Heavier rumen–reticulum organs in white-tailed deer (*Odocoileus virginianus*) is consistent with dietary bulk not quality

F.W. Weckerly, G. Bhaskar, A. Duarte, R.S. Luna, and H.D. Starns

**Abstract:** The organs that make up the gastrointestinal tract have high energy demands. Therefore, when these organs vary in mass, they should impact metabolic requirements. Mass of the rumen–reticulum organs, the organs that comprise the largest part of the gastrointestinal tract of ruminants, might vary from bulk or nutrient availability of the diet. We examined differences in mass of the rumen–reticulum organs in white-tailed deer (*Odocoileus virginianus* (Zimmermann, 1780)) from two sites in Texas, USA, with different diet types. Specifically, at one site deer were fed a pelleted ration and at the other site deer consumed a natural browse diet. Accounting for body mass, deer consuming the browse diet had rumen–reticulum organ masses that were about 1.7 times heavier than deer consuming the pelleted diet. Deer consuming the browse diet also had lower diet quality, as indexed by crude protein concentration, than deer consuming the pelleted diet. The digesta loads of deer, however, were similar for the two types of diet. Our study findings are consistent with increased mass of rumen–reticulum organs from greater bulk, not diet quality. Understanding variation in rumen–reticulum organ mass has implications for understanding energy conservation in white-tailed deer.

**Key words:** bulk, diet, gastrointestinal tract, nutrient availability, *Odocoileus virginianus*, Texas, white-tailed deer.

**Introduction**

The mass of the organs that make up the gastrointestinal tract can vary from nutrition and type of food consumed (Ortigues and Doreau 1995). When the mass of the gastrointestinal tract increases, the energetic demands of the tract also increase because the mass-specific energy requirements of the tissue remain unchanged (McLeod and Baldwin 2000). Furthermore, a heavier gastrointestinal tract probably imposes a substantial metabolic cost to the animal, owing to the high energetic demands of this tissue (McBride and Kelly 1990). The implication is that animals should not commit to increases in the mass of gastrointestinal tract organs unless there is a return from ingested nutrients or it is vital to digestion and acclimation to local conditions.

The rumen and reticulum, which are separated by a reticular fold, are the largest organs in the gastrointestinal tract and account for a majority of fermentation and absorption of nutrients in ruminants (Barboza et al. 2006; Ramzinski and Weckerly 2007). The primary function of the reticulum is to move smaller food particles to the omasum and trap dense or heavy particles within the honeycomb surface of the reticulum (Van Soest 1994). These dense or heavy food particles are then regurgitated for rumination and subsequently moved to the rumen, where fermentation takes place and volatile fatty acids are produced. The wall of the rumen–reticulum is lined by papillae, a serous membrane, and a muscular tunic (Van Soest 1994). The papillae contribute to nutrient absorption, active transport of sodium and chloride, and passive transport of volatile fatty acids and water (Van Soest 1994). The muscular tunic provides motility to move food particles and fluid through the rumen–reticulum.

Two hypotheses that might explain variation in rumen–reticulum organ masses (hereafter, rumen–reticulum mass) are the bulk and...
nutrient availability of forage (Ortigues and Doreau 1995). In species such as white-tailed deer, the diet is primarily browse, which often contains bulky, fibrous material like cactus, seeds, fruits, leaves, and stems of woody plant (Hewitt 2011). A diet composed of these forages might require a rumen–reticulum mass sufficient to generate the force needed for rumen motility, especially if rumen–reticulum fill is high (Ortigues and Doreau 1995; Bonin et al. 2016). The force needed for rumen motility might require a thicker muscular tunic, which would lead to a heavier rumen–reticulum mass (Álvarez-Rodríguez et al. 2012). White-tailed deer also consume diets that vary in quality due to overall nutrient availability (Weckerly and Kennedy 1992). All else being equal, when deer ingest forage that is more digestible, additional surface area of the papillae is probably needed to increase absorptive capacity (Van Soest 1994). The additional epithelial tissue might lead to an increased rumen–reticulum mass (McLeod and Baldwin 2000).

We had the opportunity to examine whether the bulk hypothesis or the nutrient availability hypothesis was consistent with differences in the rumen–reticulum mass of white-tailed deer from two sites in Texas, USA. Deer were strictly fed a nutrient-rich, pelleted ration at one site and had access to a natural browse forage at the other site (Parra et al. 2014; Aiken et al. 2015). Notably, bulk (volume/dry mass) differences in browse forage and pelleted rations are apparent, with pelleted rations having greater food density and a lower volume:mass ratio than browse forage (Hubert et al. 1980; Van Soest 1994). We examined differences between sites in rumen–reticulum mass, diet quality, and digesta load (i.e., the wet mass of contents in the rumen–reticulum lumen). If site differences in rumen–reticulum mass was consistent with the bulk hypothesis, then animals consuming a browse diet would require heavier rumen–reticulum mass. The bulk hypothesis would be further supported if deer consuming browse forage had dietary quality similar to or less than deer with access to a strictly pelleted ration and a concomitant digesta load similar to or lighter than deer consuming a pelleted ration (Table 1).

Materials and methods

Study areas and diets

One study site was the Donnie E. Harmel deer pens at Kerr Wildlife Management Area (hereafter Kerr pens), Kerr County, in central Texas, USA. The mean annual precipitation was 69.7 cm. Daytime temperatures in summer could reach 35 °C with moderate winter temperatures averaging 16 °C (Parra et al. 2014). 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 and surrounded by a 2.7 m high fence 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 1 kg (dry mass) of alfalfa (Medicago sativa L.) and straw hay per animal each week (Parra et al. 2014). The pens included bare ground, some ground vegetation, and live oak (Quercus virginiana Mill.) that provided 25%–50% canopy cover (Lockwood et al. 2007). Prevalent ground species were common horehound (Sneezingum glutinosum DC.), tanglehead (Heteropogon contortus (L.) P. Beauv. ex Roem. & Schult.), woolly croton (Crotton capitantus Michx.), Hooker’s palaffoxia (Dalposia hookeriana Torr. & A. Gray), coastal sandbur (Cenchrus spinifex Cav.), little bluestem (Schizachyrium scoparium (Michx.) Nash), king ranch bluestem (Bothriochloa ischaemum (L.) Kent), and Johnson grass (Sorghum halepense (L.) Pers.). Also, from January through October, protein feed was supplied through gravity feeders that were placed throughout the site at a density of 1 per 107 ha (Aiken et al. 2014; Parra et al. 2014). Deer did not have access to alternative food sources because a 2.4 m high fence enclosed the entire property.

Deer at south Texas were considered to be in a high nutritional plane in November 2011 when animals were collected. Female deer at south Texas had back fat thicknesses similar to females from the Kerr pens and noticeably thicker than free-ranging females from Kerr Wildlife Management Area (Luna et al. 2012; Duarte et al. 2014; Parra et al. 2014; Aiken et al. 2015). Male deer at Kerr pens had thinner back fat thicknesses than male deer at south Texas, probably because males at Kerr pens were collected near the peak of the mating season (see below).

Table 1. Predictions of the bulk effect and nutrient availability hypotheses.

<table>
<thead>
<tr>
<th>Rumen–reticulum variable</th>
<th>Hypothesis</th>
<th>Bulk effect</th>
<th>Nutrient availability</th>
</tr>
</thead>
<tbody>
<tr>
<td>Organ masses</td>
<td>Heavier</td>
<td>Lighter</td>
<td></td>
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<tr>
<td>Diet quality</td>
<td>Similar or lower</td>
<td>Higher</td>
<td></td>
</tr>
<tr>
<td>Digesta load</td>
<td>Lighter or similar</td>
<td>Heavier or similar</td>
<td></td>
</tr>
</tbody>
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Note: Predictions are listed for browse versus pelleted diets of white-tailed deer (Odocoileus virginianus).

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Specimen and data collection

At Kerr pens, 24 female and 20 male white-tailed deer were collected in late November or early December 2011 and 2014. These deer were collected near the apparent peak of the mating season, which is thought to be in late November (Robinson et al. 1965; Dye et al. 2012). At south Texas, 32 female and 44 male white-tailed deer were collected in October 2011. October is 2 months prior to the peak of the mating season of white-tailed deer in this region (Webb et al. 2007).

Deer at Kerr pens were dispatched using two techniques. In 2011, deer were shot with a high-powered rifle; in 2014, deer were euthanized in a self-contained and portable CO2 chamber (Kinsey et al. 2016). A prior analysis indicated that rumen–reticulum mass, body mass, and rumen–reticulum fill did not differ between the 2 years (Blaskar 2015). At south Texas, free-ranging deer were net-gunned from a helicopter and restrained before being dispatched with a 22 caliber rifle at a central processing station. At both sites, the time of day that each animal was dispatched was also recorded. The collections followed the Institutional Animal Care and Use protocol from Texas State University (permits 00933_09-06-0314BFISD and 1018_1029_24).

Whole body mass minus any blood loss was recorded to the nearest kilogram. The deer were then field dressed and dressed mass (i.e., whole mass minus the mass of the internal organs and the mesentery) was recorded. We used dressed mass as our measure of body mass because it did not include masses of the rumen–reticulum organs. The rumen–reticulum organs were 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). Afterward, the rumen–reticulum organs were 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 organs were then wrung out to rid excess water and then weighed to the nearest 0.1 kg to measure rumen–reticulum mass (Luna et al. 2012). Digesta load was the difference between the mass of the rumen–reticulum organs with and without contents.

We used ruminal crude protein concentration to index diet quality because ruminal crude protein concentration has been shown to be consistent with patterns of dietary quality in other whitetailed deer populations (Simard et al. 2008) and western roe deer (Capreolus capreolus (Linnaeus, 1758)). Approximately 0.4 L of thoroughly mixed rumen contents were obtained from 10 female and 10 male deer at south Texas and 23 female and 17 male deer at Kerr pens. Each sample was dried for 48 h at 60 °C and then ground to particle sizes 1 mm or less. Nitrogen concentration expressed as a proportion was assayed from a nitrogen gas analyzer and then multiplied by 6.25 to obtain crude protein concentration.

All deer for this study were at least 2.5 years of age. Each deer at Kerr pens was uniquely ear-tagged at birth, enabling us to know its exact age. Also, reproduction by each female was monitored. Therefore, we knew whether females had young that survived to at least 90 days of age that year, which is the age juvenile deer are usually weaned (Short 1964). At south Texas, deer were aged by tooth replacement and wear, which is an accurate technique to separate deer less than 2.5 years of age (Severinghaus 1949). Female reproduction that year was determined by the presence of milk (lactation) in the teats. We assumed that lactating females at south Texas had one or more young that survived to at least 90 days of age. We only used reproductive females in analyses because nonreproductive females that were at least 2.5 years old were scarce at both sites.

### Statistical analyses

We fitted general linear regression models to assess effects on the three response variables; rumen–reticulum mass, ruminal crude protein concentration, and digesta load. For rumen–reticulum mass and digesta load, the potential fixed effects were body mass, site, and sex. Time of day that animals are dispatched was included as a covariate because a preliminary analysis with fixed effects of body mass, site, and sex did not consider time that the animal was dispatched. The empty rumen–reticulum organs were then wrung out to rid excess water and then weighed to the nearest 0.1 kg to measure rumen–reticulum mass. Digesta load was the potential fixed effects were body mass, site, and sex. Time of day that animals are dispatched can influence digesta load (Weckerly 2010; Aiken et al. 2014). In this study, however, we did not consider time that the animal was dispatched because a preliminary analysis with fixed effects of body mass, site, sex, and dispatch time indicated little influence of dispatch time ($P = 0.189$). For ruminal crude protein, the potential effects were site and sex. To accommodate heteroscedasticity and potential nonlinear relationships between body mass, rumen–reticulum mass, and digesta load, we analyzed the natural logarithms of these variables. We also report the adjusted $r^2$ and residual standard deviation for each model. All analyses were conducted in the program R (R Core Team 2016).

### Results

As expected, rumen–reticulum mass was positively related to body mass and the relationship differed between sites (Table 2). Rumen–reticulum mass, however, did not differ between females and males. The model provided a reasonable fit to the data because the $r^2$ value was 0.81 (Fig. 1). On average, rumen–reticulum mass was about 1.7 times heavier for female and male deer at mean body mass (47 kg) was 5.4 kg (SE = 0.44 kg) and 3.8 kg (SE = 0.2 kg), respectively.

### Discussion

We examined the relationship between rumen–reticulum metrics and white-tailed deer diet type and quality. Deer with access to a browse diet had a lower dietary quality, but a digesta load that was similar to that of deer that had access to a nutrient-rich, pelleted ration. Therefore, the heavier rumen–reticulum mass of deer with access to bulky browse does not appear to be from greater nutrient availability or heavier digesta loads. Collectively, our findings indicate the heavier rumen–reticulum mass is related to greater bulk in the rumen–reticulum, results that are consistent with the bulk hypothesis and not the nutrient availability hypothesis.

Hypothetically, there are at least two ways that rumen–reticulum mass can vary. One way is from changes in epithelial tissue (or size and density of papillae) and another way is from variation in the muscular tunic (Van Soest 1994; Álvarez-Rodríguez et al. 2012). Variation in epithelia tissue and absorptive capacity are evident in white-tailed deer (Zimmerman et al. 2006; Bonin et al. 2016). Variation in the thickness of the muscular tunic has not been examined in white-tailed deer, but it is apparent within and among other ruminant species (Knott et al. 2004; Álvarez-Rodríguez et al. 2012). Yet, to our knowledge, no one has examined the covariation between epithelia and muscular tunic variation and variation in rumen–reticulum mass.

Whether the difference in rumen–reticulum mass (1.7 times) between deer consuming natural browse diet and a pelleted ration is extraordinary and difficult to gauge because there is only one other study that we are aware of which measured rumen–reticulum mass of white-tailed deer consuming different diets. White-tailed deer on Anticosti Island, Quebec, Canada, that were collected in autumn had rumen–reticulum masses and digesta loads that were 1.46 and 2.61 times, respectively, greater than deer from a nearby mainland site (Bonin et al. 2016). The increased digesta load in deer from Anticosti Island was probably due to deer elevating food intake to compensate for lower forage nutrition when compared with the mainland population. Heavier rumen–reticulum mass in the Anticosti Island deer was probably required for rumin motility.

An apparent difference in findings between our study and the one on Anticosti Island was that we found females and males differed in digesta load, but a difference in rumen–reticulum mass was not supported, which was somewhat surprising. The difference in digesta loads between females and males in our study might not have been extensive ($5.4/3.8 = 1.52$) enough to result in substantial differences in rumen–reticulum mass. As such, the difference between sites in deer diets might have had the greatest effect on rumen–reticulum mass.

Our results rely on our ability to accurately measure or index diet quality. We did not include ruminal fiber, as indexed by neutral detergent fiber or acid detergent fiber, in our measure of dietary quality. This was because of the contrasting diets in our study.
study. When deer mostly consume browse, there is considerable chewing that is required to comminute particles. Generally, less digestible diets require more chewing and have slower passage through the gut. Ruminal fiber concentration in such cases can indicate dietary quality (Duarte et al. 2014). Pelleted, nutrient-rich diets require less chewing because food particles are small. Consequently, indigestible material passes more quickly through the gastrointestinal tract. Thus, variation in ruminal fiber concentration is more likely to reflect time since the last meal and recalcitrant particles remaining in the rumen–reticulum than diet quality (Aiken et al. 2015). On the other hand, diet quality can be assayed from crude protein concentration of contents in the rumen, but only when it captures digestibility of the diet (Lukas et al. 2005). At Kerr pens, ruminal crude protein appeared to reflect diet digestibility because the crude protein concentration exceeded pellet crude protein concentration by 10%. We suspect the additional crude protein in the rumen was related to metabolic nitrogen. Since the browse forages consumed by free-ranging deer at south Texas are noted for containing a variety of secondary compounds that reduce digestibility, it might seem that ruminal crude protein could be an unreliable index for those deer (Campbell and Hewitt 2005; Adams et al. 2013). Yet, if diet digestibility was greatly curtailed in deer from south Texas such that animals were on a low nutritional plane, then these deer should also have a relatively poor body condition. This was not the case because south Texas deer appeared to possess a body condition comparable with deer at Kerr pens (Aiken et al. 2015). Thus, we are confident the concentration of ruminal crude protein in the rumen was a reliable index of diet quality.

In the literature of both domestic and free-ranging ruminants, there are inconsistent findings about bulk and nutrient availability on gastrointestinal tract mass (Sibbald and Milne 1993; Ortigues and Doreau 1995; Arnold et al. 2015). In studies with domestic ruminants, diets are often nutrient-rich such that metabolizable energy intake is high in both forage and concentrate diets (Van Soest 1994; McLeod and Baldwin 2000). Usually the forage diets contain some amount of concentrate that is often in a pelleted form. In our study, the browse diet had negligible concentrate material and the pelleted diet had negligible amounts of forage to stimulate rumination and maintain rumen–reticulum function. Inconsistent findings in the literature might also reflect inconsistencies among studies. Some studies use growing animals and others use adult animals that reached asymptotic body mass. Growing animals have somatic and skeletal growth and a developmental trajectory for the gastrointestinal tract, which is something quite different from adult animals that have a developed gastrointestinal tract and are at asymptotic body size (Short 1964; McLeod and Baldwin 2000; Knott et al. 2004; Veiberg et al. 2009). Additional inconsistency might be from the available diet and heterogeneity among individual animals. In some studies, animals are provided the same diet, whereas in other studies, animals might have been transitioning between diets. In our study, reproductive state was heterogeneous in males. Males from one site were collected at the peak of the mating season, whereas males at the other site were selected 2 months before the mating season began. The heterogeneity from mating season would seem-
ingly affect digesta load in males (Mysterud et al. 2008; Weckerly and Foster 2010). Yet, we did not detect differences in digesta loads of males between the two sites. Either there was not as much heterogeneity from the mating season as supposed or, perhaps, dietary differences complicated effects from mating season on digesta loads.

White-tailed deer have the largest geographic range of any cervid species in the western hemisphere, extending from tropical ecosystems in the northern part of South America to boreal ecosystems at higher latitudes of North America (Hewitt 2011). They are able to inhabit a wide variety of environments due, in part, to plasticity in life-history strategies. Our study indicates that increased mass of rumen–reticulum organs is related to greater bulk in the gastrointestinal tract, not diet quality. Given the high energy demands of tissue from the gastrointestinal tract, it is credible that a heavier rumen–reticulum mass might impose increased metabolic demands on deer (McLeod and Baldwin 2000). Thus, variation in energetic demands due to variation in the masses of the gastrointestinal tract and other visceral organs might also contribute to the species’ wide geographic range.

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