

BODY SIZE, RUMEN-RETICULUM FUNCTIONS, AND DIETARY NUTRITION OF  
WHITE-TAILED DEER

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by

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San Marcos, Texas  
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BODY SIZE, RUMEN-RETICULUM FUNCTIONS, AND DIETARY NUTRITION OF  
WHITE-TAILED DEER

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## **ABSTRACT**

# **BODY SIZE, RUMEN-RETICULUM FUNCTIONS, AND DIETARY NUTRITION OF WHITE-TAILED DEER**

by

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May 2013

**SUPERVISING PROFESSOR: FLOYD W. WECKERLY**

Ruminants have a highly specialized digestive system which allows them to obtain nutrients from fibrous forage. The morphology of this digestive system changes with respect to the quality and quantity of consumed forage. Few studies have explicitly examined variation in ruminant digestive system morphology in semi-arid environments at low latitudes. The aim of my dissertation was to examine scaling relationships of anatomical and physiological rumen-reticulum attributes, dietary nutrition, rumen-reticulum fill, reserve capacity, and surface area of rumen mucosa across a body mass

gradient of white-tailed deer in a semi-arid environment. My findings indicate that scaling relationships between body mass and rumen-reticulum capacity were isometric. With regard to nutrition, juveniles and sub-adults consumed a higher quality diet (assessed by the ratio of protein to less digestible and indigestible carbohydrates), which should aid in meeting their high mass-specific metabolic demands. Factors governing rumen-reticulum function were complex because rumen-reticulum fill, reserve capacity, and absorptive surface area of the rumen mucosa were influenced by differing factors. One key finding was that surface area of the rumen mucosa had an inverse relationship with reserve capacity. This inverse relationship would allow individuals in a semi-arid environment to conserve metabolically expensive rumen-reticulum tissue, yet still allow them to accommodate sudden changes in forage quality. Additionally, my research indicates that white-tailed deer in a semi-arid environment had less pronounced seasonal changes in their surface area of rumen mucosa than deer at higher latitudes. My findings contain relevant information to intraspecific scaling relationships, forage niche partitioning, and anatomical patterns of the rumen-reticulum of deer inhabiting semi-arid environments.

## CHAPTER I

### INTRODUCTION

Ruminants have a highly specialized mode of digestion which allows them to obtain nutrients from fibrous forage (Van Soest 1994). The ruminant digestive system is characterized by pre-gastric forage retention and fermentation which is dependent on symbiotic relationships with micro-organisms. The ruminant forestomach can be regarded as a versatile, but highly efficient and well regulated fermentation chamber.

The rumen and reticulum of ruminant species are the gastrointestinal organs with the largest capacity and where most of the fermentation occurs (Van Soest 1994). Fermentation in the rumen-reticulum allows ruminants to extract energy from forage and convert non-protein nitrogen to microbial protein, which is more useful to the ruminant (Allen 1996). Fermentation rates differ with forage quality, therefore, fermentation rates impact rumen turnover and forage intake. For example, if the ingested forage has low digestibility, the composition of cellulose, which is recalcitrant to digestion, or lignin and cutin, which are completely indigestible, will be high and forage intake might be limited by rumen-reticulum capacity (Hummel et al. 2006, Van Soest 1994). Thus, to accommodate greater forage intake, rumen-reticulum capacity would have to increase to allow greater digesta loads.

The digesta load is comprised of the contents within the rumen-reticulum which consists of forage water, forage particles, and digestive fluids (Van Soest 1994). Digesta loads have been shown to fluctuate with forage intake, fermentation rates, and the nutritional content of the forage (Barboza et al. 2006; Van Soest 1994). Digesta load is typically measured by wet weight of the digesta in the rumen-reticulum. The wet weight of digesta can be greatly influenced by forage water and digestive fluids; however relationships between the wet weight and dry weight of digesta have not been thoroughly examined. Correlations between the wet weight and the dry weight of the rumen-reticulum contents are rarely estimated. The relationship between wet and dry weight of rumen-reticulum contents might have implications on rumen-reticulum functions.

Body size should also influence an animal's digestive efficiency (Barboza and Bowyer 2000; Van Soest 1994). Gut capacity increases as animal energy requirements increase (Barboza et al. 2009) such that larger bodied individuals will have greater gut capacity than small bodied individuals. Also, large bodied individuals will have greater absolute metabolic demands than their smaller bodied counterparts. Differences in metabolic demands can affect the type of forage selected as well as the amount of time spent foraging (Demment 1983; Demment and Van Soest 1985; Janis 1976; Prins and Geelen 1971; Van Soest 1994). Furthermore, the frequency of feeding and energy intake increases with mass-specific metabolic demands (Barboza et al. 2009). Scaling relationships of body size to metabolic rate and gut capacity have provided a theoretical basis for predicting that diet quality should vary inversely with body size.

Studies by Jarman (1968, 1974) and Bell (1971) indicated that larger ruminants could tolerate a poor quality diet more easily than their smaller bodied counterparts. Geist

(1974) coined this concept the Jarman-Bell principle. The Jarman-Bell principle is based upon two scaling relationships: for every 1% change in body weight there is a 0.67-0.75% change in metabolic rate and food intake, and gut capacity changes isometrically with body weight (scalar = 1.0). The allometric scaling of metabolic rate and the isometric scaling of gut capacity should allow for greater digesta loads and increased mean retention time as body weights increase. A greater mean retention time would prolong exposure of the digesta to microbial activity within the fermentation chamber. The increased time of exposure to microbes should enable the animal to increase nutrient extraction from forage containing high concentrations of recalcitrant structural carbohydrates.

While the Jarman-Bell principle is viable among species (Bell 1971; Bell 1970; Geist 1974; Jarman 1974; Sensenig et al. 2010; Yoshihara et al. 2008), it is not well supported within species (Duarte et al. 2011; Gross et al. 1996; Perez-Barberia et al. 2008; Perez-Barberia et al. 2007; Weckerly 2010; Weckerly and Nelson 1990). Weckerly (2010) demonstrated that white-tailed deer (*Odocoileus virginianus*) gut capacity could scale allometrically not isometrically with body weight. Moreover, the Jarman-Bell principle is difficult to apply given the enormous variability in rumen-reticulum capacity observed within species (Tulloh 1966; Weckerly 2010). The majority of variation in rumen-reticulum capacity appears to be linked with changes in metabolism and forage intake resulting from life history demands such as breeding, gestation, or lactation, however, rumen-reticulum capacity can also be influenced by season and age (Gross et al. 1996; Jenks et al. 1994; Jiang et al. 2009; Ramzinski and Weckerly 2007; Vetharanim et al. 2009).

As a result of the positive relationship between digestive capacity and body mass, large bodied individuals should be able to capitalize on increased forage retention times. The increase in retention time of forage should allow for an increase in exposure of digesta to micro-organisms and greater digestive efficiency. There is also evidence that smaller bodied animals display highly selective feeding behavior which results in targeting immature plants that are more nutritious due to low concentration of structural carbohydrates (Laca et al. 2010; Van Soest 1996). Therefore, animals that differ in body size might also differ in nutrition.

In addition to body size, environmental conditions can also influence forage intake and digestion. Hot environments have been shown to increase the animal's maintenance requirements and reduce voluntary forage intake (Silanikove 1992). Ungulates will decrease forage intake when they are dehydrated or in conditions where water availability is restricted (Balch et al. 1953; Silanikove 1985). The change in voluntary forage intake is likely the result of dry matter intake and water intake being correlated (MacFarlane and Howard 1972; Silanikove 1987). The change in forage intake could also be the result of a decrease in rumination when the animal is facing heat stress and dehydration (Gordon 1965; Silanikove 1992). Although forage intake might decrease with increasing ambient temperature, studies on steers (Warren et al. 1974) and sheep (Silanikove 1987) indicated that there was an increase in digestibility associated with heat stress because of reduced rumen motility.

Heat stress has also been shown to increase rumen volume in Bedouin goats (Silanikove 1992), beef cows (Silanikove and Tadmor 1989), and swamp buffalo (Chiayabutr et al. 1987). The increase in rumen volume might be an attempt to be able to

consume greater amounts of senesced forage, increase retention time, and increase exposure to micro-organisms. Additionally, there is a decrease in the outflow of rumen fluid, in an attempt to conserve water, when the animal is in a state of dehydration (Silanikove and Tadmor 1989). Therefore, the quantity of forage within the rumen and the amount of rumen fluid can fluctuate due to environmental influences.

### *Scope of This Dissertation*

The aim of my research was to examine variation in rumen-reticulum function of white-tailed deer in a semi-arid environment, how rumen-reticulum function is influenced by body mass, and the influence of body mass on nutrition. The three chapters of my dissertation are: (1) Scaling relationships between rumen-reticulum capacity and body mass, 2) Covariation of dietary quality with body sizes, and 3) Changes in rumen-reticulum attributes (rumen-reticulum fill, surface area of rumen mucosa, and reserve capacity) across seasons and years in a semi-arid environment. The information gathered from these studies provides greater understanding of scaling relationships, dietary nutrition, and rumen-reticulum morphology and function across a gradient of deer body sizes in a semi-arid environment.

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## CHAPTER II

### RUMEN-RETICULUM CHARACTERISTICS, SCALING RELATIONSHIPS AND ONTOGENY IN WHITE-TAILED DEER (*ODOCOILEUS VIRGINIANUS*)

Scaling relationships between body mass and gut capacity have been used to help explain digestive efficiency among and within species. Studies by Jarman (1974) and Bell (1971) indicated that larger species of ruminants digest a poorer-quality diet more completely than smaller species. Geist (1974) coined this phenomenon the Bell-Jarman principle. The Bell-Jarman principle is based upon 2 scaling relationships: for every 1% change in body mass there is a 0.67-0.75% change (i.e.,  $\text{Body mass}^{0.67-0.75}$ ) in metabolic rate and food intake, whereas gut capacity changes 1% for every 1% change in body mass ( $\text{Body mass}^{1.0}$ ). The isometric scaling of gut capacity should allow for greater digesta weight and increased mean retention time (MRT) as body mass increases because MRT should be the difference between gut capacity and food intake scalars (0.25-0.33). Prolonged exposure of digesta to microbial activity within the fermentation chambers should allow the animal to obtain nutrients from forages that are more recalcitrant to digestion. The Bell-Jarman principle has been useful to explaining differences in dietary patterns among species (Yoshihara et al. 2008; Sensenig et al. 2010); however, there is growing evidence that the Bell-Jarman principle is not suitable to explain some

phenomenon. There have been a number of studies that have indicated that digesta retention time does not scale to  $BM^{0.25-0.33}$  (Clauss et al. 2007; Clauss et al. 2009; Muller et al. 2011; Steuer et al. 2011). Additionally, some studies have shown forage intake to scale higher than  $BW^{0.75}$  (Minson 1990; Reid et al. 1990; Hackmann and Spain 2010). It is unclear whether the problem is due to the Bell-Jarman principle not considering additional factors that influence forage retention and digestion or because of variability in scaling relationships.

The majority of research conducted on scaling relationships and the Bell-Jarman principle has been used in explaining dietary patterns across species. Yet, the Bell-Jarman principle has been applied within species (Gross et al. 1996, Barboza and Bowyer 2000). Weckerly (2010) reported that gut capacity of white-tailed deer (*Odocoileus virginianus*) scaled allometrically (scalar = 0.67-0.75) not isometrically with body mass. Moreover, the Bell-Jarman principle is difficult to apply within ruminant species given the enormous variability in rumen-reticulum capacity (Tulloh 1966; Weckerly 2010). Much of the variability in rumen-reticulum capacity has been linked with life history demands such as mating, gestation, or lactation. In particular, increases in digestive-tract fill have been well documented during lactation (Smith and Baldwin 1974; Jenks et al. 1994; Vetharanim et al. 2009).

Weckerly (2010) was the first to estimate an allometric, intraspecific scaling relationship between body mass and the 2 most commonly used measures of rumen-reticulum capacity (wet weight of digesta and volume). Nonetheless, this study had some limitations. First, influences of nutrition and body condition were not accounted for, and these variables can influence wet weight of contents (Demment 1983; Barboza et al.

2009). Second, no explanations were given to account for why the scaling relationship was allometric instead of isometric.

Ruminants probably adjust the fill and capacity of their rumen-reticulum in response to changes in forage quality, except with the lowest quality diets. When forage quality is < 50% digestible dry matter, white-tailed deer may be limited in gut capacity and unable to adjust food intake to meet metabolic demands (Gray and Servello 1995). When forage quality is moderate or better, that is digestible dry matter is > 50%, rumen turnover is probably less limited by rumen capacity and animals have greater flexibility in food intake to meet metabolic demands (Gray and Servello 1995). Without the capability to alter the capacity and fill of the digestive tract to accommodate fluctuations in food intake with diets that have moderate or better forage quality, body condition would be affected. Moreover, a reduction in the absorption of nutrients would occur when forage intake increases (Tyrrell and Moe 1975; Demment 1983; Demment and Van Soest 1985; Barboza et al. 2006; Lechner et al. 2010).

Being able to accommodate changes in digesta weights as a result of variability in the amount of forage consumed is paramount for juveniles because they have high mass-specific food intakes to meet the demands of growth (Welch 1982; Hooper and Welch 1983). Yet, little is known about how juvenile ruminants accommodate increased digesta weights. Juveniles might have greater capacity or accommodate greater fill of the rumen-reticulum.

The greatest change in rumen-reticulum capacity occurs during weaning. Short (1964) indicated that during the second month of age, the weight of the rumen organ with

its contents increased 400%. The dramatic increase in rumen-reticulum capacity is needed to provide the space for fermentation and absorption of fermentation byproducts in the transition from consuming milk to plant forage (Short 1964). Consequently, there might be further anatomical development of the rumen-reticulum after weaning (Short 1964; Knott et al. 2004). An outcome of incomplete rumen-reticulum development might be less rumen-reticulum organ tissue in juveniles compared with adults. Because adding more gut tissue is metabolically expensive (Kelly et al. 1991; McLeod and Baldwin 2000), having less rumen-reticulum organ tissue might allow juveniles greater rumen-reticulum elasticity without having to accommodate an increase in metabolic demands.

I conducted a study on white-tailed deer to estimate scaling relationships of body mass and rumen-reticulum characteristics, and how these scaling relationships influence rumen-reticulum elasticity and fill. I set out to determine if there is a mechanism to explain allometric scaling relationships between body mass and rumen-reticulum capacity. Determining why rumen-reticulum capacity scales allometrically with body mass would aid in understanding how ruminants accommodate space for ingesta to meet demands of growth and production when gut tissue is metabolically expensive. I hypothesize that requirements of growth and a small body mass (and thus a proportionally high metabolic rate) require small bodied individuals (juveniles and sub-adults) to have a rumen-reticulum that, relative to their body mass, 1) weighs less, 2) is capable of a greater elasticity, and 3) contains more digesta than that of larger bodied individuals (adult deer). As such, there should be allometric scaling relationships between body mass and rumen-reticulum variables. Organ weight should have a scalar  $>1.0$  and measures of elasticity and digesta weight should have scalars  $<1.0$ . By having a rumen-

reticulum capable of increased elasticity, juvenile and sub-adults would be able to increase capacity without requiring additional metabolically expensive gut tissue, thereby resulting in proportionally greater fill. The proportionally greater fill associated with increased mass-specific food intake would enable juvenile and sub-adults the means to accommodate higher forage intake, thereby aiding the individual in meeting their high mass-specific metabolic demands.

## **Methods**

### *Study area*

My study occurred on Kerr Wildlife Management Area (WMA) in Kerr County, Texas, USA from 2009 to 2011. The WMA encompasses 2,628 ha and is surrounded by a 2.6 m high game fence. Warren and Krysl (1983) reported that the primary deer forage on Kerr WMA in autumn and early winter was various oaks (*Quercus* spp.), Ashe juniper (*Juniperus ashei*), bladderpods (*Lesquerella* spp.), spurges (*Euphorbia* spp.), redseed plantain (*Plantago rhodosperma*), filaree (*Erodium* spp.), silverleaf nightshade (*Solanum elaeagnifolium*), globemallows (*Sphaeralcea* spp.), whorled nodviolet (*Hybanthus verticillatus*), common horehound (*Marrubium vulgare*), and wintergrass (*Nassella leucotricha*).

### *Sample collection*

White-tailed deer were obtained during September and November 2009-2010. All deer were collected with high powered rifles by licensed public hunters or Texas Parks and Wildlife personnel. Collection procedures followed an Institutional Animal Care and Use protocol from Texas State University (permit # 00933\_09\_06-03141BF15D). After

harvest, the time of kill was recorded, and the deer were transported to a check station where they were processed within 3 h post mortem. Time of kill was included because wet weights of digesta have been shown to fluctuate throughout the day, which is likely indicative of synchronized patterns of feeding, resting, and ruminating (Conradt 1998; Weckerly et al. 2003).

Whole weights minus blood loss were taken to the nearest 0.1 kg and depth of back fat was measured to the nearest 1.0 mm by making an incision just above the lower lumbar vertebrae (L4-L5) and measuring the thickness of fat between the muscle layer and the hide (Veiberg et al. 2009). Ages were estimated with tooth replacement and wear (Severinghaus 1949). Females were assessed for lactation by the presence or absence of milk within their udder. The animal was eviscerated and the mesentery removed to expose the rumen-reticulum. The rumen-reticulum was separated from the rest of the entrails by ligating the esophagus approximately 5 cm above its junction with the reticulum and making a second incision at the reticulo-omasal sphincter (Weckerly et al. 2003; Ramzinski and Weckerly 2007). The rumen-reticulum along with its contents was then weighed to the nearest 0.1 kg. The contents in the rumen-reticulum were then removed; the rumen-reticulum was inverted and rinsed thoroughly to ensure that all particulate matter had been removed. After rinsing, the rumen-reticulum was reverted and the organ weight was recorded. Wet weight of the digesta in the rumen-reticulum was the difference between weight of the rumen-reticulum organ with contents and rumen-reticulum organ without contents.

A subsample consisting of 800 g of fill was collected and dried at 60°C for 48 h. After the drying period, the subsample was reweighed, and the dry weight of the digesta

subsample was extrapolated to estimate the total dry weight of rumen-reticulum digesta. Next, nitrogen (%) and acid detergent fiber (ADF %) were determined with an N gas analyzer using an induction furnace and thermal conductivity using a Leco FP-528 (AOAC 1997). The crude protein (CP %) was determined as nitrogen (%) times 6.25. Acid detergent fiber consists of lignin, cutin and cellulose that are within the plant cell. Typically, cellulose is recalcitrant to digestion which requires longer fermentation times because digesta needs increased rumen microbial exposure (Hummel et al. 2006). Other components of ADF, specifically lignin and cutin, are completely indigestible (Van Soest 1994). Due to its composition, ADF was used as an index for measuring forage quality within a sample. All digesta analyses were conducted by A&L Plains Agricultural Laboratory, Lubbock, Texas, USA.

Elasticity was measured by volume of water held in the rumen-reticulum. The rumen-reticulum organ was placed in a plastic drum that contained 208 l of tap water. Keeping the opening of the reticulum at water level for hydrostatic support, water was poured into the rumen-reticulum and the amount of water the organ held was recorded to the nearest 0.1 liters. The measurement was taken in triplicate.

#### *Data analysis*

I constructed a series of models to estimate changes in rumen-reticulum characteristics associated with body mass. The response variables were wet weight of the digesta, dry weight of digesta, rumen-reticulum organ weight, and rumen-reticulum volume (hereafter referred to as rumen-reticulum capacity). Each response variable was logarithmically transformed for purposes of estimating the scalar. Hereafter, each

reference to a response variable will refer to the natural logarithm of that response variable. Covariates were body mass, time of kill, CP (%) in digesta, ADF (%) in digesta, whether the animal was lactating, sex, and depth of back fat. The above listed covariates would account for changes in forage quality as well as body condition changes; therefore, the month of kill was not included as a covariate. Because digesta weights have been shown to fluctuate with crepuscular foraging periods (Teer et al. 1965; Tulloh and Hughes 1965; Beier and McCullough 1990), time of kill was included as a covariate. Natural logarithmic transformation of body mass was done to meet the assumption of homoscedasticity and to remain consistent with previous studies that estimated scaling relationships of gut capacity (Demment and Van Soest 1985; Weckerly et al. 2003; Ramzinski and Weckerly 2007; Weckerly 2010). Depth of back fat was also transformed using the natural logarithm of back fat plus one because of nonlinear relationships, and depth of back fat on some animals being 0.

Sixteen models were built to assess the influence of body mass, kill time, nutrition (CP and ADF), sex, lactation, and back fat as well as combinations of these covariates on each response variable. I used Akaike information criterion corrected for small sample size ( $AIC_c$ ) to select models (Burnham and Anderson 2002). After calculating the  $AIC_c$  I computed the  $\Delta AIC_c$  ( $AIC_c - \min AIC_c$ , min refers to the model with the smallest  $AIC_c$ ) for each of the 16 models for every response variable. The  $\Delta AIC$  was then used to calculate the relative likelihood ( $RI = e^{(-0.5 * \Delta AIC_c)}$ ). From the relative likelihoods I identified competing models by calculating the likelihood ratio ( $RI_i / RI_{\min}$ ). Competing models had likelihood ratios  $\geq 0.125$  (Burnham and Anderson 2002). I used the “model.avg” function within the MrMIn package in R to estimate coefficients and

standard errors averaged among competing models (Barton 2009), after which I calculated 95% confidence intervals (CI). A coefficient was statistically significant if the 95% CI excluded 0. Also, if the 95% confidence intervals for the body mass coefficient included 1.0, it suggested an isometric scaling relationship.

Because of the numerous adults in the data set (see Results) I assessed whether there was an influence from age on the scaling relationships. A dichotomous categorical covariate coded for age (juveniles – sub-adults, adults) was added to the model with the smallest  $AIC_c$  for every response variable to determine if scaling relationships differed between juveniles – sub-adults and adults.

## Results

During the 2 year study, 108 white-tailed deer were collected, of which 73 were females (4 juvenile, 10 sub-adults, and 59 adults) and 35 were males (1 juvenile, 19 sub-adults, and 15 adults). Body masses ranged from 14 to 24 kg for fawns, 29 to 45 kg for sub-adults, and 31 to 76 kg for adults. Animals collected during the sampling period had ADF values that ranged from 22.3 to 60.7%, CP ranged from 9.4 to 26.1%, and depth of back fat from 0 to 2.1 cm (Table 2.1).

Rumen-reticulum organ weight and rumen-reticulum capacity each had 7 competing models, whereas, wet weight of digesta and dry weight of digesta had, respectively, 4 and 3 competing models (Table 2.2). For rumen-reticulum organ weight, the influential covariates were: body mass, CP, sex, and lactation (Table 2.3). Rumen-reticulum organ weights of males were lighter than either lactating or non-lactating females. For a given body mass, male rumen-reticulum organ weights were about 73% of

rumen-reticulum weights of lactating females, and about 83% of the rumen-reticulum weight of non-lactating females. Rumen-reticulum capacity was influenced by the covariates of body mass and lactation. Wet weight of the digesta was influenced by body mass, sex, lactation, and back fat. Influential covariates of dry weight of digesta were body mass, ADF, lactation, and back fat. For every response variable, body mass and lactation were the only two covariates that were influential.

There was not an age effect (juveniles – sub-adults, adults) on any rumen-reticulum response variable. For each response variable, I added an age covariate to the model with the smallest AIC<sub>c</sub>. The age covariate had 95% CI that included zero for rumen-reticulum organ weight (-0.21 – 0.34), rumen-reticulum capacity (-0.35 – 0.20), dry weight of digesta (-0.30 – 0.12), and wet weight of digesta (-0.21 – 0.15).

## Discussion

I hypothesized that as a result of their small body mass, juvenile and sub-adults would have rumen-reticulums that, relative to their body mass, weighed less, had greater elasticity, and contained more digesta than their larger bodied counterparts. Therefore, I expected to find allometric scaling relationships between body mass and each of my response variables; however, each response variable had an isometric scalar for my study. My hypothesis was not supported by my findings. The development of the rumen-reticulum of juvenile and sub-adults in this study appears similar to adults.

Body mass, energetic demands from growth and reproduction, and diet quality varied across age classes and likewise each response variable was influenced by a different set of covariates. I expected that the ontogenetic development of the rumen-

reticulum extended beyond the time of weaning and influenced the scaling of rumen-reticulum capacity. Yet, the isometric scalar for organ weight suggests that the rumen-reticulum is developed by the time the bulk of the diet of juvenile animals is solid food. To accommodate the primarily browse diet, juvenile white-tailed deer need papillae for absorption, musculature for rumen motility, and a vascular rumen wall for nutrient transport (Knott et al. 2004). In spite of the metabolic demands of gut tissues, juvenile and sub-adult animals do not appear to have a rumen-reticulum organ that is lighter, relative to body mass, than adults.

It is hard to tell what rumen-reticulum capacity, which is obtained by water displacement, is measuring. It is possible that there are varying degrees of post-mortem influence in the tension of the rumen-reticulum tissue, which might affect the capacity measurements. I thought that lighter organ weights would be positively associated with greater capacity, a finding reported by Sibbald and Milne (1993). Yet, lactating females in my study had the greatest rumen-reticulum capacity when these organs were the heaviest. Heavier organ weights in lactating females presumably accommodate heavier digesta weights (Jenks et al. 1994; Gross et al. 1996; Ramzinski and Weckerly 2007; Jiang et al. 2009). Weckerly (2010), however, found that rumen-reticulum capacities were not associated with digesta weights. It appears that the only consistent finding about rumen-reticulum capacity is that the values are most often, but not always, greater than wet weight of digesta measurements (Tulloh and Hughes 1965; Sibbald and Milne 1993; Weckerly et al. 2003; Ramzinski and Weckerly 2007; Weckerly 2010).

In studies where rumen-reticulum fill and capacity are measured from animal dissection, wet weight of digesta is the most commonly used measure (Demment and Van

Soest 1985; Freudenberger 1992; Forchhammer and Boomsma 1995; Veiberg et al. 2007). I also measured dry weight to assess rumen-reticulum fill and capacity without the influence of ruminal fluid. Dry weight of rumen-reticulum contents is influenced by three processes; forage intake, rate of digestion, and passage rate. My findings suggested that animals with greater dry weight of rumen-reticulum contents also had less back fat. It is likely that this relationship is due to food intake, diet selection, forage processing or all three processes being influenced by metabolic demands and body condition. Most likely, animals undergoing the demands of growth (little back fat) or that were in poorer condition had greater food intake because Verme and Ozoga's (1980) manuscript indicated animals had increased food intake after they were first presented a nutritionally restricted diet. My study is the first, to my knowledge, to consider and show the relationship between gut fill and back fat.

Because I sampled animals over 2 autumns I measured CP and ADF in the rumen-reticulum to capture temporal variation in dietary nutrition. The nutritional quality of the food is known to influence rumen fill, which then has ramifications on scaling relationships. Juvenile and sub-adult animals, relative to adults, should have had the flexibility to increase rumen fill in response to demands from growth which means I should have had the potential to estimate allometric scalars ( $<1.0$ ) for wet and dry weights of digesta, however both of these predictors had isometric scalars. It is likely that the influences on rumen-reticulum digesta weight are more complex than I thought when I began the study. Rumen-reticulum fill is probably influenced by type of forage, dietary nutrition, life history demands and body condition, forage processing via chewing, and microbial activity (Jenks et al. 1994; Van Soest 1994; Barboza and Hume 2006; Jiang et

al. 2009; Veiberg et al. 2009; Weckerly 2010; Duarte et al. 2011).

Crude protein concentration measured in the rumen is affected by nitrogen content of the diet and digestive functions in the rumen-reticulum. Consequently, it is difficult to say that the positive relationship between CP and wet weight of rumen-reticulum contents is due solely to forage availability and selection. Digestive functions that could influence rumen CP concentrations are urea recycling and micro-organism abundance related to fermentation (Barboza and Bowyer 2000). Micro-organism abundance in the rumen is of a magnitude where microbial N might comprise a substantive part of rumen CP (Van Soest 1994; Barboza and Hume 2006). Because CP did not have a strong influence on dry weight of rumen-reticulum contents, these two measures probably do not capture the same forage selection and digestive processes. The differing influence CP had on dry and wet weights might be the result of the CP associated with wet weight of digesta being inflated due to contributions of N from micro-organisms in the rumen liquor. Therefore, when considering the effect of forage quality on the scaling relationships, it is advisable to use dry weight of rumen-reticulum contents to negate the influence of rumen liquor, and to measure dietary nutrition (CP and ADF) to account for spatial and temporal variation in the diet.

The findings of this study, unfortunately, do not resolve whether the intraspecific scaling relationship between body mass and rumen-reticulum capacity is allometric or isometric and, thus, whether the Bell-Jarman principle is a viable hypothesis to explain dietary variation across body sizes of conspecific animals. For white-tailed deer, this study and Weckerly (2010) had large sample sizes and attempted to account for the covariates influencing the scaling relationship between body mass and the rumen-

reticulum. Yet, each study reached a different conclusion. The Weckerly (2010) study might have been limited by not including important covariates (analyses included response variables of rumen-reticulum volume and weight, and predictors of body mass, digesta wet weight, sex, and year). My study included a greater number of covariates, some of which indicated that there is strong evidence that rumen-reticulum relationships with body mass are isometric. There are numerous factors that can influence rumen-reticulum fill; body mass, type of diet, nutrition, digestive processes, life history, and body condition. The extent to which and how these factors directly and indirectly influence rumen-reticulum fill has yet to be explored. There should be consequences to scaling relationships if these factors have direct and indirect effects on rumen-reticulum fill. For example, body mass, ADF, and back fat have direct influences on rumen-reticulum fill since each of these covariates influenced rumen-reticulum dry weight of digesta in this study. Body mass might also have indirect influences on rumen-reticulum fill through ADF in the diet and amount of back fat, patterns that cannot be detected in a regression analysis estimating scaling relationships. In which case the intraspecific scalar estimated from a data set is not only influenced by the set of life history, diet, body condition, and other environmental covariates considered in an analysis but also the study-specific values of each of the covariates.

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Table 2.1.--Summary of the characteristics of sampled white-tailed deer (*Odocoileus virginianus*) from Kerr Wildlife Management Area, Texas, USA. Data shows mean, standard error (SE), and range of crude protein (%) and acid detergent fiber (%) (measured from rumen contents), as well as depth of back fat with respect to sex and across an array of age classes.

Sex	Age	n	BM	CP (%)			ADF (%)			Back Fat (cm)		
				Mean	SE	Range	Mean	SE	Range	Mean	SE	Range
Female	Juvenile	4	17.6	18.2	0.75	16.6-20.1	38.1	2.56	31.3-43.6	0.1	0.04	0-0.2
	Sub-adult	10	34.5	19.2	1.18	14.0-26.1	41.2	2.74	28.9-56.8	0.3	0.07	0-0.8
	Adult	59	40.3	18.7	0.41	10.7-24.3	43.6	1.09	22.3-60.7	0.3	0.04	0-2.1
Male	Juvenile	1	23.5	20.8	N/A	N/A	50.5	N/A	N/A	0.0	N/A	N/A
	Sub-adult	19	36.1	17.3	0.89	9.4-23.5	41.5	1.67	30.3-56.6	0.3	0.04	0-0.7
	Adult	15	56.4	16.5	0.82	9.5-22.0	43.3	2.05	31.3-56.2	0.4	0.10	0-1.3
Combined		108	40.3	17.8	0.32	9.4-26.1	42.7	0.77	22.3-60.7	0.3	0.03	0-2.1

N/A represents not applicable, n=sample size, BM=average body mass, CP=crude protein, ADF=acid detergent fiber

Table 2.2.---Models analyzed using AIC<sub>c</sub> and models selected for model averaging analysis (bold) for the response variables of rumen-reticulum organ weight, rumen-reticulum capacity, wet weight of digesta, and dry weight of digesta of white-tailed deer (*Odocoileus virginianus*) sampled in a 2628 ha enclosure at Kerr Wildlife Management Area, Kerr County, Texas.

Model predictors	nPar	Ln RR organ weight			Ln RR capacity			Ln wet weight of RR digesta			Ln dry weight of RR digesta		
		Δ	r <sup>2</sup>	likelihood ratio	Δ	r <sup>2</sup>	likelihood ratio	Δ	r <sup>2</sup>	likelihood ratio	Δ	r <sup>2</sup>	likelihood ratio
BW,KT	4	47.81	0.49	≤0.01	13.63	0.14	≤0.01	32.29	0.44	≤0.01	28.61	0.29	≤0.01
BW,KT,NUT	6	44.85	0.51	≤0.01	11.37	0.18	≤0.01	29.80	0.46	≤0.01	26.15	0.32	≤0.01
BW,KT,SEX & LACT	6	<b>1.29</b>	<b>0.67</b>	<b>0.52</b>	<b>0.59</b>	<b>0.26</b>	<b>0.75</b>	7.23	0.56	0.03	11.35	0.40	≤0.01
BW,KT,BF	5	49.51	0.49	≤0.01	15.45	0.14	≤0.01	21.21	0.50	≤0.01	19.31	0.35	≤0.01
BW,KT,NUT,SEX & LACT	8	<b>2.05</b>	<b>0.68</b>	<b>0.36</b>	<b>0.00</b>	<b>0.28</b>	<b>1.00</b>	7.91	0.57	0.02	6.32	0.44	0.04
BW,KT,NUT,BF	7	46.55	0.51	≤0.01	12.99	0.17	≤0.01	17.92	0.52	≤0.01	17.99	0.37	≤0.01
BW,KT,SEX & LACT, BF	7	<b>3.58</b>	<b>0.67</b>	<b>0.17</b>	<b>2.83</b>	<b>0.25</b>	<b>0.24</b>	<b>0.13</b>	<b>0.60</b>	<b>0.94</b>	6.74	0.44	0.03
BW,KT,NUT, SEX & LACT,BF	9	4.43	0.68	0.11	<b>2.38</b>	<b>0.27</b>	<b>0.30</b>	<b>0.16</b>	<b>0.60</b>	<b>0.92</b>	<b>2.38</b>	<b>0.47</b>	<b>0.30</b>
BW	3	50.47	0.48	≤0.01	12.90	0.15	≤0.01	38.13	0.40	≤0.01	26.66	0.30	≤0.01
BW,NUT	5	44.12	0.51	≤0.01	12.23	0.16	≤0.01	31.07	0.45	≤0.01	24.17	0.32	≤0.01
BW,SEX & LACT	5	<b>0.42</b>	<b>0.67</b>	<b>0.81</b>	<b>1.75</b>	<b>0.24</b>	<b>0.42</b>	10.88	0.54	≤0.01	9.11	0.41	0.01
BW, BF	4	51.99	0.47	≤0.01	14.76	0.13	≤0.01	27.01	0.46	≤0.01	17.21	0.36	≤0.01
BW, NUT, SEX & LACT	7	<b>0.00</b>	<b>0.68</b>	<b>1.00</b>	<b>2.01</b>	<b>0.25</b>	<b>0.37</b>	8.62	0.56	0.01	<b>4.07</b>	<b>0.45</b>	<b>0.13</b>
BW, NUT, BF	6	45.70	0.51	≤0.01	13.95	0.16	≤0.01	19.00	0.51	≤0.01	15.85	0.38	≤0.01
BW,SEX & LACT, BF	6	<b>2.66</b>	<b>0.67</b>	<b>0.26</b>	<b>3.84</b>	<b>0.23</b>	<b>0.15</b>	<b>2.73</b>	<b>0.58</b>	<b>0.26</b>	4.50	0.44	0.11
BW, NUT, SEX & LACT, BF	8	<b>2.33</b>	<b>0.68</b>	<b>0.31</b>	4.27	0.25	0.12	<b>0.00</b>	<b>0.60</b>	<b>1.00</b>	<b>0.00</b>	<b>0.48</b>	<b>1.00</b>

BW, natural logarithm of body mass; KT, kill time; Nut, nutrition (CP and ADF); LACT, lactation; BF, ln(back fat+1)

Table 2.3.—Model averaged parameter estimates, standard errors (SE), and confidence intervals of rumen-reticulum organ weight, rumen-reticulum capacity, wet weight of digesta, and dry weight of digesta of white-tailed deer (*Odocoileus virginianus* Zimmermann, 1780) sampled in a 2628 ha enclosure at Kerr Wildlife Management Area, Kerr County, Texas. Estimates highlighted in bold represent the statistically significant covariates for each response variable.

Coefficients	Response variable															
	Ln RR organ weight				Ln RR capacity				Ln wet weight of RR digesta				Ln dry weight of RR digesta			
	SE	lb <sup>+</sup>	Coef. Est.	ub <sup>+</sup>	SE	lb <sup>+</sup>	Coef. Est.	ub <sup>+</sup>	SE	lb <sup>+</sup>	Coef. Est.	ub <sup>+</sup>	SE	lb <sup>+</sup>	Coef. Est.	ub <sup>+</sup>
Intercept	0.286	-4.345	-3.778	-3.211	0.631	-2.323	-1.072	0.180	0.428	-4.215	-3.365	-2.515	0.485	-4.670	-3.708	-2.745
Ln body mass	<b>0.074</b>	<b>0.792</b>	<b>0.938</b>	<b>1.085</b>	<b>0.170</b>	<b>0.419</b>	<b>0.755</b>	<b>1.092</b>	<b>0.116</b>	<b>0.940</b>	<b>1.169</b>	<b>1.399</b>	<b>0.133</b>	<b>0.801</b>	<b>1.065</b>	<b>1.330</b>
Kill time	0.004	-0.005	0.004	0.012	0.009	-0.037	-0.018	0.001	0.006	-0.002	0.011	0.024	0.007	-0.014	0.000	0.015
CP	<b>0.540</b>	<b>0.071</b>	<b>1.142</b>	<b>2.213</b>	1.277	-1.284	1.250	3.784	1.391	-0.876	1.885	4.645	0.926	-2.855	-1.017	0.820
ADF	0.221	-0.519	-0.081	0.357	0.496	-0.191	0.794	1.778	0.321	-0.814	-0.178	0.458	<b>0.381</b>	<b>-1.680</b>	<b>-0.925</b>	<b>-0.170</b>
Sex	<b>0.050</b>	<b>-0.287</b>	<b>-0.189</b>	<b>-0.091</b>	0.114	-0.315	-0.089	0.137	<b>0.075</b>	<b>-0.299</b>	<b>-0.150</b>	<b>-0.002</b>	0.087	-0.293	-0.120	0.052
Lactation	<b>0.045</b>	<b>0.035</b>	<b>0.124</b>	<b>0.214</b>	<b>0.101</b>	<b>0.053</b>	<b>0.254</b>	<b>0.455</b>	<b>0.070</b>	<b>0.005</b>	<b>0.143</b>	<b>0.282</b>	<b>0.083</b>	<b>0.030</b>	<b>0.195</b>	<b>0.360</b>
Ln(back fat+1)	0.088	-0.177	-0.002	0.174	0.199	-0.360	0.035	0.430	<b>0.127</b>	<b>-0.655</b>	<b>-0.402</b>	<b>-0.149</b>	<b>0.150</b>	<b>-0.669</b>	<b>-0.372</b>	<b>-0.074</b>

The natural logarithm is indicated by Ln, RR represents rumen-reticulum, Coef. Est represents the coefficient estimate, CP indicates crude protein, and ADF is acid detergent fiber.

<sup>+</sup> Coefficient estimates are given with lower (lb) and upper bounds (ub) of 95% confidence intervals. Covariates are statistically significant if confidence intervals exclude 0.

### CHAPTER III

#### INTRA-SPECIFIC FORAGE NICHE PARTITIONING: THE INFLUENCE OF BODY SIZE ON DIETARY NUTRITION OF WHITE-TAILED DEER

Differentiation among feeding strategies due to morphology should occur when feeding efficiency varies between or among morphs (Schluter 1995). A herbivore's body mass is one morphological feature that is a driving force of forage niche partitioning (Main et al. 1996; Perez-Barberia and Gordon 1998b; Barboza and Bowyer 2000; Barboza and Bowyer 2001), and can also influence feeding strategies (Illius and Gordon 1992). Different-sized species of ruminants are able to coexist and utilize the same patches of habitat by selecting forage that differs in quality and abundance (Bell 1970; 1971; Jarman 1974; McNaughton 1976; Illius and Gordon 1987; Illius and Gordon 1992). Use of the same forage patch is likely feasible because of dissimilar energy requirements associated with differing body masses. Energy requirements of animals are determined by metabolic size, which scales to the 0.67-0.75 power of body mass (Kleiber 1961). Consequently, small homeothermic animals will have high metabolic costs per unit of body mass (Welch 1982; Hooper and Welch 1983). Differences in metabolic demands are associated with feeding selectivity and time spent foraging (Prins and Geelen 1971; Janis 1976; Demment 1983; Demment and Van Soest 1985; Van Soest 1994). The

frequency of feeding and energy intake increase with mass-specific metabolic demands (Barboza et al. 2009). Individuals with small body mass will have greater mass-specific metabolic demands compared to their larger bodied counterparts. As a result of greater mass-specific metabolic demands, small bodied individuals will have greater mass specific energy demands, which results in an increase in feeding frequency (Barboza et al. 2009). As such, small bodied individuals should feed more frequently and select forages with greater nutrient concentrations to meet these demands.

Body size should also influence an animal's digestive efficiency (Van Soest 1994; Barboza and Bowyer 2000). Gut capacity increases as animal energy requirements increase (Barboza et al. 2009) such that larger bodied individuals will have greater gut capacity than small bodied individuals because large bodied individuals have greater absolute metabolic demands than their smaller bodied counterparts. In addition to metabolic rates, forage selection also might be conditional on the gut capacity of the individual. Scaling relationships of body mass to gut capacity and metabolic rate, coined the Bell-Jarman principle (Geist 1974), have provided a theoretical basis for predicting that diet quality should vary inversely with body mass. The Bell-Jarman principle states that larger bodied individuals are able to feed on diets of poorer quality (i.e., high cellulose content) as a result of their lower metabolism requirement/gut capacity ratio (Demment and Van Soest 1985). As a result of an increase in gut capacity associated with an increase in body mass, large-bodied individuals have a digestive advantage in that they can retain digesta longer, thereby increasing the time that forage is exposed to micro-organisms in the digestive tract (Barboza and Bowyer 2000). Thus, larger bodied individuals are able to tolerate a diet comprised of lower-quality forage. The Bell-Jarman

principle is supported on an inter-specific level (Bell 1970; 1971; Geist 1974; Jarman 1974), but the principle is not fully supported to explain dietary variation on an intra-specific level. In size-dimorphic species, males are typically larger. In the size-dimorphic Nubian ibex (*Capra nubiana*) there was little difference in digestive efficiency between sexes (Gross et al. 1996). However, in another study using the sexually dimorphic Soay sheep (*Ovis aries*), males were shown to be slightly more efficient at digesting forage than females that were 30% smaller (Perez-Barberia et al. 2008). Consequently, more research is needed to determine the applicability of the Bell-Jarman principle to the intra-specific level. Moreover, isometric scaling of gut capacity with body mass, which is an assumption of the Bell-Jarman principle, may not occur within all species (Weckerly 2010; Duarte et al. 2011). Gut capacity scaling relationships can be used in conjunction with metabolic scaling relationships to explain differences in digestive efficiency across species. However, attempts to correlate digestive efficiency with body mass using the Bell-Jarman principle has been unsuccessful on an intra-specific level (Weckerly and Nelson 1990; Perez-Barberia et al. 2007).

One factor that can affect conspecific digestive efficiency is variation in mastication efficiency. Mastication efficiency is the rate of particle breakdown, and is the main mechanism to decrease particulate size of forages. Digestive processes in the abomasum and small intestine, as well as bacterial fermentation in the rumen, ceacum, and proximal large intestine have little effect on particle size (Poppi et al. 1980; Uden and Van Soest 1982; McLeod and Minson 1988; Lechner-Doll and Von Engelhardt 1989; Freudenberger 1992). Mastication efficiency has two possible components, chewing effort (chews/gm of intake) and tooth morphology. Tooth morphology affects the degree

to which forage particulate matter is degraded through chewing (Veiberg et al. 2009). The teeth of a larger-bodied individual would contain greater distances between the enamel ridges compared with a smaller-bodied individual. If large and small-bodied individuals have the same chewing effort, mastication efficiency should be greater in small-bodied browsing ungulates because of shorter distances between enamel ridges. Consequently, mastication by a large-bodied individual can result in a slower rate of particulate breakdown compared to a smaller individual (Fritz et al. 2009). Because rate of particle breakdown affects digestion rate, mastication efficiency should influence rates of forage intake and rumen turnover (Perez-Barberia and Gordon 1998a; Logan 2003). A change in rate of rumen turnover should affect the fill and nutrient composition in the rumen (Short 1975; Van Soest 1994).

In addition to greater mastication efficiency, smaller-bodied individuals also might meet their metabolic demands by greater forage selectivity. Forage selectivity is food intake in relation to forage time (Hodgson 1982). Therefore, forage selectivity should increase with an increase in forage time. Smaller-bodied individuals might display more selectivity to obtain a more digestible diet than would large-bodied animals (Van Soest 1994).

A high-quality diet can be defined operationally by the ratio of crude protein (CP) to acid detergent fiber (ADF) in digesta (Van Soest et al. 1991). Crude protein is a nutrient required for growth, maintenance, and reproduction; whereas ADF measures plant material that is either completely indigestible to the animal (e.g. lignin and cutin; Van Soest 1994) or is recalcitrant to digestion (e.g. cellulose; Hummel et al. 2006). Through mastication efficiency, food selection, or both, body weight should covary with

the CP:ADF of rumen digesta.

On an intra-specific level, smaller-bodied individuals cannot afford to ingest low quality forage because of processing constraints (i.e., they are less efficient at extracting the nutrients from low-quality forage compared to larger bodied individuals). Animals may compensate for changes in dietary nutrients by adjusting food intake and concomitantly, gut fill (Holand 1994; Gross et al. 1996). In order to meet metabolic demands, small bodied individuals are likely to be more selective for high-quality forage to maximize energy intake per bite. Therefore, I expect to see an inverse relationship between diet-quality (as indexed by CP:ADF) and body size.

I conducted a study on white-tailed deer (*Odocoileus virginianus*) to examine if body mass was inversely related to diet quality. I hypothesize that small-bodied individuals are likely to have greater CP content of rumen digesta as a means to meet their higher mass-specific metabolic demands. Although metabolic demands are usually associated with energy, protein is needed for growth, maintenance, and reproduction (Barboza et al. 2009). Therefore, as a result of forage selectivity, body mass should covary inversely with the CP:ADF ratio of rumen digesta. Identifying body mass-diet quality relationships should provide information useful to furthering the understanding of resource selection and niche partitioning by sexually dimorphic ungulates. Forage niche partitioning could reduce the effects of intra-specific competition, which could potentially have ramifications on recruitment and carrying capacity of the habitat. Additionally, by understanding how forage is utilized across body sizes, wildlife managers could augment available forage according to the composition of the local population in order to increase recruitment or enhance body condition of older age class

individuals.

## Methods

### *Study area*

I conducted research in Kerr County, Texas, USA, on the Kerr Wildlife Management Area (WMA). The Kerr WMA encompasses an area of 2,628 ha and is enclosed with a 2.6 m high game fence. The primary forage for white-tailed deer during autumn and early winter on Kerr WMA was various oaks (*Quercus* spp.), Ashe juniper (*Juniperus ashei*), bladderpods (*Lesquerella* spp.), common horehound (*Marrubium vulgare*), filaree (*Erodium* spp.), globemallows (*Sphaeralcea* spp.), redseed plantain (*Plantago rhodosperma*), silverleaf nightshade (*Solanum elaeagnifolium*), spurges (*Euphorbia* spp.), whorled nodviolet (*Hybanthus verticillatus*), and wintergrass (*Stipa leucotricha*; Warren and Krysl 1983).

### *Sample collection*

I sampled deer in September, November, and the first week of December in 2009 and 2010. The samples were obtained from harvested white-tailed deer during culling efforts (September) and from four management hunts and one trophy hunt (November and December). A cull or a management deer was any female, or any male that had one un-branched antler. Trophy hunts allowed for take of males with greater than 16" antler spread and eight or more tines. All white-tailed deer were collected by licensed public hunters (November and December) or Texas Parks and Wildlife personnel (September) utilizing high powered rifles. Collection procedures followed an Institutional Animal Care and Use protocol from Texas State University (permit # 00933\_09\_06-03141BF15D). After each animal was harvested, it was transported to a check station

where it was processed within 3 hours post mortem. Each animal was given a unique identification number upon arrival at the check station, and time of kill was recorded. Sex and whole weight minus blood loss (measured to the nearest 0.10 kg) of each animal was obtained. Back fat thickness was recorded from each carcass by making an incision along the spine above the L4-L5 lumbar vertebrae (Komers et al. 1994; Veiberg et al. 2009). The thickness of the back fat between the muscle layer and the hide was measured to the nearest 1.0 mm. Females were assessed for lactation by examining their udder for presence of milk. The animals were eviscerated and the mesentery removed to expose the rumen-reticulum. The rumen-reticulum was separated from the remainder of the entrails by ligations made at the esophagus just above the reticulum and at the reticulo-omasal sphincter (Weckerly et al. 2003; Ramzinski and Weckerly 2007). The rumen and reticulum are the gastrointestinal organs with the largest capacity and where most fermentation occurs (Van Soest 1994).

The rumen-reticulum was weighed and then emptied of digesta by inverting the organ. The rumen-reticulum organ (void of any digesta) was then reweighed and the difference was recorded as the wet weight of the digesta. In a semi-arid environment primary productivity often differs due to fluctuations in precipitation from one season to the next, as well as across years (Teer et al. 1965; Beatley 1969; Noy-Meir 1973; Robertson 1987; Polis et al. 1997; Marshal et al. 2002; 2005), so I obtained nutritional composition (CP, ADF, and NDF) of the digesta. Crude protein is a nutrient required for growth, maintenance, and reproduction; whereas ADF measures plant material that is either completely indigestible to the animal (e.g. lignin and cutin; Van Soest 1994) or is recalcitrant to digestion (e.g. cellulose; Hummel et al. 2006). Neutral detergent fiber

represents total plant fiber or cell wall content including hemicelluloses, cellulose and lignin (Van Soest 1994).

A sample consisting of 800 g of wet digesta was collected and dried at 60°C for 48 h. After the drying period, the sample was reweighed, and the dry weight of the digesta was extrapolated to estimate the total dry weight of rumen-reticulum digesta. After the sample was reweighed, it was ground to a uniform size of approximately 1 mm. A Leco FP-528 apparatus was utilized to determine the percent nitrogen from a 1-g sample of the dried particulate (AOAC 1997). The percent CP was calculated by multiplying percent nitrogen by 6.25 (protein is approximately 16% nitrogen,  $1/0.16=6.25$ ).

A second 1-g sample of the dried and ground digesta was placed into a filter bag and put in a hexadecyltrimethyl-sulphuric acid solution. The sample was then removed and rinsed three times with boiling water. After rinsing with boiling water, the sample was rinsed a final time with acetone and allowed to air dry. After the sample was dry, it was weighed. Nitrogen and ADF were determined from the dried sample by an N gas analyzer using an induction furnace, and thermal conductivity using a Leco FP-528 (AOAC 1997). The weight obtained in relation to the initial weight represented the percent of ADF in the sample. Neutral detergent fiber was determined according to methods of Van Soest et al. (1991). Assays of all digesta samples were conducted by A&L Plains Agricultural Laboratory, Lubbock, Texas, USA. Results of the analyses were then used to calculate the grams of ADF, NDF, and CP within each rumen. The weights obtained were then used to assess differences between individuals across a spectrum of body masses.

### *Data analysis*

I constructed a series of 28 a priori models to assess the relationship between body mass and dietary nutrition using response variables of CP, ADF, and NDF. Crude protein, ADF, and NDF were log-transformed to meet the assumption of homoscedasticity. Covariates were body mass, age, sex, whether the animal was lactating or not, year, back-fat thickness, and time of kill. Interaction terms between age and body mass as well as sex and body mass were also included in the analysis. A categorical covariate coded for age (juvenile, sub-adult, adult). Year was included as a covariate to account for the possibility of variation in available forage during the 2-year study. The values of back fat were transformed using natural logarithm to accommodate nonlinear relationships. Because some individuals had a back fat value of zero, I added one to each value and then performed a natural log-transformation. Time of kill was measured in military time with minutes expressed as a portion of the hour to eliminate issues with time being a circular variable.

I used Akaike information criterion corrected for small sample size ( $AIC_c$ ) to select models (Burnham and Anderson 2002). After calculating the  $AIC_c$  I computed the  $\Delta AIC_c$  ( $AIC_c - \min AIC_c$ , min refers to the model with the smallest  $AIC_c$ ) for each of the 28 models for every response variable. The  $\Delta AIC_c$  was then used to calculate the relative likelihood ( $RI = e^{(-0.5 * \Delta AIC_c)}$ ). From the relative likelihoods I identified competing models by calculating the likelihood ratio ( $RI_i / RI_{\min}$ ). Competing models had  $\Delta AIC_c \leq 2$  and likelihood ratios  $\geq 0.125$  (Burnham and Anderson 2002). I used the “model.avg” function within the MrMIn package in R to estimate coefficients and standard errors averaged

across all models, after which I calculated 95% confidence intervals (CI). A coefficient was statistically significant if the 95% CI excluded 0.

I used predicted values from regressions to estimate CP:ADF for a particular body mass using the back transformed predicted values. The predicted values and standard errors of response variables were estimated across the spectrum of body mass (15 to 80 kg) using the `predict.lm` code (R Development Core Team, 2009). The mean values of covariates (besides body mass) in a reduced model were used in the multiple regression of a given response variable, with the exception of lactation. Lactation was given a value of 0 (no lactation) because juvenile, sub-adult, and male deer in this population were not lactating. These ratios were used to estimate if smaller white-tailed deer had a diet higher in CP content. To assess uncertainty of ratios, standard errors were estimated for the back transformed ratios. A coefficient was statistically significant if the 95% CI excluded 0. All statistical analysis was conducted in program R (R Development Core Team, 2009).

## Results

Over the course of the 2-year study, a total of 108 white-tailed deer were collected, of which 73 were females and 35 were males (Table 3.1). The response variables were influenced by different covariates (Table 3.2).

From the 28 models assessed, there were five competing models for CP, two competing models for ADF, and three competing models for NDF (Table 3.2). The model with the greatest model weight for CP was  $bm+age+bf+yr+age \times bm$  (model weight=0.24; see Table 3.2). The top model for ADF was  $bm+age+bf+yr$  (model weight=0.33); and the top model for NDF was  $bm+sex+lact+bf+yr+sex \times bm$  (model weight=0.35; see Table 3.2). After conducting model averaging across all models, the

covariates that had a statistically significant influence on CP were body mass, lactation, back fat, year, and the interaction between body weight and age (Table 3.3). Covariates influential to ADF were body mass, lactation, back fat, year, and the interaction between body weight and sex (Table 3.3). Covariates statistically significant to NDF were body mass, lactation, back fat, and year (Table 3.3). Back fat had inverse relationships with NDF, ADF, and CP.

The relative variable importance after model averaging of CP models were: body mass=1.00, Year=1.00,  $\ln(\text{back fat} + 1)$ =0.79, lactation=0.53, sex=0.53, age=0.47, age x body mass=0.25, sex x body mass=0.20, and time of kill=0.04. With respect to ADF models, relative variable importance was: body mass=1.00, year=1.00,  $\ln(\text{back fat} + 1)$ =0.72, age=0.53, lactation=0.47, sex=0.47, sex x body mass=0.31, time of kill=0.13, and age x body mass=0.10. Models of NDF had relative variable importance of: body mass=1.00, year=0.95, lactation=0.82, sex=0.82,  $\ln(\text{back fat} + 1)$ =0.74, sex x body mass=0.46, age=0.18, time of kill=0.09, age x body mass=0.03.

Lactation had a positive relationship with CP, NDF, and ADF; as did year. With regard to the interaction terms, the interaction between body mass and sex had an inverse relationship with ADF, and the interaction between body mass and the sub-adult category of age had a positive relationship with CP. None of the interactions were significant with regard to NDF.

To account for rumen-reticulum fill influences on CP and ADF, I reported the relationship between body mass and CP:ADF. This ratio used the back-transformed predicted values and indicated that body mass was inversely related to the ratio of CP:ADF (Figure 3.1).

## Discussion

Body mass co-varied negatively with CP:ADF. In support of my hypothesis, small-bodied individuals exhibited greater CP:ADF than their larger-bodied counterparts. These findings indicate that smaller-bodied individuals had higher CP content in their rumen-reticulum digesta, which presumably can be attributed to consuming a higher quality diet. According to my low  $r^2$  values for my regressions, the covariates selected did not encompass all influencing factors. Therefore, specifics about diet selection cannot be assessed within this study.

Crude protein in the rumen-reticulum can originate from one of four sources: forage, micro-organisms, urea, and endogenous secretions. Herbivores that consume forage low in nitrogen can undergo urea recycling as a means of obtaining nitrogen (Barboza et al. 2009). Urea in the blood is capable of passing back into the gastrointestinal tract where it can be broken down by micro-organisms and used as a nitrogen source (Stewart and Smith 2005). Endogenous secretions such as saliva contain urea and proteins which can also be used as a source for nitrogen (Van Soest 1994). Urea and amides are converted to ammonia in the rumen-reticulum because ammonia is the form of nitrogen utilized by rumen organisms. Ammonia within the rumen-reticulum can either be absorbed across the rumen wall or utilized within the rumen-reticulum (Van Soest 1994). When consuming high quality forage (high N content), recycling urea nitrogen back to non-essential amino acids is low.

By utilizing digesta samples for my CP measurements, the contribution of microbial protein, urea, and endogenous secretions were not differentiated from dietary proteins. To better quantify differences in protein intake, microbial protein within the

rumen-reticulum should be distinguished from dietary protein, as well as the amount of dietary protein fermented in the rumen-reticulum (Van Soest 1994). It has been noted that bacteria numbers within the rumen-reticulum fluid are correlated with forage quality (Van Soest 1994; Cantalapiedra-Hijar et al. 2009), and follow seasonal patterns (Barboza et al. 2006). Also, urea concentrations in digesta are typically very low. Most of the endogenous nitrogen is probably associated with proteins from mucosal cells as well as salivary proteins (Barboza et al. 2009).

If small-bodied individuals are recently weaned juveniles, then these animals might be learning what to eat from the mother which could negate the possibility of differential forage selection (Provenza and Balph 1987; Mirza and Provenza 1990; Thorhallsdottir et al. 1990; Mirza and Provenza 1994). However, it is feasible that fawns and their adult counterparts can consume different forages within the same foraging area. Spalinger et al. (1997) noted that diet selection by juvenile white-tailed deer was largely an innate behavior rather than a learned response.

Forage selectivity by small-bodied individuals is likely a means to efficiently meet their greater mass-specific metabolic demands, which can also influence the duration and frequency of foraging bouts and forage selection (Irvine et al. 2000; Aikman et al. 2008; Laca et al. 2010). There were notable differences between the covariates that influenced CP, ADF and NDF in the rumen-reticulum. My findings support previous studies which noted that animals adjust their forage intake in response to changing nutrient concentrations of the diet (Holand 1994; Gross et al. 1996).

In addition to consuming a greater amount of CP to more efficiently meet metabolic demands, forage selectivity by small-bodied individuals also might have

ramifications on forage niche partitioning. Because there were differences in the CP:ADF across a range of body masses, habitat use on the same forage patch might be mitigated, which could decrease competition. The decreased competition between deer of differing body masses within the same foraging area might be the result of either different sized individuals selecting different forages, or possibly, different parts of the same forage. Also, the abundance of high quality forage is likely to be rarer on the landscape compared with lower quality forage. Therefore, the base of the diet is likely composed of low quality forage, and supplemented with high quality forage. The small-bodied individuals in my study might be acquiring a greater amount of CP by spending more time foraging in order to seek out the less abundant high quality forage.

Large-bodied individuals require greater absolute dry matter intake to meet greater absolute metabolic demands than smaller-bodied individuals (Van Soest 1994). Larger body masses consequently should have larger rumen-reticulums which accommodate longer ruminal retention times, thereby increasing digesta exposure to rumen microbes to facilitate more efficient digestion of lower-quality forage (Barboza and Bowyer 2000). Small-bodied individuals are likely to forage differentially than their larger-bodied counterparts to maximize intake of highly nutritious forage; which might result in quicker rumen turnover. Although large-bodied individuals will take advantage of high quality forage, they are not as reliant on consuming forage with the highest nutrient content as smaller-bodied individuals. Therefore, individuals of varying body masses are likely able to partition forage within the same foraging area.

Sex and reproductive status can influence forage intake (Barboza et al. 2009). We, surprisingly, did not detect differences based on sex. However, the influence of lactation

might have overshadowed any influence attributed to sex due to my adult female data set being comprised largely of lactating individuals (78%). With respect to lactation, I did detect higher CP values for lactating individuals. The increased CP intake of lactating females is likely attributed to increased metabolic demands associated with lactation (Barboza et al. 2009). Lactating females meet their high metabolic demands for energy and protein by selecting higher quality forage in addition to consuming greater amounts of forage compared to non-lactating females (Barboza and Bowyer 2000).

Typically, on an intra-specific level adult males and females do not compete for forage when they are segregated spatially (McCullough 1979; Kie and Bowyer 1999). Large males select areas where they can best meet their nutritional demands, which frequently results in moving to areas where forage is more abundant, but contains higher fiber content (Bowyer 1984; Clutton-Brock et al. 1987). The positive relationship between body mass and NDF I detected is consistent with the notion that larger animals feed in areas with more abundant and lower quality forage.

With respect to body condition, I noted a relationship between the amount of back fat and the amount of CP in the digesta. As fat stores are depleted, there is an increase in the rate of depletion of protein stores (Torbit et al. 1985; Cook et al. 2001). In my study, there was an inverse relationship between back fat and CP, ADF, and NDF; indicating individuals will likely be increasing food intake to replenish fat storages or to meet demands of growth.

Previous research has noted that lambs were capable of selecting forage that would maximize their growth (Cropper et al. 1986; Kyriazakis and Oldham 1993) and the proportion of protein in the diet decreased with increasing age (Cropper et al. 1985).

Also, results of a controlled feeding experiment indicated that yearling white-tailed deer were selectively consuming forages which contained the greatest CP content (Dostaler et al. 2011). Gains in body mass resulting from consuming a high quality diet increase the probability of survival for juvenile ungulates (Pettorelli et al. 2007). In order to increase their chances of survival, juveniles should maximize intake of high quality forage. By primarily selecting high quality forage, thereby increasing CP intake, digestibility will increase as well as rumen turnover time (Oikawa et al. 2011), thereby maximizing nutrients available to meet demands of growth. Perhaps the amount of protein within the forage that causes satiety for an animal of young age could result in varying degrees of malaise in older individuals (Provenza 1995). If I use body mass as a proxy for age, my study followed the trend reported in domesticated sheep by Cropper et al. (1985) in that younger (lighter) animals consume a greater amount of protein than the older (heavier) animals.

My study indicates that small-bodied individuals had a diet higher in CP than their larger-bodied counterparts. To increase their CP intake, small-bodied individuals might exhibit differential forage selection. By selectively choosing which forage items to consume, small-bodied individuals could increase rumen turnover which would aid in meeting growth demands. Also, differential forage selection between small and large-bodied individuals would reduce competition and enable small-bodied individuals to efficiently meet their high mass-specific metabolic demands. My study provides empirical evidence that foraging strategies probably differ across a body mass gradient within species. Therefore, forage partitioning is likely occurring which would decrease dietary overlap and limit intra-specific competition.

Wildlife managers could use the information presented herein to better understand nutritional needs across body sizes. Additionally, by assessing landscapes, managers can use my information to determine how their property meets the forage needs of current populations. Depending on the age class of white-tailed deer populations and the quality and quantity of available forage, augmentations may be required to the landscape to increase high quality forage. Augmentations to the landscape that increase forage quality would enable the young age classes to more efficiently meet their metabolic demands. This would potentially increase recruitment, as well as overall body condition of the population in general.

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Table 3.1.--Summary of the characteristics of white-tailed deer (*Odocoileus virginianus*) sampled during September, November, and December 2009 and 2010 in a 2628 ha enclosure at Kerr Wildlife Management Area, Kerr County, Texas, USA. Data shows mean, standard error (SE), and range of crude protein, acid detergent fiber, and neutral detergent fiber in grams (measured from rumen contents) with respect to sex and across an array of age classes.

Sex	Age	n	BM	CP			ADF			NDF		
				Mean	SE	Range	Mean	SE	Range	Mean	SE	Range
Female	Juvenile	4	17.6	0.05	0.01	0.04-0.08	0.10	0.03	0.07-0.18	0.15	0.02	0.12-0.22
	Sub-adult	10	34.5	0.12	0.02	0.05-0.15	0.25	0.03	0.15-0.36	0.33	0.04	0.17-0.47
	Adult	59	40.3	0.14	0.01	0.05-0.25	0.33	0.01	0.17-0.55	0.44	0.02	0.21-0.73
Male	Juvenile	1	23.5	0.10	N/A	N/A	0.25	N/A	N/A	0.30	N/A	N/A
	Sub-adult	19	36.1	0.10	0.01	0.05-0.19	0.23	0.02	0.13-0.35	0.31	0.02	0.21-0.43
	Adult	15	56.4	0.14	0.02	0.04-0.37	0.37	0.07	0.12-1.21	0.50	0.08	0.17-1.43
Combined		108	40.3	0.11	0.01	0.05-0.21	0.26	0.03	0.13-0.53	0.34	0.03	0.18-0.66

N/A represents not applicable, n=sample size, BM=average body mass, CP=crude protein, ADF=acid detergent fiber, NDF=neutral detergent fiber. Nutritional components (CP, ADF, NDF) are in grams per rumen.

Table 3.2.-- Models analyzed using AIC<sub>c</sub> and competing models (bold) for the response variables of crude protein, acid detergent fiber, and neutral detergent fiber from digesta of white-tailed deer (*Odocoileus virginianus*) sampled during September, November, and December 2009 and 2010 in a 2628 ha enclosure at Kerr Wildlife Management Area, Kerr County, Texas, USA.

Model predictors	nPar	CP				ADF				NDF			
		AIC <sub>c</sub>	Δ AIC <sub>c</sub>	Model Weight	r <sup>2</sup>	AIC <sub>c</sub>	Δ AIC <sub>c</sub>	Model Weight	r <sup>2</sup>	AIC <sub>c</sub>	Δ AIC <sub>c</sub>	Model Weight	r <sup>2</sup>
bm	3	123.570	67.110	0.000	0.083	109.200	49.730	0.000	0.188	86.590	36.900	0.000	0.202
bm+yr	4	76.520	20.050	0.000	0.408	76.910	17.450	0.000	0.398	73.220	23.530	0.000	0.295
bm+bf	4	120.220	63.750	0.000	0.112	105.990	46.530	0.000	0.212	81.420	31.730	0.000	0.240
bm+kt	4	119.800	63.340	0.000	0.115	110.480	51.020	0.000	0.179	88.610	38.910	0.000	0.188
bm+yr+kt	5	78.700	22.230	0.000	0.402	76.600	17.130	0.000	0.406	73.620	23.920	0.000	0.300
bm+yr+bf	5	72.110	15.650	0.000	0.437	73.320	13.850	0.000	0.424	68.080	18.390	0.000	0.335
bm+sex+lact	5	96.220	39.760	0.000	0.297	87.300	27.840	0.000	0.344	58.730	9.040	0.000	0.390
bm+sex+lact+yr	6	<b>58.180</b>	<b>1.720</b>	<b>0.100</b>	<b>0.511</b>	63.780	4.310	0.040	0.479	52.630	2.940	0.080	0.480
bm+sex+lact+kt	6	94.370	37.910	0.000	0.316	89.450	29.990	0.000	0.339	60.880	11.190	0.000	0.385
bm+sex+lact+bf	6	95.450	38.990	0.000	0.309	86.590	27.120	0.000	0.356	56.980	7.280	0.010	0.407
bm+sex+lact+sex x bm	6	96.350	39.890	0.000	0.304	84.730	25.270	0.000	0.367	58.010	8.320	0.010	0.401
bm+sex+lact+yr+kt	7	60.450	3.990	0.030	0.510	63.020	3.550	0.060	0.488	52.650	2.960	0.080	0.437
bm+sex+lact+yr+sex x bm	7	59.500	3.040	0.050	0.511	62.540	3.070	0.070	0.490	52.760	3.070	0.080	0.436
bm+sex+lact+kt+sex x bm	7	95.100	38.640	0.000	0.319	87.020	27.550	0.000	0.361	60.030	10.340	0.000	0.397
bm+sex+lact+bf+sex x bm	7	94.430	37.970	0.000	0.324	82.190	22.730	0.000	0.389	54.620	4.930	0.030	0.426
bm+sex+lact+bf+yr	7	<b>56.940</b>	<b>0.470</b>	<b>0.190</b>	<b>0.522</b>	62.920	3.460	0.060	0.489	<b>50.970</b>	<b>1.270</b>	<b>0.180</b>	<b>0.445</b>

Table 3.2.--Continued

Model predictors	nPar	CP				ADF				NDF			
		AIC <sub>c</sub>	$\Delta$ AIC <sub>c</sub>	Model Weight	r <sup>2</sup>	AIC <sub>c</sub>	$\Delta$ AIC <sub>c</sub>	Model Weight	r <sup>2</sup>	AIC <sub>c</sub>	$\Delta$ AIC <sub>c</sub>	Model Weight	r <sup>2</sup>
bm+sex+lact+bf+yr+sex x bm	8	<b>57.390</b>	<b>0.930</b>	<b>0.150</b>	<b>0.526</b>	<b>60.070</b>	<b>0.600</b>	<b>0.240</b>	<b>0.508</b>	<b>49.690</b>	<b>0.000</b>	<b>0.350</b>	<b>0.458</b>
bm+age	5	103.890	47.430	0.000	0.245	90.430	30.960	0.000	0.325	66.070	16.370	0.000	0.348
bm+age+yr	6	62.390	5.930	0.010	0.491	64.030	4.560	0.030	0.477	58.120	8.420	0.010	0.401
bm+age+kt	6	102.270	45.800	0.000	0.264	92.580	33.110	0.000	0.319	68.180	18.490	0.000	0.342
bm+age+yr	6	62.390	5.930	0.010	0.491	64.030	4.560	0.030	0.477	58.120	8.420	0.010	0.401
bm+age+kt	6	102.270	45.800	0.000	0.264	92.580	33.110	0.000	0.319	68.180	18.490	0.000	0.342
bm+age+bf	6	99.800	43.330	0.000	0.281	86.530	27.060	0.000	0.356	59.710	10.020	0.000	0.392
bm+age+age x bm	7	106.650	50.190	0.000	0.243	92.920	33.450	0.000	0.325	69.100	19.410	0.000	0.344
bm+age+yr+kt	7	64.530	8.070	0.000	0.487	62.480	3.020	0.070	0.491	57.380	7.680	0.010	0.412
bm+age+yr+age x bm	8	63.040	6.580	0.010	0.500	66.620	7.150	0.010	0.477	61.100	11.400	0.000	0.398
bm+age+kt+age x bm	8	104.630	48.170	0.000	0.265	95.100	35.630	0.000	0.319	71.360	21.660	0.000	0.338
bm+age+bf+age x bm	8	102.340	45.880	0.000	0.281	89.280	29.810	0.000	0.355	62.740	13.040	0.000	0.389
bm+age+bf+yr	7	<b>56.760</b>	<b>0.300</b>	<b>0.210</b>	<b>0.523</b>	<b>59.460</b>	<b>0.000</b>	<b>0.330</b>	<b>0.505</b>	<b>51.690</b>	<b>1.990</b>	<b>0.130</b>	<b>0.442</b>
bm+age+bf+yr+age x bm	9	<b>56.460</b>	<b>0.000</b>	<b>0.240</b>	<b>0.535</b>	62.050	2.580	0.090	0.505	54.450	4.760	0.030	0.441

Note: bm, body mass; kt, time of kill; lact, lactation; bf, ln(back fat+1); yr, year; nPar, number of parameters.

Table 3.3.-- Model averaged parameter estimates, standard errors (SE), and confidence intervals for crude protein, acid detergent fiber, and neutral detergent fiber taken from digesta of white-tailed deer (*Odocoileus virginianus*) sampled during September, November, and December 2009 and 2010 in a 2628 ha enclosure at Kerr Wildlife Management Area, Kerr County, Texas, USA.

Coefficients	CP				ADF				NDF			
	SE	lb <sup>+</sup>	Coef. Est.	ub <sup>+</sup>	SE	lb <sup>+</sup>	Coef. Est.	ub <sup>+</sup>	SE	lb <sup>+</sup>	Coef. Est.	ub <sup>+</sup>
Intercept	0.412	-4.087	-3.270	-2.453	0.476	-3.464	-2.520	-1.576	0.378	-2.920	-2.170	-1.420
bm	<b>0.004</b>	<b>0.015</b>	<b>0.023</b>	<b>0.031</b>	<b>0.005</b>	<b>0.006</b>	<b>0.016</b>	<b>0.026</b>	<b>0.011</b>	<b>0.009</b>	<b>0.032</b>	<b>0.054</b>
sex	0.237	-0.387	0.083	0.554	0.348	-0.356	0.334	1.024	0.299	-0.383	0.210	0.803
lact	<b>0.084</b>	<b>0.104</b>	<b>0.270</b>	<b>0.436</b>	<b>0.085</b>	<b>0.060</b>	<b>0.229</b>	<b>0.398</b>	<b>0.082</b>	<b>0.112</b>	<b>0.274</b>	<b>0.436</b>
bf	<b>0.160</b>	<b>-0.679</b>	<b>-0.362</b>	<b>-0.045</b>	<b>0.156</b>	<b>-0.665</b>	<b>-0.355</b>	<b>-0.045</b>	<b>0.155</b>	<b>-0.652</b>	<b>-0.344</b>	<b>-0.036</b>
yr	<b>0.064</b>	<b>0.307</b>	<b>0.434</b>	<b>0.561</b>	<b>0.068</b>	<b>0.209</b>	<b>0.344</b>	<b>0.479</b>	<b>0.064</b>	<b>0.048</b>	<b>0.174</b>	<b>0.300</b>
age F	0.008	-0.017	-0.001	0.014	0.008	-0.029	-0.014	0.001	0.008	-0.026	-0.011	0.004
age SA	0.598	-2.054	-0.868	0.318	0.503	-1.836	-0.838	0.160	0.432	-1.650	-0.793	0.064
kt	0.660	-2.074	-0.765	0.544	0.302	-0.881	-0.282	0.317	0.322	-0.966	-0.327	0.312
wt:age F	0.054	-0.087	0.019	0.126	0.055	-0.050	0.059	0.168	0.053	-0.066	0.039	0.144
wt:age SA	<b>0.019</b>	<b>0.002</b>	<b>0.040</b>	<b>0.078</b>	0.020	-0.021	0.018	0.056	0.019	-0.016	0.021	0.058
wt:sex	0.009	-0.029	-0.011	0.007	<b>0.009</b>	<b>-0.037</b>	<b>-0.019</b>	<b>-0.001</b>	0.009	-0.033	-0.015	0.002

Coef. Est represents the coefficient estimate; bm, body mass; lact, lactation; bf, ln(back fat+1); yr, year; age F, fawns; age SA, sub-adults (reference category adult); kt, time of kill; wt:age F, interaction between body mass and age (fawn); wt:age SA, interaction between body mass and age (sub adult); and wt:sex, interaction between body mass and sex. N/A represent not applicable.

<sup>+</sup> Coefficient estimates are given with lower (lb) and upper bounds (ub) of 95% confidence intervals. Covariates are statistically significant if confidence intervals exclude 0.

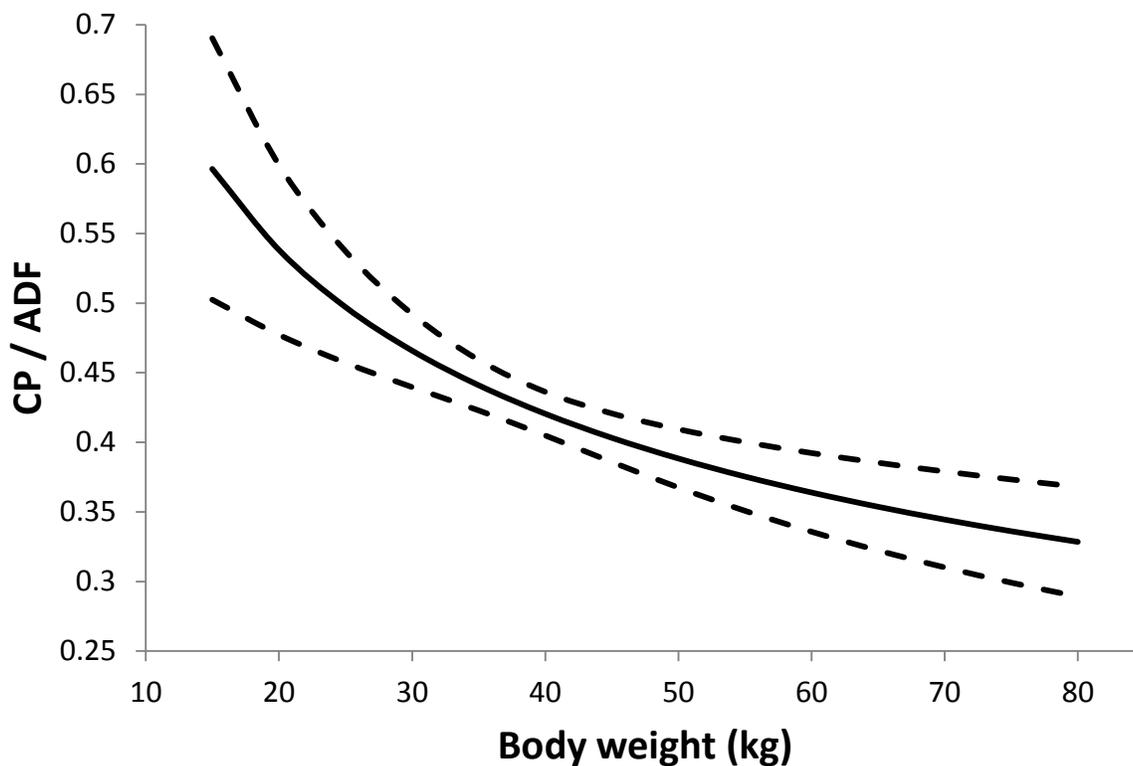


Figure 3.1.--Ratio of CP:ADF across a spectrum of body masses with 95% confidence intervals. Ratios were derived from back-transformed predicted values of crude protein [CP (g)] divided by back-transformed predicted values of acid detergent fiber [ADF (g)] of white-tailed deer (*Odocoileus virginianus*) sampled during September, November, and December 2009 and 2010 in a 2628 ha enclosure at Kerr Wildlife Management Area, Kerr County, Texas, USA. This ratio in relation to body mass indicated smaller white-tailed deer possessed a greater amount of CP in relation to ADF in the rumen-reticulum.

## CHAPTER IV

### TEMPORAL VARIATIONS IN RUMEN-RETICULUM FILL, RESERVE CAPACITY, AND ABSORPTIVE CAPACITY IN SOUTHERN WHITE-TAILED DEER

In semi-arid and arid environments, periods of drought are punctuated with brief periods of rainfall, which results in an ephemeral flush of green and succulent plants (Ostrowski et al. 2006). Therefore drought, either seasonal or those lasting multiple years, is likely the primary limiting factor affecting survival of herbivores inhabiting arid and semi-arid regions (Nagy 1994). Plant productivity in arid and semi-arid landscapes is largely dependent on precipitation events (Lane et al. 1998). As a result of infrequent and sporadic precipitation events, forage availability is likely to be episodic, and plants can often be senesced resulting in low nutritional quality (Shoemaker et al. 1976; Zimmerman and Tracy 1989). To better cope with the challenges of inhabiting an arid or semi-arid environment, many animals have undergone physiological, behavioral and morphological adaptations (Schmidt-Nielsen and Schmidt-Nielsen 1951). For example, some species of herbivores, in particular the Bedouin goats (*Capra hircus*) in the Middle East, have become well adapted to arid environments, and are able to graze on meager pastures and often withstanding water deprivation for 2-4 days (Brosh et al. 1986; Shkolnik and Choshniak 1984). However, not all herbivores inhabiting arid and semi-arid environments are as well adapted as the Bedouin goats. Adaptations such as those

exhibited by Bedouin goats are likely to differ across species and with regard to the severity of the environment (Silanikove et al. 1980).

Physiological changes, specifically to the rumen, can affect forage digestion and nutrient assimilation in ruminant herbivores. The rumen-reticulum is the largest chamber where most fermentation occurs in the gastro-intestinal tract of ruminants (Van Soest 1994). To accommodate variation in diet and food intake, the rate of fermentation, composition of products from fermentation (short-chain fatty acids) and the surface area of the absorptive rumen mucosa vary (Barboza et al. 2006; Zimmerman et al. 2006). During periods when forage plants are growing animals elevate food intake, fermentation increases, and the surface area of the rumen mucosa (hereafter surface enlargement factor, SEF) increases to enhance absorptive capacity for passive and active transport of nutrients across the rumen wall (Barboza et al. 2006; Martens et al. 2012; Storeheier et al. 2003; Zimmerman et al. 2006). Whereas when forage plants are non-growing the opposite occurs, animals are hypophagic, rate of fermentation declines, and so does SEF. The decrease in SEF during hypophagia is likely because maintaining large surface area of rumen mucosa is uneconomical when concentrations of short-chain fatty acids are low (Martens et al. 2012).

Often an increase in dry matter intake is associated with an increase in rumen-reticulum fill (Short 1964; Spalinger et al. 1993). Increases in dry matter intake and rumen-reticulum fill can be associated with consumption of diets that are of low quality (Barboza and Bowyer 2000). Therefore, increases in rumen-reticulum fill typically coincide with an increase in rumen-reticulum capacity (Barboza and Bowyer 2000; Demment and Van Soest 1985; Duarte et al. 2011; Weckerly 2010; Weckerly et al.

2003). Changes in dry matter intake, rumen-reticulum fill, and rumen-reticulum capacity are largely coupled with the quality and quantity of the food supply.

During times when forage quality decreases, ruminants must be able to increase dry matter intake as well as digestive efficiency in order to meet metabolic demands (Jiang et al. 2006). Variations in forage intake in ruminants can influence rumen-reticulum fill mainly as a result of differences in diet quality, type of diet, and fermentation rates (Barboza et al. 2006; Clauss et al. 2006). When forage is of high quality, it might be advantageous for the animal to invest in more rumen-reticulum organ tissue to increase capacity as well as SEF in spite of the metabolic costs of investing in organ tissue (Kelly et al. 1991; McLeod and Baldwin 2000). An investment in rumen-reticulum organ tissue might be detrimental to survival, however, when there are unpredictable changes in forage quality or quantity. Unpredictable environmental events have been shown to influence the quality and quantity of forage (Fritz and Duncan 1994; Spalton 1999). In areas where there is environmental heterogeneity, inherent unpredictability in future forage quality and quantity exists; therefore, it might be beneficial to have a rumen-reticulum that is capable of accommodating changes in forage intake without adding metabolically expensive tissue. By accommodating changes in forage intake in a manner that does not require metabolically expensive tissue, ruminants would be poised to capitalize on sudden changes in forage quality resulting from precipitation events.

In semi-arid environments where the availability of high quality forage is unpredictable the quality of the forage and the demands of the animal are likely to drive rumen-reticulum fill. Forage quality will also have a direct effect on the SEF due to

changes in the amount of short-chain fatty acids produced during fermentation. As a result of environmental heterogeneity in forage quality ruminants in these environments are likely to maintain a rumen-reticulum that is able to adapt to and accommodate sudden changes in forage intake as a result of alterations in forage quality. It then seems plausible that in semi-arid environments reserve capacity should remain constant across seasons so that there is always space in the rumen-reticulum to accommodate sudden changes in forage intake to be able to capitalize on high quality forage when it is available.

While attention has been given to rumen function in response to heat and drought, how animals and the rumen-reticulum respond to unpredictability in the food supply considering the energetic demands of reproduction has received little attention. At high latitudes, animal demands are greatest when digestible forage is most abundant (Argo et al. 1999; Bowyer 1991; Lawler and White 1997; Schwartz et al. 1988). A strong coupling between the food supply and animal demands might be less evident at low latitudes, specifically in semi-arid environments where precipitation events are less predictable. Therefore, individuals in a semi-arid environment might need to maintain sufficient rumen-reticulum tissue to capitalize on sudden increases in forage quality resulting from irregular precipitation events.

I conducted a study on white-tailed deer (*Odocoileus virginianus*) in a semi-arid environment to examine if rumen-reticulum reserve capacity is maintained at a relatively constant level across seasons in an effort to be able to capitalize on unpredictable changes in forage quality or quantity. I conducted a study to examine two hypotheses: the economy workload hypothesis, and the constant reserve capacity hypothesis. The economy of workload states that there should be just enough tissue for maximum

capacity and absorption. Thus, fill is likely to be positively related to reserve capacity, and reserve capacity positively related to SEF. The constant reserve capacity states that reserve capacity should be constant with changes in fill; and fill can change with respect to diet quality and animal demands, but reserve capacity does not. I hypothesize that white-tailed deer in a semi-arid environment will follow the constant reserve capacity hypothesis, which would enable them to respond in a more expedient way to changes in forage quality.

## Methods

### *Study area*

My study was conducted at Kerr Wildlife Management Area (KWMA) located in Kerr County, Texas, USA (30° 3'N, 99° 30'W). The KWMA encompasses an area of 2,628 ha, and is enclosed with a 2.6 m high game fence. The composition of the landscape at KWMA is roughly 8.7% savannah, 51.7% woodland, and 39.6% forest. The dominant tree species are plateau live oak (*Quercus fusiformis*) 41.7%, Ashe juniper (*Juniperus ashei*) 29.8%, post oak (*Quercus stellata*) 10.4%, shin oak (*Quercus sinuata*) 8.7%, Netleaf hackberry (*Celtis reticulata*) 6.2%, blackjack oak (*Quercus marilandica*) 1.8%, Texas oak (*Quercus buckleyi*) 1.8% , and mesquite (*Prosopis glandulosa*) 0.5% (Wills 2005). Kerr WMA is a subtropical savanna, summers are hot with day time temperatures often exceeding 35°C and winters are mild with day time temperatures ranging from 10 – 22°C. Annual precipitation averages 70.5 cm but varies across years. During the three years that data was collected at KWMA, precipitation was 62.74 cm in 2009, 76.6 cm in 2010, and 33.3 cm in 2011. The primary forage for white-tailed deer on Kerr WMA was various oaks (*Quercus* sp.), Ashe juniper (*Juniperus ashei*), bladderpods

(*Lesquerella* spp.), common horehound (*Marrubium vulgare*), filaree (*Erodium* spp.), globemallows (*Sphaeralcea* spp.), redseed plantain (*Plantago rhodosperma*), silverleaf nightshade (*Solanum elaeagnifolium*), spurges (*Euphorbia* spp.), whorled nodviolet (*Hybanthus verticillatus*), and wintergrass (*Stipa leucotricha*) (Warren and Krysl 1983).

### *Sampling*

White-tailed deer were collected in November (2009, 2010), March (2010, 2011), and September 2010. By sampling during these periods, I assessed the influence of major life history events (lactation, breeding season, and gestation) which alter metabolic demands of the animal. Furthermore, variation in quality of the food supply is likely to occur over the length of time animals were sampled because of variation in precipitation and temperature (Teer et al. 1965).

All white-tailed deer collected in November were by licensed public hunters and by Texas Parks and Wildlife personnel during the other months. During the public hunts, hunters were allowed to supplementally feed corn (1 day prior to the hunt). Animals were harvested using high powered rifles, and collection procedures followed an Institutional Animal Care and Use protocol from Texas State University (permit # 00933\_09\_06-03141BF15D) and ASM guidelines (Sikes et al. 2011). After each animal was harvested, it was transported to a check station where it was processed within 3 hours post mortem. Each animal was given a unique identification number upon arrival at the check station; and their sex, reproductive condition of females (pregnant, lactating, neither), and whole weight minus blood loss (measured to the nearest 0.10 kg) was obtained. The animals were then eviscerated and the mesentery removed from the entrails to expose the rumen-reticulum. Dressed weight was then taken (whole weight minus weight of internal organs

and mesentery). The rumen-reticulum was separated from the remainder of the entrails by ligations made at the esophagus just above the reticulum and at the reticulo-omasal sphincter (Ramzinski and Weckerly 2007; Weckerly et al. 2003).

The rumen-reticulum was inverted and emptied of all digesta matter. The pH of the digesta was obtained using an Oakton pH 100 series portable pH/mV/°C meter. All digesta matter within the rumen-reticulum was collected, weighed and set aside. The rumen-reticulum was then rinsed to ensure that it was void of any digesta. Once the rumen-reticulum was void of vegetative matter, it was reverted and a sample of the rumen wall, approximately 3 cm<sup>2</sup>, was collected from the atrium ruminis, dorsal sac, ventral sac, and the caudal-dorsal blind sac. Rumen wall samples were stored in 10% buffered formalin until processed (Mathiesen et al. 2000; Soveri and Nieminen 1995). I assumed that any changes in the samples due to fixation of the tissue samples were consistent for all samples (Lentle et al. 1997). Using a Nikon SMZ 745 stereo dissecting microscope with 1 cm<sup>2</sup> ocular grid consisting of 0.1 mm measurements, 10 papillae were randomly chosen from each of the 4 rumen wall locations and their length and width to the nearest 0.1 mm was measured. The density of papillae per 1 cm<sup>2</sup> was also counted. Surface enlargement factor (SEF) was calculated using the equation [(2 x papillae surface) x papillae number + base surface] / base surface, where papillae surface was papillae length multiplied by papillae width and base surface was the area of the subsample (Hofmann and Nygren 1992). The average SEF was calculated for each individual by adding the calculated SEF for each of the rumen sections and dividing it by the number of rumen wall locations.

To measure the volume of the rumen-reticulum, the organ was inverted and rinsed

of all particulate matter. The reverted rumen-reticulum organ was weighed to the nearest 0.1 kg and placed in a plastic drum filled with 208 l of tap water. Water was poured into the rumen-reticulum and the amount of water held by the rumen-reticulum was recorded to the nearest 0.1 L. The measurement was taken in triplicate and the mean of the three measurements was used in analyses (Ramzinski and Weckerly 2007; Weckerly 2010).

Approximately 800 g of digesta was collected from the rumen-reticulum, weighed and then dried at 60°C for 48 h after which it was weighed again. After the sample was dry, nitrogen was determined with a N gas analyzer using an induction furnace and thermal conductivity using a Leco FP-528 (AOAC 1997). The crude protein was determined as nitrogen times 6.25. Acid detergent fiber consists of lignin, cutin and cellulose that comprise the plant cell wall. Typically, cellulose is recalcitrant to digestion (Hummel et al. 2006), and lignin and cutin are completely indigestible (Van Soest 1994). Due to its composition, ADF was used as an index of forage quality. All digesta analyses were conducted by A&L Plains Agricultural Laboratory, Lubbock, Texas, USA.

#### *Statistical analysis*

The response variables were rumen-reticulum fill (wet weight of rumen-reticulum contents), reserve capacity (rumen-reticulum volume  $\div$  wet weight of rumen-reticulum contents<sup>-1</sup>), and SEF. Potential predictors were dressed body weight, sex and whether females were pregnant or lactating, season, CP, ADF, season, pH, and dry weight of the rumen-reticulum contents (hereafter dry fill). Sex, pregnancy, lactation, and season were categorical variables. Season was the month the animal was collected and was included to capture heterogeneity not measured by the other predictors. Models (least-squares regressions) were built to estimate the influence of diet composition (CP, ADF), animal

demand (sex, lactation, pregnant), season or combinations of these predictors on rumen-reticulum fill and reserve capacity. For rumen-reticulum fill I included dressed body weight in every model to account for potential heterogeneity from body size. I considered dry fill and pH in some models predicting SEF because pH is associated with concentration and composition of short-chain fatty acids (Crater et al. 2007; Martens et al. 2012; Short et al. 1966; Short et al. 1969). Dry fill was a predictor in some models because it is unclear whether diet composition or amount of material to ferment influences SEF (Storeheier et al. 2003).

Model selection was guided by Akaike Information Criterion corrected for small sample size ( $AIC_c$ ). The  $AIC_c$  uses fit of model to the data and parsimony as criteria for model selection (Burnham and Anderson 2002). The model with the smallest  $AIC_c$  was selected and I reported  $\Delta$ , the change in  $AIC_c$  between a model and the model with the smallest  $AIC_c$ . I also report the adjusted coefficient of determination ( $r^2$ ) for each model. Because season was a predictor in every selected model I conducted a Tukey's HSD multiple comparison procedure to assess similarities and differences among predicted monthly means (i.e., least squares means) of the response variables (Quinn and Keough 2002). Because Tukey's HSD multiple comparison procedure adjusts for experiment-wide error the detected differences are more conservative than t-tests of regression coefficients comparing the response between a reference category (i.e. September in this analysis) and another month.

## Results

Average monthly temperatures and precipitation amounts varied between sampling periods and across years (see Table 4.1). I also report temperate and

precipitation the month before sampling because climatic conditions during that time are likely to influence food supplies in the month I sampled deer (Teer et al. 1965).

Temperatures were noticeably cooler in February and March than in the other months. A wet period occurred in the first year of the study. For example, in October – November, 2009 and February – March, 2010, precipitation was more than three times the amounts recorded in these same months in the next year.

Crude protein concentration of rumen-reticulum contents ranged from 0.16 in November, 2009, to 0.21 in March, 2011, and concentration of acid detergent fiber ranged from 0.38 in March, 2011, to 0.46 in November, 2010 (Table 4.2). Digesta CP did not covary with ADF ( $r = 0.11$ ,  $t_{137} = 1.33$ ,  $P = 0.910$ ). Rumen-reticulum fill was variable across months, the lowest rumen-reticulum fill was in March, 2010, and the greatest rumen-reticulum fill was in March, 2011. The pH of rumen-reticulum contents ranged from 5.62 to 6.30 and SEF was lowest (9.2) in November, 2009, and highest (13.4) in September, 2010. Reserve capacity was more than twice as much in November, 2009, as it was in September, 2010.

Selected models had  $\Delta$  of 0.0 (Tables 4.3, 4.4, 4.5). The coefficients of determination ranged from 0.32 to 0.81 for the three selected models. Season was influential in every selected model (Table 4.6, 4.7, 4.8). Rumen-reticulum fill was influenced by both life history and diet composition, reserve capacity was influenced by diet composition, and SEF was also influenced by diet composition. Because of seasonal variation in every response variable (Tables 4.3, 4.4, 4.5) I predicted monthly means using non-lactating females and monthly means for all other predictors in these models (Figure 4.1). Rumen-reticulum fill of non-lactating females was least in November, 2009

and 2010, and greater in the other months. Reserve capacity and SEF showed similar monthly differences but in the opposite direction. Reserve capacity was greatest in Novembers and least in the other months. In contrast, SEF was least in the Novembers and greatest in the remaining months.

### **Discussion**

Because of the much greater precipitation in the first year of the study and the warmer temperatures in August and September it is likely that heterogeneity in food supplies did occur during the study because rumen-reticulum fill varied temporally. The findings from my study, however, did not support the economy of workload hypothesis nor the constant reserve capacity hypothesis. The economy of workload hypothesis predicts that rumen-reticulum fill is positively related to reserve capacity and reserve capacity is positively related to SEF. The constant reserve capacity hypothesis stated that reserve capacity should be constant with changes in fill; but fill can change with respect to diet quality and animal demands. Neither hypothesis was supported because the factors that influenced rumen-reticulum fill differed from the factors that influenced reserve capacity and SEF as well as because reserve capacity was not constant across seasons. Season, animal demands and diet composition influenced rumen-reticulum fill but only season and diet composition, not animal demands, influenced reserve capacity and SEF.

Animal demands, specifically lactation, influenced rumen-reticulum fill. Lactating females in September, for example, had greater rumen-reticulum fill suggestive of greater food intake (Weckerly 2010). Additionally, the September sampling period had the highest ambient temperatures of the times I sampled. It is conceivable that the increase in rumen-reticulum fill during September could also be affected by animals being heat

stressed (Silanikove 1985). When animals are heat stressed rumen motility might be less and turnover of material in the rumen slowed.

Diet composition, particularly ADF concentration, affected rumen-reticulum fill, reserve capacity, and SEF. Diets that are high in ADF indicate a larger fraction of the ingested forage is indigestible and forage intake will likely decrease because of slower rumen turnover (Barboza et al. 2006; Holter et al. 1977; Thompson et al. 1973; Wheaton and Brown 1983). Consumption of forage that has high fiber content can be restricted by limitations on rumen-reticulum distension (Allen 1996). Therefore, consuming large amounts of a low quality diet (i.e., high ADF) would decrease reserve capacity. I found an inverse relationship between reserve capacity and ADF, which is supportive of the findings of Balch and Campling (1962). An inverse relationship was also detected between ADF and SEF. This finding is consistent with another study that found that diets comprised of low quality forage (i.e., ADF) result in a decrease in rumen papillation (Mathiesen et al. 2000). Papillae has been noted to respond within a short time period to dietary changes (Nockels et al. 1966; Tamate et al. 1962), therefore SEF is likely a direct indicator of dietary nutrition (Lentle et al. 1996). In my study, dietary nutrition likely varied across seasons which helps explain why SEF varied across seasons.

It is unlikely that hunters having the opportunity to provide corn a day before the hunt had much influence on deer nutrition. Rumen-reticulum fill varied between the two Novembers, when hunts occurred, as did CP and ADF (Table 1). The patterns in these three variables are more consistent with precipitation resulting in a more nutritious food supply in November, 2009, than in November, 2010, that resulted in more rapid rumen turnover. It is likely that deer intake of corn was meager during the hunts.

The positive relationship between pH and SEF probably reflects a change in concentration and composition of short-chain fatty acids associated with nutrient concentration and composition of the diet (Barboza et al. 2006; Crater et al. 2007; Martens et al. 2012; Short et al. 1966; Short et al. 1969). What was unexpected was that the relationship between pH and SEF was positive. Most studies that measure diet quality, short-chain fatty acids, and pH in the rumen-reticulum find that increased dietary quality is associated with increased short-chain fatty acids concentrations and more acidic rumen conditions. One factor that could potentially influence pH is the period of time postmortem before rumen pH is sampled. Studies have indicated an increase in short-chain fatty acid production post mortem, which drives down pH (Cole et al. 1998; Thomson 1969). However, these studies indicated that pH drop is minimal for the first 4 hours postmortem. In my samples pH was taken no longer than 3 hours post mortem.

An unexpected finding was that reserve capacity was greatest when SEF was less (Figure 4.1). To my knowledge, no such pattern has been reported. Because ADF influenced both reserve capacity and SEF it is likely that the inverse relationship between these two response variables is coupled to diet quality. A large amount of space in the rumen-reticulum should not be needed when consuming a high quality diet because of quicker rumen turnover. What is needed in the rumen when consuming a high quality diet is the capacity to absorb nutrients which requires greater SEF (Mathiesen et al. 2000; Zimmerman et al. 2006). The inverse relationship between reserve capacity and SEF is consistent with the patterns reported by Hofmann (1973). Species with more voluminous rumens (grazers) have less of the rumen lumen covered with papillae than species that are primarily browsers where all of the lumen is covered with papillae and rumen-reticulum

capacity is less. This general pattern reported among ruminant species might be relevant within a species as well. There might be a direct connection between reserve capacity, rumen volume, and SEF.

What are unclear are the anatomical changes that would result in a reduction in reserve capacity with increased SEF. When the rumen has longer and wider papillae there must be reworking of connective tissue between the muscle layer and the epithelium and the papillae must be networked with vascular tissue (Hofmann 1973). The restructuring of rumen wall anatomy to accommodate a high SEF might alter the ability of the rumen to distend.

The largest ratio in SEF was between March, 2010, and November, 2009 (Figure 4.1,  $13.42/9.19 = 1.5$ ). For white-tailed deer from a higher latitude ( $43^{\circ}\text{N}$ ) in the Black Hills of South Dakota, the deviation in SEF between February and August was about 1.9 – 2.1 (Zimmerman et al. 2006). The presumed difference in the magnitude of change between the two studies is probably not due to technique. Both studies preserved rumen wall samples and estimated SEF in the same way. Yet Zimmerman et al. (2006) did not sample rumen tissue from the atrium ruminis. The atrium ruminis in my specimens and in other studies is noted for greater SEF than in other parts of the rumen (Appendix 4.1, Forsyth and Fraser 1999; Mathiesen et al. 2000). Consequently, the SEF measurements that I report were probably not constrained by obtaining tissue samples that were only from parts of the rumen with a lower SEF. It is plausible that the magnitude of change in SEF between winter and summer differs in animals from low and high latitudes

Plasticity of rumen-reticulum functions are likely to differ between animals inhabiting semi-arid ecosystems and animals at high latitudes. At high latitudes animal

demands are greatest during a short growing season when nutritious food resources are ubiquitous. At high latitudes, animals display hyperphagia during the growing season to meet the energetic demands of reproduction and to replenish nutritional reserves lost in the previous non-growing season and to add reserves for the upcoming non-growing season when nutritious forage is going to be scarce and cold temperatures tax thermoregulation (Barboza and Hume 2006; Barboza et al. 2006; Parker et al. 2009). In semi-arid environments the non-growing and the growing seasons are more unpredictable and winter temperatures typically do not exert great demands on thermoregulation. Therefore, periods of hypo- and hyperphagia might not be as extensive as at high latitudes (Holter et al. 1977; Thompson et al. 1973; Wheaton and Brown 1983). Also, due to unpredictability in quality and quantity of forage available in semi-arid environments, ruminants inhabiting these areas might be more conservative in adding additional metabolically expensive tissue to accommodate changes in forage. Findings presented herein shed light on how ruminants in a semi-arid environment are able to accommodate sudden changes in forage intake resulting from changes in forage quality without having to account for major changes in metabolically expensive rumen-reticulum tissue.

Exploiting palatable forage to meet animal demands in a wide variety of environmental settings requires plasticity in rumen-reticulum fill, reserve capacity, and SEF. Yet, understanding how rumen-reticulum functions vary across the spectrum of environmental heterogeneity and animal demands has often focused on capacity with less regard to how capacity is coupled to other attributes that affect rumen form and functions. Understanding how plasticity in rumen-reticulum functions is coupled with environmental heterogeneity is vital to predicting how ruminants will respond to and

effect ecosystem processes in a constantly changing world.

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Table 4.1.—Summary of the characteristics of sampled white-tailed deer (*Odocoileus virginianus*) from Kerr Wildlife Management Area, Texas, USA. Data shows the mean ( $\bar{X}$ ) and standard deviation ( $s$ ).

covariates	Nov-09		Mar-10		Sep-10		Nov-10		Mar-11	
	$\bar{X}$	$s$								
$n$	46		20		10		49		14	
ADF	0.403	0.079	0.418	0.036	0.397	0.025	0.461	0.080	0.380	0.030
DW	29.924	8.171	29.436	3.708	28.492	4.310	30.178	8.284	28.100	4.978
CP	0.161	0.032	0.209	0.025	0.207	0.025	0.192	0.026	0.211	0.024
RR fill	2.469	0.909	2.207	0.343	3.654	0.752	2.469	0.919	3.810	1.012
pH	5.690	0.342	6.299	0.330	5.615	0.200	5.848	0.384	5.979	0.254
SEF	9.191	1.590	12.431	2.755	13.424	2.077	9.811	2.527	11.971	2.677
RC	2.538	0.712	1.663	0.632	1.180	0.344	2.381	0.713	1.308	0.877

$n$  indicates sample size, ADF represents acid detergent fiber (%), DW is dressed body weight (kg), CP represents crude protein (%), RC is reserve capacity of the rumen-reticulum (Volume [L] · rumen-reticulum fill [kg]<sup>-1</sup>), RR indicated rumen-reticulum, and SEF is surface enlargement factor.

Table 4.2.—Models analyzed and summaries of models analyzed for the response variable of rumen-reticulum fill (wet weight) of white-tailed deer (*Odocoileus virginianus*) sampled from Kerr Wildlife Management Area, Texas, USA. Each model had a predictor of dressed body weight. Model summaries are number of parameter estimates (nPar),  $\Delta$ -the change in  $AIC_c$  between a particular model and the model with the smallest  $AIC_c$ , and the coefficient of determination ( $r^2$ ).

Model	nPar	$\Delta$	$r^2$
Sex, lact, preg	6	152.050	0.405
Season	7	113.801	0.552
ADF, CP	5	54.032	0.704
Sex, lact, preg, season	10	95.046	0.619
Sex, lact, preg, ADF, CP	8	41.036	0.737
Season, ADF, CP	9	20.114	0.776
Sex, lact, preg, season, ADF,CP	12	0.000	0.811

lact represents lactating, preg indicated pregnant, ADF is acid detergent fiber, CP is crude protein.

Table 4.3.—Models analyzed and summaries of models analyzed for the response variable of rumen-reticulum reserve capacity (volume · wet weight<sup>-1</sup>) of white-tailed deer (*Odocoileus virginianus*) sampled from Kerr Wildlife Management Area, Texas, USA. Model summaries are number of parameter estimates (nPar),  $\Delta$ -the change in AIC<sub>c</sub> between a particular model and the model with the smallest AIC<sub>c</sub>, and the coefficient of determination ( $r^2$ ).

Model	nPar	$\Delta$	$r^2$
Sex, lact, preg	5	50.167	0.142
Season	6	14.647	0.341
ADF, CP	4	69.797	0.003
Sex, lact, preg, season	9	19.360	0.335
Sex, lact, preg, ADF, CP	7	48.787	0.164
Season, ADF, CP	8	0.000	0.416
Sex, lact, preg, season, ADF,CP	11	5.985	0.407

lact represents lactating, preg indicated pregnant, ADF is acid detergent fiber, CP is crude protein.

Table 4.4.—Models analyzed and summaries of models analyzed for the response variable of surface enlargement factor (SEF) of white-tailed deer (*Odocoileus virginianus*) sampled from Kerr Wildlife Management Area, Texas, USA. Model summaries are number of parameter estimates (nPar),  $\Delta$ -the change in AIC<sub>c</sub> between a particular model and the model with the smallest AIC<sub>c</sub>, and the coefficient of determination ( $r^2$ ).

Model	nPar	$\Delta$	$r^2$
Dwfill	3	39.560	0.052
ADF,CP	4	30.014	0.115
ADF,CP,pH	5	15.543	0.209
Season	6	4.717	0.275
Dwfill,ADF,CP	5	27.190	0.140
Dwfill,ADF,CP,pH	6	14.031	0.224
Season,CP,ADF	8	7.240	0.274
Season,CP,ADF,pH	9	0.000	0.317
Dwfill,season,CP,ADF	9	8.037	0.276
Dwfill,season,CP,ADF,pH	10	0.617	0.320

Dwfill is the dry weight of rumen-reticulum fill, ADF is acid detergent fiber, CP is crude protein.

Table 4.5.—Parameter estimates of the selected model for rumen-reticulum fill (wet weight) of white-tailed deer (*Odocoileus virginianus*) sampled from Kerr Wildlife Management Area, Texas, USA.

Coefficient	Estimate	SE	<i>t</i>	<i>P</i>
Intercept	-0.863	0.257	-3.36	0.001
Dressed weight	0.491	0.067	7.03	<0.001
SexM	-0.014	0.046	-0.31	0.758
Lactation	0.175	0.042	4.12	<0.001
Pregnancy	0.014	0.103	0.14	0.888
Season SP1	-0.321	0.118	-2.71	0.008
Season SP2	-0.131	0.098	-1.33	0.186
Season W1	-0.410	0.060	-6.89	<0.001
Season W2	-0.242	0.055	-4.36	<0.001
ADF	1.631	0.144	11.33	<0.001
CP	0.143	0.555	0.26	0.798

SexM indicates that males were the reference category, SP1 indicates spring 2010, SP2 represents spring 2011, W1 is winter 2010, W2 is winter 2011, ADF represents acid detergent fiber, and CP is crude protein. The intercept is in natural log scale.

Table 4.6. Parameter estimates of the selected model for reserve capacity (rumen-reticulum volume  $\cdot$  wet weight of contents<sup>-1</sup>) of white-tailed deer (*Odocoileus virginianus*) sampled from Kerr Wildlife Management Area, Texas, USA.

Coefficient	Estimate	SE	<i>t</i>	<i>P</i>
Intercept	0.563	0.558	1.01	0.314
Season SP1	0.338	0.268	1.26	0.210
Season SP2	0.135	0.252	0.54	0.593
Season W1	1.610	0.242	6.65	<0.001
Season W2	1.582	0.224	7.06	<0.001
ADF	-1.609	0.528	-3.05	0.003
CP	5.022	2.243	2.24	0.027

RRfill represents rumen-reticulum fill, SP1 indicates spring 2010, SP2 represents spring 2011, W1 is winter 2010, W2 is winter 2011, CP is crude protein, and ADF represents acid detergent fiber.

Table 4.7.—Parameter estimates of the selected model for surface enlargement factor (SEF) from white-tailed deer (*Odocoileus virginianus*) sampled from Kerr Wildlife Management Area, Texas, USA.

Coefficient	Estimate	SE	<i>t</i>	<i>P</i>
Intercept	3.799	3.594	1.057	0.292
Season SP1	-2.158	0.947	-2.279	0.024
Season SP2	-2.302	0.952	-2.418	0.017
Season W1	-3.937	0.835	-4.713	≤ 0.001
Season W2	-3.469	0.799	-4.343	≤ 0.001
CP	8.761	6.950	1.261	0.210
ADF	-7.225	3.130	-2.308	0.023
pH	1.902	0.624	3.049	0.003

SP1 indicates spring 2010, SP2 represents spring 2011, W1 is winter 2010, W2 is winter 2011, CP is crude protein, and ADF represents acid detergent fiber.

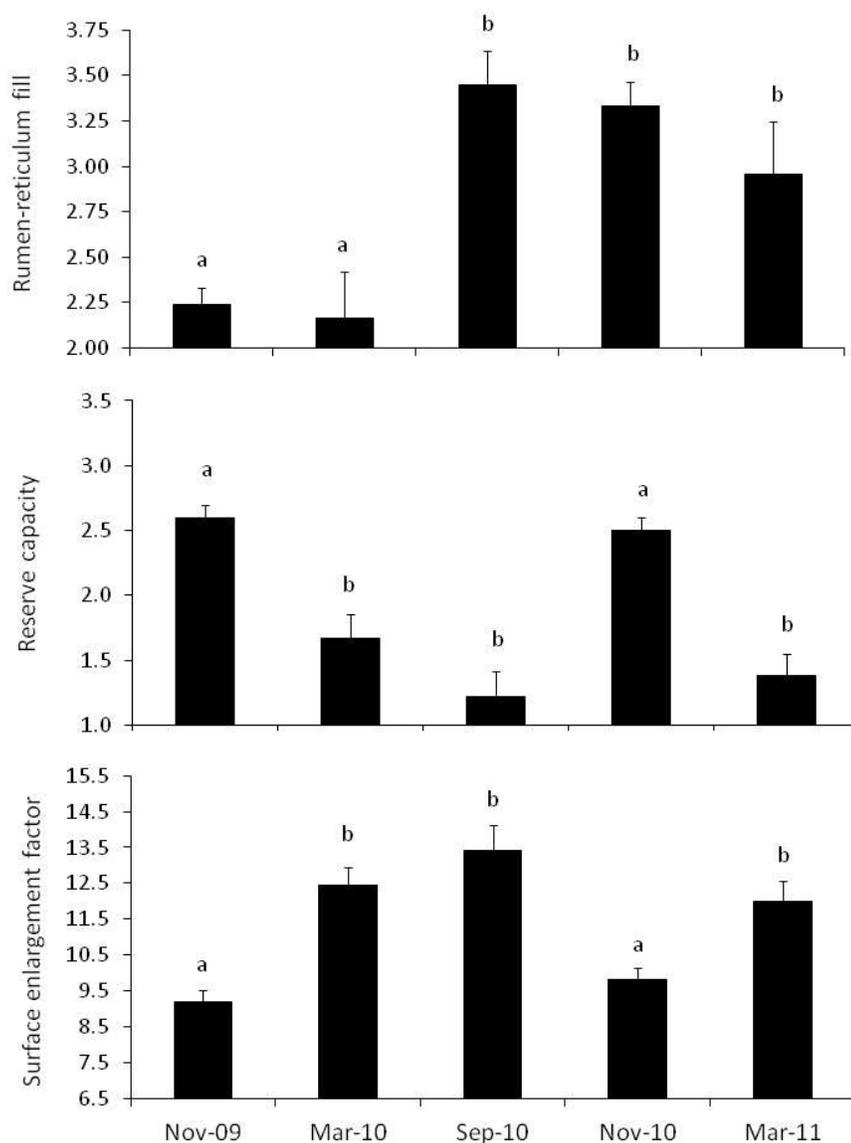


Figure 4.1.-- Bar charts with one standard error bars of monthly predicted means of rumen-reticulum fill (kg dry weight of rumen-reticulum contents divided by dressed weight in kg), reserve capacity (rumen-reticulum volume · wet weight<sup>-1</sup>), and surface enlargement factor of non-reproductive females (not lactating or pregnant). Predicted means of response variables were estimated by adjusting for influence of monthly means of crude protein, acid detergent fiber, or pH predictors that were in selected models. Letters above error bars denote months that were similar as determined from a Tukey's HSD multiple comparison procedure.

Appendix 4.1—Summary of the surface enlargement factor (SEF) characteristics for each region sampled from the rumen-reticulum. Total SEF is also noted. Samples were obtained from white-tailed deer from Kerr Wildlife Management Area, Texas, USA. Data shows the mean ( $\bar{X}$ ) and standard deviation ( $s$ ).

Region	Nov-09		Mar-10		Sep-10		Nov-10		11-Mar	
	$\bar{X}$	$s$								
AR	12.44	3.19	19.83	5.94	21.37	4.57	14.56	4.80	19.40	5.36
VS	9.06	1.67	9.54	5.14	11.18	2.71	9.24	2.58	9.48	2.54
DS	7.91	2.00	9.39	3.16	9.85	2.09	7.36	2.70	9.19	3.64
CDBS	7.37	2.13	10.97	5.16	11.32	3.05	8.08	2.73	10.47	3.37
Total SEF	9.19	1.59	12.43	2.75	13.42	2.08	9.81	2.53	11.97	2.68

Regions of the rumen-reticulum are denoted as follows: AR indicates atrium ruminis, VS represents ventral sac, DS is the dorsal sac, and CDBS signifies the caudal dorsal blind sac.

## CHAPTER V

### SUMMARY AND SYNTHESIS

The aim of this dissertation was to examine variation in rumen-reticulum function of southern white-tailed deer, how rumen-reticulum function is influenced by body mass, and the influence of body mass on nutrition. Overall, this dissertation extends our knowledge of factors that affect rumen-reticulum attributes and scaling relationships in white-tailed deer. When considering the influence of ontogeny on scaling relationships between body mass and response variables of rumen-reticulum capacity, rumen-reticulum organ weight, and digesta mass, I was expecting to find an allometric relationship as reported by Weckerly (2010); however, I found that the scaling relationships were isometric. These findings imply that juvenile and sub-adult individuals had scaling relationships similar to their larger bodied counterparts. Regardless of energetic demands from growth and metabolic costs associated with maintaining gut tissue, my findings suggested that juvenile and sub-adult white-tailed deer have rumen-reticulum organs that, in relation to body mass, express similar scaling relationships to those displayed in adult individuals.

My study contradicted findings of Weckerly (2010) which indicated that the scaling relationship between body mass and rumen-reticulum capacity of white-tailed deer had allometric scaling relationships. The discrepancy in scaling relationships

between my study and the Weckerly (2010) study might be due to my study assessing a greater number of covariates than were accounted for by Weckerly (2010). Nonetheless the disagreements regarding the scalars between the fore mentioned studies indicate that there are likely numerous factors that influence rumen-reticulum capacity and fill, body mass, nutrition, body condition, life history demands, and further study is necessary to determine the extent to which each of these factors directly and indirectly influence rumen-reticulum attributes. Although scaling relationships in my study were similar between juvenile, sub-adult, and adults, there were differences in nutritional components within the rumen when assessed across a body mass gradient.

With regard to nutrition, body mass covaried negatively with the CP:ADF ratio. This finding supported my hypothesis that small-bodied individuals exhibited greater CP:ADF than their larger bodied counterparts. Also, the inverse relationship between body mass and CP:ADF suggested that smaller-bodied individuals were likely exhibiting some form of selective foraging which resulted in consumption of a higher quality diet. By consuming a higher quality diet smaller-bodied individuals should be able to more efficiently meet their high mass-specific metabolic demands. Small-bodied individuals are likely to forage differentially than their larger-bodied counter parts to maximize nutrient intake from quicker rumen turnover which should aid in meeting growth demands. Additionally, competition on the same forage patch might be mitigated as a result of different sized individuals differing in forage selectivity and forage niches. Forage selection has been shown to differ across ages, particularly in association with carbohydrate-rich foods (McCullough 1985). A study of white-tailed deer in New Zealand indicated that diet consumption between juveniles and adults differed (Nugent

and Challies 1988). In theory, juvenile and sub-adults should differ in dietary consumption compared to adults due to their high mass specific metabolic demands; however, this is not always the case (Weckerly and Nelson 1990). If juvenile and sub-adults do exhibit selective foraging and consume high quality forage, they will likely increase their body mass, which has been shown to also increase their probability for survival. Furthermore, as a juvenile grows into adulthood, the proportion of protein consumed in their diet decreases (Cropper et al. 1985). Changes in the proportion of protein in the diet with increasing age might be indicative of larger-bodied individuals requiring a greater forage intake in order to meet metabolic demands.

As a result of their greater absolute metabolic demands, large-bodied individuals require greater absolute dry matter intake to meet greater absolute metabolic demands (Van Soest 1994). Although large-bodied individuals will take advantage of high quality forage, they are not as reliant as small-bodied individuals on consuming forage with high nutritional yields in order to meet their mass-specific metabolic demands. Individuals with larger body mass will also have larger rumen-reticula that can provide longer ruminal retention times, thereby increasing digesta exposure to rumen microbes which would increase efficiency in digesting lower-quality forage (Barboza and Bowyer 2000).

My study indicated that when individuals ate a diet that contained low amounts of protein and ADF, rumen-reticulum fill was greater. Rumen-reticulum fill was shown to be influenced by the composition of the diet as well as the individual's metabolic demands. Typically, when consuming diets that contain low amounts of ADF, forage intake will increase to a limit that is probably determined by the capacity to absorb digested metabolites and maintain the ruminal environment by secretions of buffers

(Barboza et al. 2006; Holter et al. 1977; Thompson et al. 1973; Wheaton and Brown 1983). Additionally, diet should be a driving force affecting SEF because microbial activity produces volatile fatty acids which have a direct influence on SEF (Barboza et al. 2006; Crater et al. 2007; Martens et al. 2012; Mathiesen et al. 2000; Short et al. 1966; Short et al. 1969).

The largest differentiation in SEF in my study was between November 2009 and March 2010. Variation in SEF between September and March in my study was less than reported from similar seasonal periods in deer inhabiting higher latitude (Zimmerman et al. 2006). The different degrees of papillation are likely attributed to the effects of my deer living in a semi-arid environment which undergoes less environmental heterogeneity. At higher latitudes, animal demands are greatest during the growing season when quality food resources are ever-present. During this time period, animals are likely to display hyperphagia in order to meet current metabolic demands, replenish depleted nutritional reserves, as well as add additional reserves for the upcoming winter where individuals face scarce nutritional resources as well as ambient temperatures that tax thermoregulation (Barboza and Hume 2006; Barboza et al. 2006; Parker et al. 2009). However, in a semi-arid environment, there is less fluctuation in nutritional supplies across seasons. Therefore, in semi-arid environments seasonal variation in rumen-reticulum fill, microbial populations, and SEF are likely to be less pronounced when compared to animals that inhabit higher latitudes where seasonal changes are more pronounced. Although, there is less fluctuation across seasons in a semi-arid environment, animals in these habitats must be able to adapt to periods of drought and high ambient temperatures.

Many ungulates in semi-arid and arid environments use heterothermy as a mechanism to reduce evaporative water loss (Schmidt-Nielsen et al. 1957). Heterothermy is the ability to store body heat during the day and dissipate the heat at night by non-evaporative means, which thereby reduces evaporative water loss for the individual (Schmidt-Nielsen et al. 1957). Heterothermy has been observed in large desert ungulates (Fuller et al. 2005; Mitchell et al. 2002), as well as some small ungulates such as the Arabian sand gazelle and Arabian Oryx (Ostrowski and Williams 2006; Ostrowski et al. 2003). However, heterothermy does not occur in all desert dwelling ungulates (Fuller et al. 2004; Mitchell et al. 2002). It is unlikely that animals used heterothermy during my sampling periods due to the relatively mild ambient temperatures. It is possible that these white-tailed deer might use some degree of heterothermy during the summer when ambient temperatures exceed 40°C. Heterothermy has been documented in ungulates when ambient temperatures exceed 40°C (Ostrowski and Williams 2006; Ostrowski et al. 2003; Schmidt-Nielsen et al. 1957); however heterothermy has not been explicitly studied in white-tailed deer. Although my study was conducted in a semi-arid environment, the sampling periods were not during times when the animals were heat stressed. Therefore, further research could be conducted to determine if high ambient temperatures during the summer had any influence on the various rumen-reticulum attributes I studied.

Overall, the studies of my dissertation examined the relationships of anatomical and physiological rumen-reticulum attributes on scaling relationships, nutrition, rumen-reticulum fill, reserve capacity and SEF across a body mass gradient in a semi-arid environment. My findings indicate that scaling relationships between body mass and rumen-reticulum capacity were isometric. With regard to nutrition, juveniles and sub-

adults consumed a higher quality diet (when assessing the CP:ADF ratio), which should aid in meeting their high mass-specific metabolic demands. Dietary nutrition was shown to be influential to rumen-reticulum fill and rumen-reticulum fill had a positive relationship with fluid in the rumen reticulum. Surface area of the rumen mucosa covaried with dietary nutrition. One of my most important findings was that reserve capacity and SEF had an inverse relationship. This inverse relationship would minimize the amount of metabolically expensive rumen tissue, yet would still enable the individual to accommodate sudden changes in forage quality. Additionally, my research indicated that white-tailed deer in a semi-arid environment, in which there is less environmental heterogeneity, have less pronounced changes in their SEF across seasons compared to deer at higher latitudes. Findings presented herein contain information that is relevant to intraspecific scaling relationships, forage niche partitioning, and anatomical differences in the rumen-reticulum of individuals inhabiting sub-tropical, semi-arid environments.

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## VITA

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