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Authors: Jones, Phillip D., Strickland, Bronson K., Demarais, Stephen, Rude, Brian J., Edwards, Scott L., et al.

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Original article

Soils and forage quality as predictors of white-tailed deer *Odocoileus virginianus* morphometrics

Phillip D. Jones, Bronson K. Strickland, Stephen Demarais, Brian J. Rude, Scott L. Edwards & James P. Muir

Biologists tasked with managing cervids could benefit from models predicting physical characteristics. Differences in white-tailed deer *Odocoileus virginianus* morphometrics across soil resource areas in Mississippi, USA, provide opportunity to test the predictive capacity of soil chemical and forage quality variables. Using principal components analysis (PCA), we modeled variation in body mass and antler score of $\geq$ 1.5-year-old male deer against seven soil chemical variables and 12 forage quality variables to elucidate potential nutritional factors corresponding with physical variation among 21 deer populations. We developed separate sets of models at the levels of state and soil resource area (Delta, Thin Loess and Lower Coastal Plain) and compared statewide models with general linear models (GLM) that related deer morphometrics to nominal classification variables representing the three soil resource areas. PCA distinguished a gradient of increasing soil fertility and forage quality that explained 58% of body mass and 52% of antler score variation statewide. However, the GLM using soil resource area as the explanatory variable explained 78 and 61%, respectively, indicating that management models should use soil resource area to designate areas with broadly similar nutritional planes. Within soil resource areas, the region with the greatest soil fertility and forage quality (Delta) did not model successfully for either body mass or antler score. The Thin Loess was successfully modeled for antler score, but only the Lower Coastal Plain, which had the lowest level of soil and forage quality, was successfully modeled for both morphometric variables. The Delta may have represented an area with habitat quality sufficiently high to render small variations non-influential. In contrast, the generally poorer soil quality of Thin Loess and Lower Coastal Plain soils and forages may act as a limiting factor on physical expression, which allowed some response to relatively small fluctuations in range quality. The potential utility of soil and forage metrics within soil resource areas to estimate deer physical qualities appears to be primarily for fine-tuning estimates largely determined by factors such as density and land use.

Key words: antler size, body mass, forage quality, Odocoileus virginianus, soil fertility, white-tailed deer

Phillip D. Jones, Bronson K. Strickland & Stephen Demarais, Department of Wildlife, Fisheries, and Aquaculture, Mississippi State University, Box 9690, Mississippi State, Mississippi, USA 39762 - e-mail addresses: pjones@cfr.msstate.edu (Phillip D. Jones); bstrickland@cfr.msstate.edu (Bronson K. Strickland); sdemarais@cfr.msstate.edu (Stephen Demarais)
Brian J. Rude, Department of Animal and Dairy Science. Mississippi State University, Box 9815, Mississippi State, Mississippi, USA 39762 - e-mail: brude@ads.msstate.edu
Scott L. Edwards, Mississippi Department of Wildlife, Fisheries, and Parks, Box 9690, Mississippi State, Mississippi, USA 39762 - e-mail: sedwards@cfr.msstate.edu
James P. Muir, Texas AgriLife Research, 1229 North US Highway 281, Stephenville, Texas, USA 76401 - e-mail: jmuir@ag.tamu.edu

Corresponding author: Phillip D. Jones

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Individual physical performance has been correlated with soil and forage quality in a variety of cervids, including moose *Alces alces* (Herfindal et al. 2006), roe deer *Capreolus capreolus* (Gaillard et al. 1996, Lehoczki et al. 2010), red deer *Cervus elaphus* (Mysterud et al. 2001, Pettorelli et al. 2005) and white-tailed deer *Odocoileus virginianus* (Simard et al. 2008). Several habitat suitability models for roe deer (Radeloff et al. 1999), moose (Allen et al. 1987), elk (Roloff 1997, Roloff et al. 2001) and white-tailed deer (Short 1986, Crawford & Marchinton 1989) incorporate measures of soil fertility and forage quality. However, the utility of each variable may vary with scale (Mysterud et al. 2000, Strickland & Demarais 2006).

Management for white-tailed deer in North America is increasingly focused on producing herds with desirable age structure and physical qualities, rather than merely promoting abundance (Hamilton et al. 1995, Collier & Krementz 2006, Enck & Brown 2009). Deer exhibit measurable physical and physiological responses to habitat quality (Cheatum & Severinghaus 1950, Shea et al. 1992, Strickland & Demarais 2000, Simard et al. 2008) and expression of genetic potential is limited by access to necessary nutrition (French et al. 1956, McEwen et al. 1957, Asleson et al. 1996). Models quantifying relationships between habitat characteristics and deer physical qualities would assist managers in establishing reasonable expectations for deer response.

We examined relationships among forage quality, soil chemical variables and deer morphometrics to determine if soil and forage quality factors would contribute to models explaining body mass and antler development at both statewide and intra-regional scales. Body mass and antler development of deer in Mississippi exhibit spatial variation that has been correlated with soil characteristics at a statewide scale (Jacobson 1984, Strickland & Demarais 2000, 2006). However, previous studies did not thoroughly address the variety of potentially influential soil chemical constituents (Strickland & Demarais 2006), test within soil resource areas (Jacobson 1984), nor did they include forage variables (Jacobson 1984, Strickland & Demarais 2006), which may provide a better characterization of available nutrients than soil variables. We predicted that body mass and antler development would increase in concert with soil and forage quality, both across the broad scale of the state and within soil resource areas, thus providing a foundation for including measurements of soil and forage quality in predictive equations for deer morphometrics. Understanding the relationships of soil and forage quality with deer morphometrics may aid in developing models for cervid management at a variety of scales.

Material and method

Study area

We sampled from properties in three soil resource areas in Mississippi, USA (Pettry 1977; Fig. 1). Soils of the Delta resource area are typically alluvial soils created from flooding of the Mississippi River and its tributaries; land use is primarily row-crop agriculture. The Thin Loess resource area comprises soils developed from windblown material, generally ≤ 1.3 m thick, which becomes progressively thinner as it merges with soils of the Upper and Lower Coastal Plains. The silty soils are highly susceptible to erosion, and the loess material is often eroded to expose the underlying loamy materials. Soils in the



Figure 1. Locations of properties sampled for soils and deer forages during spring and summer 2008 in Mississippi, USA.

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Lower Coastal Plain (LCP) resource area are generally less fertile, more acidic and used mostly for timber production. To expand the potential sampling pool, we combined the Upper and Lower Thin Loess into a single region (Thin Loess) based on their similar derivation and erosion potential (Pettry 1977). The climate is subtropical, with a mean annual temperature of 18.7°C and a mean annual rainfall of 159 cm (National Oceanic and Atmospheric Administration 2008). Data from the 15 weather stations (five/region) in closest proximity to the sampling sites indicated that precipitation averaged 18.7% (SE = 2.7) below normal from January to July 2008 and that the deficit was similar among regions ($F_{2,12} = 3.16$; $P = 0.079$).

Study design

We collected deer forage plant samples on 13 public and eight private properties in the Delta, Thin Loess and Lower Coastal Plain (N = 7 in each), which we assumed represented regions of high, moderate and low soil fertility, respectively (see Fig. 1). We selected properties to provide geographically representative samples of each region. Because harvest and population management may interact with inherent site differences, we selected sites with long histories of management under the Mississippi Deer Management Assistance Program (Guynn et al. 1983). We selected eight forage species of moderate to high annual importance to deer in Mississippi (Warren & Hurst 1981) likely to be present statewide: common ragweed *Ambrosia artemisiifolia*, partridge pea *Chamaecrista fasciculata*, late boneset *Eupatorium serotinum*, Japanese honeysuckle *Lonicera japonica*, pokeweed *Phytolacca americana*, Southern dewberry *Rubus trivialis*, roundleaf greenbrier *Smilax rotundifolia* and Canada goldenrod *Solidago canadensis*. We collected spring samples between 15 April and 5 May 2008 and summer samples between 21 July and 1 August 2008. We located plant species by searching for appropriate habitats and attempted to collect ≥ 150 g wet weight of each species from each property. Samples consisted of all leaves and growing stem tips from selected plants. We sampled plants with little or no evidence of depredation or disease, and avoided sampling in areas which might have had a recent history of fertilization, such as wildlife food plots or agricultural fields. We placed samples on wet ice for transport to Mississippi State University (MSU) and then stored the samples at -16°C. We freeze-dried a representative portion of each sample and tested for condensed tannin content using a modified butanol-HCl assay (Terrill et al. 1992, Wolfe et al. 2008). We oven-dried the remaining sample portions at 60°C for 72 hours, ground dried samples in a Wiley mill to pass a 1-mm screen, then tested them for N content using the Kjeldahl procedure (Jurgens 2002) and for neutral detergent fiber and acid detergent fiber (ADF) using van Soest analysis (Goering & van Soest 1970). According to Jones et al. (2010), we calculated crude protein (CP) as 6.25× % N and adjusted CP in forage samples containing condensed tannins with the formula $\%CP_{adj} = \%CP - (0.025 \times \%CT)$. In accordance with Jurgens (2002), we calculated digestible energy (DE) as 4.618 - (0.0573 × ADF). We also assayed oven-dried samples for macro- and micro-mineral content, including P, K, Ca, Mg, S, Fe and Mn. For each property, we calculated seasonal means for CP, DE, P, K, Ca and Ca:P within and across seasons using the LSMEANS statement in SAS 9.1 (SAS Institute, Cary, North Carolina), yielding 12 forage variables for use in modeling (Table 1).

We collected soil samples congruent with plant samples. Each sample consisted of ≥ 6 cores of soil 15 cm deep taken according to instructions from the MSU Soils Laboratory (Crouse & McCarty 1998). We combined and mixed soil cores thoroughly by

Table 1. Soil and forage variables used in a principal component analysis of 21 properties in three soil resource areas of Mississippi, USA.

Description	Code
Soil variables	
Acidity	pH
Calcium (kg/ha of extractable nutrient)	Ca
Cation exchange capacity (milliequivalents/100 g)	CEC
% organic matter	OM
Phosphorus (kg/ha of extractable nutrient)	P
Potassium (kg/ha of extractable nutrient)	K
Sodium (kg/ha of extractable nutrient)	Na
Forage variables	
Spring and summer calcium content (in %)	SpCa, SuCa
Spring and summer calcium:phosphorus ratio	SpCa:P, SuCa:P
Spring and summer crude protein content (in %)	SpCP, SuCP
Spring and summer digestible energy (in kcal/g)	SpDE, SuDE
Spring and summer phosphorus content (in %)	SpP, SuP
Spring and summer potassium content (in %)	SpK, SuK

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hand to create a composite sample for each sampling site. Because species often grew intermingled, each soil sample represented the growing medium for 1-5 species. We analyzed soil samples for organic matter, cation exchange capacity, pH, % base saturation and extractable levels of P, K, Ca, Mg and Na. We averaged the results of soil samples for each property using the LSMEANS statement in SAS to yield seven sets of composite values per region.

We obtained hunter harvest data for white-tailed deer for each property from the Mississippi Department of Wildlife, Fisheries and Parks. Although hunter selectivity for larger animals may bias the results, we assumed that any bias would be similar across all regions. Our data included sex, age as delineated by tooth eruption and wear (Severinghaus 1949), eviscerated body mass (body mass) to the nearest 0.45 kg, number of antler points $\geq$ 2.54 cm, antler beam basal circumferences, antler beam lengths, inside spread of antler beams, date of harvest and the property where each animal was collected. Rather than compare multiple antler characteristics, we calculated the antler size index (analogous to Boone and Crockett score) developed to reduce antler characteristics to a single variable (Strickland & Demarais 2000). Relative deer density has the potential to strongly influence physical characteristics and is likely to vary widely through time (Keyser et al. 2006). Because relative density was unknown for each property, we sought to minimize the potential influence of density by using 13 years of harvest data (1995-2007) to calculate mean body mass and antler score for $\geq$ 1.5-year-old males on each property. Because Mississippi altered harvest regulations beginning in 1995 to require harvested males to have $\geq$ 4 antler points, we opted not to include earlier harvest data to avoid changes in hunter selectivity. We calculated a mean body mass and antler size value to represent each property after accounting for age and date of harvest as covariates for body mass and age as a covariate for antler size (Littell et al. 2006).

Data analysis

We used principal components analysis (PCA) of sites to examine relationships of soil and forage variables among sites and soil resource areas (Figs. 2 and 3) and assess their potential as explanatory variables for body mass and antler score among and within soil resource areas. We included seven soil chemical variables and 12 forage quality variables (see Table 1). We performed PCA in PCORD 5.0 (MjM Software Design, Gleneden Beach, Oregon) using a correlation coefficients cross-products matrix. We used PCA scores from the first four principle components (PC) to model deer morphometrics using soil and forage characteristics at the levels of state (all three soil resource areas) and soil resource area. We used a stepwise procedure in Proc REG in SAS 9.1 to develop models, requiring $P \leq 0.05$ for a variable to enter the model, and $P \leq 0.10$ to remain in the model during subsequent steps.

For comparison with the statewide soil-based and forage-based models, we used the GLM procedure in SAS to construct two 1-way ANOVAs with male

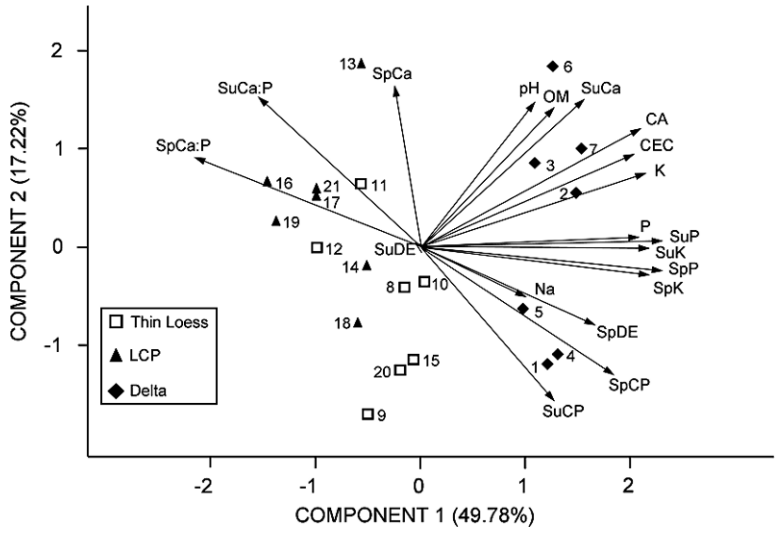


Figure 2. Axes 1 and 2 of a principal components analysis incorporating soil chemical and forage quality variables from 21 properties across three soil resource areas in Mississippi, USA, during 2008. See Table 1 for variable abbreviations. The numbers next to site symbols designate the site's rank for body mass of $\geq$ 1.5-year-old male white-tailed deer.

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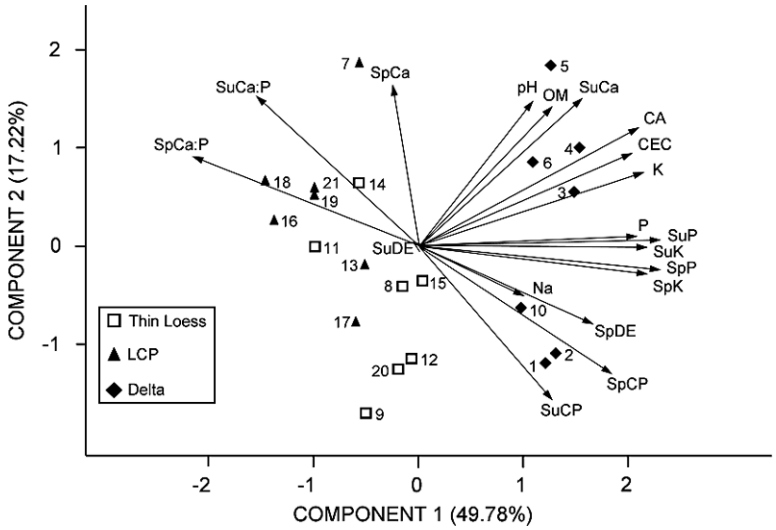


Figure 3. Axes 1 and 2 of a principal components analysis incorporating soil chemical and forage quality variables from 21 properties across three soil resource areas in Mississippi, USA during 2008. See Table 1 for variable abbreviations. The numbers next to site symbols designate the site's rank for mean antler score of $\geq$ 1.5-year-old male white-tailed deer.

eviscerated mass and antler size as response variables and soil resource area (Delta, Thin Loess and LCP) as the treatment. We then qualitatively compared the fitted GLMs to the statewide regression models (that used PCA scores as variables) using R^2 to determine which technique produced the better predictive model.

Table 2. Eigenvector loadings of soil and forage variables from a principal components analysis of 21 properties in three soil resource areas of Mississippi, USA.

	Principle component			
Factor[a]	1	2	3	4
OM	1668	-3155	1815	-1146
K	2797	-1661	2086	-715000
P	2725	-224	-674	882
CA	2724	-2656	1050	-232
PH	1411	-3256	-3703	1395
CEC	2652	-2082	3181	-1208
NA	1293	1127	5328	-3842
SPCP	2378	2833	-2654	515
SUCP	1657	3477	-522	161
SPDE	2164	1810	-2086	-2963
SUDE	-69	-131	-3845	-7156
SPP	3062	552	-798	751
SUP	2999	-127	134	1257
SPCA	-319	-3638	-785	-2421
SUCA	2021	-3328	-1341	1887
SPK	2855	578	-813	-2161
SUK	2844	13	-2335	607
SPCAP	-2810	-2039	-586	-1671
SUCAP	-2019	-3382	-1610	66

[a] See defined abbreviations in Table 1.

Results

In the PCA, the first four eigenvectors combined to explain 82.1% of the total variance. The first axis (PC1) explained 49.78% of total variance (see Figs. 2 and 3), and eigenvector loadings clearly separated Delta sites from LCP and Thin Loess sites on the basis of greater forage P, forage K, soil P, soil K, soil Ca and cation exchange capacity (Table 2). Thin Loess and LCP sites were associated with greater Ca:P ratios than Delta sites, but the Thin Loess and LCP sites did not cluster distinctly. The second axis (PC2) explained 17.22% of total variance (see Figs. 2 and 3) and was associated with reduced organic matter, soil pH, soil Ca, forage Ca and summertime Ca:P, and with greater forage CP. This axis presented greater potential for differentiating among sites within soil resource areas. PC3 comprised 7.96% of the total variance and was associated with greater soil Na and CEC, and decreasing pH, spring CP and summer DE. PC4 comprised 7.13% of the total variance and was associated with decreasing DE and soil Na. Subsequent principal components each comprised $<$ 5% of the total variance, and we did interpret them or use them in subsequent modeling.

Statewide, both body mass and antler score were successfully modeled using PCA scores from PC1 (Table 3). However, both 1-way GLMs using the nominal classification of soil resource area explained greater variation in either mean population body mass ($F_{2,18} = 31.25$, $P \leq 0.001$, $R^2 = 0.78$) or mean population antler score ($F_{2,18} = 14.17$, $P \leq$

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Table 3. Regression models relating antler score and eviscerated body mass of ≥ 1.5-year-old male white-tailed deer to principal component (PC) scores based on soil chemical or forage characteristics in three soil resource areas of Mississippi, USA.

Dependent variable	Area	Model[a]	F-value	P-value	R^2
Body mass	Statewide[b]	60.18 + 2.46PC1	26.75	≤ 0.001	0.58
	Delta	none			
	Thin Loess	none			
	LCP[c]	50.44 - 2.19PC2 + 2.01PC4	89.78	≤ 0.001	0.98
Antler score	Statewide[b]	261.15 + 8.02PC1	20.65	≤ 0.001	0.52
	Delta	none			
	Thin Loess	234.61 - 7.49PC1 + 14.52PC3	40.14	0.002	0.95
	LCP[c]	225.42 - 12.75PC2	11.97	≤ 0.001	0.71

[a] Independent variables refer to principle components presented in Table 2.
[b] Includes all three soil resources areas.
[c] Lower Coastal Plain

0.001, $R^2 = 0.61$) than their analogous statewide linear regression models using PCA score.

Modeling within soil resource areas we met with mixed success. Neither body mass nor antler score were successfully modeled in the Delta sites. Likewise, body mass was not successfully modeled in the Thin Loess, although a model with PC3 (partial $r^2 = 0.81$) and PC1 (partial $r^2 = 0.15$) as variables accounted for nearly all the variability in antler score. Body mass in the LCP was negatively associated with PC2 (partial $r^2 = 0.74$) and positively associated with PC4 (partial $r^2 = 0.24$); antler score was likewise negatively associated with PC2 ($r^2 = 0.71$).

Discussion

PC1 provided a good representation of the soil fertility gradient assumed among the three soil resource areas, with nearly all soil and forage variables loading positively. The 21 properties clustered tightly within soil resource areas along this axis, indicating relatively little intra-regional variation in soil or forage quality. The successful modeling of both body mass and antler score across this gradient was in line with a habitat suitability model proposed for roe deer (Radeloff et al. 1999), which assumed large differences in habitat quality among areas of different soil provenance. Similarly, Lehoczki et al. (2010) reported a strong effect of 10 levels of soil fertility on roe deer antler size in Hungary. However, the superior performance of the 1-way linear model indicates that the statewide models will be simpler and more accurate using nominal variables in place of soil and forage quality metrics.

Lack of variability in either dependent or independent variables could explain the inconsistent results of intra-regional modeling. However, soil and forage metrics in the Delta resource area typically had a greater range and variability than in the Thin Loess or LCP, and the range and variability of morphometrics in the Delta resource area were intermediate. The lack of modeling success in the Delta may have been due to a threshold effect. Deer in this region have markedly greater body mass and antler size than those in either the Thin Loess or LCP (Strickland & Demarais 2000), and that was reflected in our study by the rankings of properties for these variables. We believe that it is likely that superior forage quality in the Delta resource area allowed deer to meet or exceed optimum nutritional requirements for growth, thereby eliminating any discernible effect of variation in forage quality. Similarly, Pettorelli et al. (2005) reported no relationship between preferred plant occurrence and roe deer fawn survival in rich habitats, though correlation did occur in poorer habitats. The availability of agricultural crops in the Delta may also have dampened any effect of inherent site differences (Murphy & Porath 1969, Kissell et al. 2002, Strickland 2005). Thus, models specific to the Delta should be concerned with issues other than soil and forage quality. Conversely, habitat quality in the Thin Loess and LCP may be seen as limiting physical development through a generally lower nutritional plane. Thus, small changes in nutrient availability may have had greater opportunity to affect morphometrics and should be investigated further to determine which factor(s) would be of particular use in predictive models.

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In areas of limited soil fertility, forage selection by ungulates may be predominantly driven by mineral requirements, even at the cost of reducing energy or protein intake (Belovsky & Jordan 1981, Ben-Shahar & Coe 1992). The LCP model indicated that deer were larger at sites with greater Ca availability, though such sites had relatively lesser protein availability. Given the vital role of Ca in skeletal and antler growth, it is not surprising that small variations in Ca availability would have measurable effect on body mass and antler size. Although soil and forage quality were not associated with size of roe deer in Denmark (Klein & Strandgaard 1972) that study used only nitrogen as an index of forage quality. The wider array of variables used in our study may have allowed detection of a more refined response. Furthermore, Klein & Strandgaard (1972) found substantial effect of land use, while land use on our LCP sites was predominantly pine *Pinus taeda* and *P. palustris* forestry. Expanding our sampling into areas with markedly different land uses could have introduced a large source of variation that might have obscured the effect of foraging habitat.

Density has been posited as the primary driver of deer physical development (Keyser et al. 2005) with the likely exception of areas of marginal range (Osborne et al. 1992, Shea et al. 1992, Shea & Osborne 1995). However, evidence from other studies of cervids indicates that there is some interaction between density and nutritional plane. Density reportedly affected body mass of moose less in areas of greater forage quality (Hjeljord & Histøl 1999), and Herfindal et al. (2006) found that moose body mass responded more strongly to changes in forage quality in less dense populations. Moreover, roe deer have been shown to respond to greater nutritional availability with both greater population density and greater body mass (Gaillard et al. 1996, Pettorelli et al. 2001). Density is generally accepted to affect deer physical parameters through intraspecific competition for higher quality forages (McCullough 1979, Messier 1991, Jacobson 1992, Simard et al. 2008). Thus, forage availability is important in determining carrying capacity and relative density. Land use patterns may have substantial effects on deer mass and antler size through their influence on forage production (Murphy & Porath 1969, Kissell et al. 2002, Strickland 2005, Strickland & Demarais 2008). However, the effect of any given land use may differ among soil resource areas (Strickland & Demarais 2008). Also, because dominant land use may differ among soil resource areas, it is likely that influential landscape variables will be region-specific (Klein & Strandgaard 1972, Strickland 2005).

Genetics may also influence morphometric differences among soil resource areas. In 1929, the statewide deer population of Mississippi was estimated at < 500 individuals, and was confined primarily to the Delta region (Leopold 1929, Blackard 1971). Restoration efforts from 1931 to 1965 included both intrastate translocations and releasing deer from source populations as distant as Mexico and Wisconsin, USA (Blackard 1971). Examination of 17 micro-satellite loci among 16 Mississippi deer populations found substantial genetic variation; however, $\geq 93\%$ of the variation was contained within the populations, and populations were not necessarily more similar within soil resource areas (DeYoung et al. 2003). Deer may modify their life history strategies so as to adjust body size to available nutrition while maintaining consistent reproductive characteristics (Simard et al. 2008). Because ≥ 35 generations have elapsed since the reintroduction efforts began, it is possible that natural selection has favoured localized adaptations to persistent nutritional limitations. Evidence from pen-reared deer representing the same soil resource areas as our study indicates at least some genetic influence on interregional morphometric differences (S. Demarais, unpubl. data). However, there is as yet no evidence for a genetic role within soil resource regions, and thus no known reason to consider genetics as a predictive factor.

Conclusions

Soil resource areas in Mississippi were defined by similarities in climate, topography and soil parent material (Pettry 1977), and apparently represented relatively homogeneous areas of differing fertility. In developing models predicting deer morphometrics across well-defined soil resource areas, our results suggest that managers can incorporate soil resource area as a nominal variable to indicate a fairly distinct baseline nutritional plane. These region-level models may then subsequently incorporate site-specific soil and forage variables, except in areas where very high range quality renders such variables non-influential. The range of variation

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observed within these regions may be largely explained by land use and relative animal density influences on forage availability. Density (McCullough 1984, Keyser et al. 2005) and forage availability resulting from large-scale land use (Strickland & Demarais 2008) or site-specific habitat management (Jones et al. 2009, Mixon et al. 2009, Iglay et al. 2010) should be useful predictors of deer population phenotype within broad soil resource regions, with local soil and forage quality potentially fine-tuning expectations. Thus, deer population phenotype is not fixed within soil resource regions but instead demonstrates genetic growth potential amenable to deer population and habitat management.

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