (Stewart et al., 2000; Melnycky et al., 2013; Mattioli et al., 2021). We did not directly consider changes to male body size because mass loss of males through the hunting season would be difficult to account for across our sites (Strickland et al., 2017), but we would expect male body mass had a similar trend to female body mass and male antler size. The relationship between body and antler size may be nonlinear in some systems (Lemaître et al., 2014; Sontheimer et al., 2024), but our results confirm that individuals with larger body size in cooler climates produce larger antlers when factors directly influencing forage availability also are considered.

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

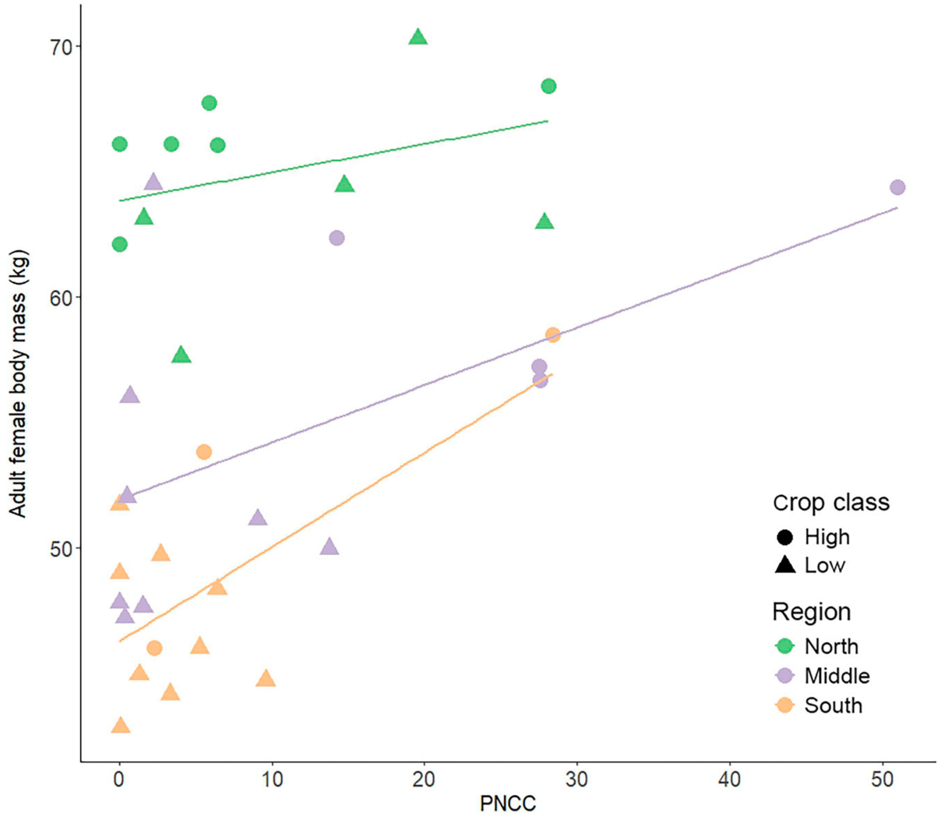

FIGURE 4 Effects plot predicting the relationship between nutritional carrying capacity using a 0.3% phosphorus constraint (P NCC) and average adult female white-tailed deer (*Odocoileus virginianus*) body mass by region and crop classification.

TABLE 6 Corrected Akaike information criterion (AIC_c) for small sample size scores predicting average antler size of mature male white-tailed deer (*Odocoileus virginianus*) at the fine scale at 30 sites across the eastern United States, 2021–2023.

Model	AIC_c	ΔAIC_c	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

Note: Properties were grouped into three region groups (South, Middle, North) based on latitude, and two 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} digestible energy constraint, respectively. Weight represents the likelihood of a model relative to other candidate models.

landscapes (Strickland & Demarais, 2008; Hefley et al., 2013; Quebedeaux et al., 2019), as crops such as soybean and alfalfa provide nutritious and selected food resources during the growing season (Harper, 2019). Forage also is more concentrated in agricultural areas, which allows deer to consume high-quality plants without expending great amounts of calories searching for forage (Emlen, 1966; MacArthur & Pianka, 1966). Greater numbers of large-antlered males across the midwestern United States are associated with interspersion of forest and cropland (Cain et al., 2019), as forest cover may be a limiting factor to deer populations in some areas with extensive crop coverage. The greatest row crop coverage in the landscape surrounding our sites was 77%, so it is unlikely forest 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. Of course, the specific crop planted may influence observed morphology. However, we did not model the specific crop present because we were primarily interested in the effects of broad land-use categories at that scale rather than fine-scale effects, which we measured at the fine scale

TABLE 7 Beta values (β), 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 fine scale at 30 sites across the eastern United States, 2021–2023.

Model	β	SE	p
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

Note: Properties were grouped into three region groups (South, Middle, North) based on latitude, and two 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} digestible energy constraint, respectively. The Middle region and high crop serve as the references which are included in the intercept calculation.

where we collected forage biomass in each cover type present. For example, several sites in the South planted cotton (*Gossypium hirsutum*) within the 10-km buffer. Cotton is not widely considered as desirable as forage for deer, yet deer readily eat cotton leaves and they are relatively nutritious (Milroy et al., 2009; Hand et al., 2024). Row crop in all regions was dominated by soybeans and corn, which were rotated and certainly served as sources of additional nutrition to deer at the landscape level. Epigenetics play a key role in the relative 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). We expected epigenetic effects would mask some effects of fine-scale forage availability, yet we still observed a positive correlation between forage availability and morphology at the fine scale.

NCC using a P constraint positively influenced morphology 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 & Sturaro, 2014), but few have related morphology with forage availability at the fine scale. Rankins et al. (2023) considered the influence of forage quantity and quality on deer morphology at four sites in South Texas but were largely unable to link morphology with high-quality forage availability. We used lactation-level NCC estimates as our forage availability covariate, which simultaneously accounts for both forage quantity and quality, and this 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 a limiting nutrient across the eastern United States (Jacobson, 1984; Lashley et al., 2015; Dykes et al., 2018; Turner et al., 2025), which our results support. Plant species composition moderates P availability more than variation in plant quality related to soil nutrients, as forbs tend to provide adequate nutrition regardless of soil quality (Harper et al., 2025). It is possible that our estimates of NCC would have improved with multiple sampling events at each site over time, as the nutritional quality of plants varies over time (McKinney et al., 2023). We attempted to minimize this effect by sampling young and old leaves of each forage separately, but multiple sampling events may have improved model fit. Deer also likely used forage located on adjacent properties that we were unable to sample that may have added noise to the model. Nonetheless, after accounting for landscape and climate covariates, our results suggest fine-scale forage availability influences deer morphology.

Fine-scale forage availability had a stronger influence on female body mass than male antler size. Body size positively influences 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. Some males harvested on a given property also may have been harvested during an excursion outside of their home range or following a home range shift during fall (Karns et al., 2011; Resop et al., 2024), and their summer home range may have had different forage availability than we measured on the study site where they were harvested. Differential dispersal rates also may be important, as more males than females in the harvest data likely were born to mothers living off the properties we sampled (Kilgo et al., 1996; Long et al., 2005; Stewart et al., 2011). Given

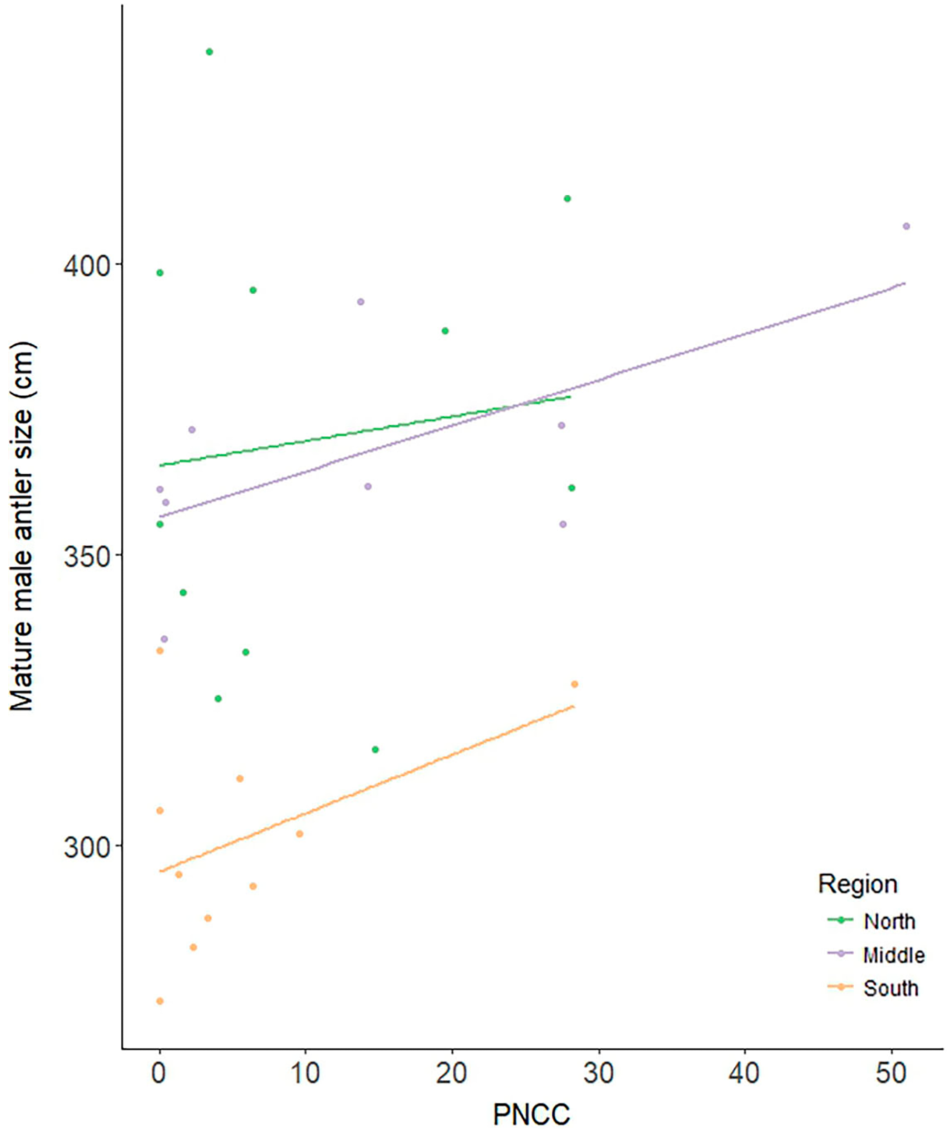

FIGURE 5 Effects plot predicting the relationship between nutritional carrying capacity using a 0.3% phosphorus constraint (P NCC) and average mature male white-tailed deer (*Odocoileus virginianus*) antler size across three geographic regions.

the influence of epigenetics on lifelong antler and body size (Monteith et al., 2009, Michel et al., 2016), greater rates of dispersal for males and the associated delay in settling into a permanent home range could increase the importance of landscape composition and delay effects of site-specific nutrition. Finally, male harvest data may less accurately reflect average population morphology than female harvest data, as harvest bias in males is common (Strickland et al., 2001; Turner, Harper, et al., 2024). For example, most of our sites had average antler sizes between 300 and 400 cm, but one site was an outlier at 436.4 cm. We chose to retain this site in our analysis because the data were accurately collected, but the sample was obviously biased toward large-antlered males as it would be unlikely to have a population with average antlers that large (Demarais & Strickland, 2017). Although many of our sites used age-based harvest restrictions, none used antler point restrictions (beyond those present in agency regulations) that would promote greater harvest bias (Strickland et al., 2001). Despite these potential limitations with male harvest data, our data indicated fine-scale P NCC influences 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 & 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 increased 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. Additionally, forage availability during other periods of the year likely contributes to morphology. We chose to focus our sampling when nutritional demands were greatest, but forage availability during the dormant season may allow deer to enter the following spring in better condition (Jackson et al., 2021). Some variation in winter forage availability would have been captured in our landscape analysis through crops (i.e., cereal grains) providing winter nutrition. Even when forage is limited during the dormant season, morphology likely is most strongly influenced by summer forage (Lesage et al., 2001). Finally, it is possible morphology varied based on environmental factors within a given year (Toïgo et al., 2006; Strickland, Demarais, et al., 2013; Strickland et al., 2020), but all our sites collected harvest data for ≥3 years. Therefore, our samples likely represented site-level averages which were suitable for our analysis without accounting for additional covariates. Future studies should consider pairing long-term harvest datasets with fine-scale vegetation data collection to evaluate various ecological hypotheses, as these data provide valuable insights into animal condition.

CONCLUSIONS

Our study found that temperature, landscape coverage of agriculture, and site-specific forage availability influenced deer morphology across the eastern United States. Deer body and antler size were negatively correlated with temperature, which could be related to heat regulation or factors associated with net primary productivity at a different scale than we measured. Landscape-level nutritional availability and site-specific measures of P NCC were correlated with larger female body and male antler size, but temperature-related gradients in size may be relatively fixed. Thus, the upper limit of deer body size may be constrained by thermoregulatory mechanisms imposed by heat conservation or dissipation, and the lower limit constrained by minimum body size needed for survival and reproduction. Within the upper and lower limits, food availability (i.e., the Resource Rule) may best explain population-level variation in deer size.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data (Turner, 2026) are available from Dryad: https://doi.org/10.5061/dryad.47d7wm3vc.

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