NRC Research Press

ARTICLE

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.

Résumé : Les organes qui constituent le tube digestif ont d'importants besoins énergétiques. Des variations de la masse de ces organes devraient donc avoir une incidence sur les exigences métaboliques. La masse du réticulo-rumen, le couple d'organes qui constitue la plus grande partie du tube digestif des ruminants, pourrait varier en fonction de la disponibilité de fibres alimentaires ou de nutriments dans le régime alimentaire. Nous avons examiné les variations de la masse du réticulo-rumen chez des cerfs de Virginie (*Odocoileus virginianus* (Zimmermann, 1780)) en deux sites au Texas (États-Unis) caractérisés par différents types de régimes alimentaires. Plus précisément, en un des sites, les cerfs étaient nourris d'aliments en boulettes alors que dans l'autre, ils consommaient un régime de viandis naturel. En tenant compte de la masse corporelle, la masse des réticulo-rumens des cerfs qui consommaient un régime de viandis était environ 1,7 fois plus grande que celle des cerfs consommant des aliments en boulettes. L'alimentation des cerfs consommant le régime de viandis était également de moindre qualité, indiquée par la concentration de protéines brutes, que celle des cerfs mangeant des aliments en boulettes. Les charges de digesta des cerfs étaient toutefois semblables pour les deux types d'alimentation. Nos observations concordent avec une masse plus importante du réticulo-rumen pour des régimes à plus grandes teneurs en fibres alimentaires, et non de meilleure qualité. La compréhension des variations de la masse de ces organes est importante pour la compréhension de la conservation d'énergie chez les cerfs de Virginie. [Traduit par la Rédaction]

Mots-clés : fibres alimentaires, régime alimentaire, tube digestif, disponibilité des nutriments, *Odocoileus virginianus*, Texas, cerf de Virginie.

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

F.W. Weckerly, G. Bhaskar, A. Duarte,* R.S. Luna,† and H.D. Starns.‡ Department of Biology, Texas State University, San Marcos, TX 78666, USA.
Corresponding author: F.W. Weckerly (email: fw11@txstate.edu).
*Present address: Oregon Cooperative Fish and Wildlife Research Unit, Department of Fisheries and Wildlife, Oregon State University, Corvallis, OR 97331, USA.
†Present address: Department of Natural Resource Management, Sul Ross State University, Alpine, TX 79832, USA.
‡Present address: Department of Natural Resource Ecology and Management, Oklahoma State University, Stillwater, OK 74078, USA.

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 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 (*Marrubium vulgare* L.) and cowpen daisy (*Verbesina encelioides* (Cav.) Benth. & Hook. f. ex A. Gray). Notably, live oak (species of the genus *Quercus* L.) trees had been browsed out of reach of white-tailed deer since 1974, and ground vegetation was nonpalatable to deer (Wolcott et al. 2015). Consequently, vegetation in the pens was not a substantial part of the food available for deer consumption at this site.

The other study site was a 2994 ha private ranch located in Jim Hogg County, south Texas, USA (hereafter south Texas). The annual precipitation during this study was 60.5 cm (Aiken et al. 2014). The subtropical climate was hot in summer, with daytime temperatures reaching as high as 37 °C and moderate winters with a mean daytime temperature of 11 °C. The predominant forage available to white-tailed deer at south Texas was prickly pear

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

Rumen–reticulum variable	Hypothesis	
	Bulk effect	Nutrient availability
Organ masses	Heavier	Lighter
Diet quality	Similar or lower	Higher
Digesta load	Lighter or similar	Heavier or similar

Note: Predictions are listed for browse versus pelleted diets of white-tailed deer (*Odocoileus virginianus*).

(species of the genus *Opuntia* Mill.), honey mesquite (*Prosopis glandulosa* Torr.), cenizo (*Leucophyllum frutescens* (Berland.) I.M. Johnst.), retama (*Parkinsonia aculeata* L.), western ragweed (*Ambrosia psilostachya* DC.), tanglehead (*Heteropogon contortus* (L.) P. Beauv. ex Roem. & Schult.), woolly croton (*Croton capitatus* Michx.), Hooker's palafoxia (*Palafoxia hookeriana* Torr. & A. Gray), coastal sandbur (*Cenchrus spinifex* Cav.), little bluestem (*Schizachyrium scoparium* (Michx.) Nash), king ranch bluestem (*Bothriochloa ischaemum* (L.) Keng), 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).

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 CO_2 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 (Bhaskar 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_06-03141BF15D 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 white-tailed 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 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 ($e^{(-0.992+0.53)}/e^{-0.992}$) for deer that consumed the browse diet (south Texas).

Ruminal crude protein concentration also did not differ between females and males but did differ between sites (Table 3). The mean concentration of ruminal crude protein was 0.26 (95% confidence interval (CI): 0.25–0.27) for deer at Kerr pens and 0.21 (95% CI: 0.19–0.23) for deer at south Texas. Dietary quality was higher for deer that were fed the pelleted diet (Kerr pens).

Digesta load was positively related to body mass and female deer had heavier loads than male deer (Table 4). Nonetheless, we detected no site effect on digesta load. Deer from both Kerr pens and south Texas had similar digesta loads. Estimated digesta loads

Table 2. Parameter estimates, standard errors, and Student's *t* test statistics from a regression model testing the effects of body mass, site, and sex on mass of the rumen–reticulum organs in white-tailed deer (*Odocoileus virginianus*).

Coefficient	Estimate	Standard error	*t*	*P*
Intercept	−0.992	0.337	−2.94	0.004
Body mass	0.208	0.098	2.11	0.037
Site	0.530	0.030	17.88	<0.001
Sex	0.082	0.065	1.26	0.211

Note: Organ and body masses were natural log transformed so estimates are also in logarithmic scale. Females and Kerr pens were the reference categories. The adjusted r^2 of the model was 0.81 and the residual degrees of freedom and standard error were 116 and 0.1459, respectively.

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 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 rumen 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 oracid detergent fiber, in our measure of dietary quality. This was because of the contrasting diets in our

Fig. 1. Scatterplot with predicted values summarizing the relationship between body mass and rumen–reticulum mass of reproductive female and male white-tailed deer (*Odocoileus virginianus*). Circles and solid line represent deer from Kerr pens and diamonds and broken line represent deer from south Texas. Females are indicated by solid symbols and males are indicated by open symbols.
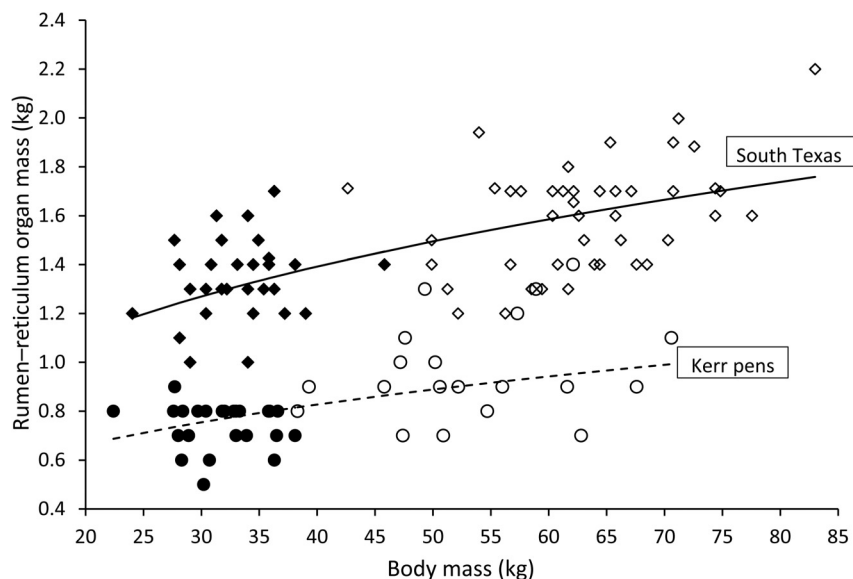
Table 3. Parameter estimates, standard errors, and Student's *t* test statistics from a regression model testing the effects of site and sex on concentration of ruminal crude protein of white-tailed deer (*Odocoileus virginianus*).

Coefficient	Estimate	Standard error	t	P
Intercept	0.254	0.007	36.88	<0.001
Site	−0.054	0.010	−5.54	<0.001
Sex	0.013	0.009	1.40	0.166

Note: Females and Kerr pens were the reference categories. The adjusted r^2 of the model was 0.34 and the residual degrees of freedom and standard error were 57 and 0.036, respectively.

Table 4. Parameter estimates, standard errors, and Student's *t* test statistics from a regression model testing the effects of body mass, site, and sex on mass of digesta loads in the rumen–reticulum organs of white-tailed deer (*Odocoileus virginianus*).

Coefficient	Estimate	Standard error	t	P
Intercept	−0.388	0.669	−0.58	0.563
Body mass	0.531	0.196	2.72	0.008
Site	0.024	0.059	0.41	0.680
Sex	−0.339	0.129	−2.63	0.010

Note: Organ and body masses were natural log transformed so estimates are also in logarithmic scale. Females and Kerr pens were the reference categories. The adjusted r^2 of the model was 0.05 and the residual degrees of freedom and standard error were 116 and 0.289, respectively.

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.

Acknowledgements

References

Adams, R.P., Muir, J.P., Taylor, C.A., and Whitney, T.R. 2013. Differences in chemical composition between browsed and non-browsed *Juniperus ashei* Buch. trees. Biochem. Syst. Ecol. **46**: 73–78. doi:10.1016/j.bse.2012.09.020.

Aiken, M.R.E., Duarte, A., Luna, R.S., Wolcott, D.M., and Weckerly, F.W. 2014. Daytime declines in rumen–reticulum fill of male white-tailed deer (*Odocoileus virginianus*) from south Texas. Can. J. Zool. **92**(7): 637–642. doi:10.1139/cjz-2013-0232.

Aiken, M.R.E., Wolcott, D.M., Duarte, A., Luna, R.S., Starns, H.D., and Weckerly, F.W. 2015. Use of rumen–reticulum fill to examine nutrient transfer and factors influencing food intake in white-tailed deer (*Odocoileus virginianus*). Can. J. Zool. **93**(6): 439–445. doi:10.1139/cjz-2014-0286.

Álvarez-Rodríguez, J., Monleón, E., Sanz, A., Badiola, J.J., and Joy, M. 2012. Rumen fermentation and histology in light lambs as affected by forage supply and lactation length. Res. Vet. Sci. **92**: 247–253. doi:10.1016/j.rvsc.2011.03.010. PMID:21458834.

Arnold, W., Belglbock, C., Burmester, M., Guschlbauer, M., Lengauer, A., Schroder, B., Wilkens, M., and Breves, G. 2015. Contrary seasonal changes of rates of nutrient uptake, organ mass, and voluntary food intake in red deer (*Cervus elaphus*). Am. J. Physiol. **309**: R277–R285. doi:10.1152/ajpregu.00084.2015. PMID:26017492.

Barboza, P.S., Peltier, T.C., and Forster, R.J. 2006. Ruminal fermentation and fill change with season in an arctic grazer: responses to hyperphagia and hypophagia in muskoxen (*Ovibos moschatus*). Physiol. Biochem. Zool. **79**: 497–513. doi:10.1086/501058. PMID:16691516.

Bhaskar, G. 2015. Rumen–reticulum–liver relationships in white-tailed deer (*Odocoileus virginianus*) differ between females and males. M.S. thesis, Texas State University, San Marcos.

Bonin, M., Tremblay, J.-P., and Cote, S.D. 2016. Contributions of digestive plasticity to the ability of white-tailed deer to cope with a low-quality diet. J. Mammal. **97**: 1406–1413. doi:10.1093/jmammal/gyw091.

Campbell, T.A., and Hewitt, D.G. 2005. Nutritional value of guajillo as a component of male white-tailed deer diets. Rangel. Ecol. Manage. **58**: 58–64. doi:10.2111/1551-5028(2005)58<58:NVOGAA>2.0.CO;2.

Duarte, A., Luna, R.S., Starns, H.D., and Weckerly, F.W. 2014. Intraspecific scaling of rumen–reticulum fill might depend on dietary fiber. Am. Midl. Nat. **172**: 329–337. doi:10.1674/0003-0031-172.2.329.

Dye, M.P., Demarais, S., Strickland, B.K., Jones, P.D., McDonald, C.O., and Prochaska, D.F. 2012. Factors affecting conception date variation in white-tailed deer. Wildl. Soc. Bull. **36**: 107–114. doi:10.1002/wsb.98.

Hewitt, D.G. 2011. Biology and management of white-tailed deer. CRC Press, Boca Raton, Fla.

Hubert, G.F., Jr., Woolf, A., and Post, G. 1980. Food habits of a supplementally-fed captive herd of white-tailed deer. J. Wildl. Manage. **44**: 740–746. doi:10.2307/3808032.

Kinsey, J.C., Foster, J.A., and Reitz, R.L. 2016. Development of a self-contained carbon dioxide euthanasia trailer for large-scale euthanasia of feral swine. Wildl. Soc. Bull. **40**: 316–320. doi:10.1002/wsb.664.

Knott, K.K., Barboza, P.S., Bowyer, R.T., and Blake, J.E. 2004. Nutritional development of feeding strategies in arctic ruminants: digestive morphometry of reindeer, *Rangifer tarandus*, and muskoxen, *Ovibos moschatus*. Zoology, **107**: 315–333. doi:10.1016/j.zool.2004.07.005. PMID:16351947.

Lockwood, M.A., Frels, D.B., Armstrong, W.E., Fuchs, E., and Harmel, D.E. 2007. Genetic and environmental interaction in white-tailed deer. J. Wildl. Manage. **71**: 2732–2735. doi:10.2193/2005-517.

Lukas, M., Sudekum, K.-H., Rave, G., Friedel, K., and Susenbeth, A. 2005. Relationship between fecal crude protein concentration and diet organic matter digestibility in cattle. J. Anim. Sci. **83**: 1332–1344. doi:10.2527/2005.8361332x. PMID:15890810.

Luna, R.S., Duarte, A., and Weckerly, F.W. 2012. Rumen–reticulum characteristics, scaling relationships, and ontogeny in white-tailed deer (*Odocoileus virginianus*). Can. J. Zool. **90**(11): 1351–1358. doi:10.1139/cjz-2012-0122.

McBride, B.W., and Kelly, J.M. 1990. Energy cost of absorption and metabolism in the ruminant gastrointestinal tract and liver: a review. J. Anim. Sci. **68**: 2997–3010. doi:10.2527/1990.6892997x. PMID:2170320.

McLeod, K.R., and Baldwin, R.L. 2000. Effects of diet forage:concentrate ratio and metabolizable energy intake on visceral organ growth and in vitro oxidative capacity of gut tissues in sheep. J. Anim. Sci. **78**: 760–770. doi:10.2527/2000.783760x. PMID:10764085.

Mysterud, A., Bonenfant, C., Loe, L.E., Langvatn, R., Yoccoz, N.G., and Stenseth, N.C. 2008. Age-specific feeding cessation in male red deer during rut. J. Zool. (Lond.), **275**: 407–412. doi:10.1111/j.1469-7998.2008.00453.x.

Ortigues, I., and Doreau, M. 1995. Responses of the splanchnic tissues of ruminants to changes in intake: absorption of digestion end products, tissue mass, metabolic activity and implications to whole animal energy metabolism. Ann. Zootech. **44**: 321–346. doi:10.1051/animres:19950401.

Parra, C.A., Duarte, A., Luna, R.S., Wolcott, D.M., and Weckerly, F.W. 2014. Body mass, age, and reproductive influences on liver mass of white-tailed deer (*Odocoileus virginianus*). Can. J. Zool. **92**(4): 273–278. doi:10.1139/cjz-2013-0201.

Ramzinski, D.M., and Weckerly, F.W. 2007. Scaling relationship between body weight and fermentation gut capacity in axis deer. J. Mammal. **88**: 415–420. doi:10.1644/06-MAMM-A-213R1.1.

R Core Team. 2016. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Available from https://www.r-project.org/.

Robinson, R.M., Thomas, J.W., and Marburger, R.J. 1965. The reproductive cycle of male white-tailed deer in central Texas. J. Wildl. Manage. **29**: 53–59. doi:10.2307/3798631.

Severinghaus, C.W. 1949. Tooth development and wear as criteria of age in white-tailed deer. J. Wildl. Manage. **13**: 195–216. doi:10.2307/3796089.

Short, H.L. 1964. Postnatal stomach development of white-tailed deer. J. Wildl. Manage. **28**: 445–458. doi:10.2307/3798196.

Sibbald, A.M., and Milne, J.A. 1993. Physical characteristics of the alimentary tract in relation to seasonal changes in voluntary food intake by the red deer (*Cervus elaphus*). J. Agric. Sci. **120**: 99–102. doi:10.1017/S0021859600073640.

Simard, M.A., Cote, S.D., Weladji, R.B., and Huot, J.L. 2008. Feedback effects of chronic browsing on life-history traits of a large herbivore. J. Anim. Ecol. **77**: 678–686. doi:10.1111/j.1365-2656.2008.01374.x. PMID:18312337.

Van Soest, P.J. 1994. Nutritional ecology of the ruminant. 2nd ed. Cornell University, Ithaca, N.Y.

Veiberg, V., Mysterud, A., Irvine, R.J., Sormo, W., and Langvatn, R. 2009. Increased mass of reticulo-rumen tissue and contents with advancing age in Svalbard reindeer. J. Zool. (Lond.), **278**: 15–23. doi:10.1111/j.1469-7998.2008.00538.x.

Webb, S.L., Hewitt, D.G., and Hellickson, M.W. 2007. Survival and cause-specific mortality of mature male white-tailed deer. J. Wildl. Manage. **71**: 555–558. doi:10.2193/2006-189.

Weckerly, F.W. 2010. Allometric scaling of rumen–reticulum capacity in white-tailed deer. J. Zool. (Lond.), **280**: 41–48. doi:10.1111/j.1469-7998.2009.00642.x.

Weckerly, F.W., and Foster, J.A. 2010. Blind count surveys of white-tailed deer and population estimates using Bowden's estimators. J. Wildl. Manage. **74**: 1367–1377. doi:10.2193/2009-432.

Weckerly, F.W., and Kennedy, M.L. 1992. Examining hypotheses about feeding strategies of white-tailed deer. Can. J. Zool. **70**(3): 432–439. doi:10.1139/z92-066.

Weckerly, F.W., Bleich, V.C., Chetkiewicz, C.-L.B., and Ricca, M.A. 2003. Body weight and rumen–reticulum capacity in tule elk and mule deer. J. Mammal. **84**: 659–664. doi:10.1644/1545-1542(2003)084%3C0659:BWARRC%3E2.0.CO;2.

Wolcott, D.M., Reitz, R.L., and Weckerly, F.W. 2015. Biological and environmental influences on parturition date and birth mass of a seasonal breeder. PloS ONE, **10**: e0124431. doi:10.1371/journal.pone.0124431. PMID:25885545.

Zimmerman, T.J., Jenks, J.A., and Leslie, D.M. 2006. Gastrointestinal morphology of female white-tailed and mule deer: effects of fire, reproduction, and feeding type. J. Mammal. **87**: 598–605. doi:10.1644/05-mamm-A-356R1.1.