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Variation Across Years in Rumen-Reticulum Capacity and Digesta Load in White-tailed Deer (*Odocoileus virginianus*)

Ryan S. Luna[1,*] and Floyd W. Weckerly[1]

Abstract - How gut capacity and digesta loads vary with unpredictable forage quality and abundance has not been examined in ruminants. *Odocoileus virginianus* (White-tailed Deer) should have greater rumen-reticulum capacity during drought years to accommodate heavier digesta loads due to diets that contain a greater fraction of indigestible material. In contrast, in years with above-average precipitation, digesta loads should be lighter due to a greater fraction of digestible material in the diet which would result in less need for a large rumen-reticulum capacity. Data were collected from White-tailed Deer obtained during October, 2006–2008, from a 214-ha enclosure at the Mason Mountain Wildlife Management Area, Mason County, TX. Digesta load, liver weights (used as a proxy to indicate metabolic workload), empty rumen-reticulum organ weights, and rumen-reticulum volume were measured. Findings, adjusted for body weight, indicated that in the year with above-average precipitation, liver weights and rumen-reticulum capacity were less than in drought years. Although the influence of year on rumen-reticulum organ weight, adjusted for body weight, was not statistically significant, graphical representation did show a trend that followed yearly precipitation. Digesta loads, adjusted for body weight, progressively increased over the study, which did not coincide with changes in precipitation. Overall, this study provided information on how rumen-reticulum attributes change with environmental heterogeneity across years.

Introduction

Environmental changes across years can affect the nutritional content and availability of forage for large herbivores. Variation across years in forage quality and quantity may be coupled to changes in the capacity of the gastrointestinal organ of herbivores. Capacity of the gastrointestinal organ should increase during periods of hyperphagia and decrease during hypophagia. However, variation in gut capacity within a season across years has not been explicitly examined in long-lived herbivores. Flexibility in gastrointestinal organs may be needed to accommodate erratic climatic conditions that influence temporal availability of forage (Canale and Henry 2010). In semiarid environments, abundance and quality of ruminant forages such as browse and forbs are positively correlated with precipitation, which is capricious in both space and time, and the predictability of precipitation from one year to the next is poor (Beatley 1969; Marshal et al. 2002, 2005; Noy-Meir 1973; Polis et al. 1997; Robertson 1987; Teer et al. 1965). Variation among years in forage quality and quantity should be coupled to the capacity of gastrointestinal organs so that ruminants can adjust to density-independent factors that influence survival and reproduction (Canale and Henry 2010).

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The capacity of gastrointestinal organs can change in predictable ways across seasons for several species of ruminants (Jenks et al. 1994, Jiang et al. 2009, Weckerly 1989). These changes in capacity are largely due to changes in diet quality, which will have direct effects on the amount of food a ruminant consumes (Barboza et al. 2009). *Ovibos moschatus* Zimmermann (Muskoxen), for example, experience changes in digesta loads of over 150 percent between seasons when hypo- and hyperphagia occur (Barboza et al. 2006). During hyperphagia, digesta load increases and tissue is added to the gastrointestinal tract to enlarge capacity (Jenks et al. 1994, Jiang et al. 2009, Weckerly 1989). The increased capacity occurs when nutritious forage is abundant and predictable from one year to the next. The animal then has the capability to ingest enough nutrients to meet life-history demands and replenish fat stores lost during seasons when hypophagia occurs. An investment in gastrointestinal tissue, which has high energy demands, is returned by the animals' ability to elevate forage intake and retain digesta long enough so that plant material can be fermented (Barboza et al. 2006, Holand 1994).

In contrast to Barboza et al. (2006), numerous studies have shown that as diet quality decreases, forage intake increases (Barboza et al. 2009, Karasov and Martinez del Rio 2007). An increase in forage intake attributed to a decrease in forage quality was termed the instantaneous response strategy by Meyer et al. (2010). The instantaneous response strategy has been noted in numerous trials and on a variety of mammals including rodents, marsupials, pigs, primates, horses, and ruminants (Baer et al. 1985; Dinius and Baumgardt 1970; Edwards and Ullrey 1999a, 1999b; Laut et al. 1985; Owen and Ridgman 1968; Peterson and Baumgardt 1971; Plowman 2002; Schwartz et al.1988; Wellard and Hume 1981). Artificial feeds were used in the trials documenting the instantaneous response; even though it is assumed that the same food intake strategies would apply in herbivores consuming natural forage (Karasov and Martinez del Rio 2007), the strategy has not been directly tested.

When forage quality and quantity become unpredictable, it seems unlikely that variation in gut capacity will follow the pattern noted in ruminants at high latitudes where forage availability changes predictability from winter to summer. Animals inhabiting semi-arid environments might not have a marked change in forage quality and quantity between seasons. Because changes in forage quality and quantity are less predictable in semi-arid environments, animals inhabiting these environments might have gut capacities that respond differently than observed in animals that inhabit high latitudes. Variation in gut capacity in less predictable environments may be influenced by the quality of the recent diet (Barboza and Hume 2006). However, the metabolic expense of adding gut tissue may be too risky in environments with unpredictable forage resources (Naya et al. 2007), which may play a role in semi-arid environments. When the quality of the diet is high, excess gut capacity may not be critical because the fraction of the diet that is indigestible is low resulting in increased rates of digesta passage. Conversely, when animals consume a low-quality diet, a greater amount of time may be required to extract nutrients from forage. For this reason, gut capacity may increase by stretching of the existing gut tissue, thereby not requiring any additional tissue to increase capacity.

In addition to understanding variation in gut capacity, liver weight should also be noted. Liver weight can be used as an indicator of metabolic workload; therefore, liver weights should be obtained when considering the influence of forage quality. Liver weights of *Cervus elaphus* L. (Red Deer) have been shown to decrease in conjunction with a reduced forage intake (Wolkers et al. 1994). Numerous studies have noted co-variation of liver weights with nutrition and animal demands (Gerhart et al. 1996, McLeod and Baldwin 2000, Reynolds et al. 2004, Swanson et al. 1999, Verme and Ozoga 1980, Wolkers et al. 1994). Therefore, variations in liver weight should be coupled with variations in rumen-reticulum morphology.

We measured rumen-reticulum capacity, digesta load, and liver weight in male and female *Odocoileus virginianus* Zimmermann (White-tailed Deer) in central Texas across three consecutive Octobers. In this semi-arid environment, primary productivity often differs from one autumn to the next as a result of fluctuations during summer and early autumn in precipitation. We set out to determine how rumen-reticulum capacity and digesta loads fluctuate in a semi-arid environment across years within a season. We tested predictions about how rumen-reticulum capacity and digesta load should vary across years of drought and above-average precipitation. During drought years, nutritious forage in summer and early autumn should be scarce. Therefore, we predicted that White-tailed Deer would exhibit greater liver weights and rumen-reticulum capacity during a drought year as a result of consuming forage with a greater fraction of indigestible material, which thereby should also result in increased digesta loads. We hypothesized that in years with above-average precipitation, rumen-reticulum capacity would be decreased because less rumen-reticulum capacity is needed to accommodate lighter digesta loads. The lighter digesta loads in above-average precipitation years would presumably result from the consumption of forage that has a greater fraction of digestible material.

Methods

Study area

Animals were obtained from a 214-ha enclosure at Mason Mountain Wildlife Management Area (WMA), Mason County, TX. Daytime temperatures are hot (35–40 °C) in summer and mild (15–20 °C) in winter. Mason Mountain WMA has an average annual precipitation of approximately 66 cm with a coefficient of variation = 21% and first order serial $r = 0.09$. Precipitation varies from year to year, and it is also unpredictable across years. The vegetation in the enclosure is primarily comprised of various *Quercus* spp. (oaks), *Aloysia gratissima* Gillies and Hook. (Whitebrush), and grassland with *Bouteloua* spp. (grama species), *Eragrostis* spp. (love grasses), *Schizachyrium scoparium* Michx. (Little Bluestem), and *Bothriochloa saccharoides* Steud. (Silver Bluestem). The entire enclosure was fenced with a 2.46-m-tall game fence.

Gut variables

We measured liver weight and three rumen-reticulum variables: organ weight, digesta load, and capacity. Variation in liver weight was used to assess whether changes in precipitation resulted in changes in nutrition of deer. We measured rumen-reticulum organ weights and capacity. Distension of the rumen-reticulum is needed to accommodate digesta load changes (Weckerly 2010). Rumen-reticulum volume was used to measure distension of these organs and concomitantly capacity, because rumen-reticulum organ weights do not necessarily measure the extent to which these organs distend (Sibbald and Milne 1993). The remaining rumen-reticulum variable measured was digesta load.

Experiment

In 2006, 2007, and 2008, deer were trapped from sites in central Texas and translocated to the enclosure from February through April (Weckerly 2010). The deer were provided supplemental corn for two weeks after introduction to the enclosure. Supplemental corn was dispensed from 5 feeders programmed to release 1.13 kg of corn 0.5 hrs before sunrise and 1 hr before sunset. From May through August, deer were not provided supplemental feed, and consumed forage available within the enclosure. Supplemental feeding recommenced for 2 weeks in September as part of a population study and again when deer were harvested in October (Weckerly and Foster 2010). Numbers of deer in the enclosure were 58 in 2006, 63 in 2007, and 48 in 2008. There were 6–7 males for every 10 females in each year of the study. Precipitation was recorded at the wildlife management area by Texas Parks and Wildlife personnel. To show how precipitation was distributed across the nine months that the deer were in the enclosure, the data were combined into seasons of winter (January–March), spring (April–June), and summer (July–September) for each year of the study.

The deer were harvested by Texas Parks and Wildlife personnel with high-powered rifles in October within three hours of dawn or dusk (Weckerly 2010). Respective sample sizes were 26 (12 females, 14 males), 29 (19 f, 10 m), and 31 (21 f, 10 m) for 2006, 2007, and 2008. The carcasses were necropsied within three hours of the time of death. The whole weight of each animal minus blood loss was recorded before the animal was eviscerated. The liver was excised from the entrails and weighed. The mesentery was then removed to expose the rumen-reticulum. The rumen-reticulum was separated from the rest of the entrails by ligating the esophagus approximately five cm above its junction with the reticulum and making a second incision at the reticulo-omasal sphincter (Ramzinski and Weckerly 2007, Weckerly et al. 2003). 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 through the reticulum. The rumen-reticulum was inverted (by slightly elongating the ligation at the reticulo-omasal sphincter) and rinsed thoroughly to ensure that the rumen-reticulum was void of all particulate matter. After rinsing, the rumen-reticulum was reverted and rumen-reticulum organ weight was recorded. Digesta load was determined by the difference between the weight of rumen-reticulum organ with its contents and rumen-reticulum organ weight without contents.

To measure rumen-reticulum capacity, 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 L. The capacity measurement was taken in triplicate. Collection of animals followed an Institutional Animal Care and Use protocol from Texas State University.

Statistical analysis

Only adult animals (≥2.5 yr) were included in the analyses because gastrointestinal mucosal and submucosal morphology probably differ between yearling and adult deer (Knott et al. 2004, Pacha 2000). We conducted a multivariate analysis of covariance (MANCOVA) to account for correlations among response variables and examine overall multivariate significance of interactions between body weight and year, sex, and diel period. We used Pillai's trace as the multivariate test statistic for our MANCOVA. Body weight was used as a covariate (Sokal and Rohlf 1995) in the analysis because liver weight, rumen-reticulum organ weight, rumen-reticulum capacity, and digesta load covary with body weight (Jenks et al. 1994, Jiang et al. 2009, Weckerly 2010). Year, sex, and diel period of collection (AM, PM) have been shown to influence response variables and were main effects (Short et al. 1969, Weckerly 2010). If no interactions were detected, a reduced model MANCOVA was conducted with only main effects. A univariate ANCOVA was then performed for response variables to interpret the influence of main effects. Also, we used univariate ANCOVA models to estimate means of response variables adjusted for body weight. We also analyzed a linear contrast to assess if annual variation in response variables coincided with patterns of precipitation among years (Sokal and Rohlf 1995). Assumptions of normality and homoscedasticity were met because no patterns were observed in scatter plots between fitted values and residuals. All statistical analyses were conducted in program R (R Core Development Team 2009).

Results

Mean body weights of females and males in 2006 were 34 (range = 28–42) kg and 50 (range = 40–62) kg, respectively. In 2007, mean body weights of females were 39 (range = 32–47) kg and 59 (range = 42–73) kg for males. Mean body weights in 2008 were 37 (range = 32–41) kg for females and 50 (range = 39–61) kg for males. Precipitation for the past 20 years averaged 54 cm from January–September. Precipitation occurred in every season in each year, with seasonal precipitation in 2007 at least double the precipitation in 2006 and 2008 (Table 1). From January–September, precipitation was 76% of the 20-year average in 2006, 164% of the 20-year average in 2007, and 70% of that average in 2008.

The MANCOVA with second-order interactions of body weight, main effects, and response variables of rumen-reticulum weight, rumen-reticulum volume, digesta load, and liver weight indicated that none of the interactions were substantial (body weight:sex-*TS* = 0.031, *P* = 0.664; body weight:diel period-*TS* = 0.049, *P* = 0.436; and body weight:year-*TS* = 0.163, *P* = 0.105). Therefore, a reduced model MANCOVA was conducted which excluded the interaction terms. For the reduced MANCOVA, we detected influences from year (*TS* = 0.663, $P < 0.001$), body weight (*TS* = 0.664, $P < 0.001$), and sex (*TS* = 0.124, *P* = 0.031). There was a marginal effect of diel period (*TS* = 0.107, *P* = 0.060). The reduced MANCOVA was followed by univariate ANCOVAs on each response variable.

Every response variable in the univariate ANCOVA was influenced by body weight. Each response variable was also influenced by year, with the exception of rumen-reticulum weight. Also, rumen-reticulum organ weights and capacity varied between diel periods, and digesta loads differed between females and males (Table 2).

The variation across years in liver weight ($F_{1,82} = 6.09$, $P = 0.003$) and rumen-reticulum capacity ($F_{1,82} = 28.96$, $P < 0.001$) indicated differences across years, and matched patterns in precipitation. Means of liver weight were 0.85, 0.73, and 0.81 for 2006, 2007, and 2008, respectively. Rumen-reticulum capacity means were least in 2007 and similar in 2006 and 2008 (Fig. 1). Rumen-reticulum organ weight graphically followed the precipitation trend; however, year was not statistically significant ($F_{1,82} = 1.23$, $P = 0.297$). In contrast, variation in digesta loads did not match variation in precipitation among years ($F_{1,82} = 11.55$, $P < 0.001$). Mean digesta loads, adjusted for body weight, increased progressively from 2006 to 2008, with females having heavier digesta loads than males (Fig. 2).

Table 1. Seasonal and annual precipitation (cm) at Mason Mountain Wildlife Management Area, TX across 3 study years.

	Year		
Season	2006	2007	2008
January–March	8.5	16.9	5.8
April–June	17.5	49.3	22.2
July–September	10.3	31.3	11.5
Total	36.3	97.5	39.5

Table 2. Findings from analyses of variance examining the influence of whole weight, year, sex, and diel period (AM, PM) at time of death on response variables of liver weight, rumen-reticulum (RR) organ weight, digesta load, and RR volume of *Odocoileus virginianus* (White-tailed Deer) sampled in a 214-ha enclosure, Mason Mountain Wildlife Management Area, TX. The error degrees of freedom for each analysis was 82.

Source of variation		Liver weight		RR organ weight		RR volume		Digesta load	
	df	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*
Body weight	1	288.08	<0.001	100.59	<0.001	14.14	<0.001	19.72	<0.001
Year	2	6.09	0.003	1.23	0.297	28.96	<0.001	11.55	<0.001
Sex	1	0.85	0.359	2.75	0.101	0.12	0.730	7.97	0.006
Diel period	1	0.48	0.489	5.94	0.170	4.75	0.032	2.26	0.136

Discussion

The findings of this study, with the exception of digesta loads, supported our predictions. In 2007, when precipitation was greatest and diets were presumably higher in digestible materials, the rumen-reticulum capacity was the lowest recorded during our study. Rumen-reticulum organ weights were also low, but we did not detect a statistically significant effect. In 2006 and 2008, when there was less precipitation, rumen-reticulum capacity was greater. Greater precipitation

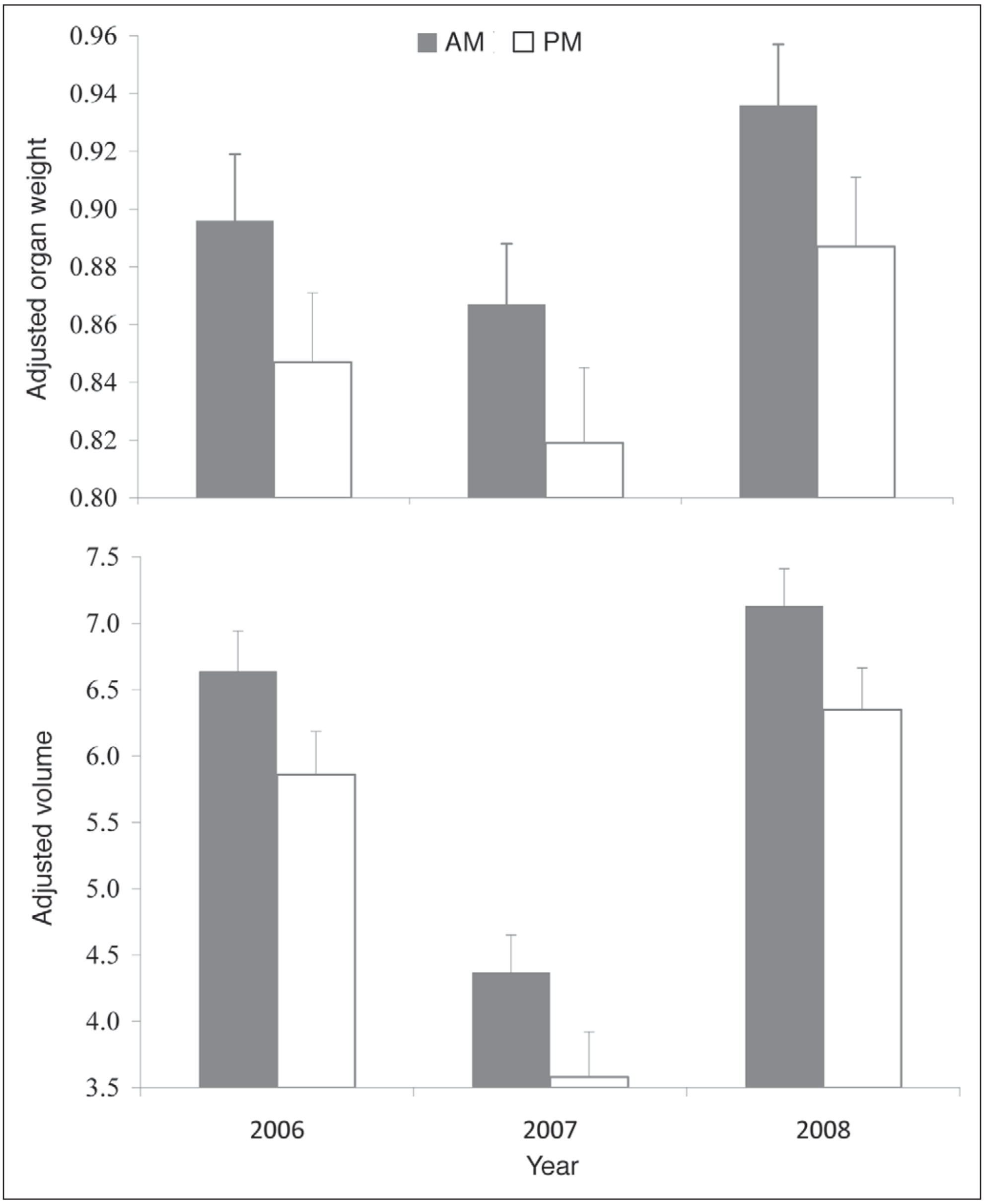

Figure 1. Rumen-reticulum organ weight (kg) and volume (L) adjusted for body weights for each diel period during 3 years at Mason Mountain Wildlife Management Area, TX. Error bars represent 1 SE.

during 2007 presumably caused an increase in the availability and nutritional content of forage within the enclosure. Changes in the quality and quantity of forage are coupled with changes in appetite and digestive function (Barboza et al. 2006). These changes in appetite and digestive function permit physiological adjustments that allow ungulates to respond to alterations in forage supplies that coincide with fluctuating environmental conditions (Barboza and Hume 2006). Numerous studies have demonstrated how the rumen-reticulum changes between seasons when forage supplies fluctuate predictably such as from winter to summer (Jenks et al. 1994, Jiang et al. 2009, Sibbald and Milne 1993). However, previous studies have not indicated how changing environmental conditions influence rumen-reticulum capacity across years. Our study is one of the first to show how rumen-reticulum capacity responds to unpredictable changes in environmental factors that influence forage resources.

Annual changes in forage quality and quantity should be coupled to forage intake and metabolic demands. Therefore, liver weights should also change among years. Our study indicated that liver weight variation coincided with precipitation patterns. Liver weights, adjusted for body weight, were lighter in the year with the greatest precipitation, which presumably corresponded with a decrease in metabolic workload as a result of increased dietary nutrition. These results differed from previous studies. Verme and Ozoga (1980) found that liver weights were heavier in White-tailed Deer fawns consuming pelleted diets high in protein (16.2%) and with more digestible energy (3030 vs. 2668 kcal/kg dry matter). In studies of cattle, goats, and sheep, liver weights increased in animals consuming

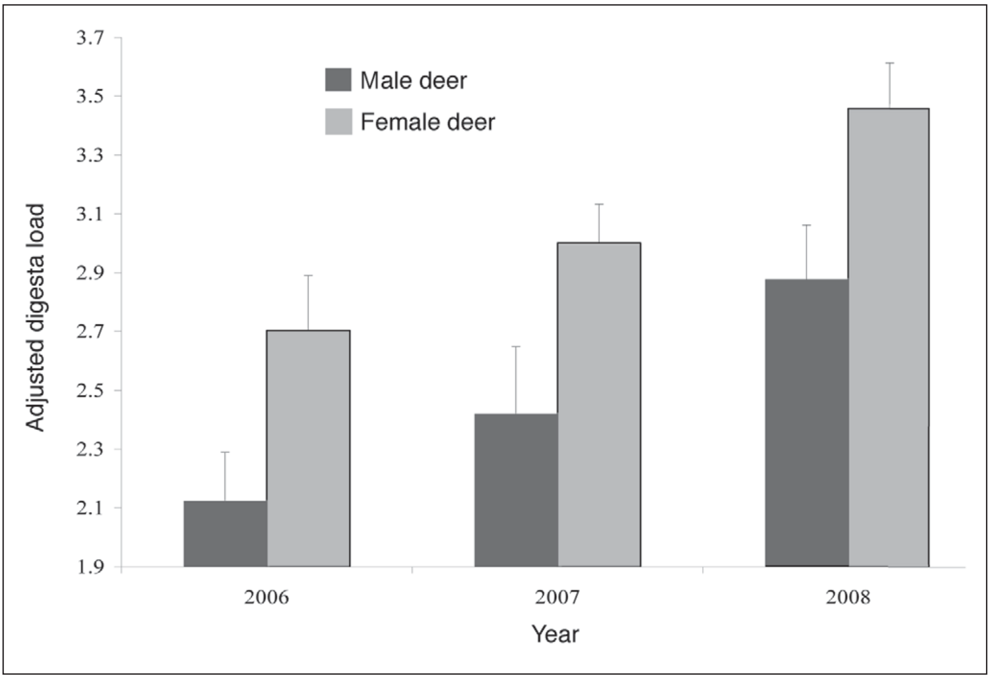

Figure 2. Digesta load weights (kg) adjusted for body weight for male and female White-tailed Deer for 3 years at Mason Mountain Wildlife Management Area, TX. Error bars represent 1 SE.

forage higher in metabolizable energy and protein (Haddad 2005, McLeod and Baldwin 2000, Swanson et al. 1999). In regards to the adult deer in this study, animals in drought conditions showed enhanced rumen-reticulum volume and slightly heavier organ weights. Hersom et al.(2004) indicated that adult castrated cattle exposed to a lower plane of nutrition had enhanced growth of the rumen-reticulum and liver, presumably to provide greater capacity to hold digesta and assimilate nutrients.

Diel changes in the capacity and weight of the rumen-reticulum were also detected. Changes in the distention of the rumen-reticulum can occur over a short period of time as a result of periods of foraging, which typically occur in the morning, or ruminating, which typically occur in the afternoon (Tulloh and Hughes 1965). Changes in rumen-reticulum capacity were 13%, 22%, and 12% between the morning and evening in 2006, 2007, and 2008, respectively. Moreover, rumen-reticulum organ weight varied by 6% between the diel periods for each respective year. The increase in rumen-reticulum organ weight associated with diel period is likely linked with rumination. During rumination, there is likely an increase in blood flow through the rumen to aid in absorption of volatile fatty acids. Exchange of metabolites, water, and minerals between the rumen and vascular system can also help explain the changes between morning and evening in rumen-reticulum organ weights (see Remond et al. 1996). The rumen-reticulum walls probably contain greater amounts of blood during periods of high nutrient exchange. Therefore the rumen-reticulum organ will have fluctuations in weight during periods of foraging compared to times of inactivity. This finding is not surprising due to reports of previous studies that have indicated that time of kill can have an influence on weights and capacities of the rumen-reticulum (Short et al. 1969, Tulloh 1966, Weckerly 2010).

Throughout the study, after adjusting for body mass, female White-tailed Deer had greater digesta loads than the males sampled. These differences in digesta load are likely the result of differing metabolic demands between the sexes. Additionally, digesta loads increased 26% from the first to the third year of the study. The observed changes in digesta load may be due to the amount of fibrous material within the forage and changes in forage availability across years. It is possible that a slight shift in age structure accounted for the observed increase in digesta loads throughout the study. Veiberg et al. (2009) detected heavier wet-rumen-reticulum fills and lower body conditions in older *Rangifer tarandus platyrhynchus* L. (Svalbard Reindeer). Veiberg et al. (2009) also noted that there might be an increase in digesta load within the rumen-reticulum due to a decrease in mastication efficiency. The mastication efficiency decreases as teeth wear, which can result in larger particles within the rumen-reticulum. As particle size and retention time of the digesta increase, there is a concomitant increase in retention time of fluid in the rumen-reticulum (Lechner et al. 2010). Therefore, larger digesta particles may also lead to more fluid in the rumen-reticulum. The resulting increase of fluid within the rumen-reticulum associated with age could have contributed to the increase in digesta load weights observed in our study. Digesta load may also vary in response to changes in the fraction of water within the forage due to diet quality and the type of diet; as a result, forage intake and fermentation rates can change as will the amount of fluid within the rumen (Barboza et al. 2006).

White-tailed Deer did not increase rumen-reticulum organ weight in response to the presumed higher-quality diet in 2007. A possible explanation for this is the high passage rates associated with high-quality forage. Also, due to the unpredictability of forage quality and quantity in semi-arid environments, it might be more beneficial for ruminants to have rumens that are elastic, and therefore do not require additional metabolically expensive tissue in order to accommodate increased digesta loads.

Slight changes in the rumen-reticulum organ weight were associated with greater changes in rumen-reticulum capacity. Therefore small changes in rumen-reticulum tissue could greatly influence capacity without incurring high energetic demands. McLeod and Baldwin (2000) reported increased intakes of metabolizable energy associated with rumen-reticulum and liver weights. During drought years, animals might increase their forage intakes to obtain more metabolizable energy. When forage is of low quality, there might be a decrease in passage rates, which would allow for longer exposure of the digesta to rumen microorganisms, thereby increasing the amount of nutrients extracted from the forage. In order to increase metabolic energy intake, rumen-reticulum capacity as well as liver weight might increase in order to accommodate the greater forage intake, digesta load, and digestive workload.

Changes in the rumen-reticulum should be directly correlated with changes in liver weights because forage that is consumed must be metabolized in order to extract nutrients. In our study, the correlation between rumen-reticulum and liver weight was present, but not very strong ($r = 0.64$). The low correlation might be the result of differences in the quality of forage between the sampling years. The liver metabolizes many nutrients (Van Soest 1994). Rumen-reticulum organ weight and capacity reflect, to some degree, the nutritional and physiological state of the animals over a long period of time, whereas digesta load may be indicative of current forage availability and life-history demands (gestation, lactation, or breeding) of the animal.

Our findings support previous studies that indicate variation in the rumen-reticulum capacity and organ weight is correlated with the quality of the forage (Kouakou et al. 1997, McLeod and Baldwin 2000). The quality of forage can be unpredictable across years in autumn due to the irregularity of precipitation. These unpredictable changes in precipitation affect forage quality, which, in turn, affects gut capacity. Previous research has shown variation in gut capacity among seasons in which there are predictable changes in seasonal forage (Barboza et al. 2006, Jenks et al. 1994, Jiang et al. 2009, Sibbald and Milne 1993). During these predictable seasonal changes, ungulates can increase dry matter intake due to an increase in gut tissue. An increase in gut capacity is needed to accommodate metabolic demands from lactation, gestation, and mating activities. In turn, the increase in gut capacity aids digestive efficiency. However, differences in forage quality can be unpredictable across years; therefore gut morphology is altered to limit energetic demands. Our findings indicated that when there is enough precipitation to yield high forage quality, there is a less pronounced increase in gut tissue. The minute increase in gut tissue results in lower rumen-reticulum organ weight and capacity compared to years with low precipitation that consequently yields low-quality forage and increased plasticity and rumen-reticulum organ weight to accommodate diets which might have high amounts of structural carbohydrates. These digestive adjustments, however, are probably energetically efficient to the animal, and allow their gut morphology to adjust to environmental changes that affect forage quality and abundance.

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