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Nutrition and ontogeny influence weapon development in a long-lived mammal

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13 Nutrition and ontogeny influence weapon allometry in a long-lived mammal

14

15 **Abstract**

16 Selection in male cervids should optimize allocation of nutritional resources to the
17 competing demands of body growth versus weapon development. We investigated
18 allocation decisions of growing and mature male white-tailed deer (*Odocoileus*
19 *virginianus* Zimmerman, 1780) from three regions of low, moderate, and high diet
20 quality. We tested (i) if deer under greater nutritional limitations would allocate
21 proportionally less to antler growth; (ii) if antler and body mass became less variable
22 with age; and (iii) if antler size consistently exhibited positive allometry with body
23 mass across age classes and nutritional planes. Greater nutrition increased antler
24 allocation in 2.5- to 4.5-year-olds, but not in yearlings or prime-aged males.
25 Variability of antler mass decreased with age and was generally less in more fertile
26 regions, but body mass was equally variable across all ages and regions. Antler mass
27 was positively allometric with body mass for all combinations of age class and region,
28 but exhibited age- and region-related differences. Our results suggest that accruing
29 body mass is more important to lifetime reproductive success than increasing weapon
30 size. Reduced allometric coefficients in older males likely stems from increasing use
31 of skeletal mineral reserves, selective pressures favoring greater body mass, and
32 possible selection for optimal weapon strength and structure.

33

34 **Keywords:** allometry, antlers, body mass, energy allocation, nutritional plane,
35 *Odocoileus virginianus*, ontogeny, white-tailed deer

36 Introduction

37 Under conditions of nutritional limitation, life history theory predicts that animals will
38 allocate nutritional resources to characteristics more likely to improve lifetime
39 reproductive success (Stearns 1992). Secondary male sex characteristics such as
40 greater body mass, ornamentation, and weaponry may contribute to mating success
41 (Deutsch et al. 1990; Hooper et al. 1999; Keyser and Hill 1999), and often develop
42 under sexual selection (Andersson 1994). Condition-dependent expression is reported
43 for sexually-selected characteristics across the spectrum of animal life forms (e.g.,
44 male horned [*Onthophagus acuminatus* Harold, 1880; Emlen 1997] and dung beetles
45 [*O. taurus* Schreber, 1759; House and Simmons 2007], sticklebacks [*Gasterosteus*
46 *spp.* Linnaeus, 1758; Boughmann 2007], wild red grouse [*Lagopus lagopus scotica*
47 Latham, 1787; Vergara et al. 2012], and amphipods [Cothran and Jeyasingh 2010]).
48 Most examinations of relationships between ontogeny and weapon allometry are
49 limited to species with a single adult age class; studies of this relationship in long-
50 lived species with continued adult development are lacking.

51 In cervids, male-male combat is the selective force sculpting the morphology of
52 males to maximize dominance and mating opportunities (Clutton-Brock 1982; Goss
53 1983). Both body mass (Clutton-Brock et al. 1982; McElligott et al. 2001; Jones et al.
54 2011) and antler mass (Severinghaus and Cheatum 1956; Hirth 1977; Kruuk et al.
55 2002) may be factors in determining mating access. However, because antler and
56 body mass are highly correlated (Anderson and Medin 1969; Van Ballenberghe and
57 Miquelle 1993; Demarais and Strickland 2011), determining which is more important
58 to reproductive success is difficult (Newbolt et al. 2017).

59 Nutritional requirements for antler growth add substantially to those for body
60 growth in cervids (Verme and Ullrey 1984; Asleson et al. 1996; Moen and Pastor

1998). Relative allocation of nutritional resources should provide evidence of the comparative importance of these characteristics to lifetime reproductive success. Body growth appears to be favored generally over horn or antler growth under nutritionally restricted conditions in bighorn rams (*Ovis canadensis* Shaw, 1804; Festa-Bianchet et al. 2004) and red deer (*Cervus elaphus* Linnaeus, 1758; Myrsterud et al. 2005), which is particularly to be expected when body reserves are important to survival (Festa-Bianchet et al. 1997; Cook et al. 2004). Diet quality may contribute to allometry plasticity, causing differences in static allometries among subjects in disparate nutritional environments (Emlen 1997). Males in areas with better nutrition should be able to consistently divert a greater proportion of nutritional resources into features of lesser importance to reproductive success. Thus, if antlers are less important than body mass, we would expect antler size to increase relative to body size as nutritional environment improves.

Ontogeny also should influence resource allocation. Fully grown males need only consider body maintenance as a competitor with antler growth, while immature males face the demands of body growth. Consequently, cervids often maximize both absolute and relative antler mass after peak body size is attained (Clutton-Brock et al. 1982; Stewart et al. 2000; Bender et al. 2003; Ungerfield et al. 2011; Gómez et al. 2012). Furthermore, cervids divert skeletal minerals to support antler growth (Banks et al. 1968; Hillman et al. 1973; Baxter et al. 1999), and males at or near maximum body size may divert greater skeletal resources to antler growth than younger males.

Immature animals are often more sensitive to environmental variation than adults (Sauer and Boyce 1983; Swihart et al. 1998; Gaillard et al. 2000; Strickland et al. 2008), and younger male cervids exhibit greater morphological response to nutritional variability than older males (Suttie and Kay 1982; Leberg and Smith 1993; Solberg and Sæther 1994). Body mass and antler characteristics may exhibit strong responses

87 to fluctuations in density or weather that affect nutritional plane (Solberg and Sæther
88 1994; Schmidt et al. 2001; Keyser et al. 2006). Greater consistency of allocation to
89 one character may indicate higher priority and thus greater fitness value.

90 Antlers are important as honest signals of male quality (Ditchkoff et al. 2001; Malo
91 et al. 2005; Vanpé et al. 2007), and as both weapons and defensive structures (Lincoln
92 1972; Goss 1983). As sexually selected characteristics, antlers face pressure to
93 maximize expression, but development is limited by opposing pressures promoting
94 survival, physiological limitations (Landete-Castillejos et al. 2012b; Ceacero 2016),
95 and species-specific breeding behaviors (Plard et al. 2011). Comparisons of
96 antler:body ratios across Cervidae (i.e., evolutionary allometry) indicate constraints
97 on allometric relationships with increasing size (Lemaître et al. 2014; Ceacero 2016).
98 Given a broad enough set of environmental circumstances, we might expect to
99 discover a similar pattern within a single species. However, intraspecific
100 investigations of this relationship are apparently rare; the single study we found
101 combined 2- to 5-year-old male reindeer (*Rangifer tarandus* Linnaeus, 1758) into a
102 single age class (Melnicky et al. 2013), thus potentially obscuring age-related
103 differences that might emerge from an analysis of separate age classes.

104 The mating system of white-tailed deer (*Odocoileus virginianus* Zimmerman,
105 1780; hereafter, deer) is polygynous and weakly polyandrous (Sorin 2004; DeYoung
106 et al. 2002, 2006), with males forming temporary tending bonds with individual
107 estrous females (Hirth 1977), and females providing all parental care. Males should
108 therefore maximize fitness by maximizing lifetime mating opportunities. We tested
109 predictions regarding relative resource allocation to antler and body mass, including
110 potential interactions between age and resource quality, using harvest data from three
111 soil resource areas with differing nutritional planes. We based our expectations on the
112 assumption that body mass would receive higher priority in nutritional allocation,

113 predicting that 1) males under greater nutritional limitations would allocate
114 proportionally less to antler growth; 2) males in areas with superior nutrition would
115 show less variation in antler mass compared to males in areas of poorer, less
116 consistent nutrition; and 3) older males would exhibit lesser variation in antler mass
117 than younger males. We also examined age- and region-specific allometric
118 relationships to identify possible effects of ontogeny and nutritional plane. Although
119 male deer are physiologically mature as yearlings, mating strategies change with
120 maturity (Sorin 2004; Holtfreter 2008; Jones et al. 2011); we thus expected 4) to find
121 ontogenetic changes in scaling. Lastly, we expected 5) to see allometry plasticity
122 related to nutritional plane among conspecifics at the same stage of growth (Moczek
123 2002; Shingleton et al. 2008).

124 **Materials and methods**

125 **Study area**

126 Mississippi, USA comprises 11 soil resource regions differing in soil origin and
127 fertility level (Pettry 1977). We sampled harvest records from the Mississippi
128 Alluvial Valley (MAV; 20,200 km²), the Thin Loess (combined Upper and Lower;
129 18,600 km²), and the Lower Coastal Plain (LCP; 17,700 km², Fig. 1) to represent
130 areas of high, moderate, and low fertility, respectively. MAV soils are typically
131 alluvial in origin, highly fertile, and devoted primarily to row-crop agriculture. Thin
132 Loess soils developed from windblown silt generally ≤ 1.3 m overlying loamy coastal
133 plain material; primary land uses are forestry, row-crop agriculture, and pasture. Soils
134 in the LCP are generally less fertile, more sandy and acidic, and used for pine (*Pinus*
135 spp.) forest production. Pine production typically creates a boom-bust cycle of forage
136 availability, with much greater quantity and quality available during brief periods with
137 open-canopy conditions (Jones et al. 2009; Iglay et al. 2010). Nutritional values of

forages in the Thin Loess are less than the MAV, but greater than in the LCP (Jones et al. 2008, 2010). Male deer from these regions exhibit substantial differences in body and antler mass across all age classes (Strickland and Demarais 2000). The climate was subtropical, with a mean annual temperature of 18.7°C and mean annual rainfall of 159 cm (National Oceanic and Atmospheric Administration 2015).

Sample collection and data preparation

We analyzed records of hunter-harvested male deer from the MAV ($n = 33,033$), Thin Loess ($n = 21,722$), and LCP ($n = 9,325$). Data were collected by Mississippi Department of Wildlife, Fisheries and Parks (MDWFP) personnel at wildlife management areas and by hunting clubs participating in the MDWFP Deer Management Assistance Program (Guynn et al. 1983) from 1991 – 2007. Records included sex, age (as delineated by tooth replacement and wear; Severinghaus 1949), eviscerated body mass (nearest 0.4 kg), number of antler points ≥ 2.54 cm, antler beam basal circumferences, antler beam lengths, maximum inside spread of antler beams, and the soil region in which each animal was harvested. For analysis we included classifications of 1.5- (i.e., yearling), 2.5-, 3.5-, 4.5-, and 5.5- to 7.5-year-olds (i.e., prime-aged).

Data analysis

To estimate antler mass, we developed predictive models using 566 sets of antlers from 1.5- to 5.5-year-old captive males housed at the Mississippi State University Rusty Dawkins Memorial Deer Unit in Starkville, Mississippi, USA during 2006 – 2012. Previous work reported that the best measurements for predicting antler volume differed between smaller (1 or 2 points) and larger (≥ 3 points) (Rogers and Baker 1965). Antlers are 3-dimensional, and estimates of mass might be improved by using a more direct indicator of antler volume (Strickland et al. 2013). We therefore created a 3-dimensional explanatory variable by multiplying basal circumference by

164 main beam length (CIRCBEAM). The best model for predicting mass of smaller
165 antlers ($R^2 = 0.90$) included both CIRCBEAM and its square-root transformation; the
166 best model for larger antlers ($R^2 = 0.89$) used only CIRCBEAM.

167 Throughout our analysis, we used eviscerated body mass to avoid unnecessary
168 variation from inconstant rumen fill (Mysterud et al. 2008; Weckerly 2010). We
169 adjusted body mass for the effect of harvest date using region- and age class-specific
170 models to estimate harvest date-corrected mass (HDCM; Strickland et al. 2017). We
171 developed the ratio antler mass:body mass by dividing predicted antler mass (g) by
172 HDCM (kg). We compared antler mass:body mass among soil regions and age
173 classes using the MIXED procedure in SAS 9.2 (SAS Institute, Cary, North Carolina,
174 USA) to build a general linear model. Because we hypothesized that variability of
175 antler allocation would vary by age and region, we included the GROUP effect to
176 compensate for heterogeneity of variance. If the restricted maximum likelihood
177 (REML) model failed to converge, we used the MIVQUE0 specification to perform
178 minimum variance quadratic unbiased estimation of the covariance parameters. Next,
179 we output the covariance parameters (residual, age $\times$ region) from our MIVQUE0
180 model to serve as starting points for a final REML model to generate least-squares
181 predicted means and variance estimates. We used the SLICE option to test post-hoc
182 comparisons. We considered differences significant if $P \leq 0.05$.

183 For allometric analysis, we used a complete analysis of covariance, with estimated
184 antler mass as the dependent variable, soil region and age class as categorical
185 variables, and HDCM as the covariate. Both antler and body mass data were log
186 transformed. The interaction terms between age class, soil region, and HDCM tested
187 whether slopes differed among models for these variable combinations. If the
188 interaction term was significant, indicating different slopes, we next examined
189 interactions between age class and HDCM and between soil region and HDCM.

Significant interactions would indicate the appropriateness of calculating separate allometric coefficients for each age class $\times$ soil region combination. We calculated allometric coefficients (i.e., slopes of reduced major axis regression models) as $\frac{sdY}{sdX}$ to account for possible measurement error in both antler mass and HDCM, again using log-transformed data (Warton et al. 2006). Because we compared two mass variables, a slope of 1 would indicate isometry, whereas slopes > 1 or slopes < 1 would indicate positive and negative allometry, respectively. We calculated bootstrapped 95% confidence intervals using 2000 replicates with N randomly selected points for each replicate in PAST 2.17 (Hammer et al. 2001).

Results

Age and soil region interacted to influence antler:body mass ratios. Ratios increased as age class increased in all regions ($P \leq 0.001$); relative antler mass for prime-aged males averaged 4.2 times greater than for yearlings (Fig. 2). Across soil regions, allocation was similar among yearlings ($\bar{x} = 3.45 \text{ g kg}^{-1}$; $P = 0.497$) and among prime-aged males ($\bar{x} = 14.59 \text{ g kg}^{-1}$; $P = 0.931$), but otherwise was greater in areas of greater soil quality ($P \leq 0.001$), in partial accordance with our first prediction. At 2.5 years, relative antler mass of MAV deer increased to 17% greater than Thin Loess deer and 22% greater than LCP deer. Among 3.5-year-olds, the difference between MAV and Thin Loess deer fell to 13%, but between the MAV and LCP it remained at 22%. At 4.5 years, differences with the MAV were reduced to 6% in the Thin Loess and 10% in the LCP.

Variability in antler mass as indicated by CV was lower in regions with greater nutritional plane for all age classes except yearlings, and generally decreased with increasing age, in accordance with predictions 2 and 3 (Fig. 3). In contrast, body mass variability was consistent across regions and age classes, averaging 12.5% CV

(Fig. 3). The ANCOVA indicated significance for all fixed effects and interactions ($P \leq 0.001$), justifying calculation of separate allometric coefficients for each combination of age class $\times$ soil region. Antler mass was positively allometric with body mass across all age classes and regions, with all confidence limits >1 (Table 1). Coefficient values exhibited an ontogenetic effect, tending to decrease with increasing age class until 4.5 years. The decrease was most apparent in the MAV, where the coefficient was reduced by nearly half between yearlings and 4+-year-olds. Confidence intervals of coefficients overlapped for all age classes between the Loess and LCP, and also for yearlings and 2.5-year-olds within both regions. Greater nutritional plane was associated with greater allometric coefficient in yearlings, but lesser coefficients for ≥ 3.5 -year-olds.

Discussion

In our study, growing males under more restricted nutrition exhibited lesser relative antler mass than their counterparts in more fertile regions. This situation suggests a greater role for body mass than antler size in lifetime reproductive success, whether by improving survival or by increasing available energy for breeding season activities. Mating opportunities for male white-tailed deer are more evenly distributed among age classes than is often assumed, especially in comparison with lekking or harem-defending cervids (DeYoung et al. 2009; Acker 2013; Turner et al. 2016). Although the searching and tending strategy of older males requires a large investment of body reserves (Johns et al. 1982, Strickland et al. 2017), yearling males may obtain matings using low-energy, non-confrontational strategies (Sorin 2004; Holtfreter 2008; Jones et al. 2011). This situation roughly corresponds to that of arthropod species with weapon or body size dimorphism that also exhibit morph-specific mating strategies

240 (Moczek and Emlen 2000; Karino et al. 2004; Zatz et al. 2011). However, whereas
241 adult arthropod body size is often fixed, deer continue to grow and to develop new
242 weapons across many mating seasons. Early diversion of energy into body
243 development thus prepares yearling males for the greater energy demands of mature
244 breeding strategies. Age-related increases in antler mass:body mass accompany a
245 shift towards mature breeding behavior (Foley et al. 2015), when the greater potential
246 for combat requires a more robust weapon.

247 Antlers act as an avenue through which genetic quality is honestly translated to
248 potential mates and rivals alike (Ditchkoff et al. 2001; Malo et al. 2005; Hoem et al.
249 2007; Vanpé et al. 2007; Ciuti and Apollonio 2011). Sexual selection pushes antler
250 size toward increasing expression, but optimal resource allocation must balance
251 advertising effectiveness, utility of antlers in combat, and physical condition of the
252 animal. Although weapon size is widely correlated with resource holding potential
253 (e.g., Barki et al. 1997; Pomfret and Knell 2005; Yoshino et al. 2011), the value of
254 relative antler size to mating success varies within Cervidae, influenced largely by
255 mating group size and mating strategy (Plard et al. 2011). Greater body mass is often
256 related to dominance ranking (Townsend and Bailey 1981; Veiberg et al. 2004;
257 Pelletier and Festa-Bianchet 2006; Taillon and Côté 2006), which in turn may
258 determine mating success (Clutton-Brock et al. 1979; McElligott et al. 2001). Male
259 deer with greater body mass can expend greater effort on reproductive activities and
260 possibly extend their period of dominance, especially in populations with relatively
261 long mating seasons, which are common in the southern US (Miller et al. 2003;
262 Mainguy and Côté 2008; Vanpé et al. 2009; Diefenbach and Shea 2011; Jones et al.
263 2011). Given the energy demands of rut, older male deer may experience increasing
264 marginal fitness gains from investment in body mass, reducing the relative value of
265 antler size. Additionally, antler strength and resistance to breakage varies by

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266 component (e.g., tines versus main beams) and beam length (Currey et al. 2009; Karns
267 and Ditchkoff 2012; Ceacero 2016); antler development may thus be constrained by
268 selection for an optimal size or structure determined by the physics of combat.

269 Two recently proposed hypotheses (the Shared Pathway Hypothesis and the
270 Resource Tradeoff Hypothesis; Hill 2011) address condition-dependent traits such as
271 antler size as evidence of the functionality of vital body systems. The Resource
272 Tradeoff Hypothesis presents allocation decisions as either/or decisions among
273 options with similar material requirements, such as antler versus skeleton growth.
274 Deer antlers contain about 22% - 24% calcium and 11% - 12% phosphorus
275 (McDonald et al. 2005; Miller et al. 1985), the investment of which poses a permanent
276 loss of these elements to the body (Muir et al. 1987). The Resource Tradeoff
277 Hypothesis could interpret lower relative antler mass in younger, growing males as
278 evidence that skeletal development receives priority over antler growth. However,
279 because both young and mature males divert skeletal resources into antler growth
280 (Cowan et al. 1968; Stephenson and Brown 1984), the ability to process or translocate
281 minerals may be more important than absolute mineral availability. The Shared
282 Pathway Hypothesis describes a situation where vital body systems share
283 physiological mechanisms with ornament production; greater ornamentation thus
284 demonstrates superior function of the shared production pathway (Hill 2011). Given
285 the necessity for calcium and especially phosphorus in nearly all aspects of animal
286 metabolism (Robbins 1993), both body and antler size may serve as honest signals
287 through demonstration of metabolic state.

288 Hunter selectivity for either larger body mass or greater antler size could introduce
289 bias into our analysis (Solberg et al. 2000; Mysterud et al. 2006). The little research
290 exploring selectivity among white-tailed deer hunters indicates that selection for body
291 mass is low during 1-day public hunts (~6%; Coe et al. 1980), but selectivity may be
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greater on properties where time is less limiting or hunter density is lower (Diekert et al. 2016). Separation of adult males (≥ 2.5 years) during the rut (Ivey and Causey 1988; Nixon et al. 1991) likely reduces opportunities for selective harvest. Generous bag limits during the period of our study (3 to 5 males/season) also likely reduced selectivity, as hunters could harvest less desirable males without forgoing a later opportunity to harvest a superior animal. We expect hunter selectivity and pressure to vary considerably across the 1003 public ($\sim 30\%$ of total acreage) and private ($\sim 70\%$) properties sampled. Given our large sample sizes and the diversity of management goals, hunting methods, and levels of competition represented, we believe hunter selection should have little influence on these models.

Investment in antlers relative to body mass by prime-aged males in this study was similar regardless of nutritional plane, indicating that increased availability of skeletal minerals eventually overcame differences in dietary mineral availability. Simultaneously, by reducing variability in mineral availability among individuals, skeletal depletion could be the primary driver of reduced allometric coefficients in older males. Because skeletal resources can provide such a large share of minerals invested in antler growth, antler mass is perhaps constrained more by skeleton size than by body mass *per se* (Landete-Castillejos et al. 2012a; Ceacero 2016). Thus, continuation of mass growth (≥ 5.5 years - Strickland and Demarais 2000; Gee et al. 2014) after skeletal growth is completed (3.5 years - Ozoga and Verme 1982; Flinn et al. 2013) may further depress allometric coefficient.

Expression of sexual ornaments may be more important in poorer environments where the ability to produce them is constrained, and is thereby more indicative of individual genetic quality (David et al. 2000; Cotton et al. 2004). The superior nutritional plane of the MAV enabled males to more nearly maximize both antler growth and body mass (Robinette et al. 1973; Ozoga and Verme 1982; Monteith et al.

2009; Michel et al. 2016), explaining the lower variability associated with antler size in the MAV relative to the other regions. Attempts to correlate antler growth and body mass with either soil or forage quality within the MAV have proven unsuccessful (Jones et al. 2010), which we would expect if high quality forages were widely available. The reduction of the allometric coefficient as nutritional plane increased suggests condition-dependent expression.

Our results demonstrate that a single allometric coefficient is insufficient to describe antler – body mass relationships in deer of different age classes. Ontogenetic changes in weapon – body relationships are widely reported (e.g., Stewart et al. 2000; Bender et al. 2003; Ungerfield et al. 2011; Gómez et al. 2012), but allometric equations are rarely included. Comparisons of allometric relationships across species (i.e., evolutionary allometry) typically use species averages derived from mature subjects within a single population (e.g., Plard et al. 2011), and our results reinforce the wisdom of this approach. However, we emphasize that continued mass accumulation after completion of skeletal growth may confound such comparisons in cervids. Age class-specific coefficients have also been reported for male and female reindeer (Melnicky et al. 2013), though age effects may have been obscured by grouping prime-aged males with physiologically mature but not fully grown individuals. Likewise, nutritional context is an important factor in weapon development (Emlen et al. 2012; Chirichella et al. 2013), and our results indicate comparisons of static allometry between areas of divergent forage quality may show substantial discrepancies.

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Table 1. Allometric relationships of antler mass with body mass in white-tailed deer (*Odocoileus virginianus* Zimmerman, 1780) in the Mississippi Alluvial Valley (MAV), Thin Loess, and Lower Coastal Plain (LCP) soil regions of Mississippi, USA. A slope >1 indicates positive allometry. Nutritional plane was greatest in the MAV, least in the LCP.

Soil region	Age class	<i>n</i>	Slope	UCL	LCL	<i>P</i>	<i>R</i> ²
MAV	1.5	2319	4.47	4.64	4.31	≤0.001	0.17
	2.5	11465	3.51	3.57	3.45	≤0.001	0.20
	3.5	11113	2.74	2.79	2.69	≤0.001	0.17
	4.5	5126	2.38	2.46	2.31	≤0.001	0.12
	5.5-7.5	3010	2.31	2.40	2.21	≤0.001	0.11
Thin Loess	1.5	2554	3.75	3.89	3.60	≤0.001	0.15
	2.5	8729	3.68	3.74	3.61	≤0.001	0.23
	3.5	6736	3.50	3.57	3.43	≤0.001	0.29
	4.5	2437	3.10	3.22	2.98	≤0.001	0.29
	5.5-7.5	1266	2.87	3.03	2.69	≤0.001	0.22
LCP	1.5	1104	3.60	3.82	3.39	≤0.001	0.11
	2.5	3912	3.60	3.68	3.50	≤0.001	0.31
	3.5	2801	3.40	3.49	3.30	≤0.001	0.36
	4.5	979	3.10	3.28	2.92	≤0.001	0.26
	5.5-7.5	529	2.92	3.15	2.66	≤0.001	0.32

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713 **Figure captions.**

714 Fig. 1. Soil resource regions from which harvested male white-tailed deer (*Odocoileus*
715 *virginianus* Zimmerman, 1780) were sampled in Mississippi, USA, 1991 – 2007.

716 Fig. 2. Least-square mean estimates of antler:body mass in white-tailed deer
717 (*Odocoileus virginianus* Zimmerman, 1780) from the Mississippi Alluvial Valley
718 (MAV), Thin Loess, and Lower Coastal Plain (LCP) regions of Mississippi, harvested
719 in 1991 – 2007. Nutritional plane was greatest in the MAV and least in the LCP.

720 Fig. 3. Variability of antler mass and body mass for white-tailed deer (*Odocoileus*
721 *virginianus* Zimmerman, 1780) from the Mississippi Alluvial Valley (MAV), Thin
722 Loess, and Lower Coastal Plain (LCP) regions of Mississippi, USA harvested in 1991
723 – 2007. Nutritional plane was greatest in the MAV and least in the LCP.

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Fig. 1. Soil resource regions from which harvested male white-tailed deer (*Odocoileus virginianus* Zimmerman, 1780) were sampled in Mississippi, USA, 1991 – 2007.

215x279mm (300 x 300 DPI)

Fig. 2. Least-square mean estimates of antler:body mass in white-tailed deer (*Odocoileus virginianus* Zimmerman, 1780) from the Mississippi Alluvial Valley (MAV), Thin Loess, and Lower Coastal Plain (LCP) regions of Mississippi, harvested in 1991 – 2007. Nutritional plane was greatest in the MAV and least in the LCP.

190x142mm (300 x 300 DPI)

Fig. 3. Variability of antler mass and body mass for white-tailed deer (*Odocoileus virginianus* Zimmerman, 1780) from the Mississippi Alluvial Valley (MAV), Thin Loess, and Lower Coastal Plain (LCP) regions of Mississippi, USA harvested in 1991 – 2007. Nutritional plane was greatest in the MAV and least in the LCP.

190x142mm (300 x 300 DPI)