DYNAMICS OF RUMEN-RETICULUM CAPACITY AND FILL IN FEMALE WHITE-TAILED DEER (*ODOCOILEUS VIRGINIANUS*)

THESIS

Presented to the Graduate Council of
Texas State University-San Marcos
in Partial Fulfillment of
the Requirements

for the Degree

Master of SCIENCE

by

Adam Duarte, B.S.

San Marcos, Texas
May, 2011

DYNAMICS OF RUMEN-RETICULUM CAPACITY AND FILL IN FEMALE WHITE-TAILED DEER (*ODOCOILEUS VIRGINIANUS*)

Committee Members Approved:

____

Floyd W. Weckerly, Chair

____

Thomas R. Simpson

____

Timothy H. Bonner

Approved:

____

J. Michael Willoughby
Dean of the Graduate College

FAIR USE AND AUTHOR'S PERMISSION STATEMENT

Fair Use

Duplication Permission

ACKNOWLEDGMENTS

I would like to first thank my wife Jennifer for supporting me in my decision to continue my education and continuously providing words of encouragement. Without her support I would not be where I am today. I would also like to thank Dr. Floyd W. Weckerly, my advisor, for his time, patience, and guidance. Much gratitude to Ryan Luna, a fellow graduate student, who answered many questions (sometimes multiple times) during my first year as a graduate student ensuring I was on the right track. I would like to thank my committee members Drs. Thomas R. Simpson and Timothy H. Bonner for guiding me to completion. Thanks to Tara Raabe, Brian Dickerson, John Kinsey, Katherine Cummings, Joe Angermire, David Morgan, and Chancey Lewis who helped during data collection. I am grateful to Dale Prochaska and the other biologists at Kerr Wildlife Management Area for going above and beyond in assisting with this research project and for allowing us to use their facilities. Thanks to the Houston Safari Club for providing funding that allowed this research project to take place.

This manuscript was submitted on 11 April 2011.

TABLE OF CONTENTS

LIST OF TABLES

Table **Page**

LIST OF FIGURES

Figure **Page**

ABSTRACT

DYNAMICS OF RUMEN-RETICULUM CAPACITY AND FILL IN FEMALE WHITE-TAILED DEER (*ODOCOILEUS VIRGINIANUS*)

by

Adam Duarte, B.S.

Texas State University-San Marcos

May 2011

SUPERVISING PROFESSOR: FLOYD W. WECKERLY

Understanding capacity and fill dynamics of the gastrointestinal tract under different environmental conditions gives insight into how herbivores meet life history demands. In female white-tailed deer (*Odocoileus virginianus*) rumen-reticulum capacity and fill presumably fluctuate with the demands of pregnancy and lactation. Other studies suggest rumen-reticulum capacity and fill decrease with higher quality diets (high crude protein-CP, low acid detergent fiber-ADF). Lower body conditions might warrant larger rumen-reticulum capacities to accommodate increased food intake. Rumen-reticulum capacity and fill might also be influenced by seasonal fluctuations in food intake associated with predictable change in forage abundance. We collected 72 adult female white-tailed deer in March, September, and November, 2009-2010, from Kerr Wildlife

Management Area, Kerr County, Texas. From each animal we measured rumen-reticulum capacity and fill (wet and dry) as well as body weight, fetus weight, mandible length, rump fat, and dietary ADF and CP. We built models and used Akaike Information Criteria to select models to understand which hypotheses explain capacity and fill dynamics. Rumen-reticulum capacity fluctuated with reproductive state and dietary nutrition. Wet rumen-reticulum fill fluctuated with the animal's body condition, dietary nutrition, and reproductive state. Dry rumen-reticulum fill fluctuated with the animal's dietary nutrition. Pregnant deer had significantly smaller rumen-reticulum capacities but relatively constant amounts of fill. Deer with a lower body condition score had larger amounts of fluid in the rumen-reticulum. Greater amounts of CP were associated with higher proportions of dry weight fill within the rumen-reticulum because CP was positively correlated with ADF. There is a nutritional tradeoff. As deer intake higher amounts of CP to meet demands they also intake higher amounts of ADF. Also, rumen-reticulum capacity and fill must adjust to influences of pregnancy and physiological condition.

CHAPTER 1

DYNAMICS OF RUMEN-RETICULUM CAPACITY AND FILL IN FEMALE WHITE-TAILED DEER (*ODOCOILEUS VIRGINIANUS*)

Introduction

Understanding the dynamics of digestive capacity and fill of herbivores is needed to understand how animals meet life history demands under a variety of environmental settings. The dynamics of digestive capacity and fill, however, might differ with the kind of digestive system. Herbivores that ferment plant material in the caecum and proximal large intestine (hindgut fermenters) display patterns of gut capacity and fill dynamics that is described as a plug flow system (Gils et al. 2008). When food intake increases, gut length also increases to provide more capacity to accommodate greater amounts of digesta and provide sufficient absorptive surface area. For herbivores that primarily ferment plant material in forestomach chambers (i.e. rumen-reticulum) a plug flow system might not be useful to understanding the dynamics of gut fill and capacity. Changes in the voluminous rumen-reticulum might not provide substantial changes in absorptive surface area or accommodate change in food intake (Barboza and Hume 2006).

Variation in rumen-reticulum capacity has been explained considering body size (Parra 1978, Demment 1982, Weckerly 2010). Across the spectrum of small to large ruminant species, larger animals require greater rumen-reticulum capacity to accommodate increased food intake to meet greater absolute energetic requirements (Van Soest 1994). Within a species, however, Weckerly (2010) revealed that for white-tailed deer (*Odocoileus virginianus*) much of the variation in rumen-reticulum capacity and wet fill could not be explained by body weight alone. Evidently, the dynamics of rumen-reticulum capacity and fill within a species are not solely influenced by body size.

Time since the animal's last meal has been shown to influence rumen-reticulum fill (Short et al. 1969, Weckerly et al. 2003, Weckerly 2010). Ruminants primarily forage at dawn and ruminate in the afternoon (Tulloh and Hughes 1965). Less rumen-reticulum fill is to be expected postprandial as the animal digests forage within the rumen-reticulum.

Dietary nutrition should also influence rumen-reticulum capacity and fill. A diet containing higher proportions of digestible fiber has a shorter retention time in the rumen-reticulum because particles require less time to ferment (Mautz and Petrides 1971, Freudenberger et al. 1994). Also, by consuming a digestible diet the animal can decrease dry matter intake and retain high levels of energy intake (Ammann et al. 1973, Baker and Hobbs 1987, Barboza et al. 2009). Therefore, a highly digestible diet should have lighter rumen-reticulum fill and require less rumen-reticulum capacity (Holand 1994).

The amount of rumen-reticulum fluid might also be coupled to diet quality. The number of microorganisms and amount of rumen-reticulum fluid can be positively correlated (Barboza et al. 2006), and microorganisms are protein in the rumen-reticulum. Therefore, fluid should be correlated with the amount of crude protein within the rumen-reticulum.

Rumen-reticulum capacity and fill has been linked to the reproductive status of females; however, this relationship is not fully understood (Short et al. 1969, Staines et al. 1982, Jenks et al. 1994, Gross et al. 1996, Zimmerman et al. 2006, Ramzinski and Weckerly 2007, Mysterud et al. 2008, Jiang et al. 2009). Greater rumen-reticulum capacity and fill is observed in lactating females, which is associated with increased food intake to meet elevated energy requirements. Though pregnant females also have high energy requirements, they should have less rumen-reticulum capacity and fill than non-pregnant females due to competition for space within the peritoneal cavity (Forbes 1986). However, when examining pregnant black-tailed deer (*O. hemionus columbianus*) early in the third trimester (when fetuses are large), Duarte et al. (2011) did not detect a reduction in wet rumen-reticulum fill.

The animal's physiological condition might also influence rumen-reticulum capacity and fill. Fat deposits are an indication of body condition (Gerhart et al. 1996) and are exploited to meet energy requirements when nutritional intake is inadequate (Short 1975, Adamczewski et al. 1993). Fat deposits are replenished by increasing food intake which should result in a greater rumen-reticulum fill (Short et al. 1969).

Large herbivores might anticipate seasonal changes in forage abundance and quality. Photoperiod length is coupled with seasonal forage availability in temperate and tropical ecosystems (Sinclair et al. 2001, Mieslerova and Lebeda 2010, Nordli et al. 2011) and ruminants increase food intake when photoperiods are longer (reviewed in Rhind et al. 2002). Therefore rumen-reticulum capacity and fill might be related to the day of the year.

Herein, we examine new and established influences on rumen-reticulum capacity and fill to better understand how female white-tailed deer physiologically adjust to meet life history demands. The four hypotheses we examined were reproductive state, physiological condition, dietary nutrition, and predictable forage (Table 1). The reproductive state hypothesis considered the animal's reproductive status. If fetuses compete with the rumen-reticulum for space within the peritoneal cavity and restrict food intake, then we expect smaller rumen-reticulum capacities and fill in pregnant than in non-pregnant females. Also, lactating females should have a greater rumen-reticulum capacity and fill than non-lactating females (Short et al. 1969, Staines et al. 1982, Jenks et al. 1994, Gross et al. 1996, Zimmerman et al. 2006, Ramzinski and Weckerly 2007, Mysterud et al. 2008). The physiological condition hypothesis included the possibility of influences of the animal's physiological (body) condition. If a decline in body condition triggers the animal to increase food intake, then we expect rumen-reticulum capacity and fill to increase as the animal's body condition declines. The dietary nutrition hypothesis included the possibility of influences of the digestibility of the selected diet. We expect lower rumen-reticulum capacities and fill when animals select a more digestible diet. The predictable forage hypothesis included the influence of Julian date. If the animal anticipates fluctuations in forage quality and quantity then we expect rumen-reticulum capacity and fill to fluctuate with the day of year. The influences included in the four hypotheses might not be mutually exclusive; therefore, combination hypotheses were also examined. Combination hypotheses were predictable forage and physiological condition, reproductive state and physiological condition, reproductive state and dietary nutrition,

Table 1. Predictions of Hypotheses.
Predictions of hypotheses to explain rumen-reticulum capacity and fill dynamics of adult female white-tailed deer (*Odocoileus virginianus*) sampled from Kerr Wildlife Management Area.

Hypotheses		Rumen-Reticulum Capacity & Fill
Reproductive State	Lactating	Increase
	Pregnant	Decrease
Physiological Condition	Poor	Increase
	Good	Decrease
Dietary Nutrition	Poor	Increase
	High	Decrease
Predictable Forage	Day	Vary with Photoperiod/ Day Length

physiological condition and dietary nutrition, and physiological condition, dietary nutrition and reproductive state.

Methods

Kerr Wildlife Management Area is a 2,628 ha high fenced ranch managed by the Texas Parks and Wildlife Department in the Edwards Plateau region, Kerr County, Texas, USA. Kerr County has highly variable year to year precipitation (Figure 1). Average annual precipitation is 69.7 cm and the mean accumulated precipitation from March through June is 26.8 cm. Average temperature is 18 °C with mean temperatures of 7 °C in January and 27 °C in July. The variable climatic conditions in this region can lead to large fluctuations in forage quality and quantity between and within seasons which allowed us to sample deer over a relatively short period but still examine the influence of a wide range in dietary quality (Beatley 1969, Marshal et al. 2005). Primary browse consumed by white-tailed deer on Kerr Wildlife Management Area includes oak (*Quercus* spp.*)* leaves, Ashe juniper (*Juniperus ashei*), and acorns (Warren and Krysl 1983). Common forbes in the diet of white-tailed deer on the Kerr Wildlife Management Area include bladderpods (*Lesquerella* spp.), spurges (*Euphorbia* spp.), redseed plantain (*Plantago rhodosperma*), filaree (*Erodium* spp.), silverleaf nightshade (*Solanum elaegnifolium*), globemallows (*Sphaeralcea* spp.), whorled nodviolet (*Hybanthus verticillatus*), and common horehound (*Marrubium vulgare*) (Warren and Krysl 1983). The only grass consumed substantially by white-tailed deer on the Kerr Wildlife Management Area is Texas wintergrass (*Stipa leucotricha*), a cool-season species (Warren and Krysl 1983).

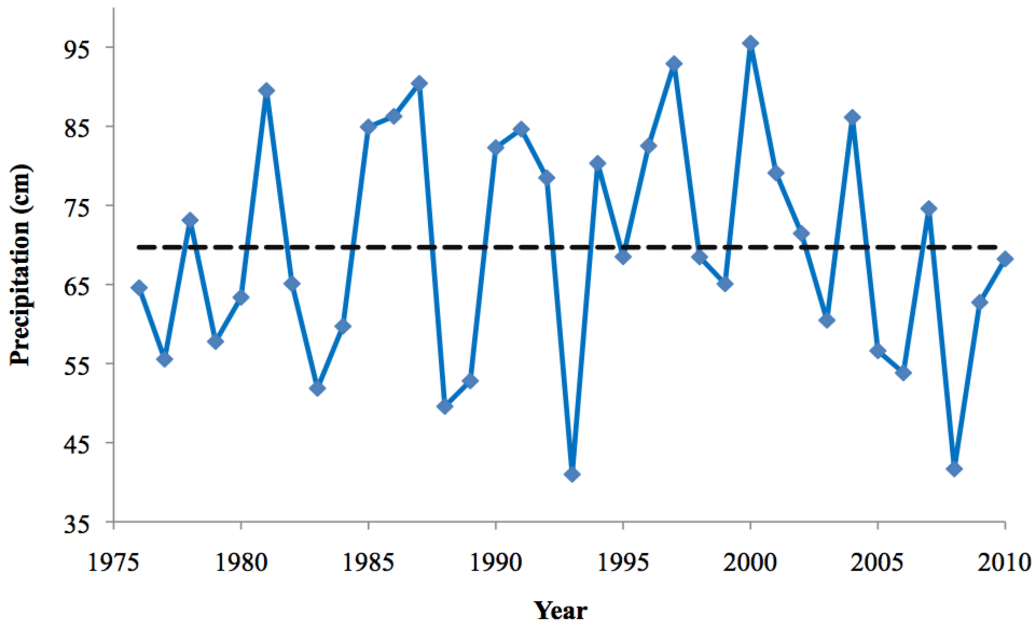

Figure 1. Average Annual Precipitation.
Average annual precipitation values on Kerr Wildlife Management Area, Kerr County, TX from 1976-2010. The dashed horizontal line indicates the mean rainfall (69.7 cm) across 24 years. The coefficient of variation and autocorrelation for the mean annual precipitation is 21 % and -0.26 to 0.41, respectively.

White-tailed deer were collected from Kerr Wildlife Management Area in November 2009 and March, September, and November in 2010. All animals were shot with a high-powered rifle. November collections were from harvests during public hunts. Collections in other months were taken by Texas Parks and Wildlife personnel. Specimen collection procedures followed the Institutional Animal Care and Use protocols from Texas State University (permit number: 0933_09_06-03141BF15D).

Animals were processed within 3 h of death. Only females aged ≥ 2 years old by tooth replacement and wear were included for the study (Severinghaus 1949). Body weight, minus blood loss, and dressed weights were measured to the nearest 0.1 kg. Fat deposits were measured by the thickness of rump fat (nearest mm; Gerhart et al. 1996). We also calculated a lifetime body condition score (LBC). Body mass corrected for the skeletal size (body mass/mandible length) is a common measure of body condition for live ungulates but is biased because of weight linked to entrails (Barboza et al. 2009). Therefore, we calculated LBCs by using dressed weights (dressed body mass/mandible length). We considered this body condition score as a measure of condition throughout life because it includes possible differences in muscle development as well as fat deposits. Lactation status was determined by examining udders for milk. Fetuses, when present, were removed from entrails and weighed to the nearest 0.1 g.

The digestive tract was separated from the other entrails and excised at the reticulo-omasal sphincter and five centimeters above the junction of the esophagus and reticulum to isolate the rumen-reticulum (Weckerly et al. 2003, Ramzinski and Weckerly 2007). The rumen-reticulum with fill was weighed then inverted and rinsed with tap water until all digesta was removed. The rinsed rumen-reticulum was then weighed.

Weights were recorded to the nearest 0.1 kg. The weight of the rumen-reticulum fill was recorded as the difference in weight between the rumen-reticulum with fill and the rinsed rumen-reticulum. The rinsed rumen-reticulum was reverted and the openings in the organ were held at the water's surface level in a 208 L plastic drum filled with tap water. Tap water was poured into the rumen-reticulum until it reached its capacity. Rumen-reticulum capacity measurements were taken in triplicate and recorded to the nearest 0.1 L. The mean of the triplicate rumen-reticulum capacity measurements was used in analyses and reported in kilograms since 1 L of water weighs 1 kg. Approximately 1 L of digesta was taken from each specimen and weighed. Digesta samples were dried at 60 ºC for 48 hours then reweighed. The weight of total dry rumen-reticulum fill was calculated as wet rumen-reticulum fill * (dry digesta sample/wet digesta sample). Rumen-reticulum fluid was the difference in weight between the wet and dry rumen-reticulum fill.

A second digesta sample was taken from each animal and dried at 60 ºC for 48 hours then ground to ≤ 1 mm particles. A 1 g sample of dried, ground digesta was analyzed in a Leco FP-528 ® to determine the percent nitrogen. Percent crude protein was calculated as percent nitrogen *6.25. Crude protein (CP) in the rumen-reticulum was then calculated by multiplying the proportion CP per g of digesta by the corresponding dry rumen-reticulum fill weight. A separate 1 g sample of dried, ground digesta was placed in a filter bag and digested in a hexadecyltrimethyl, sulphuric acid solution. The sample was then rinsed three times in boiling water, followed by an acetone rinse, then re-dried. The re-dried sample was weighed to determine the percent acid detergent fiber (ADF). Acid detergent fiber in the rumen-reticulum was calculated by multiplying the proportion acid detergent fiber per g of digesta by the corresponding dry rumen-reticulum fill weight. Acid detergent fiber is comprised of lignin, cutin, and cellulose. Lignin and cutin are indigestible and cellulose is recalcitrant to digestion by microorganisms in the rumen-reticulum (Van Soest 1994). Therefore, we used ADF as a measure of indigestible material. Digesta samples for nutrition analyses were analyzed by A&L Plains Laboratory, Inc., Lubbock, TX.

Body weight and kill time are predictors that have been shown to influence rumen-reticulum capacity and rumen-reticulum fill (Short et al. 1969, Parra 1978, Demment 1982, Weckerly et al. 2003, Weckerly 2010). Thus, body weight and kill time were in every model. Lactation and pregnancy status were included in models for the reproductive state hypothesis and coded as dummy variables (Sokal and Rohlf 1995). Rump fat measurements and LBCs were included in the models of the physiological condition hypothesis. Calculated kg dry weights of CP and ADF in the rumen-reticulum were included in the model for the dietary nutrition hypothesis. The Julian date the animal was harvested was included in the model for the predictable forage hypothesis. Since food intake fluctuates with photoperiod, we did not expect a linear relationship between Julian date and rumen-reticulum capacity and fill. Therefore, we allowed for a quadratic relationship with Julian date. All animals harvested in March were pregnant and had low values of CP and ADF. All animals harvested in September were lactating and all animals harvested in November had high values of ADF and CP. Because of multicollinearity we did not include Julian date with reproductive state or dietary nutrition in models of combination hypotheses. Response variables included rumen-reticulum capacity, wet rumen-reticulum fill, and dry rumen-reticulum fill. Analyses were conducted in program R (R Development Core Team, 2005)

A model for each response variable was selected considering Akaike Information Criterion corrected for small sample size (AIC_c), Akaike weight, and adjusted r^2 (Sokal and Rohlf 1995, Burnham and Anderson 2002). We chose a model with a large Akaike weight and adjusted r^2 (Sokal and Rohlf 1995, Burnham and Anderson 2002). Since we hypothesize that the amount of rumen-reticulum fluid is coupled with the quality of the selected diet, we also assessed the relationship between kg dry weight of crude protein and amount of fluid within the rumen-reticulum.

Results

Seventeen animals were taken in November 2009, and 15, 6, and 34 animals taken in March, September, and November, respectively, of 2010. Across all sampling periods, CP values ranged from 0.04 to 0.25 kg and ADF values ranged from 0.08 to 0.55 kg (Figure 2). Rump fat and LBC measurements range from 0 to 2.06 cm and 1.06 to 1.72 kg/cm, respectively.

For rumen-reticulum capacity we selected the model that varied with body weight, kill time, ADF, CP, and whether the animal was pregnant or lactating (Table 2). The regression was $\hat{Y}$ = 1.4976 + (0.1400*Body Weight) - (0.1779*Kill Time) + (0.8129*Lactating) - (2.8439*Fetus) + (12.8163*ADF) - (7.6842*CP). Relationships were evident because the adjusted r^2 was 0.44.

For wet rumen-reticulum fill, we selected the model that varied with body weight, kill time, rump fat, LBC, ADF, CP, and whether the animal was pregnant or lactating (Table 3). The regression was $\hat{Y}$ = -0.5053 + (0.1125*Body Weight) + (0.0105*Kill Time) - (0.0217*Rump Fat)- (2.0605*LBC) + (2.5970*ADF) + (9.4702*CP) +

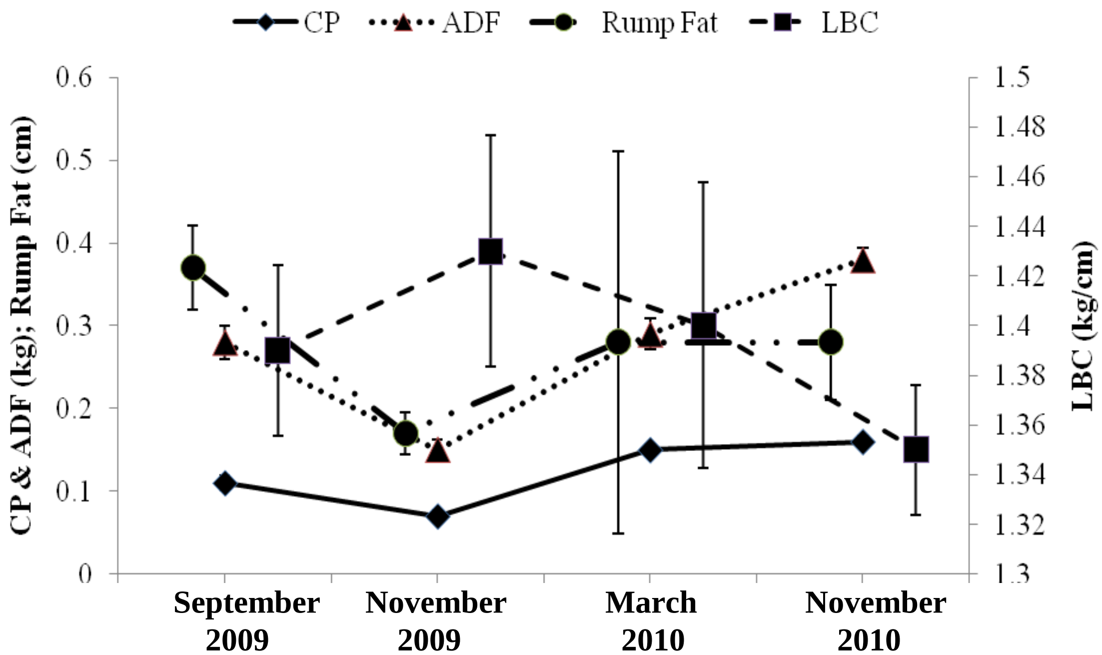

Figure 2. Summary of Data.
Summary of CP, ADF, LBC, and rump fat measurements collected from adult female white-tailed deer (Odocoileus virginianus) across all sampling periods from Kerr Wildlife Management Area. The left y-axis represents the measurements for both dietary nutrition (kg dry weight) and rump fat thickness (cm). The right y-axis represents the LBC measurements (kg/cm). Points indicate mean values recorded and error bars represent one standard error.

Table 2. Model Selection Summary (Rumen-Reticulum Capacity).
Models analyzed and summaries of model selection for rumen-reticulum capacity of adult female white-tailed deer (*Odocoileus virginianus*) sampled from Kerr Wildlife Management Area. Body weight and kill time were included in every model.

Hypothesis	Predictors *	nPar	AIC_C	AIC_C Wt.	r^2
Reproductive State	L	5	368.3	0.00	0.23
	F	5	352.0	0.09	0.39
	L,F	6	352.9	0.06	0.39
Physiological Condition	RF	5	388.5	0.00	0.00
	LBC	5	387.8	0.00	0.00
	RF,LBC	6	388.5	0.00	0.00
Dietary Nutrition	ADF	5	353.3	0.05	0.37
	CP	5	366.8	0.00	0.25
	ADF,CP	6	355.6	0.02	0.37
Predictable Season	JD,JD^2	6	349.7	0.29	0.42
Combination Models	JD,JD^2,RF,LBC	8	351.8	0.10	0.42
	L,F,RF,LBC	8	356.2	0.01	0.38
	L,F,ADF,CP	**8**	**349.4**	**0.34**	**0.44**
	RF,LBC,ADF,CP	8	359.6	0.00	0.35
	RF,LBC,ADF,CP, L,F	10	354.2	0.03	0.43

The bold-faced row denotes the model selected for rumen-reticulum capacity.
BW was body weight; KT was kill time, F was fetus; L was lactating, RF was rump fat, LBC was lifetime body condition score, ADF was acid detergent fiber, CP was crude protein, JD was Julian date, and JD^2 was allowing a quadratic relationship with Julian date. Adjusted r^2 values were reported for models with multiple predictors.

Table 3. Model Selection Summary (Wet Rumen-Reticulum Fill).
Models analyzed and summaries of model selection for wet rumen-reticulum fill of adult female white-tailed deer (*Odocoileus virginianus*) sampled from Kerr Wildlife Management Area. Body weight and kill time were included in every model.

Hypothesis	Predictors *	nPar	AIC_C	AIC_C Wt.	r^2
Reproductive State	L	5	189.3	0.00	0.39
	F	5	183.6	0.00	0.44
	L,F	6	179.3	0.00	0.48
Physiological Condition	RF	5	218.7	0.00	0.08
	LBC	5	203.4	0.00	0.26
	RF,LBC	6	205.7	0.00	0.25
Dietary Nutrition	ADF	5	131.2	0.00	0.73
	CP	5	115.7	0.00	0.78
	ADF,CP	6	106.4	0.01	0.81
Predictable Season	JD,JD^2	6	185.0	0.00	0.44
Combination Models	JD,JD^2,RF,LBC	8	157.2	0.00	0.63
	L,F,RF,LBC	8	156.0	0.00	0.64
	L,F,ADF,CP	8	107.1	0.00	0.82
	RF,LBC,ADF,CP	8	99.4	0.22	0.83
	RF,LBC,ADF,CP, L,F	**10**	**96.9**	**0.77**	**0.85**

The bold-faced row denotes the model selected for rumen-reticulum capacity.
BW was body weight; KT was kill time, F was fetus; L was lactating, RF was rump fat, LBC was lifetime body condition score, ADF was acid detergent fiber, CP was crude protein, JD was Julian date, and JD^2 was allowing a quadratic relationship with Julian date. Adjusted r^2 values were reported for models with multiple predictors.

(0.0992*Lactating) - (0.4207*Fetus). Relationships were strong because the adjusted r^2 was 0.85.

For dry rumen-reticulum fill, we selected the model that varied with body weight, kill time, ADF, and CP (Table 4). The regression was $\hat{Y}$ = 0.1185 - (0.0026*Body Weight) - (<0.0001*Kill Time) + (3.6420*CP) + (0.7096*ADF). Again, relationships were strong because the adjusted r^2 was 0.84.

Rumen-reticulum capacity and fill dynamics were influenced by reproductive state, dietary nutrition and body condition (Figure 3). Both rumen-reticulum capacity and wet fill increased during lactation and with higher amounts of ADF, but decreased during pregnancy. However, wet rumen-reticulum fill fluctuations due to reproductive state were slight. Also, rumen-reticulum capacity decreased and wet rumen-reticulum fill increased with higher amounts of CP. Wet rumen-reticulum fill decreased in animals with thicker rump fats and higher LBC scores. Dry rumen-reticulum fill increased with higher amounts of both CP and ADF.

Both wet and dry rumen-reticulum fill were influenced in part by dietary nutrition. We wanted to determine if the amount of fluid was correlated with the kg dry weight of CP in the rumen-reticulum. However, we found that as CP increased the proportion of dry weight in the rumen-reticulum also increased (Figure 4). This is contrary to what was hypothesized. In order to examine possible explanations for this pattern we estimated a Pearson's correlation coefficient to determine if CP was correlated with ADF in the rumen-reticulum (Sokal and Rohlf 1995). Crude protein was highly correlated with ADF (r=0.854, n=72, P<0.001).

Table 4. Model Selection Summary (Dry Rumen-Reticulum Fill).
Models analyzed and summaries of model selection for dry rumen-reticulum fill of adult female white-tailed deer (*Odocoileus virginianus*) sampled from Kerr Wildlife Management Area. Body weight and kill time were included in every model.

Hypothesis	Predictors *	nPar	AIC_C	AIC_C Wt.	r^2
Reproductive State	L	5	-2.2	0.00	0.34
	F	5	-11.3	0.00	0.42
	L,F	6	-14.4	0.00	0.45
Physiological Condition	RF	5	27.0	0.00	0.01
	LBC	5	20.4	0.00	0.09
	RF,LBC	6	22.8	0.00	0.08
Dietary Nutrition	ADF	5	-63.2	0.00	0.72
	CP	5	-91.5	0.01	0.81
	ADF,CP	**6**	**-99.0**	**0.56**	**0.83**
Predictable Season	JD,JD^2	6	-11.2	0.00	0.43
Combination Models	JD,JD^2,RF,LBC	8	-23.9	0.00	0.54
	L,F,RF,LBC	8	-20.5	0.00	0.52
	L,F,ADF,CP	8	-97.8	0.31	0.83
	RF,LBC,ADF,CP	8	-95.2	0.08	0.83
	RF,LBC,ADF,CP, L,F	10	-93.8	0.04	0.83

The bold-faced row denotes the model selected for rumen-reticulum capacity.
BW was body weight; KT was kill time, F was fetus; L was lactating, RF was rump fat, LBC was lifetime body condition score, ADF was acid detergent fiber, CP was crude protein, JD was Julian date, and JD^2 was allowing a quadratic relationship with Julian date. Adjusted r^2 values were reported for models with multiple predictors.

Fig. 3a

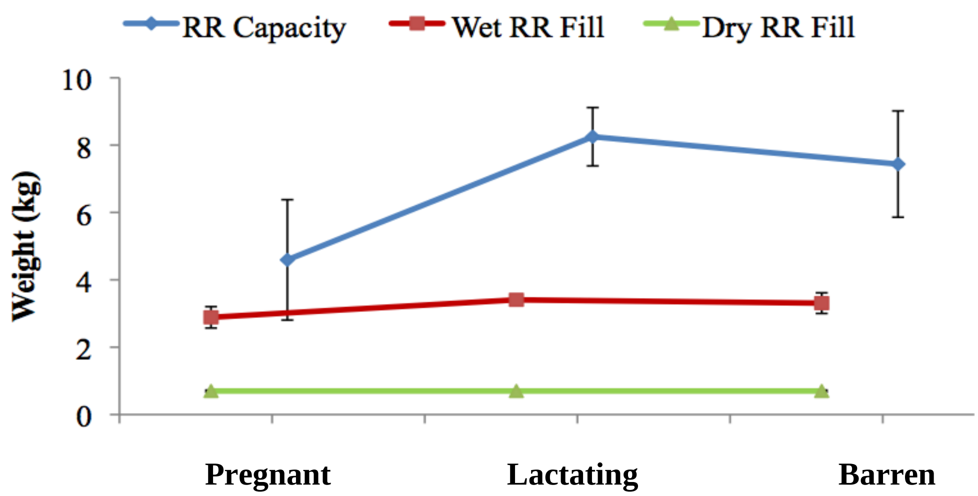

Fig. 3b

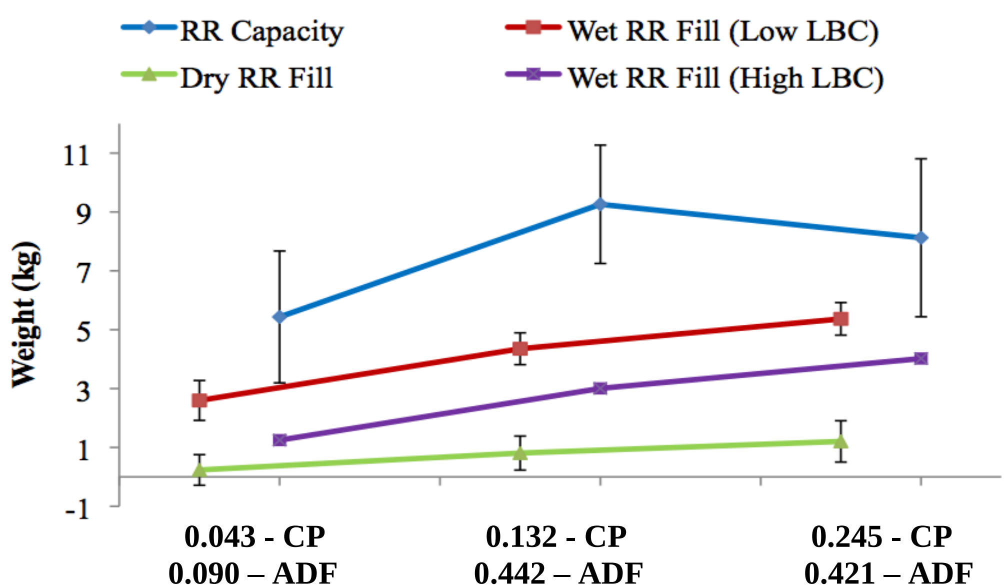

Figure 3. Rumen-Reticulum Capacity and Fill Dynamics.

Line graphs of rumen-reticulum capacity and fill from adult female white-tailed deer (*Odocoileus virginianus*) sampled from Kerr Wildlife Management Area using the regressions from the selected models. Confidence intervals (CI; 0.95) are shown at each predicted value. In some cases the CIs are too small to appear. We displayed the regression with the average body weight, kill time, and rump fat recorded. For Fig. 2a we used the mean CP, ADF, and LBC in order to illustrate the effects of reproductive state on rumen-reticulum capacity and fill. For Fig. 2b we separated wet rumen-reticulum fill by using the highest and lowest LBC scores and displayed rumen-reticulum capacity and fill dynamics across the range of CP. We displayed rumen-reticulum capacity and fill dynamics across the range in CP values because CP had a larger effect on 2 of the 3 response variables. We used the ADF that corresponded with each CP value used.

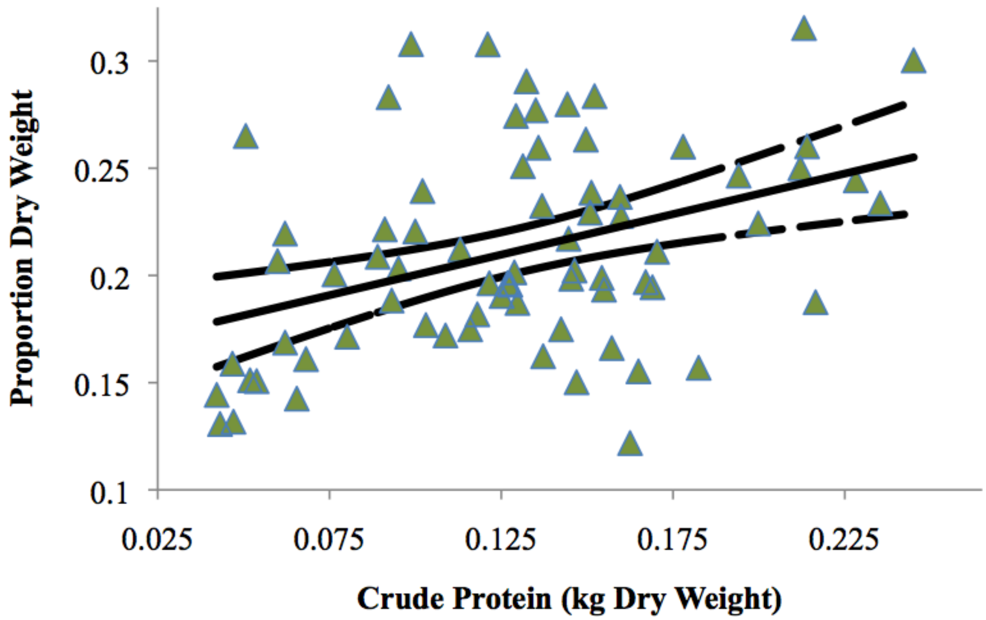

Figure 4. Proportion Dry Weight and Crude Protein.
Scatter plot of proportion of dry weight and crude protein in the rumen-reticulum of adult female white-tailed deer (*Odocoileus virginianus*) sampled from Kerr Wildlife Management Area.

Discussion

For rumen-reticulum capacity our results support the reproductive state and dietary nutrition hypotheses. The reproductive state, dietary nutrition and body condition hypotheses were supported for wet rumen-reticulum fill. However, for dry rumen-reticulum fill our results support the dietary nutrition hypothesis.

Rumen-reticulum capacity and fill should increase during lactation and be restricted during pregnancy (Short et al. 1969, Staines et al. 1982, Forbes 1986, Jenks et al. 1994, Gross et al. 1996, Zimmerman et al. 2006, Ramzinski and Weckerly 2007, Mysterud et al. 2008). However, we only detected a dramatic decrease in rumen-reticulum capacity during pregnancy and a slight increase in rumen-reticulum capacity and wet fill during lactation (Figure 3a). The lack of substantial change in wet rumen-reticulum fill during pregnancy concurs with the findings of Duarte et al. (2011), and suggests that food intake is not restricted during pregnancy. If fetuses restrict food intake, then a significant decrease in both rumen-reticulum capacity and fill should have been detected, particularly since we sampled late in the third trimester when fetuses are presumably the largest. However the dietary nutrition might be the reason we did not detect a restriction in food intake. If we sampled during a more severe drought, when ADF values are presumably higher, we might detect a restriction in food intake during pregnancy. The slight increase in wet rumen-reticulum fill in lactating deer is similar to what Jenks et al. (1994) found when sampling female white-tailed deer from Oklahoma and Arkansas, USA in August. The lack of a dramatic increase in rumen-reticulum capacity and wet fill during lactation could be due to the time of sampling. Lactating deer for this study were sampled during late September and early November. If we had sampled earlier during lactation when mothers are required to produce more milk for fawn consumption then we might have detected larger rumen-reticulum capacities and fills for lactating animals (Robbins and Moen 1975).

Rumen-reticulum fluid varied with the animal's reproductive state and body condition (Figure 3). Though dry rumen-reticulum fill did not vary across reproductive states, lactating animals had a slight increase in wet rumen-reticulum fill indicating an increase in rumen-reticulum fluid during lactation. Short et al. (1969) also detected slightly more rumen-reticulum fluid in lactating white-tailed deer. For this study, deer in poorer condition also had larger amounts of fluid in the rumen-reticulum. To our knowledge, a variation in rumen-reticulum fluid with body conditions has not been reported. Veiberg et al. (2009) detected heavier wet rumen-reticulum fills and lower body conditions in older reindeer (*Rangifer tarandus platyrhynchus*). They suggested the heavier wet rumen-reticulum fills in older animals was associated with larger particles in the rumen-reticulum due to decreased mastication efficiency. However, they also found the correlation between wet rumen-reticulum fill and age was stronger than the correlation between wet rumen-reticulum fill and particle size. This suggests that the observed increase in wet rumen-reticulum fill with age during their study is more linked to lower body conditions rather than decreased mastication efficiency.

Rump fat thickness and LBC scores varied between the sampling periods (Figure 2). Rump fat thickness increased from March to September and remained constant into November. However, November rump fat thickness was different between years. Lifetime body condition scores between November samplings were similar and the sampling period with the lowest rump fat score (March) also had the largest LBC score.

Lifetime body condition did not correlate with rump fat thickness and had a more pronounced effect on wet rumen-reticulum weights, indicating these two body condition scores were not redundant.

The positive correlation between CP and ADF was unexpected because it is generally accepted that CP is inversely correlated with ADF (Robbins 1983). A positive correlation between CP and ADF has only been reported once before (Weckerly and Kennedy 1992). We found the amount of CP and ADF increased from March to September and remained relatively constant into November (Figure 2). Differences in diet quality between the two November samplings are associated with the yearly variation in precipitation. Precipitation accumulated from March through June decreased from 2009 to 2010 (27.1 to 17.9 cm, respectively), and as plants senesce indigestible fiber increases (Van Soest 1994). This explains the on average greater kg dry weight of ADF in November of 2010 (Figure 2). Weckerly and Kennedy (1992) found similar fluctuations in CP and ADF (increased from spring/summer to autumn/winter) from white-tailed deer sampled throughout the year in Tennessee, USA. The positive correlation between CP and ADF in both these studies suggests that the cost associated with an increase in CP intake is an increased consumption of indigestible material. The increase in consumed indigestible material must be accommodated by a larger rumen-reticulum capacity, or digesta will be passed before efficient breakdown and nutrient assimilation takes place (Lechner et al. 2010).

Rumen-reticulum capacity and fill varied from year to year in November. On average, rumen-reticulum capacity and fill was greater in November 2009 (capacity 8.12 kg, wet fill 3.85 kg, dry fill 0.87 kg) than in November 2010 (7.28 kg, 2.89 kg, 0.63 kg;

used regressions from selected models and mean values for each variable from each sampling period). Weckerly (2010) found similar patterns in male and female white-tailed deer sampled in October from central Texas, USA. They sampled deer across three consecutive years (2006-2008) and found rumen-reticulum capacity decreased in the year that had above average precipitation and presumably lower amounts of indigestible material in the deer diets (Weckerly and Foster 2010). However, wet rumen-reticulum fill was not correlated with yearly fluctuations in precipitation and presumably diet quality in that study. This might be explained by the physiological state hypothesis supported for wet rumen-reticulum fill in this study. Perhaps wet rumen-reticulum fill did not correlate with fluctuations in precipitation because body conditions were on average lower each consecutive year. This would lead to an increase in the amount of fluid over the three year study period.

The dynamics of rumen-reticulum capacity and fill are complex. During this study, the amount of fill in the rumen-reticulum was mostly driven by dietary nutrition and body condition, whereas rumen-reticulum capacity was mostly driven by reproductive state and dietary nutrition. There are tradeoffs deer must make to meet life history demands. As they select for higher amounts of CP and concomitantly intake higher amounts of ADF, the amount of rumen-reticulum fill increases but the capacity of the rumen-reticulum shrinks. If this occurs during pregnancy in deer with low LBC's the rumen-reticulum capacity might not be able to accommodate an increase in food intake or maintain efficient digesta breakdown and nutrient assimilation. It is evident that the plug flow system described in hindgut fermenters should not be extended to describe gut capacity and fill dynamics in ruminant species.

LITERATURE CITED

Adamczewski, J. Z., R. J. Hudson, and C. C. Gates. 1993. Winter energy balance and activity of female caribou on Coats Island, Northwest Territories: the relative importance of foraging and body reserves. Canadian Journal of Zoology-Revue Canadienne De Zoologie 71:1221-1229.

Ammann, A. P., R. L. Cowan, C. L. Mothershead, and B. R. Baumgardt. 1973. Dry matter and energy intake in relation to digestibility in white-tailed deer. Journal of Wildlife Management 37:195-201.

Baker, D. L., and N. T. Hobbs. 1987. Strategies of digestion: digestive efficiency and retention time of forage diets in montane ungulates. Canadian Journal of Zoology-Revue Canadienne De Zoologie 65:1978-1984.

Barboza, P. S., and I. D. Hume. 2006. Physiology of intermittent feeding: integrating responses of vertebrates to nutritional deficit and excess. Physiological and Biochemical Zoology 79:250-264.

Barboza, P. S., K. L. Parker, and I. D. Hume. 2009. Integrative Wildlife Nutrition. Springer-Verlag, Berlin Heidelberg, Germany.

Barboza, P. S., T. C. Peltier, and R. J. Forster. 2006. Ruminal fermentation and fill change with season in an arctic grazer: responses to hyperphagia and hypophagia in muskoxen (*Ovibos moschatus*). Physiological and Biochemical Zoology 79:497-513.

Beatley, J. C. 1969. Dependence of desert rodents on winter annuals and precipitation. Ecology 50:721-724.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multi-model inference: a practical information-theoretic approach. 2nd edition. Springer Press, New York.

Demment, M. W. 1982. The scaling of rumenoreticulum size with body-weight in east-African ungulates. African Journal of Ecology 20:43-47.

Duarte, A., D. R. McCullough, and F. W. Weckerly. 2011. Does rumen-reticulum capacity correlate with body size or age in black-tailed deer? European Journal of Wildlife Research.1:6.

Forbes, J. M. 1986. The effects of sex hormones, pregnancy, and lactation on digestion, metabolism, and voluntary food intake. Pages 420-435 *in* L. P. Milligan, W. L. Grovum, andA. Dobson, editors. Control of digestion and metabolism in ruminants. Prentice Hall,Englewood Cliffs, New Jersey.

Freudenberger, D. O., K. Toyakawa, T. N. Barry, A. J. Ball, and J. M. Suttie. 1994. Seasonality in digestion and rumen metabolism in red deer (*Cervus elaphus*) fed on a forage diet. British Journal of Nutrition 71:489-499.

Gerhart, K. L., R. G. White, R. D. Cameron, and D. E. Russell. 1996. Estimating fat content of caribou from body condition scores. Journal of Wildlife Management 60:713-718.

Gils, J. A. v., J. H. Beekman, P. Coehoorn, E. Corporaal, T. Dekkers, M. Klaassen, R. v. Kraaij, R. d. Leeuw, and P. P. d. Vries. 2008. Longer guts and higher food quality increase energy intake in migratory swans. Journal of Animal Ecology 77:1234-1241.

Gross, J. E., P. U. Alkon, and M. W. Demment. 1996. Nutritional ecology of dimorphic herbivores: digestion and passage rates in Nubian ibex. Oecologia 107:170-178.

Holand, O. 1994. Seasonal dynamics of digestion in relation to diet quality and intake in European roe deer (*Capreolus capreolus*). Oecologia 98:274-279.

Jenks, J. A., D. M. Leslie, Jr., R. L. Lochmiller, and M. A. Melchiors. 1994. Variation in gastrointestinal characteristics of male and female white-tailed deer: implications for resource partitioning. Journal of Mammalogy 75:1045-1053.

Jiang, Z. W., S. Hamasaki, S. Takatsuki, M. Kishimoto, and M. Kitahara. 2009. Seasonal and sexual variation in the diet and gastrointestinal features of the sika deer in Western Japan: implications for the feeding strategy. Zoological Science 26:691-697.

Lechner, I., P. Barboza, W. Collins, J. Fritz, D. Gunther, B. Hattendorf, J. Hummel, K. H. Sudekum, and M. Clauss. 2010. Differential passage of fluids and different-sized particles in fistulated oxen (*Bos primigenius f. taurus*), muskoxen (*Ovibos moschatus*), reindeer (*Rangifer tarandus*) and moose (*Alces alces*): rumen particle size discrimination is independent from contents stratification. Comparative Biochemistry and Physiology a-Molecular & Integrative Physiology 155:211-222.

Marshal, J. P., P. R. Krausman, and V. C. Bleich. 2005. Rainfall, temperature, and forage dynamics affect nutritional quality of desert mule deer forage. Rangeland Ecology & Management 58:360-365.

Mautz, W. W., and G. A. Petrides. 1971. Food passage rate in white-tailed deer. Journal of Wildlife Management 35:723-731.

Mieslerova, B., and A. Lebeda. 2010. Influence of temperature and light conditions on germination, growth and conidiation of *Oidium neolycopersici*. Journal of Phytopathology 158:616-627.

Mysterud, A., C. Bonenfant, L. E. Loe, R. Langvatn, N. G. Yoccoz, and N. C. Stenseth. 2008. Age-specific feeding cessation in male red deer during rut. Journal of Zoology 275:407-412.

Nordli, E. F., M. Strom, and S. Torre. 2011. Temperature and photoperiod control of morphology and flowering time in two greenhouse grown *Hydrangea macrophylla* cultivars. Scientia Horticulturae 127:372-377.

Parra, R. 1978. Comparison of foregut and hindgut fermentation in herbivores. Pages 205-229 *in* G. G. Montgomery, editor. The ecology of arboreal folivores. Washington: Smithsonian Institution Press.

Ramzinski, D. M., and F. W. Weckerly. 2007. Scaling relationship between body weight and fermentation gut capacity in axis deer. Journal of Mammalogy 88:415-420.

R Development Core Team (2005). R: A language and environment for statistical computing, reference index version 2.2.1. R Foundation for Statistical Computing, Vienna, Austria

Rhind, S. M., Z. A. Archer, and C. L. Adam. 2002. Seasonality of food intake in ruminants: recent developments in understanding. Nutrition Research Reviews 15:43-65.

Robbins, C. T. 1983. Wildlife feeding and nutrition. Academic Press, New York.

Robbins, C. T., and A. N. Moen. 1975. Milk consumption and weight gain of white-tailed deer. Journal of Wildlife Management 39:355-360.

Severinghaus, C. W. 1949. Tooth development and wear as criteria of age in white-tailed deer. Journal of Wildlife Management 13:195-216.

Short, H. L. 1975. Nutrition of southern deer in different seasons. Journal of Wildlife Management 39:321-329.

Short, H. L., E. E. Remmenga, and C. E. Boyd. 1969. Variations in ruminoreticular contents of white-tailed deer. Journal of Wildlife Management 33:187-191.

Sinclair, T. R., P. Mislevy, and J. D. Ray. 2001. Short photoperiod inhibits winter growth of subtropical grasses. Planta 213:488-491.

Sokal, R. R., and F. Rohlf. 1995. Biometry: the principles and practice of statistics in biological research. 3rd edition. W. H. Freeman and Company, New York.

Staines, B. W., J. M. Crisp, and T. Parish. 1982. Differences in the quality of food eaten by red deer (*Cervus elaphus*) stags and hinds in winter. Journal of Applied Ecology 19:65-77.

Tulloh, N. M., and J. W. Hughes. 1965. Physical studies of the alimentary tract of grazing cattle. II. Techniques for estimating the capacity of the reticulo-rumen. New Zealand Journal of Agricultural Research 8:1070-1078.

Van Soest, P. J. 1994. Nutritional Ecology of the Ruminant. 2nd edn. Cornell University Press, Ithaca, New York.

Veiberg, V., A. Mysterud, R. J. Irvine, W. Sormo, and R. Langvatn. 2009. Increased mass of reticulo-rumen tissue and contents with advancing age in Svalbard reindeer. Journal of Zoology 278:15-23.

Warren, R. J., and L. J. Krysl. 1983. White-tailed deer food-habits and nutritional-status as affected by grazing and deer-harvest management. Journal of Range Management 36:104-109.

Weckerly, F. W. 2010. Allometric scaling of rumen-reticulum capacity in white-tailed deer. Journal of Zoology 280:41-48.

Weckerly, F.W., and J.A. Foster. 2010. Blind count surveys of white-tailed deer and population estimates using Bowden's estimators. Journal of Wildlife Management 74:1367-1377.

Weckerly, F. W., and M. L. Kennedy. 1992. Examining hypotheses about feeding strategies of white-tailed deer. Canadian Journal of Zoology-Revue Canadienne De Zoologie 70:432-439.

Weckerly, F. W., C. B. Vernon, C.-L. B. Chetkiewicz, and M. A. Ricca. 2003. Body weight and rumen-reticulum capacity in tule elk and mule deer. Journal of Mammalogy 84:659-664.

Zimmerman, T. J., J. A. Jenks, and D. M. Leslie. 2006. Gastrointestinal morphology of female white-tailed and mule deer: Effects of fire, reproduction, and feeding type. Journal of Mammalogy 87:598-605.

VITA

Adam Duarte was born 22 March 1985 to Ronald and Anna Duarte in Granada Hills, CA. He graduated from S.H. Rider High School in Wichita Falls, TX in 2003 and joined the U.S. Marine Corps Reserve. During his time in the Marine Corps, Adam was deployed to the Al Anbar Province, Iraq and also attended Texas A&M University. As an undergraduate he interned for the Texas Parks & Wildlife Department at White Oak Creek WMA. Adam married Jennifer J. Duarte in the summer of 2008 and received a B.S. in Wildlife & Fisheries Sciences from Texas A&M University in the spring of 2009. In the summer of 2009 Adam worked as a ranch hand at West End Deer Ranch. In the fall of 2009 he enrolled in the Wildlife Ecology graduate program at Texas State University-San Marcos. During his time at Texas State University, Adam has received the Houston Safari Club Dan L. Duncan Scholarship and the American Society of Mammalogists Student Travel Fellowship, and has worked as an instructional assistant teaching Functional Biology labs. In April 2011, Adam and Jennifer are expecting their first child, Elizabeth Alli Duarte.

Permanent email: ad1401@txstate.edu

This thesis was typed by Adam Duarte