RUMEN-RETICULUM AND LIVER MASS RELATIONSHIPS IN WHITE-TAILED DEER (*ODOCOILEUS VIRGINIANUS*) DIFFER BETWEEN FEMALES AND MALES.

by

Gayatri Bhaskar, B.S.

A thesis submitted to the Graduate Council of
Texas State University in partial fulfillment
of the requirements for the degree of
Master of Science
with a Major in Wildlife Ecology
December 2015

Committee Members:
Floyd W. Weckerly, Chair
Thomas R. Simpson
Clay M. Green

DEDICATION

I dedicate this work to my spiritual guru, Sri Shirdi Sai Baba.

ACKNOWLEDGMENTS

"We all need someone who inspires us to do better than we know how." I would like to express my gratitude toward my graduate advisor, Dr. Floyd Weckerly for his immense patience and tolerance for the past two years. Without his timely advice and encouragement, this thesis would not have been possible. I would like to thank my thesis committee members, Dr. Randy Simpson and Dr. Clay Green. They have been extremely cooperative and provided valuable feedback from time to time. I would also like to thank my mother, Smt. Durga Bhaskar for her unconditional love and support throughout my life. I consider myself blessed to have a brother like Mr. Maruthi Bhaskar who has always believed in me and my abilities. He is my role model and my admiration for him is inexplicable. I am indebted to my aunt and uncle Smt. Manjula Bhimraj and Mr. C. S. Bhimraj for funding my education at Texas State University. Without Mr. Jon Beaubien's help on my thesis, I would not have been able to complete the writing on time. I would like to thank Mr. Dilip Tummalapenta for his enormous amount of help for the past two years.

TABLE OF CONTENTS

	Page
ACKNOWLEDGMENTS	v
LIST OF TABLES	vii
LIST OF FIGURES	viii
ABSTRACT	ix
CHAPTER	
1. INTRODUCTION	1
2. METHODS AND MATERIALS	4
3. RESULTS	9
4. DISCUSSION	13
REFERENCES	16

LIST OF TABLES

Table **Page**

1. Second order Akaike information criterion (AICc) summary of models estimating liver mass of white-tailed deer (*Odocoileus virginianus*) sampled from the pens at Kerr Wildlife Management Area (Kerr pens), Texas, USA, and a private ranch in South Texas (SOTX), USA 10

2. Parameter estimates, standard errors (SE), and confidence intervals of models estimating liver mass of white-tailed deer (*Odocoileus virginianus*) sampled from the pens at Kerr Wildlife Management Area (Kerr pens), Texas, USA and a private ranch in South Texas (SOTX), USA 11

LIST OF FIGURES

Figure **Page**

1.(A) and (B) Scatterplot and regressions of the relationship between rumen-reticulum organ mass and liver mass for male and female white-tailed deer (*Odocoileus virginianus*) (crosses for males and squares for females). 12

ABSTRACT

Relationships between organ masses with high energetic demands influence metabolic demands in mammals. Previous studies have estimated allometric relationships between body mass and organ masses in white-tailed deer. To my knowledge, however, there has been no investigation into the relationship between rumen-reticulum organ mass and liver mass in any ungulate. Furthermore, energetically demanding life history events such as lactation in females and mating in males should affect organ workloads. Understanding the codependent relationships of these organs could be insightful to understanding the energy conservation strategy of white-tailed deer. I examined relationships between rumen-reticulum and liver mass in white-tailed deer in relation to the mating season, to see if relationships differed between females and males. I collected 151 white-tailed deer (68 males and 83 females) from Kerr Wildlife Management Area (Kerr WMA) breeding pens, Central Texas, and a private ranch in South Texas (SOTX). Deer from the Kerr WMA pens were obtained during the peak of the mating season, whereas deer from SOTX were collected two months prior to the mating season. There was a positive relationship between masses of the rumen-reticulum organ and liver at both study areas. However, this relationship differed between males and females. Males exhibited heavier livers in relation to rumen-reticulum organ masses than females at both study areas. These findings might be useful to understanding physiological changes during energetically demanding periods in male and female white-tailed deer.

1. INTRODUCTION

Visceral organs have high metabolic demands and organs with greater mass have a greater energetic burden. Knowledge of variation in relationships between organ masses is therefore useful to understanding metabolic demands and energy conservation by animals (Mueller et al. 2001, Parker et al. 2009, Parra et al. 2014). Relationships between organ masses have been detected in mammals (Johnson et al. 1990). A positive relationship has been reported which is probably due to increases in work load demands of organs with similar functions. What has not been examined, however, is whether the relationships between organ masses vary and what could be driving the change.

The mammalian liver is the largest visceral organ with several functions crucial to maintaining homeostasis. Assimilation of nutrients, their metabolism, and toxin expulsion are among the many functions of the liver. Detoxification of blood in the mammalian body is performed by hepatocytes in the liver (Barrett 2011). The liver is integral in the oxidation of fatty acids, conservation of nitrogen through urea cycling, regulating blood glucose levels by metabolizing carbohydrates (Barboza et al. 2009, Barrett 2011), and is also responsible for producing anticoagulants throughout life as well as red blood cells in early embryonic development (Leach 1961).

The rumen and reticulum are the largest compartments in the gastrointestinal tract of ruminants and these organs are where a majority of fermentation and absorption of nutrients occurs (Van Soest 1994, Clauss et al. 2003, Ramzinski and Weckerly 2007, Weckerly 2010). The rumen and reticulum are separated by a reticular fold. The primary function of the reticulum is to move smaller food particles to the omasum and trap dense or heavy particles. Dense particles get lodged in the honeycomb surface of the reticulum

(Van Soest 1994). The larger food particles are moved to the rumen, which acts as a fermentation vat producing volatile fatty acids. The wall of the rumen-reticulum is lined by epithelium, a serous membrane, and a muscular tunic (Van Soest 1994). The epithelium is where absorption, active transport of sodium and chloride, and passive transport of volatile fatty acids and water occur (Van Soest 1994). The muscular tunic provides motility to move particles and fluid through the rumen.

What makes the rumen an efficient organ of digestion is selective delay of food particles (Demment and Van Soest 1985). Selective particle delay decreases the chance of ingesta (recent forage) being passed through the rumen without digestion taking place. The rumen functions to increase retention time and further particle size reduction from rumination (Demment and Van Soest 1985). Extended exposure of digesta to microbial fermentation enables the animal to extract nutrients from food that might be recalcitrant to digestion (Luna et al. 2013). Small or less dense particles then leave the rumen by passing through the orifice between the rumen and the omasum (Barboza et al. 2009).

During energetically demanding events like lactation in females and reproductive activities by males, the workload of the liver and gastrointestinal tract can increase many fold. During the first month of lactation, for example, energy requirements of female ungulates increase 65-215% (Oftedal 1985, Robbins 1993, Parker et al. 2009). Enlargement of gastrointestinal organs in response to a presumed increase in digestive workload has been reported (Aiken et al. 2014, 2015). The elevated workload of the liver is brought about by increased food intake to meet demands or to provide energy when food intake is deficient in meeting energetic needs (Parra et al. 2014). Females faced with the enormous energetic burden of lactation increase food intake. Males spend an enormous amount of energy trying to procure mating opportunities. During the mating season, males become hypophagic and deplete fat reserves (Barboza et al. 2006, Luna et al. 2013). Adipose tissue mobilization results in fatty acid accretion in the liver (Emery et al. 1992, Gross et al. 2013). Both increase in workload and fatty acid accretion should result in heavier livers (Parra et al. 2014). The size of the liver and gastrointestinal tract probably corresponds to the demands of the ungulate and the quantity and composition of the nutrients that need to be metabolized by the liver (Anderson et al. 1974).

The difference in reproductive demands between female and male ruminants might affect relationships between rumen-reticulum organ and liver mass. During lactation both rumen-reticulum and liver masses should be heavy. Thus, there should be a positive relationship between the masses of these organs. During the mating season, the hypophagic state of males might result in a lack of relationship between the masses of the rumen-reticulum and the liver due to the differences in workloads of these organs by reproductively active males.

My objectives were to test whether the relationship between rumen-reticulum organ and livers mass differed between female and male white-tailed deer. I collected data from two populations. In one population animals were collected at the peak of the mating season and in the other population animals were collected two months before the mating season. In both populations I expected females to display a positive relationship between organ masses. I expected no relationship between organ masses in the population where males were collected at the peak of the mating season and a positive relationship in the other population where males were collected before the mating season.

2. METHODS AND MATERIALS

Study Areas

White-tailed deer were collected from two study areas. One study area was the Donnie E. Harmel deer pens at Kerr Wildlife Management Area (hereafter "Kerr pens"), Kerr County, in central Texas. The Kerr Wildlife Management Area was 2,628 ha, situated in the Edwards Plateau region. The average annual precipitation and temperature was 69.7 cm and 18 °C, respectively (Parra 2012). The research facility consisted of five to seven rearing pens and three to eight breeding pens that were each 1.2, 3, or 4 ha in size. The pens were surrounded by a 2.7-m high game fence (Wolcott et al. 2015). Deer consumed high quality, commercial pelleted rations (16% crude protein and 18.5% acid detergent fiber) ad libitum and a kg (dry weight) of alfalfa (*Medicago sativa*) and coastal hay per animal each week (Parra et al. 2014). Ground cover in the deer pens included bare ground, predominantly limestone, and non-palatable (to deer) herbaceous vegetation. Prevalent species were common horehound (*Marrubium vulgare*) and cowpen daisy (*Verbesina encelioides*). Plateau live oak (*Quercus fusiformis*) provided 25% to 50% canopy cover (Lockwood et al. 2007). Leaves and branches of the live oak trees have been browsed out of reach of white-tailed deer since 1974 (Wolcott et al. 2015).

The other study area, SOTX, was located in the brush country region of South Texas. The study area was a 2,994 ha private ranch in Jim Hogg County, Texas, USA. The average annual precipitation at this study area was 60.5 cm (Aiken et al. 2014). The sub-tropical climate was hot in summer, with daytime temperatures reaching as high as 35 °C and moderate winters with an average daytime temperature of 11 °C. A 2.4 m high fence enclosed the study area. The predominant forage consumed by white-tailed deer at

SOTX was honey mesquite (*Prosopis glandulosa*), cenizo (*Leucophyllum frutescens*), retama (*Parkinsonia aculeata*), western ragweed (*Ambrosia psilostachya*), tanglehead (*Heteropogon contortus*), woolly croton (*Croton capitatus*), Hooker's palafoxia (*Palafoxia hookeriana*), prickly pear (*Opuntia* spp.), sand bur (*Cenchrus spinifex*), little bluestem (*Schizachyrium scoparium*), king ranch bluestem (*Bothriochloa ischaemum*), and Johnson grass (*Sorghum halepense*) (Parra et al. 2014). Additionally, from January through October, protein feed was supplied through gravity feeders (1 per 107 ha) (Aiken et al. 2014).

Specimen and data collection

At the Kerr pens, 26 females and 19 males were collected in late November 2011. Another 24 females were collected in early December 2014. These deer were collected near the peak of the mating season of white-tailed deer in central Texas (Robinson et al. 1965). At SOTX, a total of 82 free ranging deer, 33 females and 49 males, were collected in October 2011. October is two months prior to the peak of the mating season of white-tailed deer in South Texas (Webb et al. 2007).

Kerr pens deer were dispatched using two techniques. In 2011 deer were shot with a high powered rifle and in 2014 deer were euthanasized in a self-contained, portable, CO_2 chamber. In the CO_2 chamber, death occurred within five minutes. At SOTX free ranging deer were net-gunned from a helicopter and restrained before being dispatched with a .22 caliber rifle at a central processing station (Parra 2012). Regardless of the dispatch method employed, deer were processed within 30 minutes. The collection followed the Institutional Animal Care and Use protocol from Texas State University (permit # 00933_09_06-03141BF15D).

Kill time was recorded when animals were dispatched. Whole mass minus any blood loss was recorded to the nearest kg (Jones and Weckerly 2008). The deer were then field dressed, and dressed mass was taken. Dressed mass is whole mass minus the mass of the internal organs and the mesentery (Luna et al. 2013). My measure of animal mass was dressed mass to reduce heterogeneity in mass from diel variation in gut fill (Weckerly et al. 2003, Aiken et al. 2015, Luna et al. 2012).

The rumen-reticulum was removed from the rest of the gastrointestinal organs at the reticulo-omasal sphincter and at the esophagus 5 cm above the junction with the reticulum. The rumen-reticulum with contents was then weighed to the nearest 0.1 kg (Weckerly et al. 2003, Ramzinski and Weckerly 2007). After this, the rumen was emptied of the digesta and thoroughly washed with tap water until the papillae on the rumen wall were free of digesta particles. The empty rumen-reticulum was then wrung out to rid excess water. The empty rumen-reticulum was then weighed to the nearest 0.1 kg (Luna et al. 2012). Hereafter empty rumen-reticulum is labeled rumen-reticulum organ mass. The liver was carefully excised and also weighed to the nearest 0.1 kg.

Body condition was assessed from back fat thickness (Gerhart et al. 1996). An incision was made approximately 3 cm parallel to the third lumbar vertebra and back fat thickness was measured with a stainless steel ruler to the nearest 0.1 cm. Males during the mating season become hypohagic (Luna et al. 2013) and thus Kerr pens males should have less back fat than SOTX males.

At both study areas deer were at least 1.5 years of age. Females also had given birth to young that year. Every pen deer was uniquely ear tagged at birth enabling me to know the age of each deer at Kerr pens. I also was able to obtain the number of young that were weaned by each female from the Kerr pens. White-tailed deer typically wean young by 90 days of age (Parra 2012). Young were considered weaned if they survived to 90 days of age. At SOTX deer were aged by tooth replacement and wear (Severinghaus 1949). Whether females reproduced that year was determined by the presence of milk (lactation) in the teats (Parra et al. 2014. Similar to the Kerr pens, only females that reproduced as indicated by lactation were included in analyses.

Statistical Analyses

I used an analysis of variance to test if back fat thickness was greater in SOTX males than Kerr pens males. Linear regression models were estimated using the least squares method. An Akaike Information Criterion (AIC) model selection approach was adopted to select models. Akaike Information Criterion uses both model fit to data and parsimony (Burnham and Anderson, 2002). Because the ratio of sample size to the model with the most parameter estimates was less than 40, I used Akaike Information Criterion corrected for small sample size (AIC_c) (Burnham and Anderson, 2002). Model selection was based on delta (Δ), the difference in AIC_cs between a model and the model with the smallest AIC_c. From my AIC_c analyses I report Δ, the number of parameters estimated by each model (nPar) and the coefficient of determination, r^2. Multiple r^2 was reported for models with a single predictor and adjusted r^2 when models had more than one predictor (Burnham and Anderson 2002, Duarte et al. 2011). Another part to AIC_c model selection was competing models. Competing models presumably summarize the data to a similar extent and better than the remaining models that are considered. Competing models can be defined as models that differ by two or fewer AIC_c units (Arnold 2010). Yet, due to how AIC is calculated, it is possible for two models that differ by one additional predictor to compete even when the one additional predictor has little effect on the response variable. When selecting models I provide statistical evidence showing that all predictors influenced the response variable by reporting the 95 percent confidence intervals of every coefficient. The model selection analysis was conducted in the MuMIn package in the statistical program R (Barton 2009, R Development Core Team 2009, Luna et al. 2013, and Aiken et al. 2014). Confidence intervals were estimated in the confint package (Stauffer 2007).

For the Kerr pens data, five models were constructed to assess the influence of sex or year on the relationship between rumen-reticulum organ mass and liver mass. Models considered the additive influence of sex or year as well as the multiplicative influence of sex or year on relationships between rumen-reticulum organ mass and live mass. For the SOTX data, three models were built to assess the additive or multiplicative influence of sex on the relationship between rumen-reticulum organ mass and liver mass.

Rumen-reticulum organ mass was measured with error whereas the other predictors were fixed (Sokal and Rohlf 2012). The error in measuring rumen-reticulum organ mass might influence parameter estimates (Ramzinsky and Weckerly 2007). Regression coefficients and standard errors estimated from least square methods, however, were virtually identical to case resampling bootstrapped estimates (Fox 2002). Thus I only report least square estimates.

3. RESULTS

Means of dressed mass from Kerr pens were 47.81 Kg (standard deviation = 12.42) for males and 34.65 Kg (4.86) for females. At SOTX, means of dressed mass were 59.77 Kg (12.14) for males and 32.93 Kg (4.09) for females. Dressed mass was positively correlated to rumen-reticulum organ mass at Kerr pens (r = 0.46,t_{67} = 4.24, $P < 0.01$) and at SOTX (r = 0.64, t_{80} = 7.63, $P < 0.01$). Thus, heavier rumen-reticulum organ masses were probably from heavier deer. For back fat, the interaction between sex and site from a two factor Analysis of Variance was statistically significant ($F_{1,147}$ =39.03, $P < 0.01$). Mean back fat of males (cm), in centimeters was thicker at SOTX (mean = 3.15, standard deviation = 1.50) than for Kerr pens males (0.67, 0.71). Mean back fat of females (cm), in centimeters were similar between the two study areas (SOTX: 0.91, 0.80; Kerr pens: 0.84, 0.88). These findings were consistent with Kerr pens males being collected near the peak of the mating season and the SOTX males being collected before the mating season.

At both SOTX and Kerr pens, I selected the model with sex having an additive influence on the relationship between rumen-reticulum organ mass and liver mass (Table 1). I selected these two models because every coefficient was statistically significant (Table 2). Each model summarized the data reasonably well (Fig. 1). At both study areas, males had heavier livers in relation to rumen-reticulum organ mass than did females.

Table 1. Second order Akaike information criterion (AIC_c) summary of models estimating liver mass of white-tailed deer (*Odocoileus virginianus*) sampled from the pens at Kerr Wildlife Management Area (Kerr pens), Texas, USA, and a private ranch in South Texas (SOTX), USA. The change in (Δ) AIC_c between a model and the model with the smallest AIC_c, number of parameters estimated (nPar) by a model, and adjusted r^2 (r^2 where there was only one predictor) are provided.

		Kerr Pens		SOTX	
Model Predictors	*n*Par	Δ	r2	Δ	r2
RROM	3	14.59	0.41	26.51	0.50
RROM,SEX	**4**	**0.00**	**0.52**	**1.69**	**0.63**
RROM,SEX,SEX*RROM	5	1.63	0.52	0.00	0.65
RROM,YEAR	4	14.7	0.42		
RROM,YEAR,YEAR*RROM	5	13.39	0.43		

*Predictors were rumen-reticulum organ mass (RROM), sex, and year. Values in boldface type denote the selected model.

Table 2. Parameter estimates, standard errors (SE), and confidence intervals of models estimating liver mass of white-tailed deer (*Odocoileus virginianus*) sampled from the pens at Kerr Wildlife Management Area (Kerr pens), Texas, USA and a private ranch in South Texas (SOTX), USA. Parameter estimates are given with lower (lb) and upper (ub) bounds of 95% confidence intervals. Predictors were rumen-reticulum organ mass (RROM), and sex.

	Kerr Pens				SOTX			
Model Predictors	Estimate	SE	lb	ub	Estimate	SE	lb	ub
Intercept	0.43	0.1	0.23	0.63	0.27	0.1	0.08	0.47
RROM	0.65	0.14	0.36	0.93	0.49	0.07	0.35	0.64
Sex	0.24	0.06	0.12	0.35	0.2	0.04	0.13	0.27

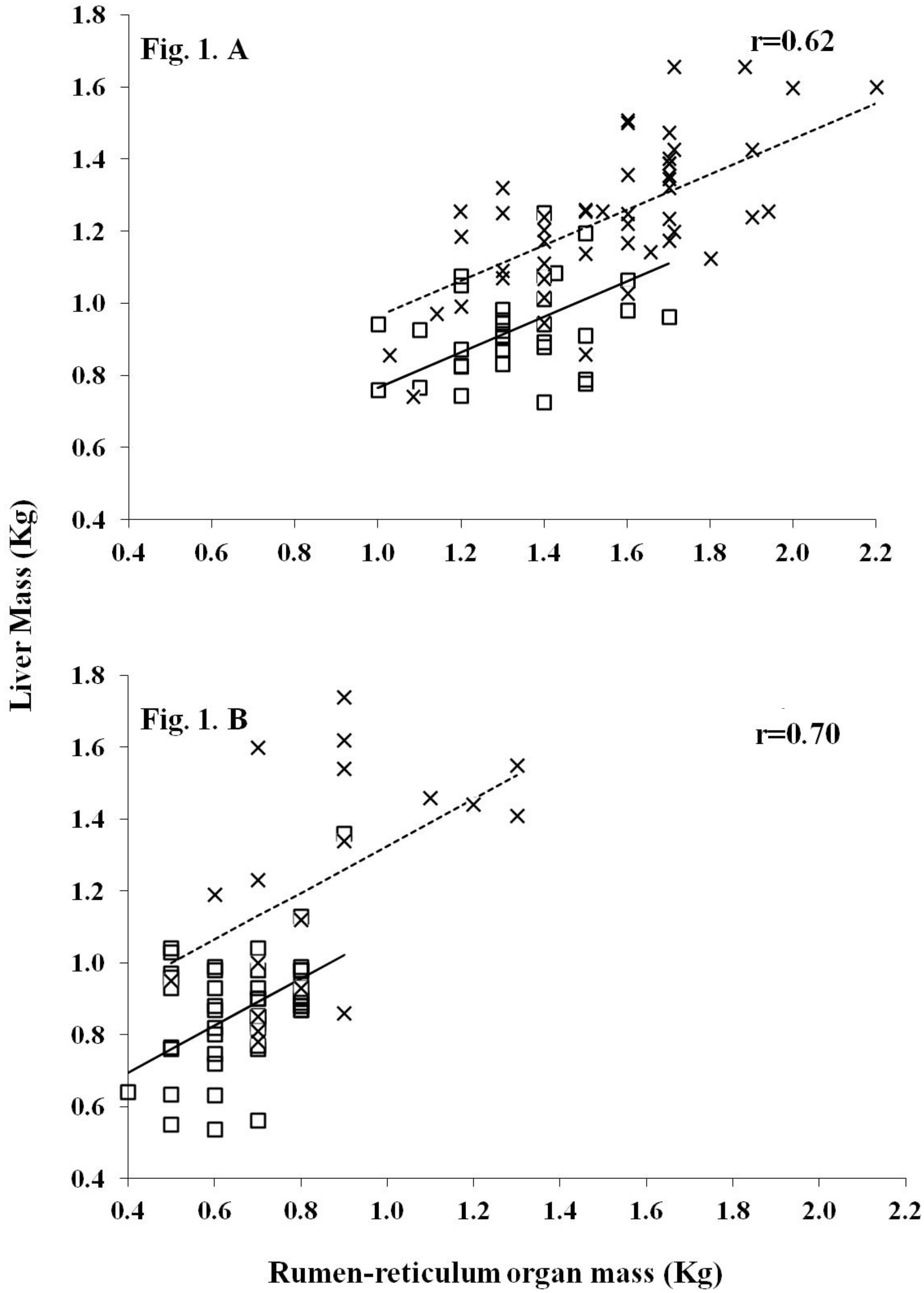

Figure 1. (A) and (B) Scatterplot and regressions of the relationship between rumen-reticulum organ mass and liver mass for male and female white-tailed deer (*Odocoileus virginianus*) (crosses for males and squares for females). Kerr pens, Texas, USA (Fig.1. A) and a private ranch in South Texas, USA (Figure. 1. B). The solid line is the female regression and the dashed line is the male regression.

4. DISCUSSION

My study design allowed me to compare the relationships between rumen-reticulum organ and liver mass of male and female white-tailed deer that differed in their diets and at the time of collection in relation to the mating season. The rumen-reticulum and liver are organs that have high energy demands (Johnson et al. 1990). Some of my findings are consistent with my expectation. Females that participated in reproduction that year did display a positive relationship between the masses of the two organs. Also, males that were collected two months before the start of the mating season also displayed a positive relationship between these two organ masses. What was unexpected was that males at the peak of the mating season displayed positive relationships between rumen-reticulum organ mass and liver mass; I expected no relationship.

During the peak of the mating season males are hypophagic to some degree (Barboza et al. 2006, Luna et al. 2013). Males can be hypophagic even when they are provided with ad libitum access to forage (Barboza et al. 2004). Hypophagia is presumably caused by a drop in secretions of thyroid hormones. Although males are hypophagic the energetic demands of mating activities are great. Males contend with other males and females rarely allow copulation until the peak of estrous (McCullough 1969). Consequently, males spend much time patrolling for females, chasing males and females, fighting, scent marking and thrashing vegetation with their antlers. Males then meet the energetic demands of these strenuous activities by mobilization of adipose tissue that takes place in the liver. The workload demands of liver tissue should be high but the workload demands of the rumen-reticulum should be less.

The unexpected findings for males from the Kerr pens were probably not due to males being collected outside of the mating season. The mean back fat for SOTX males was greater than that of the males at Kerr pens. Thinner back fat of males from the Kerr pens is consistent with those males having depleted energy reserves due to the physical rigors associated with mating activities. The consistent pattern of males having heavier livers in relation to rumen-reticulum organ masses is probably not from body size differences between females and males. Body mass was positively correlated with rumen-reticulum organ mass. Heavier rumen-reticulums were from heavier deer. The additive influence of sex on the relationship between the masses of the rumen-reticulum and liver indicates that, controlling for body mass, males had a heavier liver in relation to the mass of the rumen-reticulum than did females. The differences I observed in rumen-reticulum and liver mass in female and male white-tailed deer were also documented in reindeer from South Georgia Island (Leader-Williams and Ricketts 1982). Controlling for body mass, male reindeer had heavier livers than female reindeer throughout all seasons of the year but rumen-reticulum organ mass was similar between females and males.

The rumen-reticulum functions in digestion. The liver has digestive functions but other functions as well. The liver is involved in detoxification of expired red blood cells, urea recycling, and converting adipose tissue into energy as well as other functions (Leach 1961, Barboza et al. 2009, Barrett 2011). The multiple roles of the liver in conjunction with the differences in life histories between females and males and the polygynous mating system might have some bearing on why male livers were always heavier in relation to the rumen-reticulum organ mass than were female livers. Males live a riskier life than do females which usually results in males having a shorter life span than females (McCullough 1979). Associated with the shorter life span is that males can have compromised homeostasis associated with the intense competition among males for access to females during the mating season (Barboza et al. 2004). Polygynous males might require a greater workload on the liver than what occurs on the liver of females.

Further study is warranted to detect correlation patterns in organ mass relationships among males and females at different times of the year. Deer from the two sites differed in diet. Yet, my study design did not allow me to assess the influence of diet on organ relationships. A larger scale study, including more study areas with different habitats could examine the relationship between organs in more detail. My study examined the relationship between the rumen-reticulum organ and liver mass during stressful periods of mating in males and lactation in females. My study revealed the influence of sex on the relationship between rumen-reticulum organ mass and liver mass. Why males would have a heavier liver mass in relation to rumen-reticulum organ mass in comparison to females deserves further study to understand metabolic demands and energy conservation.

REFERENCES

Aiken, M. R. E., A. Duarte, R. S. Luna, D. M. Wolcott, and F. W. Weckerly. 2014. Daytime declines in rumen-reticulum fill of male white-tailed deer (*Odocoileus virginianus*) from south Texas. Canadian Journal of Zoology 92:637-642.

Aiken, M. R. E., D. M. Wolcott, A. Duarte, R. S. Luna, and F. W. Weckerly. 2015. Use of rumen-reticulum fill to examine nutrient transfer and factors influencing food intake in white-tailed deer (*Odocoileus virginianus*). Canadian Journal of Zoology 93:439-445.

Anderson, A. E., D. E. Medin, and D. C. Bowden. 1974. Growth and morphometry of the carcass, selected bones, organs, and glands of mule deer. Wildlife Monographs 39:3-122.

Arnold, T. W. 2010. Uninformative parameters and model selection using Akaike's Information Criterion. Journal of Wildlife Management 74:1175-1178.

Barboza, P. S., D. W. Hartbauer, W. E. Hauer, and J. E. Blake. 2004. Polygynous mating impairs body condition and homeostasis in male reindeer (*Rangifer tarandus tarandus*). Journal of Comparative Physiology. B, Biochemical, Systemic, And Environmental Physiology 174:309-317.

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.

Barboza, P. S., K. L. Parker, and I. D. Hume. 2009. Integrative wildlife nutrition. Springer, New York.

Barrett, K. E. 2011. Functional anatomy of the liver and biliary system. Pages 559-565 in H. Raff, and M. G. Levitzky, editors. Medical physiology: a systems approach. McGraw-Hill Professional Publishing, New York, New York.

Barton, K. 2009. MuMIn: multi-model inference. R package version 1.0.0 [computer program] Available from http://r-forge.r-project.org/projects/mumin/ [accessed 18 July 2015].

Burnham, K. P., R. Arnold, and G. C. White. 1998. Comparison of Akaike information criterion and consistent Akaike information criterion for model selection and statistical inference from capture-recapture studies. Journal of Applied Statistics. 25:263-282.

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

Clauss, M., M. Lechner-Doll, and W. J. Streich. 2003. Ruminant diversification as an adaptation to the physiochemical characteristics of forage. A reevaluation of an old debate and a new hypothesis. Oikos 102:253-262.

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 57:1131-1136.

Demment, M. W., and P. J. Van Soest. 1985. A nutritional explanation for body-size patterns of ruminant and nonruminant herbivores. The American Naturalist 125:641-672.

Emery, R. S., J. S. Liesman, and T. H. Herdt. 1992. Metabolism of long chain fatty acids by ruminant liver. The Journal of Nutrition 22:3166-3192.

Fox. J. 2002. Bootstrapping regression models. Appendix to An R and S-PLUS companion to Applied Regression.

Gerhart, K. L., R. G. White, R. D. Cameron, and D. E. Russell. 1996. Body composition and nutrient reserves of arctic caribou. Canadian Journal of Zoology 75:136-146.

Gross, J. J., F. J. Schwarz, K. Eder, H. A. Van Dorland, and R. M. Bruckmaier. 2013. Liver fat content and lipid metabolism in dairy cows during early lactation and during a mid-lactation feed restriction. Journal of Dairy Science. 96:5008-5017.

Johnson, D. E., K. A. Johnson, and R. L. Baldwin. 1990. Changes in liver and gastrointestinal tract energy demands in response to physiological workload in ruminants. Journal of Nutrition 120:649-655.

Jones, R. L., and F. W. Weckerly. 2008. Influence of age and sex on dressed-whole body weight relationships in black-tailed deer. California Fish and Game 94:137-142.

Leach, W. J. 1961. Functional Anatomy Mammalian and Comparative. Third edition. McGraw- Hill Book Company, Inc, New York.

Leader-Williams N., and C. Ricketts. 1982. Seasonal and sexual patterns of growth and condition of reindeer introduced into South Georgia. Oikos 38:27-39.

Luna, R. S., A. Duarte, F. W. Weckerly. 2012. Rumen-reticulum characteristics, scaling relationships, and ontogeny in white-tailed deer (*Odocoileus virginianus*). Canadian Journal of Zoology 90:1351-1358.

Luna, R. S., A. Duarte, and F. W. Weckerly. 2013. Influence of body size on dietary nutrition of White-tailed deer *Odocoileus virginianus*. Journal of Fish and Wildlife Management 4:53-62.

Lockwood, M. A., D. B. Frels, W. E. Armstrong, E. Fuchs, and D. E. Harmel. 2007. Genetic environmental interaction in white-tailed deer. Journal of Wildlife Management 71:2732-2735.

McCullough, D. R. 1979. The George Reserve Deer Herd. The Blackburn Press, Caldwell, New Jersey.

McCullough, D. R. 1969. The Tule elk: its history, behavior, and ecology. Univ. Calif. Publ. Zool. 88:1-209.

Mueller, M. J., D. Langemann, I. Gehrke, W. Later, M. Heller, C. C. Gluer, S. B. Heymsfield, and Bosy-Westphal. 2001. Effect of constitution on mass of individual organs and their association with metabolic rate in humans-a detailed view on allometric scaling. Plos One 6:e22732.

Oftedal, O. 1985. Pregnancy and lactation. Bioenergetics of Wild Herbivores 10:215-238.

Parker, K. L., P. D. Barboza, and M. P. Gillingham. 2009. Nutrition integrates environmental responses of ungulate, Functional Ecology 23:57-69.

Parra, C. A. 2012. Body weight and age influences on liver weight in White-tailed deer (*Odocoileus virginianus*): Implications for reproductive effort. Thesis, Texas State University, Texas, USA.

Parra, C. A., Duarte, R. S. Luna, D. M. Wolcott, F. W. Weckerly. 2014. Body mass, age and reproductive influences on liver weight of white-tailed deer. Canadian Journal of Zoology 92:273-278.

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.

Robbins, C. T. 1993. Wildlife feeding and nutrition. Academic Press, San Diego.

Robinson, R. M., J. W. Thomas, and R. G. Marburger. 1965. The reproductive cycle of male white-tailed deer in central Texas. Journal of Wildlife Management 29:53-59.

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

Sokal, R. R., and F. L. Rohlf. 2012. Biometry: the principle and practice of statistics in biological research. Fourth edition. W. H. Freeman and Co., New York.

Stauffer, H. B. 2007. Contemporary Bayesian and Frequentist Statistical Research Methods for Natural Resource Scientists. Humboldt State University, Arcata, California.

Van Soest, P. J. 1994. Nutritional Ecology of the Ruminant. Second edition. Cornell University, Ithaca.

Webb, S. L., D. G. Hewitt, and M. W. Hellickson. 2007. Survival and cause-specific mortality of mature male white-tailed deer. Journal of Wildlife Management 71:555-558.

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

Weckerly, F. W. 2010. Allometric scaling of rumen-reticulum capacity in white-tailed deer. Journal of Zoology 280:41-48.Wolcott, D. M., Reitz, R. L., & Weckerly, F. W. (2015). Biological and environmental influences on parturition date and birth mass of a seasonal breeder. Plos One, 10(4), e0124431 doi:10.1371/journal.pone.0124431/