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Rumen–reticulum characteristics, scaling relationships, and ontogeny in white-tailed deer (*Odocoileus virginianus*)

R.S. Luna, A. Duarte, and F.W. Weckerly

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Abstract: Scaling relationships between body mass and gut capacity are valuable to predicting digestive efficiency. Interspecific scaling relationships between body mass and gut capacity have consistently estimated a slope of 1.0; however, intraspecific scaling relationships between body mass and gut capacity have been highly variable. We examined the influence of demands of growth and production on scaling relationships of body mass and rumen–reticulum characteristics in white-tailed deer (*Odocoileus virginianus* (Zimmermann, 1780)) because little is known about how juvenile and subadult ruminants accommodate increased digesta masses. We sampled 108 animals over a 2-year period and assessed the influence of body mass, time of kill, crude protein (%), and acid detergent fiber (%) in the rumen, lactation, sex, and back fat on rumen–reticulum organ mass, rumen–reticulum capacity, wet mass of the digesta, and the dry mass of the digesta. Juvenile and subadult white-tailed deer had rumen–reticulum organ masses, capacity, and digesta masses that were similar to adults because body mass and rumen–reticulum scaling relationships all had scalars similar to 1.0. Thus, under the confines of our study, ontogeny plays only a minor role in the physiological characteristics of the rumen–reticulum and the scaling relationships of body mass and rumen–reticulum capacity.

Key words: body mass, digesta mass, *Odocoileus virginianus*, ontogenetic, rumen–reticulum, scaling.

Résumé : Les relations d'échelle entre la masse corporelle et la capacité du tube digestif sont utiles pour prédire l'efficacité de la digestion. Si les relations interspécifiques d'échelle entre la masse corporelle et la capacité du tube digestif donnent uniformément une pente estimée de 1,0, les relations intraspécifiques d'échelle entre la masse corporelle et la capacité du tube digestif sont très variables. Nous examinons l'influence des demandes de la croissance et de la production sur les relations d'échelle entre la masse corporelle et des caractéristiques du réticulo-rumen chez le cerf de Virginie (*Odocoileus virginianus* (Zimmermann, 1780)), puisque les connaissances sur l'adaptation des ruminants juvéniles et subadultes à l'augmentation des masses de digesta sont très limitées. Nous avons échantillonné 108 animaux sur une période de 2 ans et évalué l'influence de la masse corporelle, du moment de la mort, du contenu en protéines brutes (%) et en fibres au détergent acide (%) dans le rumen, de la lactation, du sexe et du gras dorsal sur la masse du réticulo-rumen, la capacité de ce dernier, la masse fraîche du digesta et la masse sèche du digesta. Les cerfs juvéniles et subadultes présentaient des masses et capacités du réticulo-rumen et des masses du digesta semblables à celles d'adultes étant donné que les relations d'échelle entre la masse corporelle et les caractéristiques du réticulo-rumen étaient toutes caractérisées par des scalaires de l'ordre de 1,0. Ainsi, dans les limites de l'étude, l'ontogénie ne joue qu'un rôle mineur dans la détermination des caractéristiques physiologiques du réticulo-rumen et des relations d'échelle entre la masse corporelle et la capacité du réticulo-rumen.

Mots-clés : masse corporelle, masse du digesta, *Odocoileus virginianus*, ontogénétique, réticulo-rumen, échelle.

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Introduction

Scaling relationships between body mass and gut capacity have been used to help explain digestive efficiency among and within species. Studies by Jarman (1974) and Bell (1971) indicated that larger species of ruminants digest a poorer quality diet more completely than smaller species. Geist (1974) coined this phenomenon the Bell–Jarman principle. The Bell–Jarman principle is based upon two scaling relationships: for every 1% change in body mass, there is a 0.67%–0.75% change (i.e., body mass$^{0.67-0.75}$) in metabolic rate and food intake, whereas gut capacity changes 1% for every 1% change

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in body mass (body mass$^{1.0}$). The isometric scaling of gut capacity should allow for greater digesta mass and increased mean retention time (MRT) as body mass increases because MRT should be the difference between gut capacity and food intake scalars (0.18 – 0.25). Prolonged exposure of digesta to microbial activity within the fermentation chambers should allow the animal to obtain nutrients from forages that are more recalcitrant to digestion. The Bell–Jarman principle has been useful in explaining differences in dietary patterns among species (Yoshihara et al. 2008; Sensenig et al. 2010); however, there is growing evidence that the Bell–Jarman principle is not suitable to explain some phenomena. There have been a number of studies that have indicated that digesta retention time does not scale to BM$^{0.18-0.25}$ (Clauss et al. 2007, 2009; Müller et al. 2011; Steuer et al. 2011). Additionally, some studies have shown forage intake to scale higher than BW$^{0.75}$ (Minson 1990; Reid et al. 1990; Hackmann and Spain 2010). It is unclear whether the problem is due to the Bell–Jarman principle not considering additional factors that influence forage retention and digestion or because of variability in scaling relationships.

The majority of research conducted on scaling relationships and the Bell–Jarman principle has been used in explaining dietary patterns across species. Yet, the Bell–Jarman principle has been applied within species (Gross et al. 1996; Barboza and Bowyer 2000). Weckerly (2010) reported that gut capacity of white-tailed deer (*Odocoileus virginianus* (Zimmermann, 1780)) scaled allometrically (scalar = 0.67 – 0.75), not isometrically, with body mass. Moreover, the Bell–Jarman principle is difficult to apply within ruminant species given the enormous variability in rumen–reticulum capacity (Tulloh 1966; Weckerly 2010). Much of the variability in rumen–reticulum capacity has been linked with life history demands such as mating, gestation, or lactation. In particular, increases in digestive-tract fill have been well documented during lactation (Smith and Baldwin 1974; Jenks et al. 1994; Vetharaniam et al. 2009).

Weckerly (2010) was the first to estimate an allometric, intraspecific scaling relationship between body mass and the two most commonly used measures of rumen–reticulum capacity (wet mass of digesta and volume). Nonetheless, this study had some limitations. First, influences of nutrition and body condition were not accounted for, and these variables can influence wet mass of contents (Demment 1983; Barboza et al. 2009). Second, no explanations were given to account for why the scaling relationship was allometric instead of isometric.

Ruminants probably adjust the fill and capacity of their rumen–reticulum in response to changes in forage quality, except with the lowest quality diets. When forage quality is <50% digestible dry matter, white-tailed deer may be limited in gut capacity and unable to adjust food intake to meet metabolic demands (Gray and Servello 1995). When forage quality is moderate or better, that is digestible dry matter is >50%, rumen turnover is probably less limited by rumen capacity and animals have greater flexibility in food intake to meet metabolic demands (Gray and Servello 1995).Without the capability to alter the capacity and fill of the digestive tract to accommodate fluctuations in food intake with diets that have moderate or better forage quality, body condition would be affected. Moreover, a reduction in the absorption of nutrients would occur when forage intake increases (Tyrrell and Moe 1975; Demment 1983; Demment and Van Soest 1985; Barboza et al. 2006; Lechner et al. 2010).

Being able to accommodate changes in digesta masses as a result of variability in the amount of forage consumed is paramount for juveniles because they have high mass-specific food intakes to meet the demands of growth (Welch 1982; Hooper and Welch 1983). Yet, little is known about how juvenile ruminants accommodate increased digesta masses. Juveniles might have greater capacity or accommodate greater fill of the rumen–reticulum.

The greatest change in rumen–reticulum capacity occurs during weaning. Short (1964) indicated that during the second month of age, the mass of the rumen organ with its contents increased 400%. The dramatic increase in rumen–reticulum capacity is needed to provide the space for fermentation and absorption of fermentation byproducts in the transition from consuming milk to plant forage (Short 1964). Consequently, there might be further anatomical development of the rumen–reticulum after weaning (Short 1964; Knott et al. 2004). An outcome of incomplete rumen–reticulum development might be less rumen–reticulum organ tissue in juveniles compared with adults. Because adding more gut tissue is metabolically expensive (Kelly et al. 1991; McLeod and Baldwin 2000), having less rumen–reticulum organ tissue might allow juveniles greater rumen–reticulum elasticity without having to accommodate an increase in metabolic demands.

We conducted a study on white-tailed deer to estimate scaling relationships of body mass and rumen–reticulum characteristics, and how these scaling relationships influence rumen–reticulum elasticity and fill. We set out to determine if there is a mechanism to explain allometric scaling relationships between body mass and rumen–reticulum capacity. Determining why rumen–reticulum capacity scales allometrically with body mass would aid in understanding how ruminants accommodate space for ingesta to meet demands of growth and production when gut tissue is metabolically expensive. We hypothesize that requirements of growth and a small body mass (and thus a proportionally high metabolic rate) require small-bodied individuals (juveniles and subadults) to have a rumen–reticulum that, relative to their body mass, (*i*) weighs less, (*ii*) is capable of a greater elasticity, and (*iii*) contains more digesta than that of larger bodied individuals (adult deer). As such, there should be allometric scaling relationships between body mass and rumen–reticulum variables. Organ mass should have a scalar >1.0 and measures of elasticity and digesta mass should have scalars <1.0. By having a rumen–reticulum capable of increased elasticity, juvenile and subadults would be able to increase capacity without requiring additional metabolically expensive gut tissue, thereby resulting in proportionally greater fill. The proportionally greater fill associated with increased mass-specific food intake would enable juvenile and subadults the means to accommodate higher forage intake, thereby aiding the individual in meeting their high mass-specific metabolic demands.

Materials and methods

Study area

Our study occurred on Kerr Wildlife Management Area (WMA) (30°3′36″N, 99°25′45″W) in Kerr County, Texas, USA, from 2009 to 2011. The WMA encompasses 2628 ha and is surrounded by a 2.6 m high game fence. Warren and

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Krysl (1983) reported that the primary deer forage on Kerr WMA in autumn and early winter was various oaks (genus *Quercus* L.), Ashe juniper (*Juniperus ashei* J. Buchholz), bladderpods (genus *Lesquerella* S. Watson = *Physaria* (Nutt. ex Torr. & A. Gray) A. Gray), spurges (genus *Euphorbia* L.), redseed plantain (*Plantago rhodosperma* Decne.), filaree (genus *Erodium* L'Hér. ex Aiton), silverleaf nightshade (*Solanum elaeagnifolium* Cav.), globemallows (genus *Sphaeralcea* A. St.-Hil.), whorled nodding violet (*Hybanthus verticillatus* (Ortega) Baill.), common horehound (*Marrubium vulgare* L.), and Texas wintergrass (*Nassella leucotricha* (Trin. & Rupr.) R.W. Pohl).

Sample collection

White-tailed deer were obtained during September and November 2009–2010. All deer were collected with high-powered rifles by licensed public hunters or Texas Parks and Wildlife personnel. Collection procedures followed an Institutional Animal Care and Use protocol from Texas State University (permit # 00933_09_06-03141BF15D). After harvest, the time of kill was recorded and the deer were transported to a check station where they were processed within 3 h of death. Time of kill was included because wet masses of digesta have been shown to fluctuate throughout the day, which is likely indicative of synchronized patterns of feeding, resting, and ruminating (Conradt 1998; Weckerly et al. 2003).

Whole masses minus blood loss were taken to the nearest 0.1 kg and depth of back fat was measured to the nearest 1.0 mm by making an incision just above the lower lumbar vertebrae (L4–L5) and measuring the thickness of fat between the muscle layer and the hide (Veiberg et al. 2009). Ages were estimated with tooth replacement and wear (Severinghaus 1949). Females were assessed for lactation by the presence or absence of milk within their udder. The animal was eviscerated and the mesentery removed to expose the rumen–reticulum. The rumen–reticulum was separated from the rest of the entrails by ligating the esophagus approximately 5 cm above its junction with the reticulum and making a second incision at the reticulo-omasal sphincter (Weckerly et al. 2003; Ramzinski and Weckerly 2007). 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; the rumen–reticulum was inverted and rinsed thoroughly to ensure that all particulate matter had been removed. After rinsing, the rumen–reticulum was reverted and the organ mass was recorded. Wet mass of the digesta in the rumen–reticulum was the difference between mass of the rumen–reticulum organ with contents and rumen–reticulum organ without contents.

A subsample consisting of 800 g of fill was collected and dried at 60 °C for 48 h. After the drying period, the subsample was reweighed and the dry mass of the digesta subsample was extrapolated to estimate the total dry mass of rumen–reticulum digesta. Next, nitrogen (%) and acid detergent fiber (ADF; %) were determined with an N gas analyzer using an induction furnace and thermal conductivity using a Leco FP-528 (AOAC 1997). The crude protein (CP; %) was determined as nitrogen (%) times 6.25. Acid detergent fiber consists of lignin, cutin, and cellulose that are within the plant cell. Typically, cellulose is recalcitrant to digestion, which requires longer fermentation times because digesta needs increased rumen microbial exposure (Hummel et al. 2006). Other components of ADF, specifically lignin and cutin, are completely indigestible (Van Soest 1994). Because of its composition, ADF was used as an index for measuring forage quality within a sample. All digesta analyses were conducted by A&L Plains Agricultural Laboratory, Lubbock, Texas, USA.

Elasticity was measured by volume of water held in the rumen–reticulum. 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 measurement was taken in triplicate.

Data analysis

We constructed a series of models to estimate changes in rumen–reticulum characteristics associated with body mass. The response variables were wet mass of the digesta, dry mass of digesta, rumen–reticulum organ mass, and rumen–reticulum volume (hereafter referred to as rumen–reticulum capacity). Each response variable was logarithmically transformed for purposes of estimating the scalar. Hereafter, each reference to a response variable will refer to the natural logarithm of that response variable. Covariates were body mass, time of kill, CP (%) in digesta, ADF (%) in digesta, whether the animal was lactating, sex, and depth of back fat. The above listed covariates would account for changes in forage quality, as well as body condition changes; therefore, the month of kill was not included as a covariate. Because digesta masses have been shown to fluctuate with crepuscular foraging periods (Teer et al. 1965; Tulloh and Hughes 1965; Beier and McCullough 1990), time of kill was included as a covariate. Natural logarithmic transformation of body mass was done to meet the assumption of homoscedasticity and to remain consistent with previous studies that estimated scaling relationships of gut capacity (Demment and Van Soest 1985; Weckerly et al. 2003; Ramzinski and Weckerly 2007; Weckerly 2010). Depth of back fat was also transformed using the natural logarithm of back fat plus one because of nonlinear relationships and because depth of back fat on some animals are 0.

Sixteen models were built to assess the influence of body mass, kill time, nutrition (CP and ADF), sex, lactation, and back fat, as well as combinations of these covariates on each response variable. We used Akaike's information criterion corrected for small sample size ($\mathrm{AIC_c}$) to select models (Burnham and Anderson 2002). After calculating the $\mathrm{AIC_c}$, we computed the $\Delta\mathrm{AIC_c}$ ($\mathrm{AIC_c} - \mathrm{minAIC_c}$, where min refers to the model with the smallest $\mathrm{AIC_c}$) for each of the 16 models for every response variable. The ΔAIC was then used to calculate the relative likelihood ($\mathrm{RI} = e^{-0.5 \cdot \Delta\mathrm{AIC_c}}$). From the relative likelihoods, we identified competing models by calculating the likelihood ratio ($\mathrm{RI}_i/\mathrm{RI}_{\mathrm{min}}$). Competing models had likelihood ratios ≥ 0.125 (Burnham and Anderson 2002). We used the "model.avg" function within the MrMIn package in R to estimate coefficients and standard errors averaged among competing models (Bartón 2009), after which we calculated 95% confidence intervals (CI). A coefficient was statistically significant if the 95% CI excluded 0. Also, if the 95% CIs for the body mass coefficient included 1.0, it suggested an isometric scaling relationship.

Because of the numerous adults in the data set (see Results), we assessed whether there was an influence from age on the

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Table 1. Summary of the characteristics of sampled white-tailed deer (*Odocoileus virginianus*) from Kerr Wildlife Management Area, Kerr County, Texas, USA.

				CP (%)			ADF (%)			Back fat (cm)		
Sex	Age	*n*	BM	Mean	SE	Range	Mean	SE	Range	Mean	SE	Range
Female	Juvenile	4	17.6	18.2	0.75	16.6–20.1	38.1	2.56	31.3–43.6	0.1	0.04	0–0.2
	Subadult	10	34.5	19.2	1.18	14.0–26.1	41.2	2.74	28.9–56.8	0.3	0.07	0–0.8
	Adult	59	40.3	18.7	0.41	10.7–24.3	43.6	1.09	22.3–60.7	0.3	0.04	0–2.1
Male	Juvenile	1	23.5	20.8	na	na	50.5	na	na	0.0	na	na
	Subadult	19	36.1	17.3	0.89	9.4–23.5	41.5	1.67	30.3–56.6	0.3	0.04	0–0.7
	Adult	15	56.4	16.5	0.82	9.5–22.0	43.3	2.05	31.3–56.2	0.4	0.10	0–1.3
Combined		108	40.3	17.8	0.32	9.4–26.1	42.7	0.77	22.3–60.7	0.3	0.03	0–2.1

Note: na, not applicable; *n*, sample size; BM, mean body mass; CP, crude protein; ADF, acid detergent fiber. Data shows mean, standard error (SE), and range of crude protein (%) and acid detergent fiber (%) (measured from rumen contents), as well as depth of back fat, with respect to sex and across an array of age classes.

scaling relationships. A dichotomous categorical covariate coded for age (juveniles–subadults, adults) was added to the model with the smallest AIC$_c$ for every response variable to determine if scaling relationships differed between juveniles–subadults and adults.

Results

During the 2-year study, 108 white-tailed deer were collected, of which 73 were females (4 juvenile, 10 subadults, and 59 adults) and 35 were males (1 juvenile, 19 subadults, and 15 adults). Body masses ranged from 14 to 24 kg for fawns, from 29 to 45 kg for subadults, and from 31 to 76 kg for adults. Animals collected during the sampling period had ADF values that ranged from 22.3% to 60.7%, CP ranged from 9.4% to 26.1%, and depth of back fat from 0 to 2.1 cm (Table 1).

Rumen–reticulum organ mass and rumen–reticulum capacity each had seven competing models, whereas wet mass of digesta and dry mass of digesta had, respectively, four and three competing models (Table 2). For rumen–reticulum organ mass, the influential covariates were body mass, CP, sex, and lactation (Table 3). Rumen–reticulum organ masses of males were lighter than either lactating or nonlactating females. For a given body mass, male rumen–reticulum organ masses were about 73% of rumen–reticulum masses of lactating females, and about 83% of the rumen–reticulum mass of nonlactating females. Rumen–reticulum capacity was influenced by the covariates of body mass and lactation. Wet mass of the digesta was influenced by body mass, sex, lactation, and back fat. Influential covariates of dry mass of digesta were body mass, ADF, lactation, and back fat. For every response variable, body mass and lactation were the only two covariates that were influential.

There was no age effect (juveniles–subadults, adults) on any rumen–reticulum response variable. For each response variable, we added an age covariate to the model with the smallest AIC$_c$. The age covariate had 95% CI that included zero for rumen–reticulum organ mass (–0.21 to 0.34), rumen–reticulum capacity (–0.35 to 0.20), dry mass of digesta (–0.30 to 0.12), and wet mass of digesta (–0.21 to 0.15).

Discussion

We hypothesized that as a result of their small body mass, juvenile and subadults would have rumen–reticulums that, relative to their body mass, weighed less, had greater elasticity, and contained more digesta than their larger bodied counterparts. Therefore, we expected to find allometric scaling relationships between body mass and each of our response variables; however, each response variable had an isometric scalar for our study. Our hypothesis was not supported by our findings. The development of the rumen–reticulum of juvenile and subadults in this study appears similar to adults.

Body mass, energetic demands from growth and reproduction, and diet quality varied across age classes and likewise each response variable was influenced by a different set of covariates. We expected that the ontogenetic development of the rumen–reticulum extended beyond the time of weaning and influenced the scaling of rumen–reticulum capacity. Yet, the isometric scalar for organ mass suggests that the rumen–reticulum is developed by the time the bulk of the diet of juvenile animals is solid food. To accommodate the primarily browse diet, juvenile white-tailed deer need papillae for absorption, musculature for rumen motility, and a vascular rumen wall for nutrient transport (Knott et al. 2004). In spite of the metabolic demands of gut tissues, juvenile and subadult animals do not appear to have a rumen–reticulum organ that is lighter, relative to body mass, than adults.

It is hard to tell what rumen–reticulum capacity, which is obtained by water displacement, is measuring. It is possible that there are varying degrees of postmortem influence in the tension of the rumen–reticulum tissue, which might affect the capacity measurements. We thought that lighter organ masses would be positively associated with greater capacity, a finding reported by Sibbald and Milne (1993). Yet, lactating females in our study had the greatest rumen–reticulum capacity when these organs were the heaviest. Heavier organ masses in lactating females presumably accommodate heavier digesta masses (Jenks et al. 1994; Gross et al. 1996; Ramzinski and Weckerly 2007; Jiang et al. 2009). Weckerly (2010), however, found that rumen–reticulum capacities were not associated with digesta masses. It appears that the only consistent finding about rumen–reticulum capacity is that the values are most often, but not always, greater than wet mass of digesta measurements (Tulloh and Hughes 1965; Sibbald and Milne 1993; Weckerly et al. 2003; Ramzinski and Weckerly 2007; Weckerly 2010).

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Table 2. Models analyzed using Akaike's information criterion corrected for small sample size (AIC_c) and models selected for model averaging analysis (values in boldface type) for the response variables of rumen–reticulum (RR) organ mass, RR capacity, wet mass of digesta, and dry mass of digesta of white-tailed deer (*Odocoileus virginianus*) sampled in a 2628 ha enclosure at Kerr Wildlife Management Area, Kerr County, Texas, USA.

		ln(RR organ mass)			ln(RR capacity)			ln(wet mass of RR digesta)			ln(dry mass of RR digesta)		
Model predictors	nPar	Δ	r^2	Likelihood ratio	Δ	r^2	Likelihood ratio	Δ	r^2	Likelihood ratio	Δ	r^2	Likelihood ratio
BW, KT	4	47.81	0.49	≤0.01	13.63	0.14	≤0.01	32.29	0.44	≤0.01	28.61	0.29	≤0.01
BW, KT, NUT	6	44.85	0.51	≤0.01	11.37	0.18	≤0.01	29.80	0.46	≤0.01	26.15	0.32	≤0.01
BW, KT, SEX & LACT	6	**1.29**	**0.67**	**0.52**	**0.59**	**0.26**	**0.75**	7.23	0.56	0.03	11.35	0.40	≤0.01
BW, KT, BF	5	49.51	0.49	≤0.01	15.45	0.14	≤0.01	21.21	0.50	≤0.01	19.31	0.35	≤0.01
BW, KT, NUT, SEX & LACT	8	**2.05**	**0.68**	**0.36**	**0.00**	**0.28**	**1.00**	7.91	0.57	0.02	6.32	0.44	0.04
BW, KT, NUT, BF	7	46.55	0.51	≤0.01	12.99	0.17	≤0.01	17.92	0.52	≤0.01	17.99	0.37	≤0.01
BW, KT, SEX & LACT, BF	7	**3.58**	**0.67**	**0.17**	**2.83**	**0.25**	**0.24**	**0.13**	**0.60**	**0.94**	6.74	0.44	0.03
BW, KT, NUT, SEX & LACT, BF	9	4.43	0.68	0.11	**2.38**	**0.27**	**0.30**	**0.16**	**0.60**	**0.92**	**2.38**	**0.47**	**0.30**
BW	3	50.47	0.48	≤0.01	12.90	0.15	≤0.01	38.13	0.40	≤0.01	26.66	0.30	≤0.01
BW, NUT	5	44.12	0.51	≤0.01	12.23	0.16	≤0.01	31.07	0.45	≤0.01	24.17	0.32	≤0.01
BW, SEX & LACT	5	**0.42**	**0.67**	**0.81**	**1.75**	**0.24**	**0.42**	10.88	0.54	≤0.01	9.11	0.41	0.01
BW, BF	4	51.99	0.47	≤0.01	14.76	0.13	≤0.01	27.01	0.46	≤0.01	17.21	0.36	≤0.01
BW, NUT, SEX & LACT	7	**0.00**	**0.68**	**1.00**	**2.01**	**0.25**	**0.37**	8.62	0.56	0.01	**4.07**	**0.45**	**0.13**
BW, NUT, BF	6	45.70	0.51	≤0.01	13.95	0.16	≤0.01	19.00	0.51	≤0.01	15.85	0.38	≤0.01
BW, SEX & LACT, BF	6	**2.66**	**0.67**	**0.26**	**3.84**	**0.23**	**0.15**	**2.73**	**0.58**	**0.26**	4.50	0.44	0.11
BW, NUT, SEX & LACT, BF	8	**2.33**	**0.68**	**0.31**	4.27	0.25	0.12	**0.00**	**0.60**	**1.00**	**0.00**	**0.48**	**1.00**

Note: BW, natural logarithm of body mass; KT, kill time; Nut, nutrition (crude protein and acid detergent fiber); LACT, lactation; BF, ln(back fat + 1); nPar, number of parameters.

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Table 3. Model averaged parameter estimates, standard errors (SE), and confidence intervals of rumen–reticulum (RR) organ mass, RR capacity, wet mass of digesta, and dry mass of digesta of white-tailed deer (*Odocoileus virginianus*) sampled in a 2628 ha enclosure at Kerr Wildlife Management Area, Kerr County, Texas.

	ln(RR organ mass)				ln(RR capacity)				ln(wet mass of RR digesta)				ln(dry mass of RR digesta)			
Coefficient	SE	lb*	Coef. est.	ub*	SE	lb*	Coef. est.	ub*	SE	lb*	Coef. est.	ub*	SE	lb*	Coef. est.	ub*
Intercept	0.286	–4.345	–3.778	–3.211	0.631	–2.323	–1.072	0.180	0.428	–4.215	–3.365	–2.515	0.485	–4.670	–3.708	–2.745
ln(body mass)	**0.074**	**0.792**	**0.938**	**1.085**	**0.170**	**0.419**	**0.755**	**1.092**	**0.116**	**0.940**	**1.169**	**1.399**	**0.133**	**0.801**	**1.065**	**1.330**
Kill time	0.004	–0.005	0.004	0.012	0.009	–0.037	–0.018	0.001	0.006	–0.002	0.011	0.024	0.007	–0.014	0.000	0.015
CP	**0.540**	**0.071**	**1.142**	**2.213**	1.277	–1.284	1.250	3.784	1.391	–0.876	1.885	4.645	0.926	–2.855	–1.017	0.820
ADF	0.221	–0.519	–0.081	0.357	0.496	–0.191	0.794	1.778	0.321	–0.814	–0.178	0.458	**0.381**	**–1.680**	**–0.925**	**–0.170**
Sex	**0.050**	**–0.287**	**–0.189**	**–0.091**	0.114	–0.315	–0.089	0.137	**0.075**	**–0.299**	**–0.150**	**–0.002**	0.087	–0.293	–0.120	0.052
Lactation	**0.045**	**0.035**	**0.124**	**0.214**	**0.101**	**0.053**	**0.254**	**0.455**	**0.070**	**0.005**	**0.143**	**0.282**	**0.083**	**0.030**	**0.195**	**0.360**
ln(back fat + 1)	0.088	–0.177	–0.002	0.174	0.199	–0.360	0.035	0.430	**0.127**	**–0.655**	**–0.402**	**–0.149**	**0.150**	**–0.669**	**–0.372**	**–0.074**

Note: Coef. est., coefficient estimate; CP, crude protein; ADF, acid detergent fiber. Estimates in boldface type represent the statistically significant covariates for each response variable.

*Coefficient estimates are given with lower (lb) and upper (ub) bounds of 95% confidence intervals. Covariates are statistically significant if confidence intervals exclude 0.

In studies where rumen–reticulum fill and capacity are measured from animal dissection, wet mass of digesta is the most commonly used measure (Demment and Van Soest 1985; Freudenberger 1992; Forchhammer and Boomsma 1995; Veiberg et al. 2007). We also measured dry mass to assess rumen–reticulum fill and capacity without the influence of ruminal fluid. Dry mass of rumen–reticulum contents is influenced by three processes; forage intake, rate of digestion, and passage rate. Our findings suggested that animals with greater dry mass of rumen–reticulum contents also had less back fat. It is likely that this relationship is due to food intake, diet selection, forage processing, or all three processes being influenced by metabolic demands and body condition. Most likely, animals undergoing the demands of growth (little back fat) or that were in poorer condition had greater food intake because Verme and Ozoga's (1980) showed animals had increased food intake after they were first presented a nutritionally restricted diet. Our study is the first, to our knowledge, to consider and show the relationship between gut fill and back fat.

Because we sampled animals over two autumns, we measured CP and ADF in the rumen–reticulum to capture temporal variation in dietary nutrition. The nutritional quality of the food is known to influence rumen fill, which then has ramifications on scaling relationships. Juvenile and subadult animals, relative to adults, should have had the flexibility to increase rumen fill in response to demands from growth, which indicates that we should have had the potential to estimate allometric scalars (<1.0) for wet and dry masses of digesta; however, both of these predictors had isometric scalars. It is likely that the influences on rumen–reticulum digesta mass are more complex than we thought when we began the study. Rumen–reticulum fill is probably influenced by type of forage, dietary nutrition, life-history demands and body condition, forage processing via chewing, and microbial activity (Jenks et al. 1994; Van Soest 1994; Barboza and Hume 2006; Jiang et al. 2009; Veiberg et al. 2009; Weckerly 2010; Duarte et al. 2011).

Crude protein concentration measured in the rumen is affected by nitrogen content of the diet and digestive functions in the rumen–reticulum. Consequently, it is difficult to say that the positive relationship between CP and wet mass of rumen–reticulum contents is due solely to forage availability and selection. Digestive functions that could influence rumen CP concentrations are urea recycling and microorganism abundance related to fermentation (Barboza and Bowyer 2000). Microorganism abundance in the rumen is of a magnitude where microbial N might comprise a substantive part of rumen CP (Van Soest 1994; Barboza and Hume 2006). Because CP did not have a strong influence on dry mass of rumen–reticulum contents, these two measures probably do not capture the same forage selection and digestive processes. The differing influence CP had on dry and wet masses might be the result of the CP associated with wet mass of digesta being inflated owing to contributions of N from microorganisms in the rumen liquor. Therefore, when considering the effect of forage quality on the scaling relationships, it is advisable to use dry mass of rumen–reticulum contents to negate the influence of rumen liquor, and to measure dietary nutrition (CP and ADF) to account for spatial and temporal variation in the diet.

The findings of this study, unfortunately, do not resolve whether the intraspecific scaling relationship between body mass and rumen–reticulum capacity is allometric or isometric

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and, thus, whether the Bell–Jarman principle is a viable hypothesis to explain dietary variation across body sizes of conspecific animals. For white-tailed deer, this study and Weckerly's (2010) study had large sample sizes and attempted to account for the covariates influencing the scaling relationship between body mass and the rumen–reticulum. Yet, each study reached a different conclusion. The Weckerly (2010) study might have been limited by not including important covariates (analyses included response variables of rumen–reticulum volume and mass, and predictors of body mass, digesta wet mass, sex, and year). Our study included a greater number of covariates, some of which indicated that there is strong evidence that rumen–reticulum relationships with body mass are isometric. There are numerous factors that can influence rumen–reticulum fill; body mass, type of diet, nutrition, digestive processes, life history, and body condition. The extent to which and how these factors directly and indirectly influence rumen–reticulum fill has yet to be explored. There should be consequences to scaling relationships if these factors have direct and indirect effects on rumen–reticulum fill. For example, body mass, ADF, and back fat have direct influences on rumen–reticulum fill since each of these covariates influenced rumen–reticulum dry mass of digesta in this study. Body mass might also have indirect influences on rumen–reticulum fill through ADF in the diet and amount of back fat, patterns that cannot be detected in a regression analysis estimating scaling relationships. In which case, the intraspecific scalar estimated from a data set is not only influenced by the set of life history, diet, body condition, and other environmental covariates considered in an analysis but also the study-specific values of each of the covariates.

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