

Correlating male white-tailed deer antler size with female body mass across multiple spatial scales

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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.

KEYWORDS

allometric scaling, harvest data, morphometrics, *Odocoileus virginianus*, secondary sexual characteristics

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, Sergeev 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 (Strickland et al. 2017, Apollonio et al. 2020). 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). These properties were primarily privately owned, and landscape composition and

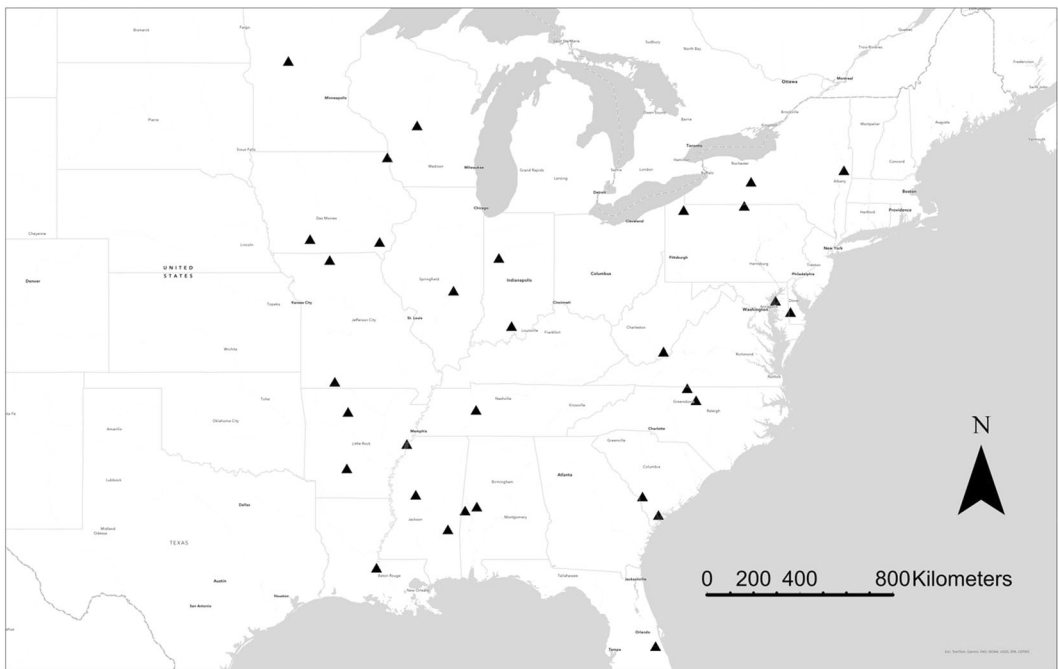


FIGURE 1 Study sites where white-tailed deer male antler size and adult female body mass were collected from harvest data, 2015–2023, to evaluate correlation between measurements of harvested deer across the eastern United States.

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 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

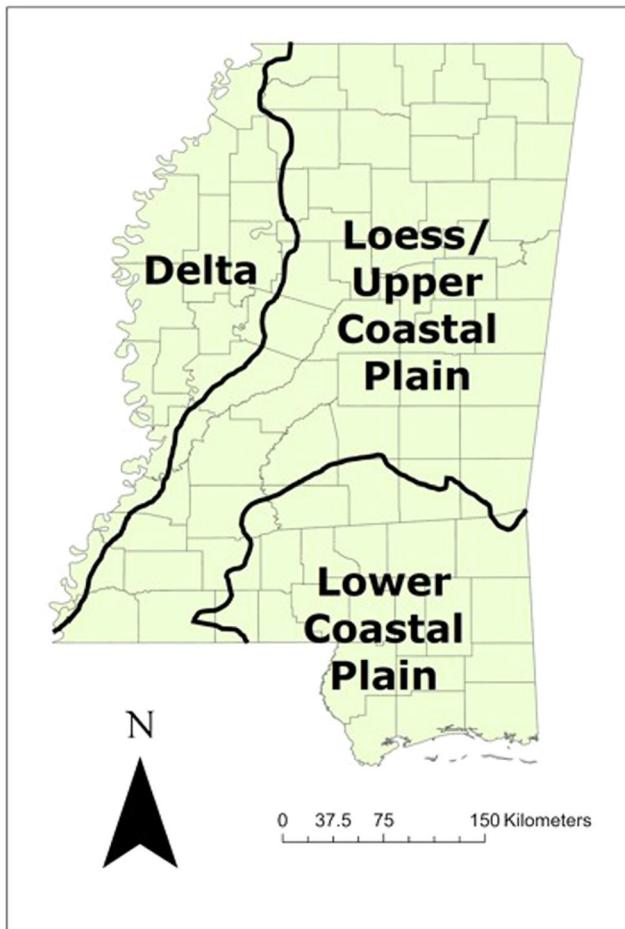


FIGURE 2 Soil resource regions in Mississippi, USA, used as covariates in a model considering the relationship between property-specific average mature white-tailed deer male antler size and adult female body mass, 1991–1994.

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 $2 \Delta AIC_c$ 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 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 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 $\alpha = 0.05$ 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 ($SE \pm 0.59$) for every 1-kg increase in adult female body mass ($P < 0.001$; Figure 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

TABLE 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 \times latitude	317.44	2.19	0.18
State dataset			
Female mass + region	1,689.47	0.00	0.78
Female mass + region + female mass \times region	1,692.33	2.85	0.19
Female mass	1,695.84	6.36	0.03

TABLE 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 \times 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 \times latitude	-0.29	0.21	0.184

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 ($SE \pm 0.59$) 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

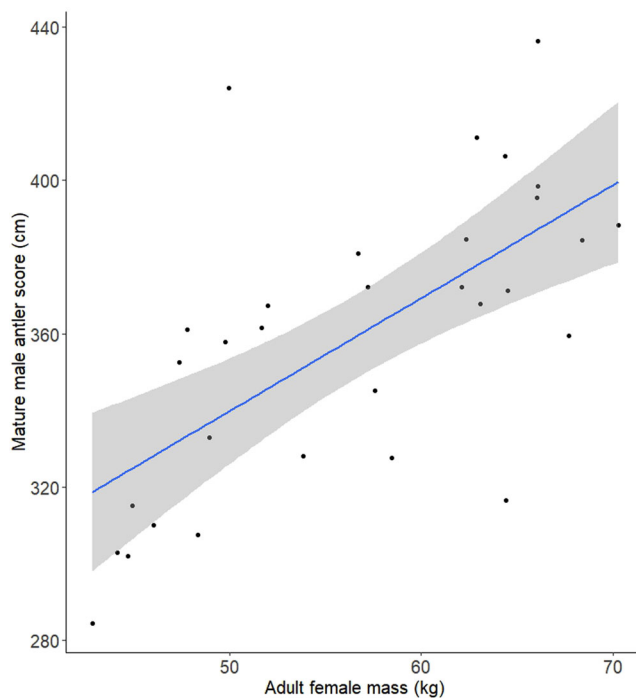


FIGURE 3 Relationship between property-specific average mature white-tailed deer male antler size and adult female body mass collected on 31 sites across 19 states in the eastern United States, 2015–2023 ($R^2 = 64.4\%$). Each point represents a property average, and the bands represent a 95% confidence interval.

Coastal Plain regions, respectively (Figure 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 Demaris 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 whether male and female morphology correlated across a variety of environmental conditions across the landscape. For example, changes in forage

TABLE 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	<i>P</i>
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 \times 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 \times LCP	1.46	2.60	0.577
Female mass \times 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

availability or quality strongly influence both antler and body size (French et al. 1956, Harmel et al. 1989). 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

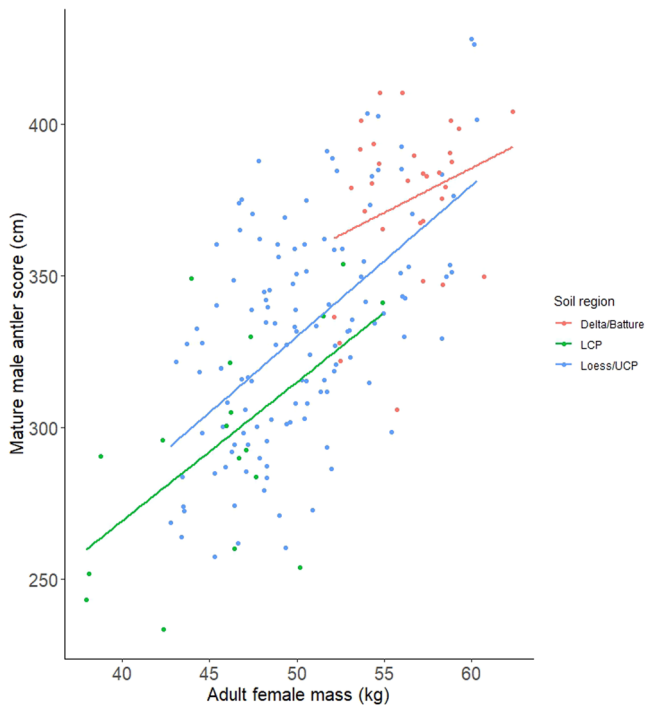


FIGURE 4 Relationship between property-specific average mature white-tailed deer male antler size and adult female body mass across 3 soil resource regions of Mississippi, USA, 1991–1994 ($R^2 = 48\%$). The red points are properties in the Delta region or inside the Mississippi River Batture (Delta/Batture), 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.

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 (Myserud 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.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

ETHICS STATEMENT

All animals were harvested legally during regulated hunting seasons and were not harvested specifically for data collection.

DATA AVAILABILITY STATEMENT

Research data are not shared.

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