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K. B. Quebedeaux

Andrew R. Little
University of Nebraska - Lincoln, alittle6@unl.edu

N. P. Nibbelink

G. J. D'Angelo

C. H. Killmaster

See next page for additional authors

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Authors
K. B. Quebedeaux, Andrew R. Little, N. P. Nibbelink, G. J. D'Angelo, C. H. Killmaster, and K. V. Miller

Variation in White-tailed Deer Antler Size: The Effects of Age, Landscape Composition, and Physiographic Province

Kathleen B. Quebedeaux, *Warnell School of Forestry and Natural Resources, University of Georgia, Athens, GA 30602*

Andrew R. Little[1]**,** *Warnell School of Forestry and Natural Resources, University of Georgia, Athens, GA 30602*

Nathan P. Nibbelink, *Warnell School of Forestry and Natural Resources, University of Georgia, Athens, GA 30602*

Gino J. D'Angelo, *Warnell School of Forestry and Natural Resources, University of Georgia, Athens, GA 30602*

Charlie H. Killmaster, *Georgia Department of Natural Resources-Wildlife Resource Division, 2065 U.S. 278 SE, Social Circle, GA 30025*

Karl V. Miller, *Warnell School of Forestry and Natural Resources, University of Georgia, Athens, GA 30602*

Abstract: Spatial variation in landscape composition can influence phenotypic expression in wildlife species and can improve management efforts to express certain phenotypic traits. We evaluated the influence of age, landscape composition, and physiographic province on white-tailed deer (*Odocoileus virginianus*) antler characteristics using data from 16,622 male deer (age range: 1.5–3.5+ years old) harvested between 1997–2016 across five physiographic provinces in Georgia. Age and physiographic province influenced antler size index (ASI; $P < 0.001$). ASI of yearling males was greatest ($\bar{x} = 53.37$; SE = 0.39) in the Upper Coastal Plain and least ($\bar{x} = 46.23$; SE = 0.51) in the Lower Coastal Plain physiographic province. Given the differences in ASI among physiographic provinces, we evaluated how landscape composition within each physiographic province influenced ASI of 7,325 yearling (1.5-year-old) males. Yearling ASI was positively related to increasing coverage of cultivated crops and suburban-urban areas (e.g., parks, small housing developments). Conversely, evergreen and deciduous forested cover consistently had a negative effect on ASI, except in the Ridge and Valley physiographic province where evergreen was positively related to ASI. Wildlife managers and hunters should recognize the effects of age, landscape composition, and physiographic province when setting antler size expectations.

Key words: age, antler size, Georgia, land cover, white-tailed deer

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Antler size is considered an important secondary sexual characteristic used to express potential fitness and genetic quality of ungulates (Ditchkoff et al. 2001, Kruuk et al. 2002, Malo et al. 2005, Vanpé et al. 2007). However, antlers are physiologically costly to produce and can be influenced by environmental conditions (Sæther and Haagenrud 1985, Ashley et al. 1998, Schmidt et al. 2001, Simard et al. 2014). For example, red deer (*Cervus elaphus*) allocate a greater amount of resources to antler development compared to body weight during favorable environmental conditions but may make tradeoffs when resources are limited (Mysterud et al. 2005). Additionally, yearling male antler size is sensitive to environmental conditions with individuals producing smaller antlers in poorer habitats (Ashley et al. 1998, Simard et al. 2014). Therefore, improving our understanding of how landscape composition influences inter-population phenotypic variation may reveal how to maximize certain phenotypic qualities (e.g., antler size and body mass).

Habitat quality and nutrition can influence phenotypic expression in ungulates (Parker et al. 2009). Nilsen et al. (2004) reported that fawn weight and litter size of roe deer (*Capreolus capreolus*) were greater in areas with increased availability of woodland land cover. Additionally, phenotypic expression (e.g., antler size and body mass) can vary across physiographic provinces, soil types, and land cover types (Severinghaus et al. 1950, Gill 1956, Strickland and Demarais 2000, Strickland and Demarais 2008, Jones et al. 2010b). In Mississippi, body mass and antler size of white-tailed deer (*Odocoileus virginianus*) was influenced by regional differences in soil quality (Strickland and Demarais 2000) and land cover characteristics (Strickland and Demarais 2008). However, a gap exists in our understanding of how these phenotypic qualities may vary in other regions within the range of white-tailed deer. Additionally, we are aware of only one other study that has incorporated data from different land ownership types and land cover types across a broad geographic area (Gill 1956).

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[1] Present address: School of Natural Resources, University of Nebraska-Lincoln, Lincoln, NE 68583

In the southeastern United States, forage resources for deer vary across cover types (Johnson et al. 1995, Ford et al. 1997, Edwards et al. 2004) and the spatial arrangement of vegetation types influences phenotypic expression (Strickland and Demarais 2008). Agricultural areas that provide high-quality food resources have a positive effect on antler size, whereas areas dominated by pine forests can negatively influence antler size (Strickland and Demarais 2008), presumably due to limited forage production and quality (Edwards et al. 2004). Acorn (*Quercus* spp.) mast production can also positively influence body and antler size in some regions (Wentworth et al. 1992, Ford et al. 1997). Additionally, increased amounts of edge habitat should positively influence antler size, as edge-dependent effects on reproductive characteristics have been observed in other cervids (McLoughlin et al. 2007, Miyashita et al. 2007).

To evaluate how animal age, landscape composition, and physiographic province influence phenotypic expression in white-tailed deer, we evaluated county-level land cover patterns nested within physiographic provinces across the state of Georgia. Our specific research objectives were to evaluate potential influences of age and physiographic province on antler size and to assess the influence of landscape composition within physiographic provinces on antler size of yearling males. We hypothesized that antler size would be positively related to increasing coverage of cultivated crops and deciduous forests as well as to increasing edge density within physiographic provinces. We also hypothesized that antler size would be negatively related to increasing coverage of evergreen forests within physiographic provinces.

Study Area

Our study area included 150 of the 159 Georgia counties. We removed data from nine counties where hunting regulations included specialized antler restrictions which could have biased our results towards larger antler sizes. Georgia spans five physiographic provinces: Ridge and Valley, Blue Ridge, Piedmont, Lower Coastal Plains, and Upper Coastal Plains (Figure 1). Ridge and Valley physiographic province is located in northwestern Georgia and contains sandstone ridges and limestone/shale valleys with elevations ranging from 180–610 m (Hodler and Schretter 1986). Soils are well-drained, highly acidic, and have a clay-enriched subsoil. Deeper soils found in this province typically support oak (*Q.* spp.)-hickory (*Carya* spp.) stands while the shallower soils, mostly on south and west aspects, support pine (*Pinus* spp.) or oak-pine forests. Valleys contain small to medium-sized farms that primarily focus on hay and pasture production with smaller areas of corn and soybean production (NRCS-Georgia Soil Survey 2017).

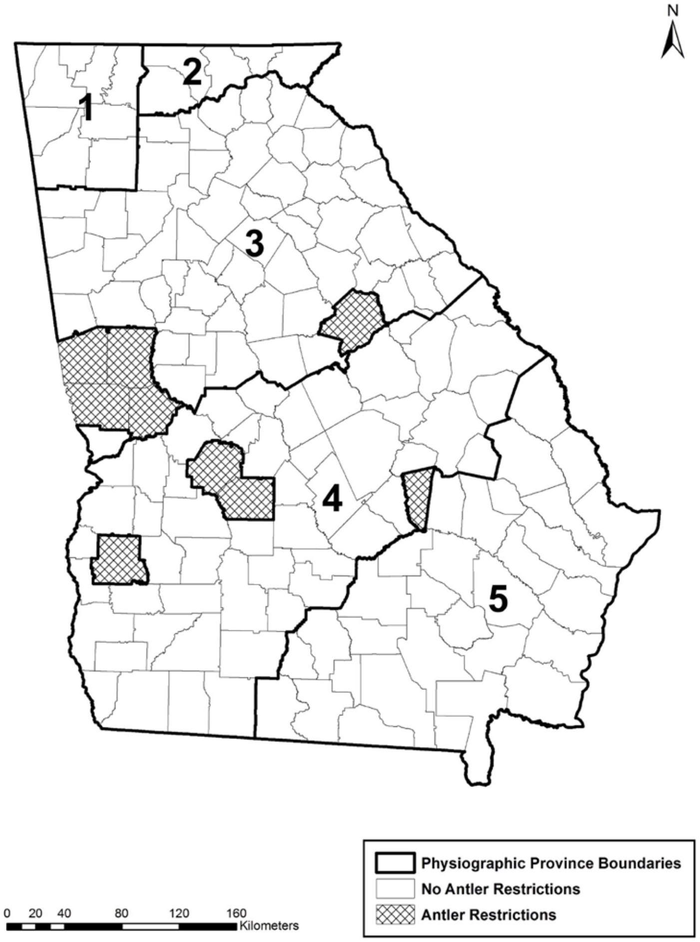

Figure 1. Counties and physiographic provinces (Ridge and Valley = 1; Blue Ridge = 2; Piedmont = 3; Upper Coastal Plain = 4; and Lower Coastal Plain = 5) in Georgia included in the study to evaluate differences in antler quality of male white-tailed deer (*Odocoileus virginianus*) harvested during 1997–2016.

Blue Ridge physiographic province is located in northeastern Georgia and is mountainous with elevations ranging from 550–1530 m (Hodler and Schretter 1986). Soils are primarily loamy with a mixture of clay, silt, and sand, and are considered acidic and well-drained. Most of the province is composed of low- to high-grade metamorphic rock with surficial deposits including colluvial material on fans and aprons along the ridges and alluvial material along the major streams (NRCS-Georgia Soil Survey 2017). This area supports a wide diversity of flora and fauna due to the highly variable topography and climatic conditions. Common tree species found in this province include: black oak (*Q. velutina*), chestnut oak (*Q. prinus*), eastern white pine (*P. strobus*), hickory, northern red oak (*Q. rubra*), scarlet oak (*Q. coccinea*), white oak (*Q. alba*), and yellow-poplar (*Liriodendron tulipifera*; NRCS-Georgia Soil Survey 2017).

Piedmont physiographic province encompasses Central Georgia including Atlanta and contains shallow to deep, generally well-drained, loamy or clayey soils. Upland areas generally support a mixture of hardwoods and pine including loblolly pine (*P. taeda*), red oak, sycamore (*Platanus occidentalis*), white oak, and yellow-poplar. Pines are commonly found on eroded sites, whereas hardwoods or mixed stands of pine and hardwoods are commonly found on slightly eroded soils and flood plains. This province contains a mixture of small farms, timberland, and suburban/urban areas and contains the highest human density in the state (GOPB 2014). Most of the Piedmont province was once cultivated but some of these areas have reverted to mixed pine-hardwood stands. In the rural areas of this province, pastures and cultivated crops including corn, cotton, soybeans, wheat, and other small grains are commonly produced (NRCS-Georgia Soil Survey 2017).

Upper Coastal Plain physiographic province is located in south-central to southwestern Georgia. Soils are generally deep and range from poor to well-drained. This province supports a mixed oak-pine forests including species such as loblolly pine, longleaf pine (*P. palustris*), shortleaf pine (*P. echinata*), slash pine (*P. elliottii*), sweetgum (*Liquidambar styraciflua*), yellow-poplar, red oak and white oak. This province also contains the greatest area in cultivated crops relative to the other provinces. Common crops produced include corn, cotton, peanuts, soybeans, and wheat (NRCS-Georgia Soil Survey 2017). Intensive timber production is also common in this physiographic province.

Lower Coastal Plain physiographic province is located in southeastern Georgia. Soils are generally deep, loamy or clayey, and are considered nutrient-poor. Soil drainage ranges from poor to well-drained. This area supports mixed oak-pine forests including species such as bald cypress (*Taxodium distichum*), loblolly and slash pine, red maple (*Acer rubrum*), swamp blackgum (*Nyssa biflora*), water tupelo (*Nyssa aquatica*), and sweetgum. Lower Coastal Plain topography is generally low, flat, and swampy where it borders the Atlantic Ocean, and grades to low rolling hills further inland. Agricultural and most other commercial activities in the Lower Coastal Plain are concentrated on higher elevations. Common crops produced in this province include corn, peanuts, soybeans, and wheat (NRCS-Georgia Soil Survey 2017). Similar to the Upper Coastal Plain, intensively-managed pine plantations are an important land cover type in this province.

Methods

We obtained deer harvest data collected at deer processing facilities by Georgia Department of Natural Resources-Wildlife Resources Division (GADNR-WRD) state biologists from 1997–2016. Biologists collected hunter name, harvest date, county of harvest, sex, estimated age (1.5, 2.5, and 3.5+ years), weight, and antler measurements (i.e., basal circumference [cm], main beam length [cm], inside spread [cm], and total number of antler points). We generated an antler score index (ASI) for each deer, based on Strickland and Demarais (2000), which included the sum of the basal circumference, main beam length, inside spread, and total number of antler points. To evaluate whether age and physiographic provinces influenced ASI, we conducted a two-way ANOVA using program R (R Core Team 2013). ASI was the response variable and age class (1.5, 2.5, and 3.5+ years) and the five physiographic provinces (Ridge and Valley, Blue Ridge, Piedmont, Lower Coastal Plains, and Upper Coastal Plains) were explanatory variables. We tested for the assumptions of a two-way ANOVA including normality, homogeneity of variance, and independence. We then evaluated the least square means for multiple comparisons using a Tukey p-value adjustment to control for the familywise error rate.

Landscape Composition and Structure

Regionally specific habitat models tend to perform better than generalized statewide models due to the variation in vegetation communities across regions (Miranda and Porter 2003). Additionally, Strickland and Demarais (2008) suggested that including populations with different spatial continuity may provide misleading results when incorporated into a statewide-only model. Therefore, we used a regionally specific approach to address whether landscape composition and structure affects yearling antler size. We chose to focus our analysis on yearling males for two reasons: 1) yearling male body morphometrics (e.g., body mass and antler size) are sensitive to environmental factors (Ashley et al. 1998, Keyser et al. 2005, Simard et al. 2014), and 2) yearling males comprised the largest sample size across all physiographic provinces. We recognize that parturition date and litter size may affect antler size (Jacobson 1995, Gray et al. 2002), but we were unable to control for these factors in our analysis.

We used the 30-m 2006 National Land Cover Database imagery (NLCD; Fry et al. 2011). We chose the 2006 NLCD because it was based on imagery collected nearest to the median of the time period from which the harvest data were collected. In addition, we compared the percent land cover by county from 2001, 2006, and 2011 NLCD imagery and found only minor differences among years; therefore, we believed using the median time period imagery from 2006 was appropriate.

Using ArcGIS 10.3.1 (Environmental Systems Research Institute Inc., Redlands, California), we reclassified the NLCD data into eight cover classes: cultivated crops, deciduous forests, developed low-medium intensity, evergreen forests, forested wetlands, mixed forests (i.e., <75% tree cover was deciduous or evergreen and interspersed throughout the landscape), non-habitat (barren land, developed high intensity, open water), and pasture/hay/herbaceous

Table 1. Descriptions of 2006 National Land Cover Database variables, Georgia, USA.

Variable Code	Description[a]
Cultivated crops	Areas used for the production of annual crops: corn, soybeans, vegetables, tobacco, and cotton, and also perennial woody crops such as orchards and vineyards.
Deciduous forest	Areas dominated by trees generally >5 meters tall and >75% of the tree species shed foliage simultaneously in response to seasonal change.
Developed low-medium intensity	Mixture of large-lot single-family housing units, parks, golf courses, and vegetation planted in developed settings for recreation, erosion control, or aesthetic purposes.
Evergreen forest	Areas dominated by trees generally >5 meters tall and >75% of the species maintain their leaves all year.
Forested wetlands	Areas where forest or shrubland vegetation >20% of vegetative cover and soil or substrate is periodically saturated with or covered with water.
Mixed forest	Areas dominated by trees generally >5 meters tall and <75% of total tree cover is deciduous or evergreen.
Non-habitat	Mixture of open water, highly developed areas (e.g., apartment complexes, row houses and commercial/industrial), and barren land (e.g., strip mines, gravel pits and other accumulations of earthen material).
Pasture/hay/herbaceous	Areas of grasses, legumes, or grass-legume mixtures planted for livestock grazing or the production of seed or hay crops.
Shrub/scrub	Areas dominated by shrubs <5 meters tall (e.g., young trees in an early successional stage).
Edge density	Meters per hectare of forest/non-forest edge

a. 2006 National Land Cover Database Legend.

Table 2. Percentage of land cover types by physiographic province using the 2006 National Land Cover Database, Georgia, USA.

	Physiographic Provinces				
Land Cover Types	Ridge and Valley	Blue Ridge	Piedmont	Upper Coastal Plain	Lower Coastal Plain
Cultivated crops	2.3	0.1	0.2	19.4	10.6
Deciduous forest	34.1	71.4	31.7	12.1	1.0
Developed low-medium intensity	12.5	6.7	16.5	6.3	6.6
Evergreen forest	13.7	8.8	20.1	23.2	24.1
Forested wetlands	0.7	0.1	3.0	14.3	31.5
Mixed forest	11.0	5.0	2.2	4.9	1.7
Non-habitat	1.5	1.5	3.6	1.3	2.0
Pasture/hay/herbaceous	19.9	5.5	20.7	14.3	13.4
Shrub/scrub	4.3	0.7	1.9	4.1	9.2
Total	100	100	100	100	100

Table 3. Explanatory variables and number of linear mixed-effects regression models evaluating the relative importance of landscape composition on antler score index of yearling, male white-tailed deer (Odocoileus virginianus) between 1997–2016 in Georgia, USA. We evaluated models within physiographic provinces using second order Akaike's Information Criterion (AICc).

Physiographic Provinces[a,b]	Variables[c,d]	Models Evaluated[e]
Ridge and Valley	DF	14
	EF	
	SS	
	NH	
Piedmont	CC	16
	EF	
	DLMI	
	FW	
	MF	
Upper Coastal Plain	CC	12
	EF	
	MF	
	SS	
Lower Coastal Plain	EF	13
	DLMI	
	MF	
	NH	

a. Physiographic provinces according to Hodler and Schretter (1986).
b. No variables were found to be important predictors of ASI in the Blue Ridge physiographic province.
c. See Table 1 for description of variables.
d. Variables: CC = cultivated crops, DF = deciduous forest, DLMI = developed low-medium intensity, EF = evergreen forest, FW = forested wetlands, MF = mixed forest, NH = non-habitat, and SS = shrub/scrub.
e. Total number of models evaluated includes null model.

(Tables 1 and 2). We also created a forest/non-forest layer (deciduous forest, evergreen forest, and mixed forest vs. all other types) for edge density calculations.

We calculated percent land cover for counties nested within each physiographic province using the Tabulate Area tool in ArcGIS 10.3.1. To calculate edge density between forested and non-forested cover types, we extracted edge pixel length using the Extract Edge Pixels tool in ArcGIS 10.3.1, which extracts the length of edge around the perimeter of each 30x30-m pixel. We used the Zonal Statistics tool in ArcGIS 10.3.1 to sum the edge in every county and calculated edge density by dividing the total length of edge (m) by total area (m^2) and converted to m/ha (McGarigal and Marks 1995). Finally, we joined each individual yearling male record by county to the percent land cover type and edge density using program R.

We implemented a two-step hierarchical variable inclusion approach in each physiographic province to reduce the number of variables in the final model selection. First, we evaluated whether ASI was related to each land cover variable by creating single variable linear mixed-effects models using package 'lme4' (Bates et al. 2015) in program R. For example, we evaluated whether a statistical relationship existed between ASI (dependent variable) and deciduous forests (independent variable) in the Ridge and Valley physiographic province. We included 'county' as a random effect in the model to account for variation in the number of deer harvested per county and percent land cover per county (Gillies et al. 2006). We removed any variable where $P \geq 0.1$, thus creating a reduced set of variables for each physiographic province. We then evaluated the variance inflation factor for all remaining variables to assess the extent of any collinearity and removed variables with variance inflations >3 (Zuur et al. 2010).

After variable reduction, we developed a set of candidate models for each physiographic province (Table 3) and implemented linear mixed-effect regression using package 'lme4' in program R.

We included 'county' as a random effect in the model to account for variation in the number of deer harvested per county and associated variation of percent land cover per county during the study period (Gillies et al. 2006). We evaluated our model set based on the information-theoretic framework (Burnham and Anderson 2002) and Akaike's information criterion (AIC) adjusted for small sample size (AICc; Burnham and Anderson 2002). All models with AICc <4.0 units from the best model were considered as candidate models. We did not model average our parameter estimates due to uncertainty in their interpretability in a mixed-effects modeling framework (Cade 2015). Therefore, we report parameter estimates for all variables in the final model set and only make inference to parameter estimates with 95% confidence intervals that excluded zero to be informative.

Results

We analyzed ASI data for 16,622 male deer harvested across 150 counties in Georgia between 1997–2016. ASIs were influenced by physiographic provinces ($P<0.001$) and age ($P<0.001$; Figure 2). ASIs of 1.5- and 2.5-year-old males were consistently

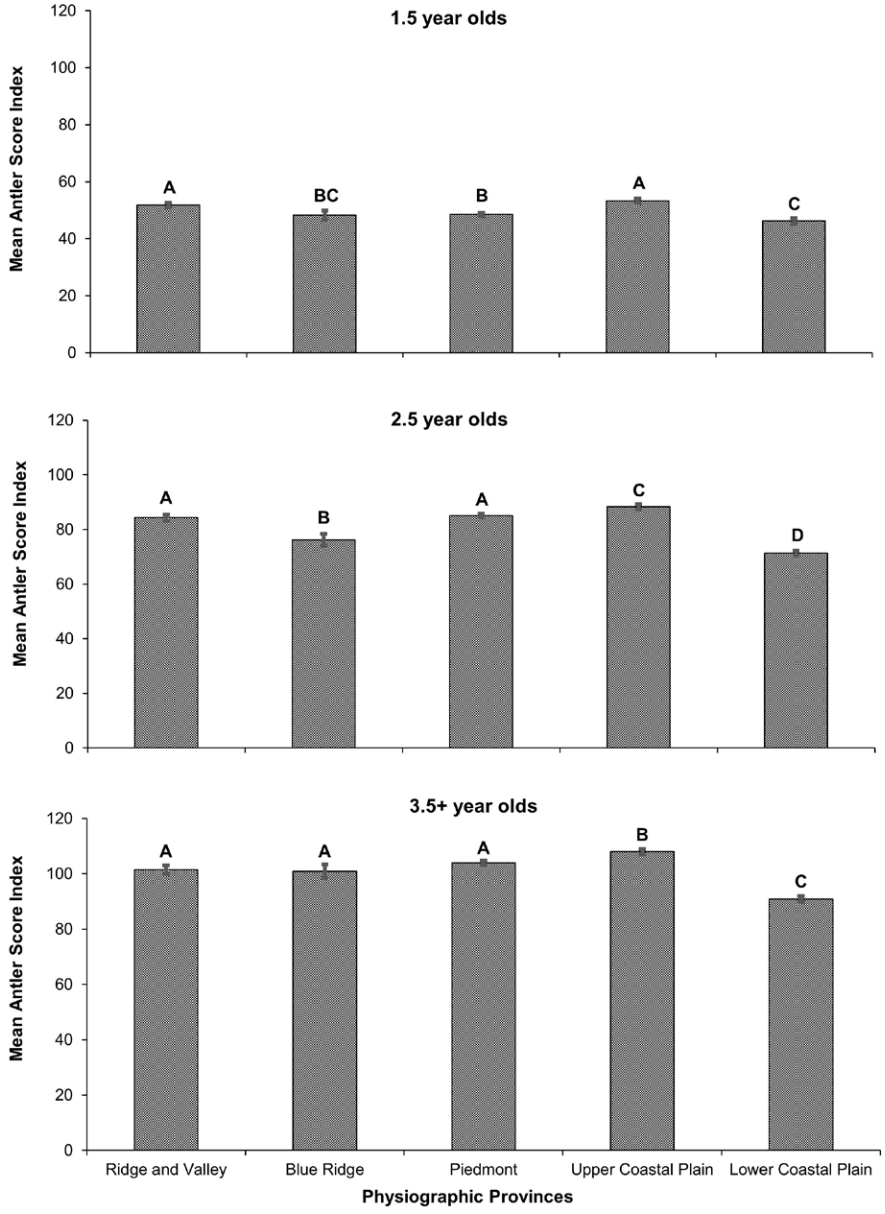

Figure 2. Least square means comparison among 1.5-year-old (A), 2.5-year-old (B), and 3.5+-year-old (C) male white-tailed deer (*Odocoileus virginianus*) harvested during 1997–2016 in different physiographic provinces, Georgia. Bars denoted by the same letter are not statistically different ($P>0.05$). We also included 95% confidence intervals for comparison among provinces.

Table 4. Linear mixed-effects regression models evaluating the relative importance of landscape composition on antler score index of yearling, male white-tailed deer (*Odocoileus virginianus*) between 1997–2016 in Georgia, USA. We evaluated models within physiographic provinces using second order Akaike's Information Criterion (AICc). Only models with ΔAICc < 4 are shown.

Physiographic Provinces[a,b]	Models[c,d]	K[e]	AICc	ΔAICc	w_i	−2LL[f]	Marginal R^2	Conditional R^2
Ridge and Valley	DF + EF	5	11349.86	0.00	0.23	−5669.91	0.029	0.041
	DF	4	11350.16	0.30	0.20	5671.06	0.026	0.040
	DF + EF + SS	6	11351.48	1.62	0.10	−5669.71	0.029	0.040
	DF + EF + NH	6	11351.56	1.71	0.10	−5669.75	0.030	0.041
	DF + NH	5	11351.65	1.79	0.09	−5670.80	0.028	0.042
	DF + SS	5	11351.87	2.01	0.08	−5670.91	0.027	0.041
	EF + NH	5	11353.08	3.22	0.05	−5671.52	0.027	0.042
	EF	4	11353.20	3.34	0.04	−5672.58	0.021	0.042
	Global (DF + EF + NH + SS)	7	11353.28	3.43	0.04	−5669.60	0.030	0.040
Piedmont	DLMI + EF + MF	6	24422.38	0.00	0.51	−12205.18	0.046	0.073
	CC + DLMI + EF + MF	7	24423.79	1.41	0.25	−12204.87	0.046	0.073
	Global (CC + DLMI + EF + FW + MF)	8	24425.24	2.86	0.12	−12204.60	0.047	0.074
Upper Coastal Plain	CC	4	13614.99	0.00	0.36	−6803.48	0.134	0.276
	CC + EF	5	13615.94	0.95	0.23	−6802.95	0.136	0.275
	CC + SS	5	13616.76	1.77	0.15	−6803.36	0.134	0.275
	CC + MF	5	13616.87	1.88	0.14	−6803.41	0.136	0.277
	CC + EF + MF	6	13617.89	2.90	0.09	−6802.92	0.137	0.276
Lower Coastal Plain	Global (DLMI + EF + MF + NH)	7	7701.46	0.00	0.75	−3843.67	0.140	0.140
	EF + MF + NH	6	7703.75	2.29	0.24	−3845.83	0.136	0.136

a. Physiographic provinces according to Hodler and Schretter (1986).
b. No variables were found to be important predictors of ASI in the Blue Ridge physiographic province.
c. See Table 1 for description of variables.
d. Variables: CC = cultivated crops, DF = deciduous forest, DLMI = developed low-medium intensity, EF = evergreen forest, FW = forested wetlands, MF = mixed forest, NH = non-habitat, and SS = shrub/scrub.
e. K parameters = variables of interest, coefficients for intercept, variances for random intercept, and error term.
f. −2LL = −2 log likelihood.

different among provinces (Figure 2A-B). Mean ASI of males in all age classes was greatest in the Upper Coastal Plain and least in the Lower Coastal Plain (Figure 2A-C). For example, mean ASI of 2.5-year-old males was 1.24 (ASI: $\bar{x} = 88$) times greater in the Upper Coastal Plain relative to the Lower Coastal Plain (ASI: $\bar{x} = 71$). However, ASIs of 3.5+-year-old males were similar for the Ridge and Valley, Blue Ridge, and Piedmont physiographic provinces with an average ASI of 102.2 (Figure 2C).

To evaluate whether landscape composition influenced ASI of yearling males, we used data from 7,325 yearling males from 147 counties (Ridge and Valley = 1,398; Blue Ridge = 375; Piedmont = 2,958; Upper Coastal Plain = 1,641; and Lower Coastal Plain = 953). We had no yearling harvest data available from three of the 150 counties. In general, parameter estimates indicated that yearling ASI increased with an increasing coverage of cultivated crops and developed low-medium intensity (Tables 4 and 5). Conversely, ASI decreased with an increasing coverage of deciduous, evergreen, and non-habitat, except in the Ridge and Valley where evergreen was positively correlated with ASI.

In the Ridge and Valley, the most parsimonious models contained deciduous and evergreen forest, non-habitat, and shrub cover (Table 4). However, deciduous and evergreen forest were the only parameters with 95% confidence intervals not including zero (Table 5). ASI was positively influenced by increasing coverage of evergreen forest, whereas ASI was negatively related to increasing coverage of deciduous forest (Table 5).

In the Blue Ridge physiographic province, no landscape variables were important for predicting ASI, thus we do not report results from those models. The suite of metrics we modeled did not affect ASI in this province and at this spatial scale.

In the Piedmont, the most parsimonious models contained cultivated crops, developed, low-medium intensity, evergreen forest, forested wetlands, and mixed forest (Table 4). However, developed, low-medium intensity, evergreen, and mixed forest were the only parameters with 95% confidence intervals not including zero (Table 5). ASI was positively influenced by increasing coverage of developed, low-medium intensity, whereas ASI was negatively related to increasing coverage of evergreen and mixed forest (Table 5).

In the Upper Coastal Plains, the most parsimonious models contained cultivated crops, evergreen forest, mixed forest, and shrub (Table 4). However, cultivated crops was the only parameter with 95% confidence intervals not including zero (Table 5). ASI was positively influenced by the increasing coverage of cultivated crops (Table 5).

Table 5. Results for linear mixed-effects regression models evaluating the relative importance of landscape composition on antler score index of yearling, male white-tailed deer (*Odocoileus virginianus*) between 1997–2016 in Georgia, USA.

Physiographic Provinces[a,b]		Model[c,d,e]	β	SE	95% CI	P
Ridge and Valley	DF + EF	Deciduous forest	−0.240	0.097	−0.451 – −0.042	0.026
		Evergreen forest	0.331	0.211	−0.107 – 0.783	0.139
	DF		−0.329	0.087	−0.520 – −0.152	0.002
	DF + EF + SS	Deciduous forest	−0.262	0.103	−0.484 – −0.053	0.021
		Evergreen forest	0.449	0.281	−0.134 – 1.062	0.135
		Shrub/scrub	−0.827	1.306	−3.723 – 1.950	0.541
	DF + EF + NH	Deciduous forest	−0.211	0.109	−0.446 – 0.010	0.071
		Evergreen forest	0.314	0.211	−0.124 – 0.764	0.158
		Non-habitat	0.489	0.871	−1.397 – 2.386	0.587
	DF + NH	Deciduous forest	−0.283	0.105	−0.512 – −0.067	0.018
		Non-habitat	0.682	0.935	−1.311 – 2.761	0.483
	DF + SS	Deciduous forest	−0.291	0.109	−0.527 – −0.067	0.018
		Shrub/scrub	0.587	1.057	−1.646 – 2.922	0.591
	EF + NH	Evergreen forest	0.493	0.210	0.052 – 0.955	0.039
		Non-habitat	1.314	0.861	−0.542 – 3.287	0.167
	EF		0.637	0.209	0.202–1.097	0.011
	Global (DF + EF + NH + SS)	Deciduous forest	−0.235	0.117	−0.487 – 0.002	0.061
		Evergreen forest	0.420	0.285	−0.173 – 1.041	0.166
		Non-habitat	0.408	0.876	−1.493 – 2.306	0.652
		Shrub/scrub	−0.720	1.310	−3.627 – 2.064	0.595
Piedmont	DLMI + EF + MF	Developed, low-medium intensity	0.150	0.043	0.066 – 0.236	<0.001
		Evergreen forest	−0.175	0.057	−0.287 – −0.055	0.004
		Mixed forest	−0.724	0.272	−1.270 – −0.173	0.012
	CC + DLMI + EF + MF	Cultivated crops	−1.085	1.398	−3.924 – 1.675	0.441
		Developed, low-medium intensity	0.153	0.043	0.068 – 0.240	<0.001
		Evergreen forest	−0.165	0.059	−0.280 – −0.042	0.007
		Mixed forest	−0.627	0.299	−1.223 – −0.014	0.044
	Global (CC + DLMI + EF + FW + MF)	Cultivated crops	−0.771	1.458	−3.717 – 2.112	0.599
		Developed, low-medium intensity	0.151	0.043	0.067 – 0.238	<0.001
		Evergreen forest	−0.150	0.062	−0.271 – −0.020	0.019
		Forested wetlands	−0.234	0.314	−0.871 – 0.388	0.460
		Mixed forest	−0.664	0.303	−1.269 – −0.046	0.035
Upper Coastal Plains	CC		0.569	0.092	0.383–0.752	<0.001
	CC + EF	Cultivated crops	0.526	0.101	0.321 – 0.726	<0.001
		Evergreen forest	−0.173	0.168	−0.511 – 0.160	0.307
	CC + SS	Cultivated crops	0.553	0.098	0.356 – 0.747	<0.001
		Shrub/scrub	−0.166	0.337	−0.843 – 0.506	0.625
	CC + MF	Cultivated crops	0.555	0.100	0.353 – 0.754	<0.001
		Mixed forest	−0.222	0.598	−1.413 – 0.980	0.712
	CC + EF + MF	Cultivated crops	0.516	0.107	0.300 – 0.728	<0.001
		Evergreen forest	−0.168	0.168	−0.508 – 0.166	0.322
		Mixed forest	−0.162	0.598	−1.350 – 1.043	0.788
Lower Coastal Plains	Global (DLMI + EF + MF + NH)	Developed, low-medium intensity	0.633	0.304	0.036 – 1.229	0.038
		Evergreen forest	−0.559	0.111	−0.777 – −0.340	<0.001
		Mixed forest	1.335	0.424	0.503 – 2.167	0.002
		Non-habitat	−0.242	0.053	−0.346 – −0.137	<0.001
	EF + MF + NH	Evergreen forest	−0.649	0.103	−0.850 – −0.448	<0.001
		Mixed forest	1.710	0.385	0.955 – 2.465	<0.001
		Non-habitat	−0.207	0.051	−0.306 – −0.108	<0.001

a. Physiographic provinces according to Hodler and Schretter (1986).

b. No variables were found to be important predictors of ASI in the Blue Ridge physiographic province.

c. See Table 1 for description of variables.

d. Variables: CC = cultivated crops, DF = deciduous forest, DLMI = developed low-medium intensity, EF = evergreen forest, FW = forested wetlands, MF = mixed forest, NH = non-habitat, and SS = shrub/scrub.

e. Null model results are not reported.

In the Lower Coastal Plains, the most parsimonious models contained developed, low-medium intensity, evergreen forest, mixed forest, and non-habitat (Table 4). ASI was positively influenced by increasing amount of developed, low-medium intensity and mixed forest, whereas ASI was negatively related to increasing amount of evergreen and non-habitat (Table 5).

Discussion

Our results indicate that antler size differs among physiographic provinces in Georgia with the Upper Coastal Plain having the greatest ASI for 2.5- and 3.5+-year-old males. Additionally, results suggest that landscape composition can influence phenotypic expression in yearling white-tailed deer populations. As reported by Strickland and Demarais (2008), we found that the variation in antler size within physiographic provinces was best explained by the composition of land cover types, and in most cases, one or two variables had the largest influence.

Among the provinces, evergreen forest cover consistently had a negative effect on ASI, except in the Ridge and Valley province were evergreen forest was positively related to ASI. In the Ridge and Valley, evergreen forest cover may have been positively related to ASI because it was a minor cover type within this province relative to other provinces and may have been a spurious finding. Within the Piedmont and Coastal Plain provinces, evergreen forests are primarily managed for fiber production. Many of these forests are monotypic plantations of loblolly or slash pine (Fox et al. 2007), and although these stands can produce high quality forage during stand establishment or following mid-rotation silvicultural treatments (Welch et al. 2004, Jones et al. 2009, Mixon et al. 2009, Jones et al. 2010a, Campbell et al. 2015), forage production is typically low (Edwards et al. 2004). Although specific silvicultural treatments such as mid-rotation thinning, prescribed fire, and selective herbicide use may increase forage abundance (Edwards et al. 2004, Jones et al. 2009, Mixon et al. 2009), relatively few pine forests are intensively-managed to optimize forage production. We found ASI to be positively related to cultivated crops, which is consistent with the findings of Strickland and Demarais (2008). Similarly, Hewson et al. (2009) reported heavier body mass of roe deer in cultivated agricultural fields compared to forested lands. Additionally, they found that nitrogen and phosphorus levels were higher in deer fecal samples in agricultural fields compared to forested lands, suggesting body mass could be linked to the availability of high-quality forage provided by the cultivated agricultural fields. Our findings suggest that the high-quality forage provided by the cultivated agricultural fields in our study benefited antler size compared to evergreen forests that are primarily managed for fiber production.

Deciduous forest cover was negatively related to ASI in the Ridge and Valley physiographic province. Although previous research has reported that acorn mast production can positively influence body and antler size of deer in areas of extensive hardwood forests (Wentworth et al. 1992, Ford et al. 1997), other cover types likely provide higher quality year-round nutrition in this province. Our results suggest that when alternate cover types are available, the amount of deciduous forest may negatively influence deer condition.

We also found developed low-medium intensity (urban and suburban areas) coverage had a positive effect on ASI in the Piedmont, which contains the highest percentage (16.5%) of this land cover type relative to other provinces. Adaptability of white-tailed deer to urban and suburban landscapes and the high-quality habitat provided in these cover types is well known (Kilpatrick and Spohr 2000, Etter et al. 2002, Grund et al. 2002, Storm et al. 2007, Kilpatrick et al. 2011). Our findings suggest yearling male ASIs likely benefit from the high-quality habitat provided in these cover types.

We expected edge density to be an important variable influencing ASI because edge density is commonly associated with an increase in game species abundance (Leopold 1933). Similar to Strickland and Demarais (2008), we did not find edge density to be an important predictor of ASI, perhaps because the non-forest category in the edge density analysis was too broad to be informative. By combining cultivated crops, developed low-medium intensity, mixed forests, non-habitat, pasture/hay/herbaceous, and shrub/scrub into the non-forest category, we may have obscured important edge classifications. Nevertheless, our models indicated that edge density itself was not related to ASI, but rather one or two variables had the greatest influence within each province on ASI.

We were unable to identify any land cover variables in the Blue Ridge physiographic province due to a lack of significant relationship between ASI with any of the land cover variables. Although the sample size of yearling males from this province was small ($n = 375$), the lack of significant relationships likely is attributable to the high proportion of forested cover types in this province.

Our models did not account for deer density and potential genetic remnants from white-tailed deer restoration. We recognize that animal density can affect the relationship between habitat quality and phenotypic expression (Pettorelli et al. 2001). Therefore, we suggest future research focus on accounting for unexplained variation by incorporating multiple data sources such as population density, genetics, and detailed stand conditions (e.g., tree age, density) into models aimed at understanding how broad-scale patterns and processes influence phenotypic expression of wildlife.

Management Implications

Our study illustrated the differences in ASI among physiographic provinces and age class of white-tailed deer. Interestingly, we observed ASI of yearling males was greatest in the Upper Coastal Plain and least in the neighboring Lower Coastal Plain physiographic province. Our study also illustrated that yearling ASI was positively related to increasing coverage of cultivated crops and suburban-urban areas (e.g., parks, small housing developments). Conversely, evergreen and deciduous forested cover consistently had a negative effect on ASI, except in the Ridge and Valley physiographic province where evergreen was positively related to ASI. Overall, our findings provide biologists and land managers with supportive evidence on how age, landscape composition, and physiographic province can affect phenotypic expression (e.g., antler size) of white-tailed deer. This information can help biologists and land managers calibrate expectations regarding the size of white-tailed deer antlers within physiographic provinces.

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