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## Factors affecting morphometrics and epiphyseal closure of white-tailed deer

Emily Brooke Flinn

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FACTORS AFFECTING MORPHOMETRICS AND EPIPHYSEAL CLOSURE OF  
WHITE-TAILED DEER

By

Emily Brooke Flinn

A Thesis  
Submitted to the Faculty of  
Mississippi State University  
In Partial Fulfillment of the Requirements  
for the Degree of Master of Science  
in Wildlife and Fisheries Science  
in the Department of Wildlife, Fisheries, and Aquaculture

Mississippi State, Mississippi

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FACTORS AFFECTING MORPHOMETRICS AND EPIPHYSEAL CLOSURE OF  
WHITE-TAILED DEER

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CLOSURE OF WHITE-TAILED DEER

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Factors affecting morphometrics and epiphyseal closure are important in understanding regional variation and growth of white-tailed deer (*Odocoileus virginianus*). I compared body and antler growth from birth to 3 years of age in captive, first-generation, male white-tailed deer from three regions with varying soil quality and deer morphometrics. I also determined gender and age effects on epiphyseal closure timing in captive white-tailed deer. I found regional morphological variation present in first-generation male deer, which may be caused by regional genetic variation or lingering maternal effects. Determining cause of regional morphological variation will require data collection through a second-generation of males raised on the controlled diet. Epiphyseal closure timing was associated positively with age. Two of the four epiphyseal plates examined were affected by gender, with females closing prior to males. Morphometric and epiphyseal data confirm that age and gender affect epiphyseal closure timing in white-tailed deer.

## DEDICATION

This thesis is dedicated to my mom, uncle John, and husband. Mom, thank you for always pursuing me to do what I love and allowing nothing to stand in my way, and without this I would not have the opportunities that I have today. John, you are more of a father than an uncle, as you have taught me the joys of hunting, and I can't thank you enough. Jeremy, you are my best friend, soul mate, and husband. The journey through graduate school would have been unimaginable without your patience, love, and never ending support. I am lucky to spend the rest of my adventures through life with you.

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## CHAPTER I

### INTRODUCTION

Age, nutrition, and genetics are significant factors affecting antler and body size of white-tailed deer (Harmel et al. 1989, Demarais 1998). Genotype determines growth potential capabilities, but phenotype is the ultimate expression of the genotype, as affected by environmental factors (e.g., nutrition; Demarais 2007). Nutrition greatly influences antler and body size of white-tailed deer (Harmel et al. 1989). Age influences morphometrics, as antler and body size increase with age until maximum size is acquired at 5 to 7 years of age and 3 to 4 years of age, respectively (Demarais 1998, Strickland and Demarais 2000).

White-tailed deer (*Odocoileus virginianus*) exhibit regional morphological variation within Mississippi and throughout their range (Richie 1970, Strickland and Demarais 2000, Monteith et al. 2009). Age of maximum antler development and body mass differed by as much as 29% across soil physiographic regions in Mississippi (Strickland and Demarais 2000).

Regional phenotypic variation in white-tailed deer might result from regional environmental differences or genetic dissimilarities (Ashley et al. 1998, Geist et al. 2000). Regional morphological variation in white-tailed deer is associated positively with soil fertility, as body mass generally increased in more fertile regions (Gill 1956,

Strickland and Demarais 2000). However, variation in genetic potential has not been eliminated as contributing to regional morphological variation. Determining how environment and genetic factors influence morphometrics is complex, but necessary to understand the species thoroughly and to implement proper management.

Understanding causes of morphological variation in white-tailed deer is important in effective management. White-tailed deer are Mississippi's most important game species (Grado et al. 2008), consequently making deer management of high importance to many stakeholders. Several state agencies have implemented harvest restrictions based on antler criteria, including number of points, inside spread, and main beam length (Strickland et al. 2001, Demarais 1998, MDWFP Deer Committee 2009). Regional morphological variation influences harvest regulations and management, so, it is important to understand the causes of variation to ensure proper management.

Factors affecting epiphyseal closure are important in understanding growth of white-tailed deer. Closure of the epiphyseal plates determines maximal length of long bones and thus potential size of deer. Understanding epiphyseal closure patterns among age and gender groups will provide insight on energy allocation and sexual dimorphism. Factors affecting closure timing in white-tailed deer have not been identified conclusively due to inadequate sample size or use of specimens with estimated age (Lewall and Cowan 1963, Purdue 1983).

My research objective of Chapter II was to determine the relative roles of nutrition and genetics in regional variation in white-tailed deer. I compared antler and body size from birth to 3 years of age in captive first-generation male white-tailed deer from three Mississippi regions when raised on optimum nutrition. The source soil

physiographic regions represented a wide range of white-tailed deer morphometrics found in Mississippi. The high quality diet removed nutritional differences deer experienced in the wild; subsequently allowing them to grow to their genetic potential. However, lingering maternal effects also can affect growth potential.

My research objective of Chapter III was to better understand the growth potential of white-tailed deer by evaluating age and gender effects on epiphyseal closure timing. At 5.5 months, 1, 2, and 3 years of age, I examined four white-tailed deer forelimb epiphyseal plates, including the distal humerus, proximal and distal radius, and metacarpal. Epiphyseal plates were examined by use of radiographic equipment to determine stage of ossification of the epiphyseal plates. Skeletal length measurements also were collected to evaluate with epiphyseal closure data. I used a captive deer herd with access to optimum nutrition and all research animals had year of birth known.

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CHAPTER II  
ENVIRONMENTAL EFFECTS ON MALE WHITE-TAILED DEER  
MORPHOMETRICS

**Abstract**

Regional variation in white-tailed deer (*Odocoileus virginianus*) antler and body size in Mississippi may be related to habitat quality or genetic limitations. I compared body and antler growth from birth to 3 years of age in captive first-generation male white-tailed deer from three physiographic regions (Delta, a greater quality area with larger body and antler size; Thin Loess [Loess], a moderate quality area with moderate body and antler size; and Lower Coastal Plain [LCP], a lesser quality area with smaller body and antler size). All deer had access to a 20% crude protein diet to eliminate nutritional differences and allow expression of genetic potential. At 1 year of age, body mass of Delta males was 19% and 12% greater than LCP and Loess males, respectively. Body mass differed among all regions at 2 and 3 years of age, with LCP males being 22% and 25% smaller than Delta males, respectively. Antler scores of 1 – 3 year-old LCP males averaged 14% smaller than Delta and Loess antler scores. Body mass trends in research deer were similar to wild deer with Delta and LCP males being the largest and smallest, respectively. Morphological variation among regions could be caused by regional differences in genetic potential or may be lingering maternal effects.

Determining the complete cause of regional morphological variation in white-tailed deer will require data collection through a second-generation of males raised on the controlled diet.

## **Introduction**

The relative impacts of nature and nurture, or more specifically genetic and environmental effects, on deer morphometrics has been debated (Jacobson 1995, Geist et al. 2000). Phenotypic variation among populations assigned to genetics may be due to environmental variation (Ashley et al. 1998, Geist et al. 2000). Genetic or environmental effects have impacted phenotypic expression of individuals (Ullrey 1982, Jacobson and Lukefahr 1998, Lockwood et al. 2007) and populations (Leberg and Smith 1993, Ashley et al. 1998, Geist et al. 2000), but quantifying the relative contribution of each to variation in morphometrics of white-tailed deer (*Odocoileus virginianus*) requires full knowledge of environmental sources of variation.

White-tailed deer morphometrics varied across physiographic regions in Illinois, Mississippi, South Dakota, and West Virginia, but sources of variation have not been thoroughly investigated (Gill 1956, Richie 1970, Strickland and Demarais 2000). The 29% variation in antler size and body mass in Mississippi was thought to be due to regional variation in habitat quality and nutritional intake, but research has not precluded genetic differences (Strickland and Demarais 2000). Further research is needed to determine the interaction of environment, genetics, and age on morphometrics in white-tailed deer.

The goal of this research was to compare antler and body development from birth to 3 years of age in captive, first-generation, male white-tailed deer from three physiographic regions when raised on optimum nutrition. I evaluated effects of source region within a year class on body and antler size of captive, male white-tailed deer. I assumed that regional variation in body and antler growth was related to regional variation in soil fertility, land use, and nutritional intake (Strickland and Demarais 2000, Strickland and Demarais 2008). I hypothesized that availability of 20% protein feed would produce similar antler and body sizes by 3 years of age among the three source regions. However, because maternal factors can influence offspring morphometrics, my alternative hypothesis was that positive effects from removal of nutritional limitations would be masked by lingering genetic or maternal effects from wild-caught dams (Mech et al. 1991, Monteith et al. 2009).

### **Study Area**

White-tailed deer originated from 29 sites throughout three source regions of Mississippi (Fig. 2.1, Table 2.1). The Delta (11 sites), Thin Loess (12 sites), and Lower Coastal Plain (6 sites) were selected as the three sources of deer because these regions represent a wide range of antler and body morphometrics found in Mississippi (Strickland and Demarais 2000).

The Delta region (Delta and Batture soil regions combined) was considered the highest quality study area. This region bordered the Mississippi River and comprised approximately 14% of the state of Mississippi. The Delta region was characterized

level flood plains with fertile alluvial soils and the predominant land use being crop production (e.g., cotton, soybean, corn, rice; Pettry 1977, Snipes et al. 2005). The combined summer and spring mean composite crude protein level of 6 deer forage species within the Delta was 18% (Jones et al. 2008). Deer from the Delta had the greatest mean eviscerated body mass, antler size, and steepest growth rate (Strickland and Demarais 2000).

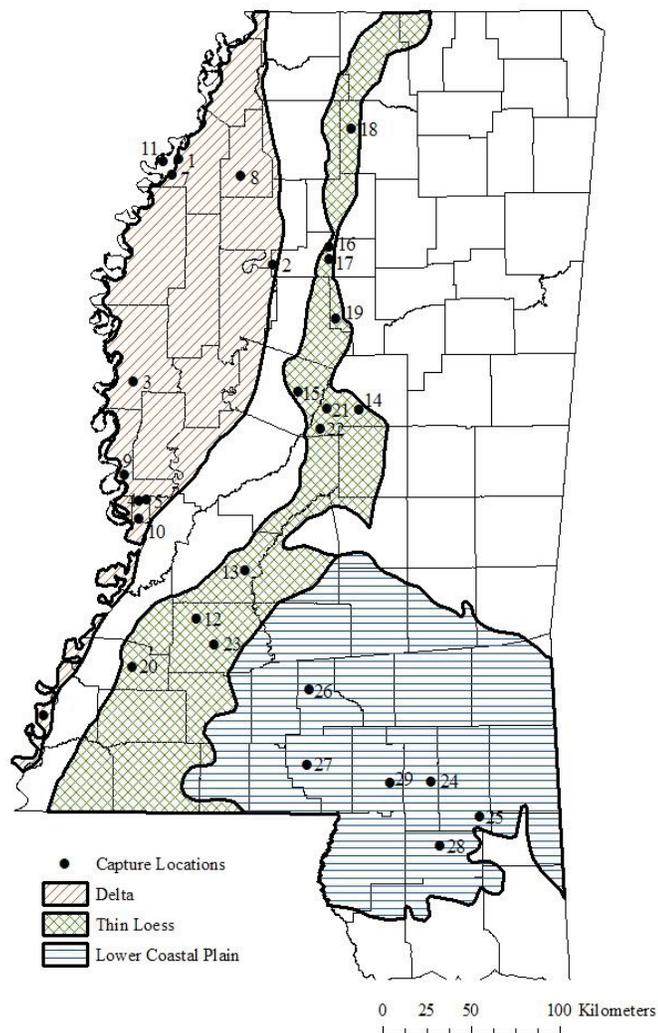


Figure 2.1 Physiographic regions of Mississippi from which captured pregnant females and fawns were captured during winters of 2005 and 2006. Numbered locations coincide with source descriptions in Table 2.1.

Table 2.1 Source and sample sizes of white-tailed deer captured from three physiographic soil regions<sup>a</sup> of Mississippi, USA during 2005 and 2006, relative to Figure 2.1.

Location	County	Region	<i>n</i>
1. Ward Lake Hunting Club	Coahoma	Delta	8
2. Malmaison WMA	Grenada	Delta	2
3. Leroy Percy WMA	Washington	Delta	1
4. Mahannah WMA	Issaquena	Delta	13
5. Steel Bayou Hunting Club	Issaquena	Delta	4
6. Big River Farms	Adams	Delta	11
7. Burkes Hunting Club	Coahoma	Delta	4
8. Info-Lab	Quitman	Delta	1
9. Tennessee Bar Hunting Club	Issaquena	Delta	3
10. Buckhorn Hunting Club	Issaquena	Delta	1
11. Coahoma Co. Cons. League	Coahoma	Delta	1
12. DeViney Property	Copiah	Loess	14
13. Florence	Rankin	Loess	1
14. Kosciusko	Attala	Loess	1
15. Holmes County State Park	Holmes	Loess	1
16. Grenada Dam	Grenada	Loess	11
17. Hugh White State Park	Grenada	Loess	9
18. Sardis Waterfowl Refuge	Lafayette	Loess	2
19. Blaylock Property	Montgomery	Loess	2
20. Deer Creek Hunting Club	Jefferson	Loess	2
21. Dr. Bryant's Property	Attala	Loess	3
22. Riverside Hunting Club	Attala	Loess	5
23. Hazelhurst	Copiah	Loess	1
24. Camp Shelby	Forrest	LCP	38
25. Leaf River WMA	Perry	LCP	3
26. Pace Hunt Club	Jefferson Davis	LCP	5
27. Walker Farms	Marion	LCP	6
28. Wiggins	Stone	LCP	1
29. Purvis	Lamar	LCP	2

<sup>a</sup> Loess = Thin Loess, LCP = Lower Coastal Plain

The Thin Loess region (Upper and Lower Thin Loess combined, Loess) was considered the medium quality study region. This region made up 14% of the state of Mississippi and had level to sloping topography composed of silty soils. Agricultural was the dominant land use, but was not as prevalent as in the Delta (Pettry 1977). The combined summer and spring mean composite crude protein level of 6 deer forage species within the Loess was 16.4% (Jones et al. 2008). This region had mid-range eviscerated body mass, antler score, and growth rates (Strickland and Demarais 2000).

The Lower Coastal Plain (LCP) was considered the lowest quality study region. This region made up 22% of Mississippi and was composed of level to steep topography with an acidic mixture of sand, loam, and clay soils. This area tended to have leaching issues, limiting most land uses to pine (*Pinus* spp.) production and livestock grazing (Pettry 1977). The combined summer and spring mean composite crude protein level of 6 deer forage species within the LCP was 15.6% (Jones et al. 2008). Of the study regions, the LCP had the least mean eviscerated body mass, antler score, and growth rate (Strickland and Demarais 2000).

Captured female white-tailed deer were taken to Mississippi State University's Rusty Dawkins Memorial Deer Unit (MSU Deer Unit) located in Starkville, Mississippi, USA. This facility included 5 main pens from 0.4 to 1.3 ha in size and 7 smaller holding pens. The deer were divided among the pens based on region of origin. Each pen contained water and two feeders supplied with ad libitum 20% protein deer pellets (Purina AntlerMax Professional High Energy Breeder 59UB, Purina, St. Louis, MO). Multiple feeders were available in each pen to reduce competition for access to feed. Forages available within the pens included Durana Clover (*Trifolium repens* [Pennington

Seed Co., Madison, GA]), Max-Q Fescue (*Festuca arundinacea shreb* [Pennington Seed Co., Madison, GA]), winter wheat (*Triticum aestivum*), and volunteer grasses and forbs.

Males born in the MSU Deer Unit at an average 5.5 months of age and wild-captured male fawns were assigned randomly to remote research pens located near Macon, Noxubee County, Kosciusko, Attala County, and Utica, Copiah County, Mississippi, USA. Remote research facilities received a random sample of one third of male fawns from each source region. Husbandry at these facilities followed MSU Deer Unit protocols.

## **Methods**

This study involved white-tailed deer with wild lineages in Mississippi. I considered deer first-generation if produced from a dam captured as an adult from the wild or captured as a wild-birthed fawn. During February – April of 2005 and 2006, Mississippi Department of Wildlife, Fisheries and Parks (MDWFP) captured adult females ( $\geq 1$  year-old) from three source regions (i.e., Delta, Loess, and LCP) (Fig. 2.1, Table 2.1). Deer came from a mixture of public Wildlife Management Areas (WMAs) and private lands that were part of the Deer Management Assistance Program (Guynn et al. 1983). I assumed these source samples adequately represented the relative genetic variation within each source region. Adult females were brought to the MSU Deer Unit under the assumption that they were bred prior to capture. During 2006, they also captured male and female fawns from the wild.

Birth location and age of first data collection varied among first-generation fawns. I located all newborn fawns at the MSU Deer Unit within two days of birth. Females

caught during 2005 produced fawns during 2005. Females caught during 2006 or females captured during 2005 that were retained in the MSU Deer Unit and bred to males from their respective source region produced fawns during 2006. I first sampled wild-birthed fawns captured during 2006 at 1 year of age. During fall 2006, I relocated wild-captured females from the MSU Deer Unit to the Kosciusko and Macon remote facilities and bred them to first-generation males from their respective source regions. I first sampled resultant fawns at 5.5 months of age, assuming the same average birth date as the MSU Deer Unit. Sex ratio within all breeding pens was 1 male for every 5 – 7 females.

I collected data on fawns born at the MSU Deer Unit within 2 days of birth. I recorded gender and birth date and measured body mass, total body length, and hind foot length (Gill 1956, Bartush and Garner 1979). I uniquely marked all fawns with a medium plastic tag (Allflex, Dallas, TX) and a numbered metal sheep-sized tag in adjacent ears (Hasco Tag Company, Dayton, KY). I also collected DNA by ear notch and freeze branded the last digit of each animal's birth year on its hindquarter.

I used a Pneu-Dart projection system (Pneu-Dart, Inc., Williamsport, PA) with telazol (4.4 mg/kg) and xylazine (2.2 mg/kg) to sedate deer for sampling at 5.5 months and older. I administered yohimbine (0.125 mg/kg; Kreeger 1996) or tolazoline (4.0 mg/kg; Miller et al. 2004) to reverse effects of xylazine. Capture, handling, and marking techniques were approved by the Mississippi State University Institutional Animal Care and Use Committee under protocol numbers 04-068 and 07-036.

At 5.5 months after the mean fawning date for each region, I anesthetized fawns for data collection, vaccinations, marking with a large plastic tag in each ear (Allflex, Dallas, TX), and removal from dams. I collected the same morphometrics sampled at

birth. I administered appropriate amounts of the antibiotic Nuflor™ (Schuering-Plough Animal Health Corp., Summit, NJ), the endectocide Ivermectin (Norbrook Laboratories, LTD., Down, Northern Ireland, UK), the clostridial vaccine Vision 7 with SPUR (Ivesco LLC, Iowa Falls, IA), and the leptospirosis vaccine Leptoferm-5 (Pfizer, Inc., New York, NY). I collected hair samples for assignment of parentage by DNA Solutions (Oklahoma City, OK). I tattooed a unique identification number (e.g., Y7501 = Delta, 2007, #501) in to one ear.

I anesthetized adult males ( $\geq 1$  year) annually during 20 October – 9 November and repeated the same prophylactics and morphometric measurements implemented at 5.5 month of age. I measured inside spread, base circumference, and beam length of antlers prior to their removal approximately 3 cm above the burr with a reciprocating saw or diamond wire.

I used two variables to represent antler size. I obtained the mass of antlers. I did not remove antler less than 3 cm long and assigned 0 gm values to these animals. I calculated an antlers score similar to the Boone and Crockett scoring system (Wright and Nesbitt 2003). After removal I recorded tine length and the second, third, and fourth circumferences only when present. For example, a main beam with 3 typical points included only three circumference measurements. Regular Boone and Crockett scoring criteria would not accurately reflect size of spikes and other small antler sets on young deer.

I quantified region of origin effects on male morphometrics by testing effects of soil region and age using a 2-way, repeated measures analysis of variance with PROC MIXED (SAS Institute, Cary, NC). Experimental units were first-generation male deer. I

used repeated measures to account for individual variation. I examined birth and 5.5 month data in a separate, but equivalent analysis due to unequal variances compared to older year classes. Response variables included body mass, antler mass and score, total body length, and hind foot length. For analysis on ages 1 – 3 years, I applied a random effect for conception and birth location, classifying whether a deer was born in the wild, conceived in the wild and born in captivity, or conceived and born in captivity. For each dependent variable, I evaluated multiple covariance structures and chose the one with the least Akaike's Information Criterion (AIC) value (Gutzwiller and Riffell 2007). If the variance for a region was three times greater than the variance for the other regions within a year class for a single dependent variable, I selected a covariance structure with a group effect for region to account for heterogeneous variance (Littell et al. 2006). Hind foot length and antler score ran best with an autoregressive covariance structure (ar[1]), whereas body mass ran best with ar[1] grouped by region. Antler mass and total body length ran best with a heterogeneous autoregressive covariance structure (arh[1]). All response variables were distributed normally. I used the LSMEANS PDIFF option to identify differences among pair wise comparisons and used the SLICE option to test the significance of one effect at each level of another effect. I compared litter size among regions to determine if it might be a confounding effect, but found no variation among regions. Therefore, litter size was not included in the final analysis because no variation was present. Differences were considered significant when  $\alpha \leq 0.050$ .

## Results

I sampled 198 deer (experimental units), with 444 observations. Males born at the MSU Deer Unit, remote facilities, or in the wild totaled 127, 38, and 33, respectively. Known ages at the time of sampling were 4.4 – 6.6 months for fawns and 1.2 – 1.4, 2.2 – 2.4, 3.2 – 3.4 years for 1, 2, and 3 year classes, respectively.

Body mass at birth and 5.5 months varied with soil physiographic region (Fig. 2.2, Table 2.2). Because the interaction effect approached significance ( $P = 0.058$ ), I also evaluated slice effects to determine age at which the region effect was most influential. Slice effects show the effect of one factor on individual levels of another factor, for example region effects at each age class. At birth, body mass did not differ among regions ( $P = 0.170$ ). At 5.5 months of age, body mass differed among regions ( $P = 0.050$ ) with Delta males weighing 14% greater than LCP males.

An interaction between age and region was present in body mass from 1 – 3 years old (Fig. 2.2, Table 2.2). Body mass differed among regions at each age ( $P < 0.001$ ). Delta males weighed 23% – 33% greater than LCP males and 10% – 14% greater than Loess males.

Soil physiographic region had varying effects on skeletal measurements at birth and 5.5 months of age. Hind foot length at birth and 5.5 months varied by region ( $P = 0.034$ ; Fig. 2.3, Table 2.2). However, I also evaluated slice effects because the interaction effect approached significance ( $P = 0.060$ ). At birth, hind foot length did not differ among regions ( $P = 0.176$ ). At 5.5 months, hind foot length exhibited a region effect ( $P = 0.042$ ), with Delta males 5% longer than Loess and LCP males. Total body length at birth and at 5.5 months did not differ by region (Fig. 2.4, Table 2.2).

Table 2.2 Morphometric measurements of white-tailed deer from birth (B) to 3 years from three soil physiographic regions in Mississippi, USA, during 2005 - 2009.

Morphometric	Age <sup>a</sup>	Source Region <sup>b</sup>						P-values <sup>c</sup>					
		Delta		Loess <sup>d</sup>		LCP <sup>d</sup>		Age	Region <sup>e</sup>	Age×Region			
		n	$\bar{X}$	SE	n	$\bar{X}$	SE				n	$\bar{X}$	SE
Hind foot length (mm)	B	46	223	2.1	46	226	2.0	35	219	2.1	<0.001	0.034	0.060
	0.5	28	371	5.7	21	352	4.4	30	354	5.0			
	B - 0.5		A <sup>f</sup>		AB			B					
	1	35	438	2.5	28	416	3.4	35	407	2.6	<0.001	<0.001	0.531
	2	31	451	3.0	25	435	4.2	31	420	2.2			
Total Body length (mm)	3	20	453	4.2	20	431	4.4	7	422	6.6			
	1 - 3		A		B			C					
	B	45	616	6.6	46	627	5.9	35	606	7.7	<0.001	0.211	0.377
Total Body length (mm)	0.5	28	1317	21.2	21	1278	18.4	30	1275	13.5			
	B - 0.5		A		A			A					
	1	35	1631	17.4	28	1551	18.1	35	1525	15.9	<0.001	<0.001	0.181
	2	31	1809	11.4	25	1722	16.9	31	1670	9.1			
	3	20	1865	15.2	20	1795	15.7	7	1704	18.4			
Body mass (kg)	1 - 3		A		B			C					
	B	46	2.5	0.1	43	2.7	0.1	35	2.4	0.1	<0.001	0.036	0.058
	0.5	28	28.5 A	1.1	21	26.3	1.4	30	25.1	0.8			
	B - 0.5		A		AB			B					
	1	36	53.2 A	1.2	28	46.8 B	1.5	34	43.1 B	1.0	<0.001	<0.001	0.001
Body mass (kg)	2	31	74.2 A	1.7	25	67.2 B	1.7	31	58.2 C	1.4			
	3	20	89.1 A	2.4	20	79.4 B	2.5	7	67.2 C	1.6			

Table 2.2 Continued.

Morphometric	Age		Source Region <sup>b</sup>						P-values <sup>c</sup>				
	a		Delta		Loess <sup>d</sup>		LCP <sup>d</sup>		Age <sup>a</sup>	Region <sup>b</sup>	Age×Region		
	n	$\bar{X}$	$\bar{X}$	SE	n	$\bar{X}$	SE	n	$\bar{X}$	SE			
Antler score (cm)	1	37	71.1	6.4	29	70.1	8.6	36	62.2	7.1	<0.001	0.006	0.058
	2	32	210.8	8.1	25	210.1	8.6	32	175.5	8.1			
	3	20	279.1	10.9	20	280.7	9.9	7	245.4	14.5			
	1-3		A		A				B				
Antler mass (gm)	1	36	80.8 A	11.5	28	79.5 A	17.2	35	62.3 A	12.4	<0.001	0.409	0.002
	2	31	458.3 A	30.6	25	433.8 A	31.4	29	317.2 B	28.1		0.002	
	3	20	850.0 A	62.1	20	810.4 A	60.6	7	578.7 B	60.8		0.007	

<sup>a</sup> All ages for a given variable significantly, except hind foot length does not vary between 2 and 3 years-old.

<sup>b</sup> Actual means presented. Treatment differences correspond to least square means.

<sup>c</sup> Degree of freedom were as follows: Age<sub>Hind Foot (B-0.5)</sub> = 1, 37; Region<sub>Hind Foot (B-0.5)</sub> = 2, 163; Age×Region<sub>Hind Foot (B-0.5)</sub> = 2, 37; Age<sub>Hind Foot (1-3)</sub> = 2, 221; Region<sub>Hind Foot (1-3)</sub> = 2, 221; Age×Region<sub>Hind Foot (1-3)</sub> = 4, 221; Age<sub>Total Body (B-0.5)</sub> = 1, 36; Region<sub>Total Body (B-0.5)</sub> = 2, 163; Age×Region<sub>Total Body (1-3)</sub> = 2, 221; Region<sub>Total Body (1-3)</sub> = 2, 221; Age×Region<sub>Total Body (1-3)</sub> = 4, 221; Age<sub>Antler Score</sub> = 4, 226; Age<sub>Antler Score</sub> = 2, 220; Region<sub>Antler Score</sub> = 2, 226; Age×Region<sub>Antler Score</sub> = 4, 220; Region<sub>Antler Score</sub> = 2, 220; Age×Region<sub>Antler Score</sub> = 4, 220

<sup>d</sup> Loess = Thin Loess, LCP = Lower Coastal Plain.

<sup>e</sup> When Age×Region is significant, Region P-values are for within-year comparisons.

<sup>f</sup> Means with different letters within a row differ significantly ( $P < 0.05$ ).

Soil physiographic region effects on skeletal measurements were consistent from 1 – 3 years of age. Hind foot length differed among regions ( $P < 0.001$ ) with Delta males averaging 7% and 5% longer than LCP and Loess males, respectively (Fig. 2.3, Table 2.2). Total body length differed among regions ( $P < 0.001$ ) at 1 – 3 years of age, with Delta males averaging 8% and 5% longer than LCP and Loess males, respectively (Fig. 2.4, Table 2.2).

Antler score varied by region ( $P = 0.006$ ; Fig. 2.5, Table 2.2). However, I also evaluated the region effect at each year class because the interaction effect approached significance ( $P = 0.060$ ). At 1 year of age antler score did not differ among regions ( $P = 0.598$ ). At 2 and 3 years of age, antler score differed among regions ( $P = 0.004$ ,  $P = 0.017$ ; respectively), with LCP antler scores 14% smaller than Delta and Loess antler scores.

An interaction between age and region was present in antler mass (Fig. 2.6, Table 2.2). Antler mass did not differ among regions at 1 year of age ( $P = 0.409$ ). Antler mass differed among regions at 2 year of age ( $P = 0.002$ ), with LCP antlers weighing 31% and 27% less than Delta and Loess antlers, respectively. Antler mass differed among regions at 3 years of age ( $P = 0.007$ ), with LCP antlers weighing 32% and 29% less than Delta and Loess antlers, respectively.

Timing of birth varied among soil physiographic regions in deer with known birth date. Average birth dates varied from 16 July for Delta, to 30 July for Loess, and 15 August for LCP.

Age affected all morphometric variables ( $P < 0.001$ ; Table 2.2). Antler score increased by 193% and 35% from 1 – 2 years-old and 2 – 3 years-old, respectively.

Antler mass increased by 440% and 85% from 1 – 2 years-old and 2 – 3 years-old, respectively. Body mass increased by 39% and 18% from 1 – 2 years-old and 2 – 3 years-old, respectively. Total body length increased by 10% and 3% from 1 – 2 years-old and 2 – 3 years-old, respectively. Hind foot length was the one exception, as it increased by 4% from 1 – 2 years-old, but did not increase after 2 years of age. ( $P = 0.683$ , Table 2.2).

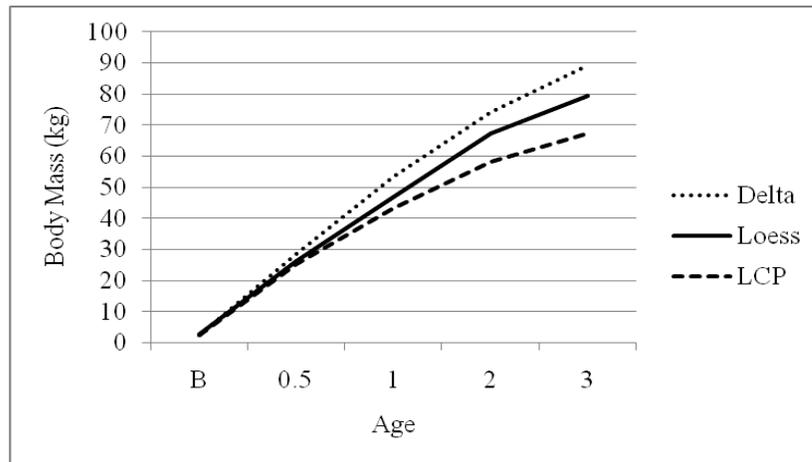


Figure 2.2 Body mass of white-tailed deer by age in years (B = birth) and region in Mississippi, USA during 2005 - 2009.

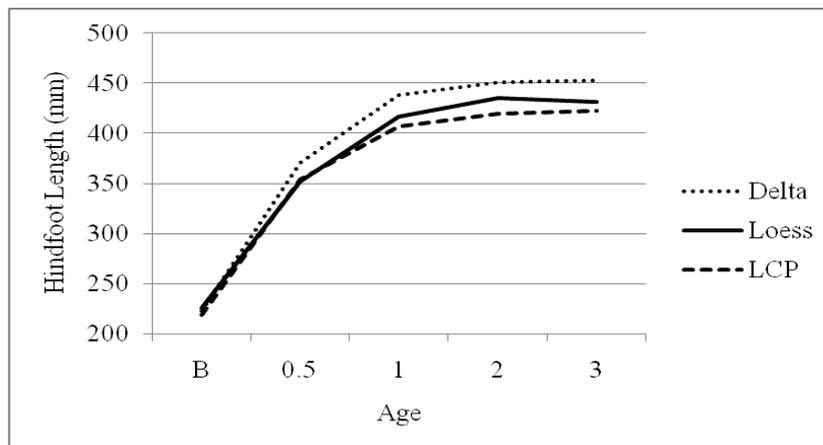


Figure 2.3 Hind foot length of white-tailed deer by age in years (B = birth) and region in Mississippi, USA during 2005 - 2009.

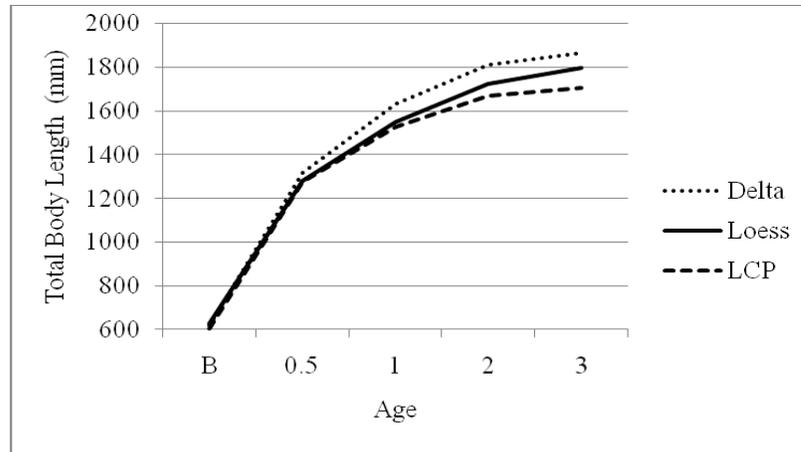


Figure 2.4 Total body length of white-tailed deer by age in years (B = birth) and region in Mississippi, USA during 2005 - 2009.

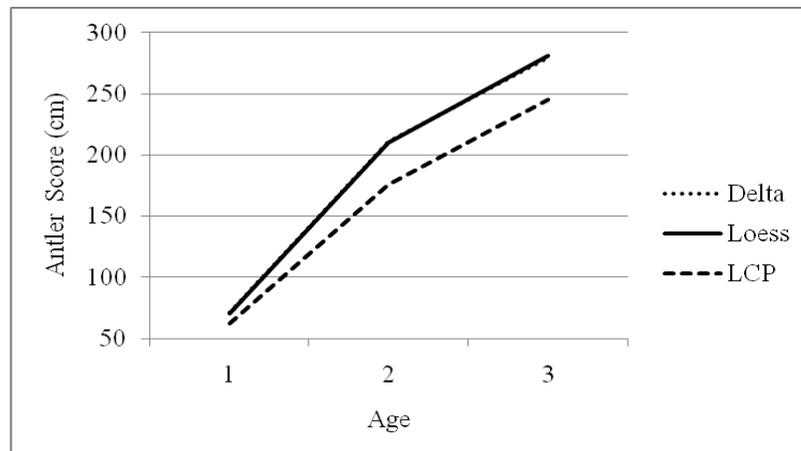


Figure 2.5 Antler score of white-tailed deer by age in years (B = birth) and region in Mississippi, USA during 2005 - 2009.

## Discussion

Source physiographic region clearly influenced growth rate in morphometrics of male white-tailed deer. Separating the relative impacts of genetic and environmental factors affecting phenotype is complicated because multiple factors occur simultaneously.

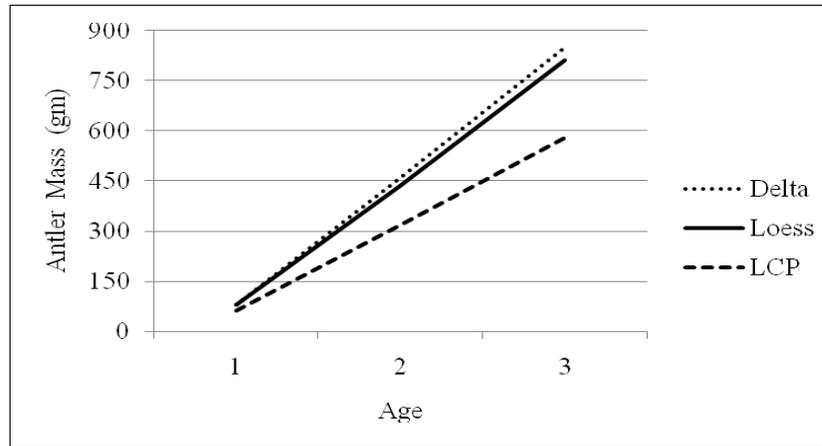


Figure 2.6 Antler mass of white-tailed deer by age in years (B = birth) and region in Mississippi, USA during 2005 - 2009.

Nutritional variation can directly and indirectly affect morphometrics of white-tailed deer during gestation and through lingering maternal effects (Dubos et al. 1966, Oftedal 1985, Mech et al. 1991). One or all of these may have influenced the varying growth rates exhibited by deer from source physiographic regions.

Nutritional variation experienced by dams during gestation can affect morphometrics of offspring (Monteith et al. 2009). A comparable study in South Dakota theorized that regional morphological variation of white-tailed deer resulted from maternal condition transmitted during gestation (Monteith et al. 2009). Body mass of female fawns their first winter was related to the nutritional intake of their dams during gestation (Mech et al. 1991). These effects could explain adult body mass which was directly related to birth body mass in male white-tailed deer from Louisiana (Schultz and Johnson 1995).

Regional variation in morphometrics of first-generation males used in my study also could have been related to maternal effects. Maternal effects are the influence of

parental phenotypes on the offspring's phenotype, regardless of genotype (Bernardo 1996, Monteith et al. 2009). Consequently, offspring characteristics might reflect environmental and nutritional conditions of past generations (Mech et al. 1991, Benton et al. 2001). Maternal effects transmitted during gestation affected growth of first-generation, male white-tailed deer, and were only partially compensated for during the second-generation (Monteith et al. 2009). Grand-maternal nutrition affected positively birth body mass of single male fawns born to 2 year-old females (Mech et al. 1991). Maternal effects might influence offspring morphometrics, growth, survival, and fitness; consequently affecting population demographics (Mech et al. 1991, Bernardo 1996, Bårdsen et al. 2008).

Maternal effects can impact fetal growth and development possibly operating through epigenetic mechanisms. Mammalian phenotype can be persistently altered through epigenetic mechanisms (Waterland and Jirtle 2004). Epigenetics is the study of how early nutrition affects fetal programming (Waterland and Jirtle 2004, Wu et al. 2004). Epigenetic changes may become heritable, and thus persist within a population, if they occur in gametes (Waterland and Jirtle 2004). During fetal development an organism may be able to alter its physiology based on maternal hormonal signals through the placenta, conceivably predicting postnatal environment (Gluckman and Hanson 2004a, b). Disruption of an individual's genetic expression might influence growth rates, allowing maternal nutrition during gestation to affect final adult body size of offspring (Chow and Lee 1964). Although dams in the current study were on optimum nutrition when the majority of fetal growth occurred (Armstrong 1950, Verme 1963, Robbins and

Robbins 1979), early nutritional variation might have affected the fetus' developmental programming through epigenetics with long term effects arising in adulthood.

Maternal effects can influence offspring for at least 2 generations, but effects diminish influence as successive generations are produced on optimum nutrition (Mech et al. 1991, Monteith et al. 2009). When raised on a highly nutritional diet, red deer (*Cervus elaphus*) and roe deer (*Capreolus capreolus*) increased antler and body size for 3 and 4 generations, respectively (Geist 1986). Geist (1986) estimated that white-tailed deer would require 14 – 16 years of production on a high quality diet to produce the maximum threshold of morphometrics. In white-tailed deer, second-generation males with lineages to low quality habitat compensated for 72% of the difference between mature body mass of first-generation males from low and high quality areas (Monteith et al. 2009). If maternal effects are causing regional variation of first-generation morphometrics in my study, additional generations must be studied.

Region effects were not demonstrated early in life possibly due to the inability of birth mass to express considerable variation as demonstrated in adults (Blaylock 2007). If fawns must have a minimum birth mass to ensure survival, but also a maximum birth mass due to limited uterine space or dystocia (i.e., parturition difficulties) then birth mass variation in fawns may be limited (Galindo-Leal and Weber 1994, Blaylock 2007). Fetal mass is an important factor affecting timing of parturition, with larger fetuses having a shorter gestation length (Verme 1969), also suggesting a maximum body mass constraint at birth. White-tailed deer birth mass varied from 1.8 kg – 3.6 kg throughout the range, with birth mass in Illinois and northern Michigan averaging 2.9 kg and ranges of 2.5 kg –

3.3 kg and 0.9 kg – 4.6 kg, respectively (Verme 1963, Sauer 1984, Nelson and Woolf 1985).

Another explanation for the lack of regional differences at birth could be an effect of higher growth hormones during gestation of later born fawns. Greater growth hormone and prolactin concentrations may have stimulated growth of fetuses carried by females with later conception dates (Verme 1985). The lack of region effects at birth could be a result of increased hormone levels due to later average birth dates of Loess and LCP fawns.

Birth date variation can affect phenotypic expression of morphometrics because late-born fawns may face issues that affect physical development (Jacobson 1995, Jacobson and Guynn 1995, Gray et al. 2002). Body mass and antler size of yearling male white-tailed deer  $\leq 17$  months-old were smaller than those  $\geq 19$  months-old (Knox et al. 1991). In Alabama, body mass, number of antler points, antler beam length, and antler beam circumference at 1 year of age were larger for males born April – May than those born in June – November; and larger for males born June – August than those born September – November (Gray et al. 2002). However, their data collected over a range of physiographic regions was potentially confounded by regional variation in morphometrics, as reported by Strickland and Demarais (2000). In contrast, birth date variation ( $> 100$  days) did not affect yearling body mass in Louisiana (Schultz and Johnson 1995). Late fawning dates and decreased physical development of yearling males may be compensated at a later age with adequate nutrition (Jacobson 1995). However, the greater regional discrepancy in morphometrics with increasing age that I

reported is contradictory to the pattern I would expect if birth date were affecting my results.

Differences in genetic potential could be the cause of regional variation in white-tailed deer morphometrics. Regional genetic variation may have arisen from an adaptation that altered morphometrics to maximize survival and fitness within a habitat. Because an individual's body size affects their absolute nutritional demand (Demment and Van Soest 1985; Sinclair and Parkes 2008), deer in habitats with environmental stochasticity may grow to a smaller body size to increase fitness and chances for nutritional support during periods of low nutritional quality. However, when body size is maintained and resources are abundant, antler size may be a beneficial investment, as large antlers can increase fitness in cervids (Clutton-Brock 1982, Kruuk et al. 2002). My results demonstrated this pattern in Loess males, as antler score was similar to the Delta at all ages, but Loess body mass averaged 12% smaller than Delta body mass at 1 – 3 years of age.

Determining if regional variation is due to maternal effects on offspring phenotypes or actual genetic differences exist will require an additional generation of research deer. Maternal effects diminish as generations are produced on optimum nutrition (Monteith et al. 2009). Therefore, if regional variation is still present after multiple generations, then maternal effects could be excluded and genetic variation would be the more likely explanation.

Multiple entwined factors affecting phenotypic expression possibly occurred in first-generation male white-tailed deer and supports the need to monitor second-generation deer in captivity on optimum nutrition. Reducing effects of maternal factors

by raising second-generation deer should allow a clearer depiction of the genotype present among the source regions. Therefore, data obtained from second-generation male white-tailed deer raised on optimum nutrition should indicate if regional variation is primarily caused by genetic differences or by nutritional variation among soil physiographic regions. The complicated relationship between genotype and environmental factors determining an individual's phenotype is essential to understanding regional variation in morphometrics and effects on population demographics.

### **Management Implications**

In first-generation, male, white-tailed deer, regional effects are not diminished when optimum nutrition is available. If lingering nutritional effects are the primary factor of morphometric differences, then improving habitat by increasing the quality and quantity of forage available to deer would improve morphometrics. However, improvement in nutrition will take longer than one generation to be recognized in morphometrics of white-tailed deer. Genetic variation caused by long-term nutritional differences also could cause regional variation. If genetics are the primary factor, then focus should be placed on managing expectations of the size of deer that can be produced in an area, instead of increasing deer morphometrics.

Presence of regional variation in wild white-tailed deer should be determined using older age class deer ( $\geq 2$  years-old) because regional variation increases significance with age. Comparison of younger aged deer would not accurately determine regional effects.

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CHAPTER III  
AGE AND GENDER EFFECTS ON EPIPHYSEAL CLOSURE IN WHITE-TAILED  
DEER

**Abstract**

Closure of the epiphyseal plates determines maximal length of long bones and thus potential body size; however, factors affecting closure timing in white-tailed deer have not been conclusively quantified. I determined effects of gender and age on epiphyseal closure timing in optimally nourished, captive, white-tailed deer (*Odocoileus virginianus*). I collected morphometric data and radiographic images of the distal humerus, proximal radius, distal radius, and metacarpal on 5.5 month, 1, 2, and 3 year-old deer. Age affected the distal radius and metacarpal epiphyseal plates ( $P < 0.001$ ), with all individuals exhibiting epiphyseal closure by 3 years of age. Gender affected epiphyseal closure timing of the distal and proximal radius epiphyseal plates ( $P \leq 0.018$ ) with females closing prior to males. The distal radius epiphyseal plate was three times more likely to be closed at 2 years of age in females than males. Scapula-to-hoof and elbow-to-hoof lengths demonstrated that most females cease growth by 2 years of age, while growth continued in males to at least 3 years of age. Morphometric and epiphyseal data confirm that age and gender affect epiphyseal closure timing in white-tailed deer.

## Introduction

Epiphyseal examination is used commonly to determine age class (Marks and Erickson 1966, Grant et al. 1972) and skeletal maturity (Vulcano et al. 1997) and to assess factors affecting morphological variation in mammals (Silberberg and Silberberg 1949, Serrano et al. 2007). Limitations of previous studies of epiphyseal closure patterns in deer include inadequate sample size or use of specimens with estimated age (Lewall and Cowan 1963, Purdue 1983). Skeletal development might influence fitness because of the relationship between ungulate body mass and skeletal size (Gill 1956) and the influence of body mass on mating success (Clutton-Brock et al. 1988) and dominance (Townsend and Bailey 1981). Knowledge of factors affecting epiphyseal closure may aid understanding of how morphological variation and fitness correlate in white-tailed deer.

Epiphyseal closure in mammals is influenced by age, environment (i.e., nutrition), and the endocrine system (Malina and Bouchard 1991). In deer, age is the primary factor affecting epiphyseal closure timing followed by gender (Purdue 1983) and possibly nutrition (Lewall and Cowan 1963). Gender variation suggests a female adaptation to prioritize energy for reproduction over growth (Clutton-Brock et al. 1982). Lewall and Cowan (1963) suggested a role of nutrition in epiphyseal closure timing in black-tailed deer (*Odocoileus hemionus columbianus*) when a restricted diet (70% of ad libitum) delayed epiphyseal closure.

The goal of my research was to determine effects of age and gender on epiphyseal closure timing in known-aged white-tailed deer. I evaluated closure rates at four epiphyseal plates for male and female captive deer aged 5.5 months to 3 years using

radiographs. I hypothesized that age would be correlated positively with epiphyseal plate closure and epiphyseal plates of females would close earlier than males.

### **Study Area**

Study animals were from wild lineages originating from 29 locations across Mississippi. Fawns were weaned naturally or at an average age of 5.5 months and maintained at one or more of four research sites. The Mississippi State University Rusty Dawkins Memorial Deer Unit (MSU Deer Unit) located near Starkville, Oktibbeha County, Mississippi, USA, was subdivided into 5 main pens from 0.4 to 1.3 ha in size and 7 smaller holding pens. Each pen contained forages, water, and two feeders supplied with ad libitum 20% protein deer pellets (Purina AntlerMax Professional High Energy Breeder 59UB, Purina, St. Louis, Missouri). Multiple feeders per pen reduced competition for feed. Male deer at 5.5 months and older were assigned randomly to remote research pens located near Macon, Noxubee County, Kosciusko, Attala County, and Utica, Copiah County, Mississippi, USA. Husbandry at these facilities followed MSU Deer Unit protocols. Planted white clover (*Trifolium repens*) and winter wheat (*Triticum aestivum*) were present at each of the facilities.

### **Methods**

During February – April of 2005 and 2006, the Mississippi Department of Wildlife, Fisheries and Parks captured and relocated wild-bred adult females ( $\geq 1$  year-old) from locations across Mississippi to the MSU Deer Unit. These wild-caught females produced fawns at the MSU Deer Unit in 2005 and 2006, and then were assigned

randomly to Kosciusko or Macon remote facilities fall of 2006 to produce fawns in 2007. During 2006, I also captured fawns born in the wild during 2005 and relocated them to the MSU Deer Unit or the remote facilities.

I collected radiographic images of epiphyseal plates to determine stage of closure (Fig. 3.1). I took images of adults (1 – 3 years-old) in October to November of 2007 and 2008. I took images of 5.5 month-old fawns in January of 2008 and December to January of 2008 – 2009. I examined four epiphyseal plates of the forelimb including: distal humerus, proximal radius, distal radius, and metacarpal. I used a VR 8020 mobile machine to collect radiographic images (Vet-Ray Inc., Arlington Heights, IL). Each epiphyseal plate was assigned a classification independently by each of 2 veterinarians: open (growth is occurring), partial (growth has ceased but epiphyseal plate has not completely ossified), or closed (growth has ceased, epiphyseal plate is fully ossified) similar to Purdue's (1983) classification system. If a closure ranking differed for a specific image, the veterinarians mutually re-evaluated and established a final closure ranking.

I collected morphometric measurements to examine the relationship between bone growth and limb length. I measured elbow-to-hoof length, which is from the proximal tip of the ulna, or elbow, to the tip of the longest nail of the front hoof. This measurement incorporated the proximal and distal radius, and metacarpal epiphyseal plates. I measured scapula-to-hoof length, which is from the most dorsal point of the scapula to the tip of the longest nail of the front hoof. This measurement incorporated all evaluated epiphyseal plates. All handling and marking techniques were approved by the Mississippi State

University Institutional Animal Care and Use Committee under protocol numbers 04-068 and 07-036.

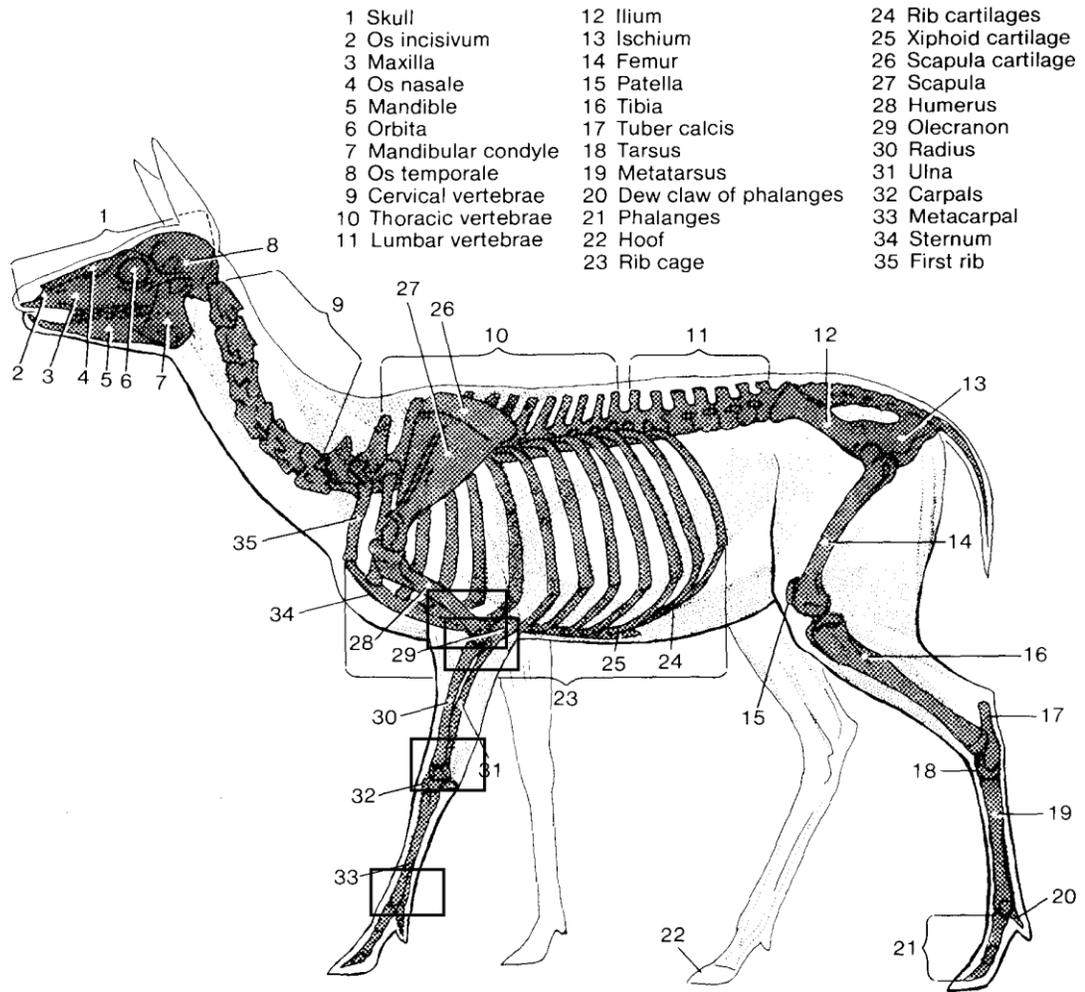


Figure 3.1 Epiphyseal plates subject to evaluation on a white-tailed deer skeleton. Drawing by Wayne Trimm.

I quantified effects of age and gender on stage of epiphyseal closure with PROC GLIMMIX (SAS Institute, Cary, NC). The treatments were age (5.5 months, 1, 2, and 3 years) and gender. Distal humerus and proximal radius had only two ages because all

epiphyseal plates closed by 1 year of age. Experimental units were white-tailed deer with known birth year. Response variables included epiphyseal closure rankings (open, partial, and closed) in ordered multinomial form (0, 1, and 2, respectively). I did not evaluate interactions in my analysis due to sample size limitations. I did not use repeated measures because deer were sampled no more than two out of the four ages. I assumed that there were no year effects on radiographs collected during 2007 to 2009 and combined data for all years. Differences were considered significant when  $\alpha \leq 0.050$ .

I tested effects of age and gender on scapula-to-hoof and elbow-to-hoof lengths using a 2-way, repeated measures analysis of variance with PROC MIXED using SAS (SAS Institute, Cary, NC). Experimental units were white-tailed deer that had at least one usable radiographic image. The treatments were age (5.5 months, 1, 2, and 3 years) and gender. If the variance for a gender group was three times greater than the variance for other gender group within an age class for a single dependent variable, I selected a covariance structure with a group effect for region to account for heterogeneous variance (Littell et al. 2006). I evaluated two covariance structures based on the Akaike's Information Criterion (AIC) value (Gutzwiller and Riffell 2007); scapula-to-hoof length ran best with an autoregressive covariance structure (ar[1]), while elbow-to-hoof length ran best with a heterogeneous autoregressive covariance structure (arh[1]). Both forelimb variables achieved normality. Differences were considered significant when  $\alpha \leq 0.050$ .

## **Results**

I collected 1,236 usable radiographic images on 231 individual white-tailed deer during 2007 to 2009, with 94 individuals having repeated sampling. I knew the birth date

of 128 deer and only birth year for 103. Known ages at the time of sampling were 3.6 – 6.7 months for fawns and 1.1 – 1.4, 2.2 – 2.4, 3.2 – 3.4 years for 1, 2, and 3 year classes, respectively. I assumed a similar range of birth dates for fawns born in the wild and at remote research pens. I collected 308 – 311 usable radiographic images for each epiphyseal plate. Sample sizes differed among epiphyseal plates because not all radiographs developed properly (Table 3.1).

Table 3.1 Sample sizes of white-tailed deer radiographic images of four epiphyseal plates classified by gender (male and female) and age (years) taken in Mississippi, USA during 2007 - 2009.

Age	Distal humerus		Proximal radius		Distal radius		Metacarpal	
	M	F	M	F	M	F	M	F
0.5	39	39	38	40	39	39	39	36
1	51	48	52	48	54	46	55	46
2	32	39	32	39	31	39	30	39
3	32	28	32	28	35	28	36	27

Age affected the distal radius and metacarpal growth plates, but was not a statistically significant factor for the distal humerus and proximal radius (Table 3.2). By 5.5 months of age 100% and 95% of the distal humerus and proximal radius epiphyseal plates, respectively, were classified as partial or closed and thus had ceased longitudinal growth at these locations. The metacarpal ceased longitudinal growth by 2 years of age, with 100% of the epiphyseal plates classified as partial or closed. The distal radius ceased longitudinal growth by 3 years of age, when 100% of the epiphyseal plates were closed.

Table 3.2 Effect of age on epiphyseal closure (%) in four growth plates of white-tailed deer by age (years) in Mississippi, USA during 2007 - 2009.

Epiphyseal Plate	Age				<i>F</i> -value	<i>P</i> -value
	0.5	1	2	3		
Distal humerus	89	100	100	100	0.00 <sup>a</sup>	0.974
Proximal radius	85	100	100	100	0.00 <sup>a</sup>	0.969
Distal radius	0	1	63	100	46.27 <sup>b</sup>	< 0.001
Metacarpal	0	1	91	100	26.54 <sup>c</sup>	< 0.001

<sup>a</sup> Degrees of freedom were as follows: Distal humerus = 1, 174; Proximal radius = 1, 174; Distal radius = 2, 305; Metacarpal = 2, 302.

Gender affected proximal and distal radius growth plates with females closing prior to males (Table 3.3). In the distal radius, females were 3 times more likely than males to be closed at 2 years of age, with females having 10% partial and 90% closed epiphyseal plates (Fig. 3.2). In contrast, males at 2 years of age were 26% open, 45% partial, and 29% closed at this location. The distal humerus approached significance, with 82% and 95% of the epiphyseal plates being closed for males and females at 5.5 months of age, respectively ( $P = 0.097$ ; Table 3.3).

Animals of known birth date provided a more detailed examination of epiphyseal closure timing for both genders. By 5.6 months all females had closed distal humerus and proximal radius epiphyseal plates. By 6.1 months all males had closed distal humerus and proximal radius epiphyseal plates. By 28.9 months all females had closed distal radius and metacarpal epiphyseal plates. By 38.5 months all males had closed distal radius and metacarpal epiphyseal plates.

Table 3.3 Effect of gender on epiphyseal closure (%) in four growth plates of white-tailed deer by age (years) in Mississippi, USA during 2007 - 2009.

Epiphyseal Plate	0.5		1		2		3		<i>F</i> -value <sup>a</sup>	<i>P</i> -value
	M	F	M	F	M	F	M	F		
Distal humerus	82	95	100	100	100	100	100	100	2.79	0.097
Proximal radius	74	95	100	100	100	100	100	100	5.76	0.018
Distal radius	0	0	0	2	29	90	100	100	19.22	< 0.001
Metacarpal	0	0	0	2	83	97	100	100	0.34	0.561

<sup>a</sup> Degrees of freedom were as follows: Distal humerus = 1, 174; Proximal radius = 1, 174; Distal radius = 2, 305; Metacarpal = 2, 302.

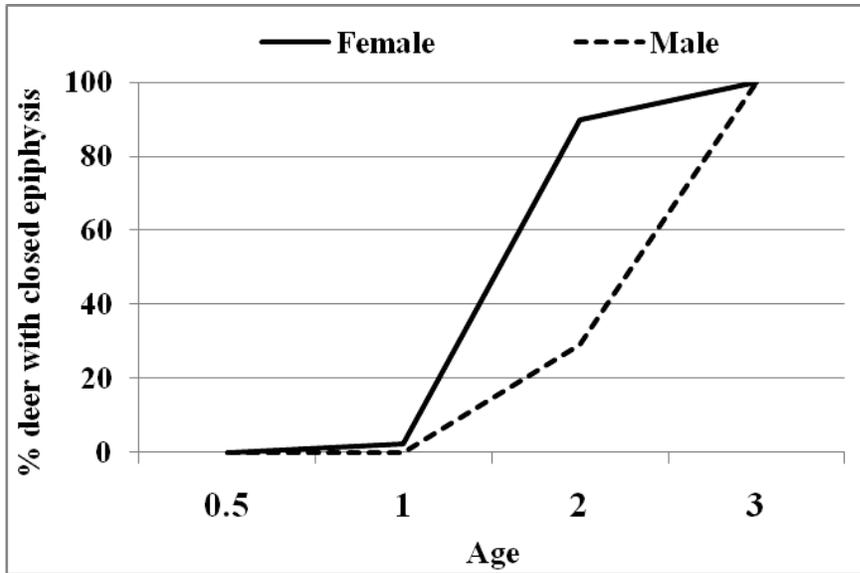


Figure 3.2 Percentage of distal radius epiphyseal plate closed in white-tailed deer by age (years) and gender in Mississippi, USA during 2007 - 2009.

An age and gender interaction was present in deer skeletal measurements ( $P < 0.001$ ; Table 3.4). Elbow-to-hoof and scapula-to-hoof lengths varied between gender groups within the same year class ( $P < 0.001$ ), except at 5.5 months. Male elbow-to-hoof and scapula-to-hoof lengths varied among all year classes ( $P \leq 0.007$ ,  $P < 0.001$ , respectively). Female elbow-to-hoof and scapula-to-hoof lengths varied among year classes ( $P < 0.001$ ), except between 2 and 3 year of age.

## **Discussion**

Age is the primary factor affecting epiphyseal closure in mammals (Thomsen and Mortensen 1946, Hale 1949). Fusion rates for the distal radius and metacarpal epiphyseal plates support the importance of age in epiphyseal closure. The lack of age effect on distal humerus and proximal radius epiphyseal plates was due to the high rate of fusion by the first sampling period at 5.5 months. Sampling prior to this age may have more clearly depicted possible variation in closure rates.

Epiphyseal plates cease growth and complete ossification, consequently, finishing elongation of the long bone and the limb. Clearly, in most specimens the distal humerus and proximal radius growth plates ceased involvement in bone elongation by 5.5 months, while the metacarpal epiphyseal plate contributed to bone elongation until 2 years of age. Longitudinal growth of the metacarpal bone ceased when this plate closed because it is the only epiphyseal plate present in the metacarpal bone (Lewall and Cowan 1963). The distal radius growth plate contributed the longest to growth of the evaluated epiphyseal plates, by ceasing growth in females by 2 years of age and males between 2 and 3 years of age.



Consistencies in epiphyseal closure timing are present between my study on optimally-nourished captive deer with known birth date and Purdue's (1983) study on wild-range deer from various environments. Purdue (1983) found the proximal radius and distal radius epiphyseal plates for males closed within 2 months of the closure timings in my study. Similarly, Purdue (1983) found the proximal and distal radius and metacarpal epiphyseal plates for females closed within 1 month of the closure timings in my study.

Inconsistencies in epiphyseal closure timing also were present between my study and Purdue's (1983) study on wild-range deer from various environments, as he reported male metacarpal epiphyseal plates closed at 29 months in contrast to my report of closure at 38 months. This discrepancy is likely a result of my sampling schedule, as a gap existed between 28.9 and 38.0 months for male deer with known birth date. Additionally, a discrepancy in Purdue's (1983) report of the distal humerus closure timing prevents an accurate comparison. While he reported in Table 3 that the distal humerus epiphyseal plate closed at 12 and 20 months for males and females, respectively, he stated in the results that this epiphyseal plate fused before and during the animal's first fall (i.e.,  $\leq 7$  months-old; Purdue 1983).

Gender is a secondary factor affecting epiphyseal closure (Purdue 1983, Malina and Bouchard 1991, Serrano et al. 2006). Epiphyseal plates closed earlier in female black bear (*Ursus americanus*; Marks and Erickson 1966) and Iberian ibex (*Capra pyrenaica*; Serrano et al. 2006) similar to my proximal and distal radius epiphyseal data and forelimb leg measurements. I may have missed gender effects in the distal humerus and metacarpal epiphyseal plates because I did not sample throughout the year. Year-round sampling may have allowed a clearer depiction of variation among year classes and gender groups.

Gender effects on epiphyseal closure timing may result from differences in the onset of sexual maturity (Silberberg and Silberberg 1949, Iuliano-Burns et al. 2009). Female red deer ceased growth earlier than males, perhaps to prioritize allocation of energy to reproduction (Clutton-Brock et al. 1982). Many more female than male white-tailed deer fawns reached sexual maturity their first winter, demonstrating the gender variation in sexual maturity (Cheatum and Morton 1946). My data suggests that female deer do not invest in body size as long as males, possibly because investment in reproduction is more beneficial. Gender variation in epiphyseal closure timing, forelimb length, and age when longitudinal growth ceases depicts how sexual dimorphism arises.

Nutrition has exhibited varying effects on timing of epiphyseal closure in ungulates. A restricted diet (70% ad libitum diet) delayed epiphyseal closure by a minimum of 12 months in black-tailed deer (Lewall and Cowan 1963). In contrast, the metacarpal epiphyseal plate closed quicker in a high density (92 individuals/km<sup>2</sup>) population of nutritionally-deprived fallow deer (*Dama dama*) compared to deer in a low density area (23 individuals/km<sup>2</sup>; Serrano et al. 2007). Purdue (1983) reported no apparent effect from nutrition, as white-tailed deer that inhabited a variety of ranges had similar epiphyseal closure times. Therefore, nutritional effects on epiphyseal closure timing should be considered inconclusive until additional, conclusive research is presented.

If nutritional variation affects epiphyseal closure timing, then significant impacts on fitness could be possible. These impacts would be produced when nutritional variation affects epiphyseal closure and subsequently body size and mass. In Mississippi, female deer within lower quality habitat had lesser body mass that did not increase after 3 years

of age, whereas female deer within greater quality habitat had greater body mass that increased until 4 years of age (Strickland and Demarais 2000). These areas of lower quality nutrition might be responsible for inhibiting growth due to increased costs of reproduction in these areas (Clutton-Brock et al. 1982, Oftedal 1985). This association may correlate to skeletal size because body mass has been correlated with skeletal development in white-tailed deer (Silberberg and Silberberg 1949, Gill 1956). Sexual maturation can cease long bone growth to increase an individual's reproductive success by closing the epiphyseal locations before genetic skeletal size is reached in suboptimal conditions (Silberberg and Silberberg 1949, Taber and Dasmann 1958). Therefore, in areas of low nutritional quality it may be more beneficial to reduce the body growth period (i.e., premature epiphyseal closure) in order to increase fitness.

### **Management Implications**

Until nutritional resource impacts are quantified on skeletal development, skeletal growth should not be precluded as a factor affecting regional body size differences. If nutritional quality is low during growth, then genetic skeletal size potential of an individual might not be acquired, which may be accredited falsely as subspecies variation. Therefore, this is of critical importance to conservation biology because maintenance of adaptive potential and evolutionary flexibility is founded on the preservation of genotypes, not phenotypes (Geist et al. 2000). I should not be over zealous in assigning subspecies designations until we completely understand morphological variation and effects of nutritional variation in epiphyseal closure. Application of resources to delineate and

protect subspecies of white-tailed deer is wasteful if the true cause of morphological variation is produced from nutritional variation.

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## CHAPTER IV

### SYNTHESIS

Body size of white-tailed deer is optimized to maximize fitness. Females exhibited epiphyseal closure prior to males, suggesting that reproduction is more beneficial to females than a larger body size. In males, the greater body size at maturity and growth period supports that they prioritize more energy to body size than females. For males a larger body size at maturity increases dominance and fitness (Clutton-Brock 1982, Stewart et al. 2000). However, animals with greater body mass at maturity require more energy for maintenance and they also reach puberty later in life (Owens et al. 1993).

Regional variation in white-tailed deer morphometrics may be a way to ensure survival and increase fitness, whether due to maternal effects or genetic variation. If lingering nutritional effects are the primary factor of morphometric differences, then improving habitat by increasing the quality and quantity of forage available to deer would improve morphometrics. However, improvement in nutrition will take longer than one generation to be recognized in morphometrics of white-tailed deer, therefore, a generational delay should be expected before results are exhibited from nutritional improvement. Genetic variation caused by long-term nutritional differences also could cause regional variation. If genetics are the primary factor, then focus should be placed

on managing expectations of the size of deer that can be produced in an area, instead of increasing deer morphometrics. However, regional variation should be determined in older age class deer ( $\geq 2$  years) because regional variation increases significance with age. Comparison of younger aged deer would not accurately determine regional effects.

Until nutritional resource impacts are quantified on skeletal development, skeletal growth should not be precluded as a factor affecting regional body size differences. If nutritional quality is low during growth, then genetic skeletal size potential of an individual might not be acquired, which may be accredited falsely as subspecies variation. Therefore, this is of critical importance to conservation biology because maintenance of adaptive potential and evolutionary flexibility is founded on the preservation of genotypes, not phenotypes (Geist et al. 2000). We should not be overzealous in assigning subspecies until we completely understand morphological variation and effects of nutritional variation. Application of resources to delineate and protect subspecies of white-tailed deer is wasteful if the true cause of morphological variation is produced from nutrition variation.

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APPENDIX A

TABLE OF PERCENTAGES OF EPIPHYSEAL PLATES OF WHITE-TAILED DEER  
EXHIBITING CLOSURE FOR FOUR GROWTH PLATES BY GENDER  
AND REGION OF ORIGIN IN MISSISSIPPI, USA FED 20%  
PROTEIN PELLETS AD LIBITUM DURING 2007-2009.

Appendix A. Percentage of epiphyseal plates of white-tailed deer exhibiting closure for four growth plates by gender and region of origin (Delta, a greater quality area with larger body and antler size; Thin Loess [Loess], a moderate quality area with moderate body and antler size; and Lower Coastal Plain [LCP], a lesser quality area with smaller body and antler size) in Mississippi, USA fed 20% protein deer pellets ad libitum during 2007 - 2009.

Epiphyseal Plate	Age	Delta				Loess				LCP			
		M		F		M		F		M		F	
		%	<i>N</i>	%	<i>N</i>	%	<i>N</i>	%	<i>N</i>	%	<i>N</i>	%	<i>N</i>
Distal humerus	0.5	82	11	88	8	71	17	94	17	100	11	100	14
	1	100	12	100	11	100	14	100	23	100	25	100	14
	2	100	12	100	9	100	15	100	18	100	5	100	12
	3	100	12	100	5	100	13	100	15	100	6	100	9
Proximal radius	0.5	82	11	88	8	53	17	94	17	100	10	100	15
	1	100	12	100	11	100	15	100	23	100	25	100	14
	2	100	12	100	9	100	15	100	18	100	5	100	12
	3	100	13	100	4	100	13	100	15	100	6	100	9
Distal radius	0.5	0	11	0	8	0	17	0	16	0	11	0	15
	1	9	12	0	11	0	16	0	21	0	26	0	14
	2	50	12	89	9	14	14	94	18	20	5	83	12
	3	100	15	100	4	100	14	100	15	100	6	100	9
Distal metacarpal	0.5	0	11	0	8	0	17	0	13	0	11	0	15
	1	0	12	10	10	0	16	0	22	0	27	0	14
	2	92	12	89	9	77	13	100	18	80	5	100	12
	3	100	16	100	3	100	14	100	15	100	6	100	9