

5-11-2013

## Effect of Dominance in Captive Female White-Tailed Deer (*Odocoileus Virginianus*)

Eric S. Michel

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Effect of dominance in captive female white-tailed deer (*Odocoileus virginianus*)

By

Eric S. Michel

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

May 2013

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2013

Effect of dominance in captive female white-tailed deer (*Odocoileus virginianus*)

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Factors associated with rank position are poorly understood whereas even fewer studies assessed if benefits were associated with increased rank position when resources were unlimited. I assessed whether age, body mass, size, and testosterone levels were important in rank establishment among 132 captive female white-tailed deer (*Odocoileus virginianus*). I also assessed if the benefit metrics of improved body condition, decreased stress level, and earlier parturition date were related to rank position. Deer in each of 9 study pens had a linear hierarchy with a mean  $h'$  of 0.39 ( $SD = 0.09$ ). Rank position was moderately related to age ( $P < 0.1$ ) and was strongly related to body mass and size ( $P < 0.01$ ). There was no relationship between benefit metrics and rank position ( $P < 0.1$ ). Although increased body mass, size, and age improved rank position there were no benefits associated with increased rank when resources were unlimited.

## DEDICATION

I dedicate this thesis to my family, friends, and the multiple people that have helped and supported me along the way. I thank my Mom and Dad, Steve and Barb Michel, who have always supported and believed in me with everything I have done. I could not have done it without you. Finally, I dedicate this thesis to my Grandfather, Frank Michel. Although you were only present in my life for a short period you were, and always will be one of the biggest influences in my life. I can only hope the way I live life would make you proud.

## ACKNOWLEDGEMENTS

I thank Mississippi Department of Wildlife, Fisheries, and Parks biologists C. Dacus, L. Wilf, W. McKinley, A. Blaylock, and A. Gary for their extensive involvement in data collection. I also thank J. Oates for his help as co-manager of the captive facility, S. Tucker as facility coordinator, and K. Warren, J. Grantham, and E. Ratcliff and multiple techs for their help collecting observations. I thank past graduate students, J. and E. Flinn in particular, for their dedication to this project. I thank R. Woods at the University of Missouri for her assistance in conducting testosterone assays. Finally, I thank my major advisor Dr. S. Demarais as well as committee members Dr. B. Strickland and Dr. J. Belant for all of their time and patience in helping me succeed with this project. I will never be able to fully describe the extent of how much I appreciate all of your help. Thank you. This thesis is supported by MDWFP, the Federal Aid in Wildlife Restoration Project W-48, Study 65, the Department of Wildlife, Fisheries and Aquaculture at Mississippi State University, and the Mississippi State University Deer Lab.

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## CHAPTER I

### INTRODUCTION

Intraspecific competition affects access to resources which can affect body condition, reproductive success, and ultimately individual fitness (Appleby 1980, Clutton-Brock et al. 1984, Dunbar and Dunbar 1977, Holand et al. 2004, Reiter et al. 1981). Agonistic interactions during competition are energetically expensive (Appleby 1980); however, dominant animals offset these costs by monopolizing food resources which balances their energetic input and output (McEwen and Wingman 2003). Furthermore, the energetic expense of interactions is reduced by successful visual assessment of dominance traits such as body mass and body size (Côté 2000, Syme and Syme 1979).

Dominance studies have been conducted on many species of ungulates such as mountain goats (*Oreamnos americanus*; Côté 2000, Fournier and Festa-Bianchet 1995, Gendreau et al. 2005), red deer (*Cervus elaphus*; Clutton-Brock et al. 1984, Veiberg et al. 2004), American bison (*Bison bison*; Rutberg 1986, Vervaecke et al. 2005), bighorn sheep (*Ovis canadensis*; Favre et al. 2008), and white-tailed deer (*Odocoileus virginianus*; Taillon and Côté 2006, Townsend and Bailey 1981). Age and body mass are important in hierarchy establishment in white-tailed deer (Taillon and Côté 2006, Townsend and Bailey 1981). Furthermore, physiological factors such as testosterone may

increase aggressiveness and therefore be associated with social rank (Pelletier et al. 2003, Wingfield et al. 1990).

There are additional benefits that dominant animals gain when they monopolize food resources. For example, when resources are limited dominant animals exhibit better body condition (Appleby 1980, Clutton-Brock et al. 1984, Holand et al. 2004, Vervaecke et al. 2005), lower stress levels (Creel 2001) and have increased reproductive success (Clutton-Brock et al. 1984, Reiter et al. 1981) compared to subordinates. In contrast, subordinate females with reduced access to resources had increased stress levels and decreased fitness due to negative effects on their metabolism and immune system (Barroso et al. 2000, Creel 2005, Ozoga et al. 1982, Sapolsky 1992).

I assessed how probable factors such as age, body mass, body size and testosterone metabolites varied with social rank in captive groups of adult female white-tailed deer having access to unlimited food resources in Chapter II. In Chapter III, I determined if benefit metrics (i.e., increased rump-fat depth, decreased glucocorticoid levels, and earlier parturition dates) were related to social rank position. Understanding factors associated with social rank and benefits associated with rank position are important because intraspecific competition influences life-history characteristics of a species (Mees 1969) and fitness of individuals (Reiter et al. 1981).

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## CHAPTER II

### FACTORS AFFECTING POSITION WITHIN A DOMINANCE HIERARCHY OF CAPTIVE FEMALE WHITE-TAILED DEER (*Odocoileus virginianus*)

Intraspecific competition affects access to resources which can affect body condition, reproductive success, and ultimately individual fitness (Appleby 1980, Clutton-Brock et al. 1984, Dunbar and Dunbar 1977, Holand et al. 2004a, Reiter et al. 1981). However, agonistic interactions during competition are energetically expensive, with negative consequences to winners and losers (Appleby 1980). Dominance hierarchies reduce energetic expense of these interactions by successful visual assessment of physical traits that increase with age such as body mass and body size (Côté 2000, Strickland and Demarais 2000, Syme and Syme 1979).

Dominance studies have been conducted on ungulates such as mountain goats (*Oreamnos americanus*; Côté 2000, Fournier and Festa-Bianchet 1995, Gendreau et al. 2005), red deer (*Cervus elaphus*; Clutton-Brock et al. 1984, Veiberg et al. 2004), American bison (*Bison bison*; Rutberg 1986, Vervaecke et al. 2005), and bighorn sheep (*Ovis canadensis*; Favre et al. 2008) with age and body mass generally being the most important traits associated with social rank position. Similarly, age and body mass are important traits associated with dominance in white-tailed deer (*Odocoileus virginianus*; Taillon and Côté 2006, Townsend and Bailey 1981). For example, Townsend and Bailey (1981) concluded age was most important in establishing social rank in adult female



white-tailed deer whereas Taillon and Côté (2006) reported that body mass was strongly related to social rank in male and female white-tailed deer fawns. Furthermore, physiological factors such as testosterone may increase aggressiveness and therefore may be associated with social rank (Pelletier et al. 2003, Wingfield et al. 1990).

Understanding factors associated with social rank is important because intraspecific competition influences life-history characteristics of a species (Mees 1969) and fitness of individuals (Reiter et al. 1981).

I assessed how probable variables such as age, body mass, overall body size and testosterone metabolites (hereafter testosterone) varied with social rank of captive groups having access to unlimited food resources. I hypothesized that age would be positively associated with social rank because social rank may increase with experience (Townsend and Bailey 1981). I also hypothesized that body mass and body size would positively affect social rank because visual assessments of body size may influence an animal's decision to interact with other animals (Veiberg et al. 2004). However, body mass and overall body size increases directly with age through physical maturity, which occurs at 3.5 years for female white-tailed deer (Strickland and Demarais 2000), and thereafter only age and experience would be expected to vary. Therefore, I hypothesized age, body mass and overall body size would be important and interrelated in hierarchy establishment among younger animals (Côté 2000, Favre et al. 2008) and differences in body mass and overall body size would be more important than age in hierarchy establishment after physical maturity is attained (Favre et al. 2008). Finally, I hypothesized that dominant females would have greater levels of testosterone compared

to subordinate females because increased levels of testosterone are associated with aggression (Grant and France 2001, Wingfield et al. 1990).

## **MATERIALS AND METHODS**

### **Study area**

I conducted this research at Johnnie R. “Rusty” Dawkins Memorial Deer Unit at Mississippi State University, a 4.9-ha facility consisting of 5 0.4–0.8-ha pens. Pens held known-aged female white-tailed deer that were 1<sup>st</sup> and 2<sup>nd</sup> generation offspring of wild dams captured from the delta, thin loess, and lower coastal plain soil regions in Mississippi (Pettry 1977). I grouped deer by soil region due to body size variation (Strickland and Demarais 2000). Deer had year-round access to a full-ration pelleted feed (20% crude protein; Purina AntlerMax Professional High Energy Breeder 59UB, Purina, St. Louis, Missouri) *ad libitum* in 2 feed troughs located at opposite ends of each pen. Durana white clover (*Trifolium repens*; Pennington Seed Co., Madison, Georgia) and Max-Q Fescue (*Festuca arundinacea shreb*; Pennington Seed Co.) grew as a supplemental food throughout each pen.

### **Dominance hierarchy**

I assessed dominance hierarchies within each pen from December through April 2008–2011 from observed social interactions collected from 0800 to 1700. I placed about 900 g of triple-cleaned corn (Southern Seed & Feed, Macon, Mississippi) in 3 piles about 1 meter apart at the beginning of each observation, creating a defensible resource to increase observable interactions (Appleby 1980, Clutton-Brock et al. 1976, Schoener

1983). I monitored interactions continuously to ensure I documented maximum number of interactions (Altmann 1974). Observation blocks ranged from 30 minutes to 4 hours.

I defined a dominance relationship as an individual deer initiating (i.e., displaying dominant behaviors) at least 3 interactions with another deer (de Vries 1998). I defined interactions as independent when a threatened female assumed normal behavior (i.e., feeding, grooming, etc.) and was at least 1 body length away from the aggressor. Independent interactions may have included multiple behaviors. I recorded interactions related to dominance, such as head high, ears back (stare from individual with ears flattened along neck), displacement, chase, foreleg kick (1 or more blows with forefoot), and rear and flail (rising on hind legs to kick with pedaling movement of forelegs; Ozoga 1972) and recorded unique ear tag number of the aggressor and subordinate. I determined the winner of an interaction when 1 of the deer withdrew from the interaction.

Matman (Noldus Information Technology version 1.1; Leesburg, Virginia) used all pairwise animal interactions among individuals to calculate a linear dominance hierarchy. Matman provides a test for linearity ( $h'$  index) which accounts for individuals in a group with no direct interactions by comparing interactions of these individuals to other individuals with observed interactions (de Vries 1995). Matman runs a randomization test to determine if the  $h'$  index for each hierarchy was different from random. Linearity ranges from 0 (absence of linearity) to 1 (complete linearity; Taillon and Côté 2006). Matman then reorganizes significantly linear hierarchies by an iterative procedure (1000 randomizations) that ranks individuals by minimizing number of inconsistencies which occur when individual  $j$  dominates individual  $i$ , when  $j$ 's rank was less than  $i$ 's.

## **Morphometric and hormonal measurements**

I chemically immobilized deer to collect measurements during November 2008–2010. I used a 2:1 mixture of Telazol (Fort Dodge Animal Health, Fort Dodge, Iowa) and xylazine HCl (Phoenix Scientific, St. Joseph, Missouri) with an estimated dosage of 6.6 mg/kg via cartridge fired dart (Pneu-Dart Inc, Williamsport, Pennsylvania). I reversed effects of xylazine HCl with 0.125 mg/kg yohimbine hydrochloride (Kreeger 1996) or 4.0 mg/kg tolazoline hydrochloride (Miller et al. 2004). I measured body mass (kg) and total body length (mm) while animals were sedated. I used body mass and total body length to calculate a scaled mass index (SMI) to supplement body mass as a measure of overall body size (Peig and Green 2009).

I assessed testosterone levels in fecal samples collected by manual removal from the rectum after immobilization during November 2010 and opportunistically by direct observation of defecation from December 2010 to March 2011. I collected at least 1 fecal sample from each deer during daylight hours and placed them in a -80° C freezer. When I collected multiple samples for an individual, I analyzed them separately and averaged their values. My research followed the American Society of Mammalogists guidelines for use of wild mammals in research (Sikes et al. 2011) and Mississippi State University Institutional Animal Care and Use Committee approved all methods under protocols 04–068 and 07–036.

I placed frozen fecal samples in a lyophilizer (Freeze-dry Specialties, Inc., Osseo, Minnesota) for 24 hours. I ground freeze-dried samples and sifted them through a stainless steel mesh (U.S. standard number 25 stainless steel) to remove large particles. I mixed about 0.2 g of dried samples in a test tube with 2.0 mL of 90% methanol at high

speed for 30 minutes. I centrifuged samples at ~1900 g for 20 minutes and stored supernatant at -20 °C (Millspaugh et al. 2002).

I measured testosterone using a commercially available testosterone I<sup>125</sup> double-antibody radioimmunoassay kit (Cat. #07189102, MP Biomedicals, Solon, Ohio). I followed manufacturer's method for testosterone I<sup>125</sup> RIA, except I halved volume of all reagents. I conducted a standard assay validation including assessment of parallelism, recovery of exogenous analyte, intra- and interassay precision, and assay sensitivity (Grotjan and Keel 1996, Jeffcoate 1981, O'Fegan 2000) to confirm the assay accurately and precisely measured testosterone metabolites in white-tailed deer feces. I conducted parallelism and recovery of exogenous testosterone validation assays on 2 pooled, directly extracted fecal mixtures (expected lesser and greater levels; each pool consisted of feces from 3 samples). Parallelism ensured the assay maintained linearity under dilution, and recovery of exogenous testosterone verified accurate measurement throughout working range of the assay (Jeffcoate 1981). I added exogenous testosterone to lesser and greater pooled fecal extracts to obtain testosterone values at greater dilution levels. I used tests for equal slopes (parallelism) to determine if log-transformed curves of serially diluted pooled fecal extracts were parallel to log-transformed testosterone standard curves. I selected 2 fecal samples and analyzed them in 2 assays; interassay variation was calculated from these 2 samples. I calculated intra-assay variation by averaging the coefficient of variation of replicate tubes from 20 randomly selected samples.

## **Data Analysis**

I estimated relationships among body mass, SMI, age, testosterone, and social rank using an analysis of covariance (ANCOVA) in the MIXED procedure in SAS (SAS version 9.2; SAS Institute, Cary, North Carolina; Littell et al. 2006). I accounted for inherent correlations between body mass and age and body mass and region (Strickland and Demarais 2000) by assigning social rank as a response variable and age as a fixed categorical variable in the model. I assigned body mass, SMI, and testosterone as continuous covariates in their respective models and made soil region a random effect to account for any regional variation. This approach allowed me to examine effects of body mass, SMI, and testosterone in the presence of age in my models. I standardized social rank according to Côté (2000) because number of deer varied across pens. The resulting hierarchy provided a rank (0 to 1) for each individual in each observed group of deer. All deer from each pen were pooled to increase power of analysis.

To assess relative importance of age in rank establishment within immature and mature animals I divided deer into immature (1.5–3.5 year-olds) and mature (3.5–5.5 year-olds) age classes. I re-standardized social rank (Côté 2000) after separating animals into age classes and analyzed them under the previously stated ANCOVA framework. I accounted for regional variation by making soil region a random effect; however, the model estimated variance at 0. Therefore, I removed soil region as a random effect to meet convergence criteria.

## **RESULTS**

I observed deer for 252 hours, averaging 28 hours per pen ( $SD = 8.2$ ). I observed 132 individual female white-tailed deer in 2–4 pens per year during 2008–2011. Across 9

total pens I averaged 15 deer per pen ( $SD = 4.4$ ). I produced a linear dominance hierarchy among deer in each of 9 pens (Table 2.1) with a mean  $h'$  of 0.39 ( $SD = 0.09$ ). Mean age of deer in respective pens was 2.8 years (range = 1.8–4.0 years; Table 2.2). Range of age and body mass within pens averaged 2.4 years and 19.89 kg, respectively.

I collected 84 fecal samples with an average of 2.1 samples (range = 1–5) from each of 39 deer for a mean testosterone level of 16.99 ng/g ( $SD = 6.44$ ). The  $I^{125}$  RIA accurately and precisely measured testosterone. Serial dilutions (1:4 to 1:128) of fecal extracts yielded displacement curves that were parallel to the testosterone standard curve (Fig. 2.1). Mean percentage recovery of added exogenous testosterone (range 0.5–2.5 ng/mL) was 111.9% ( $SE = 1.7$ ,  $n = 6$ ). Acceptable recovery of exogenous testosterone (within 90–110%) and demonstration of parallelism suggested no sample matrix effects (Grotjan and Keel 1996, Jeffcoate 1981, O’Fegan 2000). Assay sensitivity was 0.025 ng/ml. The manufacturer’s reported cross-reactivity of antisera with testosterone was 100% and less than 3.4% for other steroids. Inter-assay variation for 4 assays was 4.5% and average intra-assay variation was 2.4% for 4 assays.

Age was related to dominance rank but only in younger animals. Social rank was associated with age among immature deer ( $P = 0.073$ ,  $F_{2,89} = 2.69$ ,  $n = 93$ ; Fig. 2.2A) but not among mature deer ( $P = 0.893$ ,  $F_{2,77} = 0.11$ ,  $n = 81$ ) and when all aged deer were combined ( $P = 0.163$ ,  $F_{4,124} = 1.66$ ,  $n = 132$ ).

Body mass and SMI were related to dominance rank at all ages. Social rank was related to body mass within immature ( $P = 0.055$ ,  $F_{1,89} = 3.77$ ,  $n = 93$ ; Fig. 2.2A), mature ( $P = 0.037$ ,  $F_{1,77} = 4.49$ ,  $n = 81$ ; Fig. 2.2B), and all aged deer ( $P = 0.004$ ,  $F_{1,124} = 8.53$ ,  $n = 132$ ; Fig. 2.2C). Social rank was also related to SMI within immature ( $P = 0.059$ ,  $F_{1,89}$

= 3.67,  $n = 93$ ; Fig. 2.3A), mature ( $P = 0.039$ ,  $F_{1\ 77} = 4.39$ ,  $n = 81$ ; Fig. 2.3B), and all aged deer ( $P = 0.005$ ,  $F_{1\ 124} = 8.35$ ,  $n = 132$ ; Fig. 2.3C). Body mass was more important for mature ( $\beta = 0.011$ ) than immature deer ( $\beta = 0.009$ ). Similarly, SMI was more important for mature ( $\beta = 0.011$ ) than immature deer ( $\beta = 0.009$ ). Testosterone was not related to social rank ( $P = 0.781$ ,  $F_{1\ 34} = 0.08$ ,  $n = 39$ ). There was no interaction between age and body mass or body size ( $P > 0.1$ ) which resulted in a consistent slope for body mass by year class and body size by year class (Table 2.3). Although slopes were consistent for year class for body mass and SMI, intercepts varied by year class for body mass and SMI.

## DISCUSSION

Lack of relationship between social rank and age with all ages combined contradicts my hypothesis and previous research involving white-tailed deer (Townsend and Bailey 1981), red deer (Veiberg et al. 2004), bighorn ewes (Favre et al. 2008), and mountain goats (Côté 2000). This contradiction may be related to the relatively small range of deer ages represented in my study. Even though deer aged 1.5–5.5 were present in my overall analysis, average range within pens was only 2.4 years. This range represents a small portion of potential age range among adult female white-tailed deer, as reproductively successful wild females live up to 15.5 years (DelGiudice et al. 2007). Townsend and Bailey (1981) and Veiberg et al. (2004) did not report range of ages in their studies, but it appears they had older animals than I did. For example, Townsend and Bailey stated that their original herd was comprised of deer of various ages that were trapped from the wild. Their study lasted for almost 3 years; therefore, any mature deer (i.e., at least 3 years old) that was captured from the wild would have been at a minimum



6 years old at the end of the study. Red deer were at least 10 years old as Veiberg et al. (2004) stated that social rank peaked for animals around 10 years of age. Nevertheless, the 11 year age range in mountain goats (Côté 2000) and 12 year age range in bighorn ewes (Favre et al. 2008) represents greater potential differences in experience levels among study animals. Consequently, the relatively limited range of experience level within my study may have reduced importance of age in determining social dominance.

The relationship between social rank and age for immature and not for mature animals supports my hypothesis, as well as results of Favre et al. (2008), where social rank and age were more strongly related in immature ( $r^2 = 0.75$ ) than mature bighorn ewes ( $r^2 = 0.15$ ). Similarly, Holand et al. (2004b) found that social rank and age was highly related ( $r^2 = 0.76$ ) in female reindeer (*Rangifer tarandus*) under 8 years of age but not in females older than 8. Age may be more strongly related to social rank among immature animals because of greater gains of body mass each year until physical maturity is reached, at which time body mass becomes more independent of age (Côté 2000, Favre et al. 2008).

The significant relationships between social rank and body mass and overall body size (i.e., SMI) of female white-tailed deer supports my hypotheses and previous work with red deer hinds and calves (Veiberg et al. 2004), female American bison (Vervaecke et al. 2005), female reindeer (Holand et al. 2004b), and juvenile male and female white-tailed deer (Taillon and Côté 2006) where all studies found a positive relationship between rank position and body mass and body size. Body mass can influence social rank position by improving fighting ability and by serving as a physical attribute that is easily assessed by individuals before engaging in an interaction (Holand et al. 2004b, Veiberg et

al. 2004, Vervaecke et al. 2005). Thus, larger females in my study may have displayed an improved fighting ability and were challenged less often and therefore had an increased social rank position compared to smaller females.

My relationship between social rank and body mass for immature and mature animals supports my hypothesis and results of Favre et al. (2008). Favre et al. (2008) found that social rank was positively related to body mass in immature bighorn ewes; however, the correlation between age and body mass make it difficult to differentiate relative impacts. My relationship between social rank and body mass among mature animals also supports Favre et al. (2008) because body mass was more important than age among mature deer. Furthermore, body mass and body size were more important for mature ( $\beta = 0.011$ ,  $\beta = 0.011$ , respectively) than immature deer ( $\beta = 0.009$ ,  $\beta = 0.009$ ; respectively). Age, body mass, and body size are all important in social rank establishment among immature animals because older animals are generally larger than younger animals before physical maturity (Côté 2000, Favre et al. 2008). However, body mass becomes independent of age after maturity (i.e., the oldest animal is not always the largest) and becomes more important than age in social rank establishment among mature animals (Favre et al. 2008). Consequently, in the mature age class, older but smaller animals use body mass and body size as visual cues to determine whether to engage in an interaction because they may not have a greater fighting ability than younger but larger animals (Holand et al. 2004b, Veiberg et al. 2004, Vervaecke et al. 2005).

Presence of *ad libitum* feed and supplemental herbaceous forage year round may have decreased the relative importance of dominance and therefore, variables related to its establishment. These unlimited resources created an environment where competitive

interactions were not required for access to the resources needed to ensure animal success. Lack of clear negative consequences may have decreased the benefits associated with a strongly linear dominance hierarchy. Dominance linearity was twice as great when white-tailed deer fawns had only 1 feeder with *ad libitum* feed and no natural forage ( $\bar{X}=0.72$ ; Taillon and Côté 2006) than my study ( $\bar{X}=0.39$ ). I may have observed greater linearity and stronger relationships between social rank and measured variables in a more competitive environment with limited resources.

Lack of relationship between testosterone and social rank may be explained by the “challenge” hypothesis, which states increased testosterone levels are associated with social rank only at times of social instability (i.e., rank determination; Wingfield et al. 1990). If hierarchies were established during initial encounters among deer (Taillon and Côté 2006), my fecal sampling period from December to April may have missed the period of social instability needed to impact testosterone levels because I moved deer during November. Additionally, I was only able to collect a low number of samples per deer (i.e.,  $\bar{X} = 2.1$ ) which may have inhibited my ability to detect a relationship between social rank and testosterone. Furthermore, samples were not always collected after aggressive interactions. Collecting samples after aggressive interactions is important because testosterone levels may only be elevated for short periods after an interaction (Wingfield et al. 1987).

Unlimited resources may have influenced my results by reducing competition and aggression among deer (Barroso et al. 2000, Wingfield et al. 1987). If increased testosterone levels are related to increased aggression (Grant and France 2001, Wingfield et al. 1990) then the lack of a relationship between testosterone and social rank position

may have been due to decreased aggression due to unlimited resources. Alternatively, other hormones may be related to aggression. For example, estrogen and photoperiod may affect aggressive behavior in male house mice (*Mus musculus*) by affecting estrogen receptors in parts of the brain (Trainor et al. 2006, Trainor et al. 2007). I suggest future sampling be conducted during a period of social instability and include a wider variety of hormones sampled, such as estrogen.

The interrelationship between age and body mass makes it difficult to clearly elucidate their relationships with social rank. A controlled experiment is needed to clearly document relationships between social rank and age and social rank and body mass. Animals that have similar body mass but are of different ages need to be grouped together to document the relationship between social rank and age. Similarly, animals of the same age with a wide range of body mass need to be grouped to explore effects of body mass on social rank in the same manner as Taillon and Côté (2006). Such designed experiments with a priori assignment of animals based on ages and physical characteristics would help resolve this issue.

Body mass and SMI are traits related to increased social rank position. Increased social rank is important to resource acquisition when resources are limited (Appleby 1980). Increased social rank position and resource acquisition may also be related to improved body condition, earlier parturition date, and heavier offspring at birth (Clutton-Brock et al. 1986, Vervaecke et al. 2005) all of which may relate to increased reproductive success (Clutton-Brock et al. 1986). Therefore, older and larger females benefit from an increased social rank position which may influence future reproductive success.

Table 2.1 Total interactions,  $h$  (linearity), and  $h'$  (linearity when unknown relationships are accounted for) associated with 9 dominance hierarchies of female white-tailed deer at Mississippi State University captive research facility in Mississippi State, Mississippi, USA 2008–2010.

	Total Interactions Observed	Total Number of Deer	Directional Consistency Index	$h$	$h'$	$P$
2008-2009						
Pen 1	78	14	0.87	0.27	0.37	0.057
Pen 2	79	14	0.87	0.24	0.35	0.080
2009-2010						
Pen 1 <sup>a</sup>	567	13	0.78	0.41	0.44	0.018
Pen 2	492	13	0.81	0.37	0.38	0.034
Pen 3	193	11	0.69	0.50	0.55	0.009
Pen 4	640	13	0.89	0.40	0.44	0.015
2010-2011						
Pen 1 <sup>a</sup>	154	13	0.84	0.38	0.44	0.033
Pen 2	166	15	0.78	0.35	0.26	0.048
Pen 4	237	26	0.90	0.18	0.25	0.003
$\bar{X}$	290	15	0.83	0.34	0.39	N/A

<sup>a</sup>These pens contained the same deer during both sampling periods. The single most dominant and single most subordinate deer maintained the same rank in both years. However, multiple deer changed rank from 2009–2010 to 2010–2011 seasons.

Table 2.2 Mean and range of within-pen mean age (years), mass (kg), scaled mass index (SMI; kg), total body length (TBL; mm), and testosterone (ng/g) for 9 pens at the Mississippi State University captive research facility in Mississippi State, Mississippi, USA 2008–2010.

Variable	$\bar{X}$	<i>SD</i>	Range
Age	2.8	0.72	1.8–4.0
Mass	48.88	3.59	44.62–55.79
SMI	48.86	3.58	44.60–55.78
TBL	1616.34	40.12	1564.59–1676.40
Testosterone <sup>a</sup>	16.99	6.44	11.62–24.13

<sup>a</sup>Testosterone data was averaged across 3 pens as a result of only being collected 1 year. All other variables were averaged across 9 pens for 3 years.

Table 2.3 Slopes, intercepts, and associated *P*-values from an analysis of covariance model representing relationships between mass and SMI and social rank by age class for female, white-tailed deer at the Mississippi State University captive research facility in Mississippi State, Mississippi, USA 2008–2010. Slopes are same for each age class by variable due to a non-significant interaction between associated variables and age class.

Variable	Age	Slope	Intercept	<i>P</i>
Mass <sup>a</sup>	1	0.011	-0.235	0.706
	2	0.011	-0.074	0.145
	3	0.011	-0.030	0.845
	4	0.011	-0.083	0.444
	5	0.011	-0.091	0.929
Mass <sup>b</sup>	1	0.009	-0.124	0.023
	2	0.009	0.001	0.313
	3	0.009	0.067	0.783
Mass <sup>c</sup>	3	-0.079	0.011	0.988
	4	-0.113	0.011	0.726
	5	-0.080	0.011	0.765
SMI	1	0.011	-0.241	0.146
	2	0.011	-0.080	0.843
	3	0.011	-0.035	0.441
	4	0.011	-0.088	0.922
	5	0.011	-0.097	0.695

<sup>a</sup>Body mass for all ages (1.5–5.5).

<sup>b</sup>Body mass for immature age class (1.5–3.5 year-olds).

<sup>c</sup>Body mass for mature age class (4.5–5.5 year-olds).

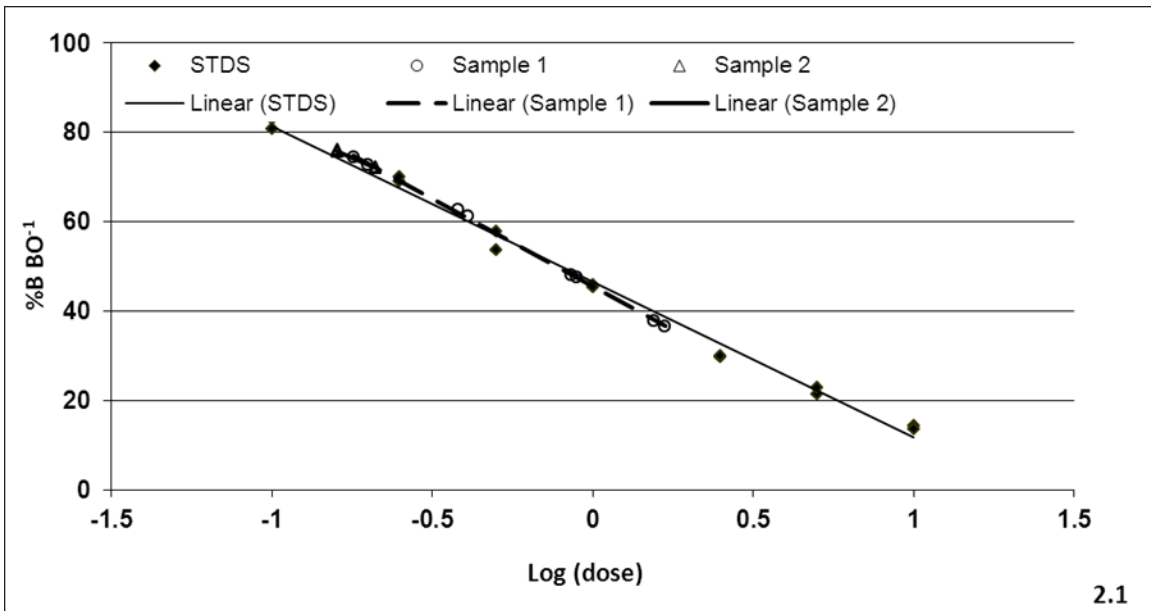


Figure 2.1 Parallelism results for fecal testosterone for white-tailed deer. Curves of percentage binding of I<sup>125</sup> tracer (%B BO-1) versus serially diluted low pool and high pool fecal extracts from white-tailed deer were parallel to testosterone standard curves (log-transformed doses). Diamonds: testosterone standard curve points, circles: serially diluted low fecal extracts, and triangles: serially diluted high pool fecal extracts.



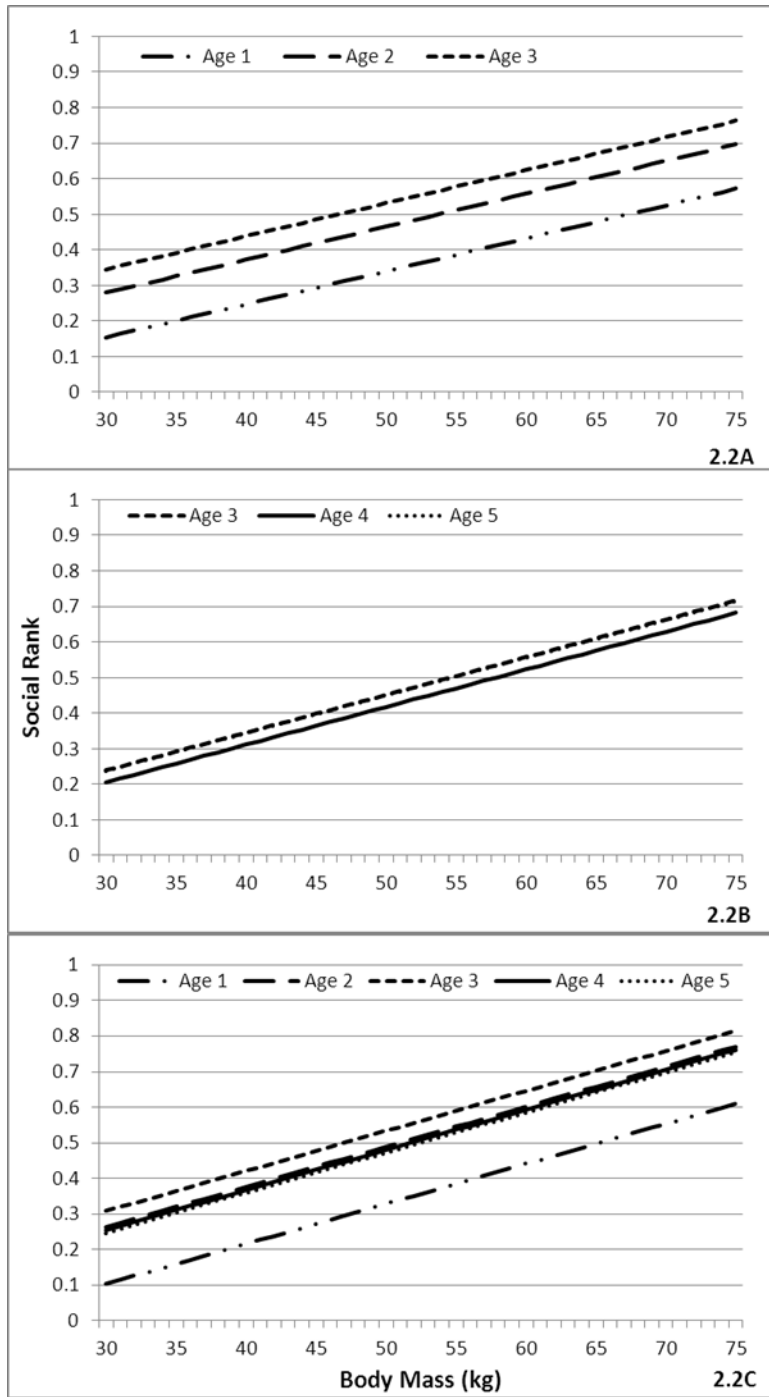


Figure 2.2 Relationship between social rank and body mass when adjusted for age for immature (i.e., 1–3;  $F_{1,89} = 3.77$ ,  $P = 0.055$ ), mature (i.e., 3–5;  $F_{1,77} = 4.49$ ,  $P = 0.037$ ), and all aged deer (i.e., 1–5;  $F_{1,124} = 8.53$ ,  $P = 0.004$ ) from an analysis of covariance model using captive white-tailed deer from Mississippi State University, Mississippi State, Mississippi, USA 2008–2011. Positive slopes indicate an increase in social rank with increased body mass and age.

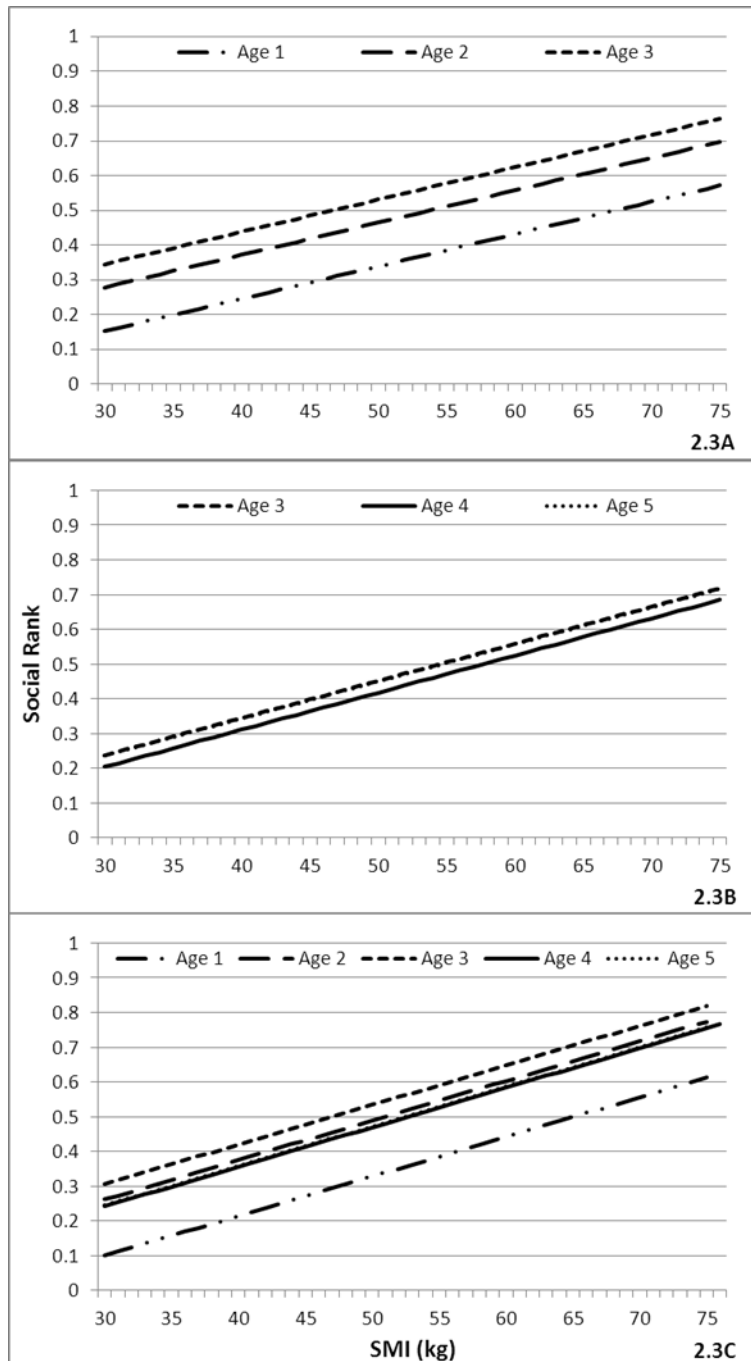


Figure 2.3 Relationship between social rank and SMI when adjusted for age for immature ( $F_{1,89} = 3.67, P = 0.059$ ), mature ( $F_{1,77} = 4.39, P = 0.039$ ), and all aged deer ( $F_{1,124} = 8.35, P = 0.005$ ) from an analysis of covariance model using captive white-tailed deer from Mississippi State University, Mississippi State, Mississippi, USA 2008–2011. Positive slopes indicate an increase in social rank with increased SMI and age.

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### CHAPTER III

#### LACK OF RELATIONSHIP BETWEEN SOCIAL RANK AND BENEFIT METRICS IN PRESENCE OF UNLIMITED RESOURCES IN FEMALE WHITE-TAILED DEER

*(Odocoileus virginianus)*.

Dominant animals offset costs associated with establishment and maintenance of social hierarchies by monopolizing food resources which balances their energetic input and output (McEwen and Wingman 2003). When resources are limited dominant animals exhibit better body condition (Appleby 1980, Clutton-Brock et al. 1984, Holand et al. 2004, Vervaecke et al. 2005), decreased stress levels (Creel 2001) and have increased reproductive success (Clutton-Brock et al. 1984, Reiter et al. 1981) compared to subordinates. In contrast, subordinate animals with reduced access to resources had increased stress levels and decreased fitness due to negative effects on their metabolism and immune system (Barroso et al. 2000, Creel 2005, Ozoga et al. 1982, Sapolsky 1992).

Although animals benefit from increased food acquisition when resources are limited (Appleby 1980, Clutton-Brock et al. 1984, Creel 2001), there has been limited effort to assess this relationship in presence of unlimited food. Brouns and Edwards (1994) found no difference in live mass gain between dominant and subordinate domesticated pigs (*Sus scrofa domesticus*) under an *ad libitum* feeding regime. Similarly, Taillon and Côté (2007) found no difference between social rank position and overwinter body mass loss in a captive population of white-tailed deer fawns (*Odocoileus*

*virginianus*) fed *ad libitum*. Lastly, dominant white-tailed deer did not observe increased survivorship compared to subordinate deer during times of abundant resources (i.e., winter cutovers; Ozoga 1972). Studying animals under ideal conditions (i.e., unlimited food resources) allows a more complete evaluation of the strength of the relationship between benefits metrics and social rank position.

I assessed if social rank of captive female white-tailed deer was associated with benefit metrics (i.e., increased rump-fat depth, decreased stress levels, and earlier parturition dates) when high-quality food was unlimited. Previous research has showed a lack of relationship between social rank position and benefit metrics (Brouns and Edwards 1994, Ozoga 1972, Taillon and Côté 2007); therefore, I hypothesized there would be no relationship between social rank and benefit metrics in presence of high-quality, unlimited food resources.

## **MATERIALS AND METHODS**

### **Study area**

I conducted this research at the Johnnie R. “Rusty” Dawkins Memorial Deer Unit at Mississippi State University, a 4.9-ha facility consisting of 5 0.4–0.8-ha pens. Deer had access to a full-ration pelleted feed (20% crude protein; Purina AntlerMax Professional High Energy Breeder 59UB, Purina, St. Louis, Missouri) *ad libitum* in 2 feed troughs located at opposite ends of each pen year round. Durana white clover (*Trifolium repens*; Pennington Seed Co., Madison, Georgia), Max-Q Fescue (*Festuca arundinacea shreb*; Pennington Seed Co.), and native volunteers grew as supplemental food throughout each pen.



## **Dominance hierarchy**

I assessed dominance hierarchies within each pen from December through April 2008–2011 from observed social interactions collected from 0800 to 1700. I placed about 900 g of triple-cleaned corn (Southern Seed & Feed, Macon, Mississippi) in 3 piles about 1 meter apart at the beginning of each observation, creating a defensible resource to increase observable interactions (Appleby 1980, Clutton-Brock et al. 1976, Schoener 1983). I monitored interactions continuously to ensure I documented the maximum number of interactions (Altmann 1974). Observation blocks ranged from 30 minutes to 4 hours.

I defined a dominance relationship as an individual deer initiating (i.e., displaying dominant behaviors) at least 3 interactions with another deer (de Vries 1998). I defined interactions as independent when a threatened female assumed normal behavior (i.e., feeding, grooming, etc.) and was at least 1 body length away from the aggressor. Independent interactions may have included multiple behaviors. I recorded interactions related to dominance, such as head high, ears back (stare from individual with ears flattened along neck), displacement, chase, foreleg kick (1 or more blows with forefoot), and rear and flail (rising on hind legs to kick with pedaling movement of forelegs; Ozoga 1972) and recorded unique ear tag number of the aggressor and subordinate. I determined the winner of an interaction when 1 of the deer withdrew from the interaction.

Matman (Noldus Information Technology version 1.1; Leesburg, Virginia) used all pairwise animal interactions among individuals to calculate a linear dominance hierarchy. Matman provides a test for linearity ( $h'$  index) which accounts for individuals in a group with no direct interactions by comparing interactions of these individuals to

other individuals with observed interactions (de Vries 1995). Matman runs a randomization test to determine if the h' index for each hierarchy was different from random. Linearity ranges from 0 (absence of linearity) to 1 (complete linearity; Taillon and Côté 2006). Matman then reorganizes significantly linear hierarchies by an iterative procedure (1000 randomizations) that ranks individuals by minimizing the number of inconsistencies which occur when individual j dominates individual i, when j's rank was lower than i's.

### **Morphometric and hormonal measurements**

I chemically immobilized deer to collect measurements during November 2008–2010. I used a 2:1 mixture of Telazol (Fort Dodge Animal Health, Fort Dodge, Iowa) and xylazine HCl (Phoenix Scientific, St. Joseph, Missouri) with an estimated dosage of 6.6 mg/kg via cartridge fired dart (Pneu-Dart Inc, Williamsport, Pennsylvania). I reversed the effects of xylazine HCl with 0.125 mg/kg yohimbine hydrochloride (Kreeger 1996) or 4.0 mg/kg tolazoline hydrochloride (Miller et al. 2004). I indexed body condition while deer were sedated using maximum rump-fat depth measured with an ultrasound (Model 180 plus, SonoSite, Bothell, Washington) only during November 2010 (Stephenson et al. 1998).

I assessed fecal glucocorticoid levels (i.e., stress) by removing fecal samples while deer were immobilized only during November 2010 and opportunistically by direct observation of defecation December 2010–March 2011. I collected at least 1 fecal sample from each deer during daylight hours and I placed them in a –80° C freezer. When I collected multiple samples for an individual, I analyzed them separately and averaged their values. My research followed American Society of Mammalogists guidelines for use

of wild mammals in research (Sikes et al. 2011) and Mississippi State University Institutional Animal Care and Use Committee approved all capture, handling, and marking techniques under protocols 04–068 and 07–036.

I estimated fecal glucocorticoid levels according to Millspaugh et al. (2002). I placed frozen fecal samples in a lyophilizer (Freeze-dry Specialties, Inc., Osseo, Minnesota) for 24 hours. I ground freeze-dried samples, sifted them through a stainless steel mesh (U.S. standard number 25 stainless steel) to remove large particles, and mixed them thoroughly. I mixed 0.2 g of sifted particles and 2.0 mL of 90% methanol at high speed for 30 minutes. I centrifuged samples at ~1900 g for 20 minutes and stored supernatant at –20 °C.

I measured corticosterone metabolites as a representation of glucocorticoid levels in supernatant using a commercially available corticosterone I<sup>125</sup> double-antibody radioimmunoassay (RIA) kit (Cat. #07120103, MP Biomedicals, Solon, Ohio). I followed manufacturer's method for corticosterone I<sup>125</sup> RIA, except I halved volume of all reagents (Wasser et al. 2000). Millspaugh et al. (2002) previously validated these procedures for white-tailed deer. Inter-assay variation was 3.7% and average intra-assay variation for 20 random samples was 1.4%.

### **Data analysis**

I estimated the relationship between social rank and dependent variables (i.e., maximum rump-fat depth, glucocorticoid levels, and parturition date) using an analysis of covariance (ANCOVA) in the MIXED procedure in SAS (SAS version 9.2; SAS Institute, Cary, North Carolina; Littell et al. 2006). I set social rank as a continuous covariate with age as a fixed categorical variable. An ANCOVA allowed me to assess the

relationship between dependent variables and social rank in presence of age in my models because age may also affect body condition (Carrión et al. 2008) and glucocorticoid level (Mooring et al. 2006). In addition to age being related to parturition date (Johns et al. 1977), body mass is also related to social rank (Chapter II). Therefore, I included body mass in the ANCOVA to account for any relationship between body mass and social rank. I transformed rank according to Côté (2000) due to varying numbers of deer. I also rank transformed parturition date by assigning the first birth as 0 and subsequent births as the number of days from first birth for each pen. All deer were pooled across pens to increase power of analysis. I evaluated pen and deer as random effects in the models but did not include them in the final analysis because the model did not converge.

## RESULTS

I observed deer for about 252 total hours averaging 28 hours per pen ( $SD = 8.2$ ). I observed 132 individual female white-tailed deer in 2–4 pens per year during 2008–2011. Across 9 total pens I averaged 15 deer per pen ( $SD = 4.4$ ) with a mean density of 18.3 per hectare ( $SD = 5.5$ ). This produced a linear dominance hierarchy among deer in each of 9 pens (Table 3.1) with a mean  $h'$  of 0.39 ( $SD = 0.09$ ).

I measured rump fat depth on 53 deer. I collected 91 fecal samples with a mean of 2.1 samples (range = 1–5) from each of 43 deer. Mean corticosterone level was 23.8 ng/g ( $SD = 19.3$ ). Mean parturition date was 2 August ( $SD = 21.6$ ) and mean percentage of does that were lactating during November was 51 ( $SD = 0.5$ ). Social rank was not associated with maximum rump-fat depth ( $P = 0.409$ ,  $F_{1,48} = 1.04$ ,  $n = 53$ ), corticosterone

levels ( $P = 0.411$ ,  $F_{1\ 38} = 0.93$ ,  $n = 43$ ), and parturition date ( $P = 0.435$ ,  $F_{1\ 109} = 0.61$ ,  $n = 116$ ).

## DISCUSSION

Lack of a relationship between preconception body condition, as measured by maximum rump-fat depth of female white-tailed deer, and social rank position supports my hypothesis. The allostatic load concept (McEwen and Wingfield 2003) may help explain this lack of relationship. Allostatic load is defined as balancing energy input with energy expenditure to conduct normal daily activities. Negative costs such as loss of body mass, diminishing body condition (i.e., decreasing maximum rump-fat depths), and death can occur when energy input is less than energy expenditure over prolonged periods (McEwen and Wingfield 2003). Social interactions may increase allostatic load thus causing an increase in energy input to balance energy expenditure. However, presence of unlimited resources may offset an increase in allostatic load. For example, Brouns and Edwards (1994) found no difference in body mass gain between dominant and subordinate domestic pig sows fed a uniform diet *ad libitum*. Similarly, there was no relationship between social rank and over-winter body mass loss in white-tailed deer fawns fed a uniform diet *ad libitum* (Taillon and Côté 2007). Furthermore, there was no difference between social rank position and winter mortality among white-tailed deer at winter cut-overs with an abundant food source (Ozoga 1972). Therefore, relatively unlimited resources within my pens likely ensured that subordinate deer were able to maintain their body condition regardless of social rank position by balancing their energy input with energy expenditure.

Sampling period might explain the lack of relationship between rank and body condition. Vervaecke et al. (2005) found a positive relationship between social rank and body condition (i.e., fatness measured on a scale from 1–5) in early lactating, semi free-ranging American bison (*Bison bison*). I estimated peak lactation to occur between 45 and 55 days after gestation by using equations derived by Moen (1973). Although most ( $\bar{X} = 51\%$ ) of my animals were still lactating during data collection in November, my collection period occurred approximately 90 days after mean parturition date. Fat reserves accumulate after peak lactation (Anderson et al. 1990). Therefore, I measured body condition while fat reserves were being replenished (i.e., pre-conception) in contrast to peak lactation when energetic demands were greatest and fat reserves may have been depleted. Furthermore, aggression is related to dominance and increases among females during late gestation regardless of food availability (Creel 2005, Townsend and Bailey 1975). Therefore, dominant females may have increased aggressive behavior towards subordinates which may have inhibited subordinates from feeding efficiently during late gestation. If social rank was stable throughout gestation (Côté 2000) and rank position influenced food acquisition during late gestation (Appleby 1980) then rank may be more related to peak lactation body condition than pre-conception body condition.

The lack of relationship between glucocorticoid levels and social rank supports my hypothesis that benefits would not be accrued when resources were abundant. The allostatic load concept suggests there should be no relationship between glucocorticoid levels and social rank when the cost of acquiring and maintaining rank is low (McEwen and Wingfield 2003, Goymann and Wingfield 2004). Cost of acquiring and maintaining social rank may have been reduced with food. This lessened cost may have reduced the

need for aggression and a resulting association between glucocorticoid levels and social rank in my study.

Other factors might be involved in the lack of relationship between social rank and stress levels. Forristal et al. (2012) reported a positive relationship between density and glucocorticoid levels in elk (*Cervus canadensis*). Hence, my animals may have experienced uniformly increased glucocorticoid levels due to relatively high density within pens ( $\bar{X} = 18.3$ ,  $SD = 5.5$ ). Alternatively, McCoy and Ditchkoff (2012) found relatively stable fecal glucocorticoid levels throughout the breeding season (i.e., my sampling period) in a penned population of female white-tailed deer. Consequently, uniformly elevated and minimally fluctuating fecal glucocorticoids in my study animals may have precluded detection of differences associated with social rank.

The relationship between social rank and parturition date is inconsistent in the literature and varies based on resource availability. For instance, lack of relationship between social rank and parturition date supports my hypothesis and results of Green and Rothstein (1991), who found no relationship between social rank and parturition date among American bison on natural range. In contrast, older female northern elephant seals (*Mirounga angustirostris*) tended to be more dominant, had earlier parturition dates, and observed increased reproductive success than younger females under a natural feeding regime (Rieter et al. 1981). This inconsistency may be related to different availability of resources. I did not consider resources as limiting in my study. Furthermore, resources may not have been limiting in Green and Rothstein's (1991) study because their population of bison was kept below carrying capacity. Conversely, resources were likely limited due to high a density of northern elephant seals found on birthing grounds (Reiter

et al. 1981). Therefore, the relationship between parturition date and social rank may only be apparent when resources are limited.

Presence of unlimited food reduced the advantage of increased social rank position among captive female white-tailed deer. Unlimited food resources ensured that all deer were able to balance their energy input with their energy output (McEwen and Wingfield 2003) and therefore, dominant animals did not display improved body conditions or earlier parturition. Similarly, cost (i.e., level of aggressiveness) of acquiring and maintaining a specific rank was reduced due to unlimited food (Goymann and Wingfield 2004) so there was no relationship between social rank and glucocorticoid levels. Although a dominance hierarchy was established among my study population with unlimited food, these conditions reduced amount of competition and aggression. Reduced costs of competition and abundant resources minimized differences in benefits between subordinate and dominant animals.



Table 3.1 Total interactions,  $h$  (linearity), and  $h'$  (linearity when unknown relationships are accounted for) associated with 9 dominance hierarchies of female white-tailed deer at Mississippi State University captive research facility in Mississippi State, Mississippi, USA 2008–2010.

	Total Interactions Observed	Total Number of Deer	Directional Consistency Index	$h$	$h'$	$P$
2008-2009						
Pen 1	78	14	0.87	0.27	0.37	0.057
Pen 2	79	14	0.87	0.24	0.35	0.080
2009-2010						
Pen 1 <sup>a</sup>	567	13	0.78	0.41	0.44	0.018
Pen 2	492	13	0.81	0.37	0.38	0.034
Pen 3	193	11	0.69	0.50	0.55	0.009
Pen 4	640	13	0.89	0.40	0.44	0.015
2010-2011						
Pen 1 <sup>a</sup>	154	13	0.84	0.38	0.44	0.033
Pen 2	166	15	0.78	0.35	0.26	0.048
Pen 4	237	26	0.90	0.18	0.25	0.003
$\bar{X}$	290	15	0.83	0.34	0.39	N/A

<sup>a</sup>These pens contained the same deer during both sampling periods. The single most dominant and single most subordinate deer maintained the same rank in both years. However, multiple deer changed rank from 2009–2010 to 2010–2011 seasons.

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## CHAPTER IV

### SYNTHESIS AND CONCLUSIONS

Dominance is an important behavior to understand because it influences resource acquisition with dominant animals having increased access to resources (Appleby 1980). Furthermore, when resources are limited dominant animals exhibit better body condition (Appleby 1980, Clutton-Brock et al. 1984, Holand et al. 2004, Vervaecke et al. 2005), decreased stress levels (Creel 2001) and have increased reproductive success (Clutton-Brock et al. 1984, Reiter et al. 1981) compared to subordinates. Although previous studies have shown a relationship between social rank and benefit metrics (i.e., improved body condition, decreased stress levels, and increased reproductive success) when resources are limited, there has been inadequate effort to assess this relationship in presence of unlimited food. Studying animals under ideal conditions (i.e., unlimited food resources) allows a more complete evaluation of the strength of the relationship between benefits metrics and social rank position.

Body mass, body size, and age are all important factors in hierarchy establishment; however, time at which these factors are important varies. Body mass and body size are important throughout maturity, whereas age is more important among immature animals. Age is important only among immature deer because of the correlation between body mass and age (Strickland and Demarais 2000). A 1 year difference in age among immature animals would lead to greater differences in body

mass compared to mature animals (Côté 2000). However, I cannot regard age as only being important among immature animals because of my relatively small range of ages observed in each pen.

Although I observed a linear hierarchy among deer, presence of unlimited food appears to reduce benefits related to increased social rank position. Unlimited food likely reduced competition by reducing the level of aggressiveness it took to acquire and maintain social rank position (Goymann and Wingfield 2004). Thus, neither dominant nor subordinate deer needed to expend more energy than they were able to intake (McEwen and Wingfield 2003); therefore, I failed to detect a relationship among body condition, stress levels, parturition date, and social rank.

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