Articles

Influence of Body Size on Dietary Nutrition of White-Tailed Deer *Odocoileus virginianus*

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Abstract

Intraspecific competition is one of the major factors that can have an effect on the resources utilized within a habitat. Differences in diet quality of selected forage have been noted in size-dimorphic ungulates. However, on an intraspecific basis, data demonstrating a body size influence on diet quality are lacking. We examined diet quality across a range of body masses (14–76 kg) in white-tailed deer *Odocoileus virginianus* (*n* = 108) in a 2,628-ha enclosure at Kerr Wildlife Management Area, Kerr County, Texas, USA. The quality of the diet consumed was determined by crude protein, acid detergent fiber, and neutral detergent fiber content of digesta in the rumen–reticulum. Results indicated that in relation to body mass, the ratio of crude protein to acid detergent fiber was greater for smaller bodied white-tailed deer. By consuming a diet higher in crude protein than did large bodied individuals, small-bodied individuals should meet their high mass-specific metabolic demands more efficiently. Furthermore, selective foraging by different-sized individuals might also reduce intraspecific competition. Information presented herein is relevant to wildlife managers in that by increasing available high-quality forage, small-bodied individuals will more efficiently meet their metabolic demands, which could have ramifications on recruitment within that population.

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Introduction

Differentiation among feeding strategies due to morphology should occur when feeding efficiency varies between or among morphs (Schluter 1995). A herbivore's body mass is one morphological feature that is a driving force of forage niche partitioning (Main et al. 1996; Perez-Barberia and Gordon 1998b; Barboza and Bowyer 2000, 2001) and can also influence feeding strategies (Illius and Gordon 1992). Different-sized species of ruminants are able to coexist and utilize the same patches of habitat by selecting forage that differs in quality and abundance (Bell 1970, 1971; Jarman 1974; McNaughton 1976; Illius and Gordon 1987, 1992). Use of the same forage patch is likely feasible because of dissimilar energy requirements associated with differing body masses. Energy requirements of animals are determined by metabolic size, which scales to the 0.67–0.75 power of body mass

(Kleiber 1961). Consequently, small homeothermic animals will have high metabolic costs per unit of body mass (Welch 1982; Hooper and Welch 1983). Differences in metabolic demands are associated with feeding selectivity and time spent foraging (Prins and Geelen 1971; Janis 1976; Demment 1983; Demment and Van Soest 1985; Van Soest 1994). The frequency of feeding and energy intake increases with mass-specific metabolic demands (Barboza et al. 2009). Individuals with small body mass will have greater mass-specific metabolic demands compared with their larger bodied counterparts. As a result of greater mass-specific metabolic demands, small-bodied individuals will have greater mass-specific energy demands, which results in an increase in feeding frequency (Barboza et al. 2009). As such, small-bodied individuals should feed more frequently and select forages with greater nutrient concentrations to meet these demands.

Body size should also influence an animal's digestive efficiency (Van Soest 1994; Barboza and Bowyer 2000). Gut capacity increases as animal energy requirements increase (Barboza et al. 2009) such that larger bodied individuals will have greater gut capacity than small-bodied individuals because large-bodied individuals have greater absolute metabolic demands than their smaller bodied counterparts. In addition to metabolic rates, forage selection also might be conditional on the gut capacity of the individual. Scaling relationships of body mass to gut capacity and metabolic rate, coined the Bell–Jarman principle (Geist 1974), have provided a theoretical basis for predicting that diet quality should vary inversely with body mass. The Bell–Jarman principle states that larger bodied individuals are able to feed on diets of poorer quality (i.e., high cellulose content) as a result of their lower metabolism requirement/gut capacity ratio (Demment and Van Soest 1985). As a result of an increase in gut capacity associated with an increase in body mass, large-bodied individuals have a digestive advantage in that they can retain digesta longer, thereby increasing the time that forage is exposed to microorganisms in the digestive tract (Barboza and Bowyer 2000). Thus, larger bodied individuals are able to tolerate a diet consisting of lower quality forage. The Bell–Jarman principle is supported on an interspecific level (Bell 1970, 1971; Geist 1974; Jarman 1974), but the principle is not fully supported to explain dietary variation on an intraspecific level. In size-dimorphic species, males are typically larger. In the size-dimorphic Nubian ibex *Capra nubiana*, there was little difference in digestive efficiency between sexes (Gross et al. 1996). However, in another study using the sexually dimorphic Soay sheep *Ovis aries*, males were shown to be slightly more efficient at digesting forage than were females that were 30% smaller (Perez-Barberia et al. 2008). Consequently, more research is needed to determine the applicability of the Bell–Jarman principle to the intraspecific level. Moreover, isometric scaling of gut capacity with body mass, which is an assumption of the Bell–Jarman principle, may not occur within all species (Weckerly 2010; Duarte et al. 2011). Gut-capacity scaling relationships can be used in conjunction with metabolic scaling relationships to explain differences in digestive efficiency across species. However, attempts to correlate digestive efficiency with body mass using the Bell–Jarman principle have been unsuccessful on an intraspecific level (Weckerly and Nelson 1990; Perez-Barberia et al. 2007).

One factor that can affect conspecific digestive efficiency is variation in mastication efficiency. Mastication efficiency is the rate of particle breakdown, and is the main mechanism to decrease particulate size of forages. Digestive processes in the abomasum and small intestine, as well as bacterial fermentation in the rumen, ceacum, and proximal large intestine, have little effect on particle size (Poppi et al. 1980; Uden and Van Soest 1982; McLeod and Minson 1988; Lechner-Doll and Von Engelhardt 1989; Freudenberger 1992). Mastication efficiency has two possible components, chewing effort (chews/g of intake) and tooth morphology. Tooth morphology affects the degree to which forage particulate matter is degraded

through chewing (Veiberg et al. 2009). The teeth of a larger bodied individual would contain greater distances between the enamel ridges compared with a smaller bodied individual. If large and small-bodied individuals have the same chewing effort, mastication efficiency should be greater in small-bodied browsing ungulates because of shorter distances between enamel ridges. Consequently, mastication by a large-bodied individual can result in a slower rate of particulate breakdown compared with a smaller individual (Fritz et al. 2009). Because rate of particle breakdown affects digestion rate, mastication efficiency should influence rates of forage intake and rumen turnover (Perez-Barberia and Gordon 1998a; Logan 2003). A change in rate of rumen turnover should affect the fill and nutrient composition in the rumen (Short 1975; Van Soest 1994).

In addition to greater mastication efficiency, smaller bodied individuals also might meet their metabolic demands by greater forage selectivity. Forage selectivity is food intake in relation to forage time (Hodgson 1982); therefore, forage selectivity should increase with an increase in forage time. Smaller bodied individuals might display more selectivity to obtain a more digestible diet than would large-bodied animals (Van Soest 1994).

A high-quality diet can be defined operationally by the ratio of crude protein (CP) to acid detergent fiber (ADF) in digesta (Van Soest et al. 1991). Crude protein is a nutrient required for growth, maintenance, and reproduction; whereas ADF measures plant material that is either completely indigestible to the animal (e.g., lignin and cutin; Van Soest 1994) or is recalcitrant to digestion (e.g., cellulose; Hummel et al. 2006). Through mastication efficiency, food selection, or both, body weight should covary with the CP : ADF of rumen digesta.

On an intraspecific level, smaller bodied individuals cannot afford to ingest low-quality forage because of processing constraints (i.e., they are less efficient at extracting the nutrients from low-quality forage compared with larger bodied individuals). Animals may compensate for changes in dietary nutrients by adjusting food intake and, concomitantly, gut fill (Holand 1994; Gross et al. 1996). In order to meet metabolic demands, small-bodied individuals are likely to be more selective for high-quality forage to maximize energy intake per bite. Therefore, we expect to see an inverse relationship between diet quality (as indexed by CP : ADF) and body size.

We conducted a study on white-tailed deer *Odocoileus virginianus* to examine whether body mass was inversely related to diet quality. We hypothesize that small-bodied individuals are likely to have greater CP content of rumen digesta as a means to meet their higher mass-specific metabolic demands. Although metabolic demands are usually associated with energy, protein is needed for growth, maintenance, and reproduction (Barboza et al. 2009). Therefore, as a result of forage selectivity, body mass should covary inversely with the CP : ADF ratio of rumen digesta. Identifying body mass–diet quality relationships should provide information useful to furthering the understanding of resource selection and niche partitioning by sexually dimorphic ungulates.

Forage niche partitioning could reduce the effects of intraspecific competition, which could potentially have ramifications on recruitment and carrying capacity of the habitat. Additionally, by understanding how forage is utilized across body sizes, wildlife managers could augment available forage according to the composition of the local population in order to increase recruitment or enhance body condition of older age-class individuals.

Study Site

We conducted research in Kerr County, Texas, USA, on the Kerr Wildlife Management Area. The Kerr Wildlife Management Area encompasses an area of 2,628 ha and is enclosed with a 2.6-m-high game fence. The primary forage for white-tailed deer during autumn and early winter on Kerr Wildlife Management Area was various oaks *Quercus* spp., Ashe juniper *Juniperus ashei*, bladder-pods *Physaria* spp., common horehound *Marrubium vulgare*, filaree *Erodium* spp., globemallows *Sphaeralcea* spp., redseed plantain *Plantago rhodosperma*, silverleaf nightshade *Solanum elaeagnifolium*, spurges *Euphorbia* spp., whorled nodviolet *Hybanthus verticillatus*, and wintergrass *Nassella leucotricha* (Warren and Krysl 1983).

Methods

We sampled deer in September, November, and the first week of December in 2009 and 2010. The samples were obtained from harvested white-tailed deer during culling efforts (September) and from four management hunts and one trophy hunt (November and December). A cull or a management deer was any female, or any male that had one unbranched antler. Trophy hunts allowed for take of males with greater than 16-in. (40.6-cm) antler spread and ≥8 tines. All white-tailed deer were collected by licensed public hunters (November and December) or Texas Parks and Wildlife personnel (September) utilizing high-powered rifles. Collection procedures followed an Institutional Animal Care and Use protocol from Texas State University (permit No. 00933_09_06-03141BF15D). After each animal was harvested, it was transported to a check station where it was processed within 3 h post mortem. We gave each animal a unique identification number upon its arrival at the check station, and recorded time of kill. We obtained sex and whole weight minus blood loss (measured to the nearest 0.10 kg) of each animal. We recorded back-fat thickness from each carcass by making an incision along the spine above the L4–L5 lumbar vertebrae (Komers et al. 1994; Veiberg et al. 2009). We measured the thickness of the back fat between the muscle layer and the hide to the nearest 1.0 mm. We assessed females for lactation by examining their udder for presence of milk. We then eviscerated the animals and removed the mesentery to expose the rumen–reticulum. We separated the rumen–reticulum from the remainder of the entrails by ligations made at the esophagus just above the reticulum and at the recticulo–omasal sphincter (Weckerly et al. 2003; Ramzinski and Weckerly 2007). The rumen and reticulum are the gastrointestinal organs with the largest capacity and those where most fermentation occurs (Van Soest 1994).

We weighed the rumen–reticulum and then emptied it of digesta by inverting the organ. We then reweighed the rumen–reticulum organ (void of any digesta) and recorded the difference as the wet weight of the digesta. In a semiarid environment, primary productivity often differs due to fluctuations in precipitation from one season to the next, as well as across years (Teer et al. 1965; Beatley 1969; Noy-Meir 1973; Robertson 1987; Polis et al. 1997; Marshal et al. 2002, 2005), so we obtained nutritional composition (CP, ADF, and neutral detergent fiber [NDF]) of the digesta. Neutral detergent fiber represents total plant-fiber or cell-wall content, including hemicelluloses, cellulose, and lignin (Van Soest 1994).

We collected a sample consisting of 800 g of wet digesta and dried it at 60°C for 48 h. After the drying period, we reweighed the sample, and extrapolated the dry weight of the digesta to estimate the total dry weight of rumen–reticulum digesta. After we reweighed the sample, we ground it to a uniform size of approximately 1 mm. We used a Leco FP-528 apparatus to determine the percent nitrogen from a 1-g sample of the dried particulate (AOAC 1997). We calculated the percent CP by multiplying percent nitrogen by 6.25 (protein is approximately 16% nitrogen, 1/0.16 = 6.25).

We placed a second 1-g sample of the dried and ground digesta into a filter bag and put it in a hexadecyltrimethyl-sulphuric acid solution. We then removed the sample and rinsed it three times with boiling water. After rinsing with boiling water, the sample was rinsed a final time with acetone and allowed to air dry. After the sample was dry, we weighed it. We determined nitrogen and ADF from the dried sample by use of an N gas analyzer using an induction furnace, and we determined thermal conductivity using a Leco FP-528 (AOAC 1997). The weight obtained in relation to the initial weight represented the percent of ADF in the sample. We determined NDF according to methods of Van Soest et al. (1991). Assays of all digesta samples were conducted by A&L Plains Agricultural Laboratory, Lubbock, Texas, USA. We used results of the analyses to calculate the grams of ADF, NDF, and CP within each rumen. The weights obtained were then used to assess differences between individuals across a spectrum of body masses.

Data analysis

We constructed a series of 28 a priori models to assess the relationship between body mass and dietary nutrition using response variables of CP, ADF, and NDF. Crude protein, ADF, and NDF were log-transformed to meet the assumption of homoscedasticity. Covariates were body mass, age, sex, whether the animal was lactating or not, year, back-fat thickness, and time of kill. Interaction terms between age and body mass, as well as between sex and body mass, were also included in the analysis. A categorical covariate coded for age (juvenile, subadult, adult). We included year as a covariate to account for the possibility of variation in available forage during the 2-y study. We transformed the values of back fat using natural logarithm to accommodate nonlinear relationships. Because some individuals had a back fat

Table 1. Summary of the characteristics of white-tailed deer *Odocoileus virginianus* sampled during September, November, and December 2009 and 2010 in a 2,628-ha enclosure at Kerr Wildlife Management Area, Kerr County, Texas, USA. Data show mean, standard error (SE), and range of crude protein (CP), acid detergent fiber (ADF), and neutral detergent fiber (NDF) in grams (measured from rumen contents) with respect to sex and across an array of age classes. N/A = not applicable, BM = average body mass. Nutritional components (CP, ADF, NDF) are in grams per rumen.

Sex	Age	*n*	BM	CP			ADF			NDF		
				Mean	SE	Range	Mean	SE	Range	Mean	SE	Range
Female	Juvenile	4	17.6	0.05	0.01	0.04–0.08	0.10	0.03	0.07–0.18	0.15	0.02	0.12–0.22
	Subadult	10	34.5	0.12	0.02	0.05–0.15	0.25	0.03	0.15–0.36	0.33	0.04	0.17–0.47
	Adult	59	40.3	0.14	0.01	0.05–0.25	0.33	0.01	0.17–0.55	0.44	0.02	0.21–0.73
Male	Juvenile	1	23.5	0.10	N/A	N/A	0.25	N/A	N/A	0.30	N/A	N/A
	Subadult	19	36.1	0.10	0.01	0.05–0.19	0.23	0.02	0.13–0.35	0.31	0.02	0.21–0.43
	Adult	15	56.4	0.14	0.02	0.04–0.37	0.37	0.07	0.12–1.21	0.50	0.08	0.17–1.43
Combined		108	40.3	0.11	0.01	0.05–0.21	0.26	0.03	0.13–0.53	0.34	0.03	0.18–0.66

value of zero, we added one to each value and then performed a natural-log-transformation. We measured time of kill in military time, with minutes expressed as a portion of the hour to eliminate issues with time being a circular variable.

We used Akaike information criterion corrected for small sample size (AIC_c) to select models (Burnham and Anderson 2002). After calculating the AIC_c, we computed the ΔAIC_c ($AIC_c - minAIC_c$; "min" refers to the model with the smallest AIC_c) for each of the 28 models for every response variable. The ΔAIC_c was then used to calculate the relative likelihood ($RL = e^{(-0.5 \times \Delta AIC_c)}$). From the relative likelihoods, we identified competing models by calculating the likelihood ratio (RL_i/RL_{min}). Competing models had $\Delta AIC_c \leq 2$ and likelihood ratios ≥ 0.125 (Burnham and Anderson 2002). We used the "model.avg" function within the MrMln package in R to estimate coefficients and standard errors averaged across all models, after which we calculated 95% confidence intervals (CI). A coefficient was statistically significant if the 95% CI excluded 0.

We used predicted values from regressions to estimate CP : ADF for a particular body mass using the back-transformed predicted values. The predicted values and standard errors of response variables were estimated across the spectrum of body mass (15–80 kg) using the predict.lm code (R Development Core Team 2009). The mean values of covariates (besides body mass) in a reduced model were used in the multiple regression of a given response variable, with the exception of lactation. We gave lactation a value of 0 (no lactation) because juvenile, subadult, and male deer in this population were not lactating. These ratios were used to estimate whether smaller white-tailed deer had a diet higher in CP content. To assess uncertainty of ratios, we estimated standard errors for the back-transformed ratios. A coefficient was statistically significant if the 95% CI excluded 0. Because of the dual nature of ratios, the relationships between body mass, CP, and ADF were also assessed and plotted on a 3 dimensional plane (see Figure S1, *Supplemental Material*). We conducted all statistical analysis in Program R (R Development Core Team 2009).

Results

Over the course of the 2-y study, 108 white-tailed deer were collected, of which 73 were females and 35 were males (Table 1; Table S1, *Supplemental Material*). The response variables were influenced by different covariates (Table 2).

From the 28 models assessed, there were 5 competing models for CP, 2 competing models for ADF, and 3 competing models for NDF (Table 2). The model with the greatest model weight for CP was bm+age+bf+yr+age × bm (model weight = 0.24; see Table 2). The top model for ADF was bm+age+bf+yr (model weight = 0.33); and the top model for NDF was bm+sex+lact+bf+yr+sex × bm (model weight = 0.35; see Table 2). After conducting model averaging across all models, the covariates that had a statistically significant influence on CP were body mass, lactation, back fat, year, and the interaction between body weight and age (Table 3). Covariates that had a statistically significant influence on ADF were body mass, lactation, back fat, year, and the interaction between body weight and sex (Table 3). Covariates that had a statistically significant influence on NDF were body mass, lactation, back fat, and year (Table 3). Back fat had inverse relationships with NDF, ADF, and CP.

The relative importance of variables after model averaging of CP models were as follows: body mass = 1.00, Year = 1.00, ln(back fat + 1) = 0.79, lactation = 0.53, sex = 0.53, age = 0.47, age × body mass = 0.25, sex × body mass = 0.20, and time of kill = 0.04. With respect to ADF models, relative variable importance was as follows: body mass = 1.00, year = 1.00, ln(back fat + 1) = 0.72, age = 0.53, lactation = 0.47, sex = 0.47, sex × body mass = 0.31, time of kill = 0.13, and age × body mass = 0.10. Models of NDF had relative variable importance as follows: body mass = 1.00, year = 0.95, lactation = 0.82, sex = 0.82, ln(back fat + 1) = 0.74, sex × body mass = 0.46, age = 0.18, time of kill = 0.09, age × body mass = 0.03.

Lactation had a positive relationship with CP, NDF, and ADF, as did year. With regard to the interaction terms, the interaction between body mass and sex had an inverse relationship with ADF, and the interaction

Table 2. Models analyzed using AIC$_c$ and competing models (bold) for the response variables of crude protein (CP), acid detergent fiber (ADF), and neutral detergent fiber (NDF) from digesta of white-tailed deer *Odocoileus virginianus* sampled during September, November, and December 2009 and 2010 in a 2,628-ha enclosure at Kerr Wildlife Management Area, Kerr County, Texas, USA.

Model predictors[a]	nPar[b]	CP				ADF				NDF			
		AIC$_c$	ΔAIC$_c$	Model weight	r^2	AIC$_c$	ΔAIC$_c$	Model weight	r^2	AIC$_c$	ΔAIC$_c$	Model weight	r^2
bm	3	123.570	67.110	0.000	0.083	109.200	49.730	0.000	0.188	86.590	36.900	0.000	0.202
bm+yr	4	76.520	20.050	0.000	0.408	76.910	17.450	0.000	0.398	73.220	23.530	0.000	0.295
bm+bf	4	120.220	63.750	0.000	0.112	105.990	46.530	0.000	0.212	81.420	31.730	0.000	0.240
bm+kt	4	119.800	63.340	0.000	0.115	110.480	51.020	0.000	0.179	88.610	38.910	0.000	0.188
bm+yr+kt	5	78.700	22.230	0.000	0.402	76.600	17.130	0.000	0.406	73.620	23.920	0.000	0.300
bm+yr+bf	5	72.110	15.650	0.000	0.437	73.320	13.850	0.000	0.424	68.080	18.390	0.000	0.335
bm+sex+lact	5	96.220	39.760	0.000	0.297	87.300	27.840	0.000	0.344	58.730	9.040	0.000	0.390
bm+sex+lact+yr	6	**58.180**	**1.720**	**0.100**	**0.511**	63.780	4.310	0.040	0.479	52.630	2.940	0.080	0.480
bm+sex+lact+kt	6	94.370	37.910	0.000	0.316	89.450	29.990	0.000	0.339	60.880	11.190	0.000	0.385
bm+sex+lact+bf	6	95.450	38.990	0.000	0.309	86.590	27.120	0.000	0.356	56.980	7.280	0.010	0.407
bm+sex+lact+sex × bm	6	96.350	39.890	0.000	0.304	84.730	25.270	0.000	0.367	58.010	8.320	0.010	0.401
bm+sex+lact+yr+kt	7	60.450	3.990	0.030	0.510	63.020	3.550	0.060	0.488	52.650	2.960	0.080	0.437
bm+sex+lact+yr+sex × bm	7	59.500	3.040	0.050	0.511	62.540	3.070	0.070	0.490	52.760	3.070	0.080	0.436
bm+sex+lact+kt+sex × bm	7	95.100	38.640	0.000	0.319	87.020	27.550	0.000	0.361	60.030	10.340	0.000	0.397
bm+sex+lact+bf+sex × bm	7	94.430	37.970	0.000	0.324	82.190	22.730	0.000	0.389	54.620	4.930	0.030	0.426
bm+sex+lact+bf+yr	7	**56.940**	**0.470**	**0.190**	**0.522**	62.920	3.460	0.060	0.489	**50.970**	**1.270**	**0.180**	**0.445**
bm+sex+lact+bf+yr+sex × bm	8	**57.390**	**0.930**	**0.150**	**0.526**	**60.070**	**0.600**	**0.240**	**0.508**	**49.690**	**0.000**	**0.350**	**0.458**
bm+age	5	103.890	47.430	0.000	0.245	90.430	30.960	0.000	0.325	66.070	16.370	0.000	0.348
bm+age+yr	6	62.390	5.930	0.010	0.491	64.030	4.560	0.030	0.477	58.120	8.420	0.010	0.401
bm+age+kt	6	102.270	45.800	0.000	0.264	92.580	33.110	0.000	0.319	68.180	18.490	0.000	0.342
bm+age+bf	6	99.800	43.330	0.000	0.281	86.530	27.060	0.000	0.356	59.710	10.020	0.000	0.392
bm+age+age × bm	7	106.650	50.190	0.000	0.243	92.920	33.450	0.000	0.325	69.100	19.410	0.000	0.344
bm+age+yr+kt	7	64.530	8.070	0.000	0.487	62.480	3.020	0.070	0.491	57.380	7.680	0.010	0.412
bm+age+yr+age × bm	8	63.040	6.580	0.010	0.500	66.620	7.150	0.010	0.477	61.100	11.400	0.000	0.398
bm+age+kt+age × bm	8	104.630	48.170	0.000	0.265	95.100	35.630	0.000	0.319	71.360	21.660	0.000	0.338
bm+age+bf+age × bm	8	102.340	45.880	0.000	0.281	89.280	29.810	0.000	0.355	62.740	13.040	0.000	0.389
bm+age+bf+yr	7	**56.760**	**0.300**	**0.210**	**0.523**	**59.460**	**0.000**	**0.330**	**0.505**	51.690	1.990	0.130	0.442
bm+age+bf+yr+age × bm	9	**56.460**	**0.000**	**0.240**	**0.535**	62.050	2.580	0.090	0.505	54.450	4.760	0.030	0.441

[a] Note: bm, body mass; kt, time of kill; lact, lactation; bf, ln(back fat + 1); yr, year.
[b] nPar, number of parameters.

between body mass and the subadult category of age had a positive relationship with CP. None of the interactions were significant with regard to NDF.

To account for rumen–reticulum fill influences on CP and ADF, we reported the relationship between body mass and CP : ADF. This ratio used the back-transformed predicted values and indicated that body mass was inversely related to the ratio of CP : ADF (Figure 1).

Discussion

Body mass covaried negatively with CP : ADF. In support of our hypothesis, small-bodied individuals exhibited greater CP : ADF than their larger bodied counterparts. These findings indicate that smaller bodied individuals had higher CP content in their rumen–reticulum digesta, which presumably can be attributed to consuming a higher quality diet. According to our low

r^2 values for our regressions, the covariates selected did not encompass all influencing factors. Therefore, specifics about diet selection cannot be assessed within this study.

Crude protein in the rumen–reticulum can originate from one of four sources: forage, microorganisms, urea, and endogenous secretions. Herbivores that consume forage low in nitrogen can undergo urea recycling as a means of obtaining nitrogen (Barboza et al. 2009). Urea in the blood is capable of passing back into the gastrointestinal tract, where it can be broken down by microorganisms and used as a nitrogen source (Stewart and Smith 2005). Endogenous secretions such as saliva contain urea and proteins, which can also be used as a source for nitrogen (Van Soest 1994). Urea and amides are converted to ammonia in the rumen–reticulum because ammonia is the form of nitrogen utilized by rumen organisms. Ammonia within the rumen–reticulum

Table 3. Model-averaged parameter estimates, standard errors (SE), and confidence intervals for crude protein (CP), acid detergent fiber (ADF), and neutral detergent fiber (NDF) taken from digesta of white-tailed deer *Odocoileus virginianus* sampled during September, November, and December 2009 and 2010 in a 2,628-ha enclosure at Kerr Wildlife Management Area, Kerr County, Texas, USA. "Coef. est" represents the coefficient estimate. Estimates in bold were statistically significant.

	CP				ADF				NDF			
Coefficients[a]	SE	Lb[b]	Coef. est.	ub[b]	SE	lb[b]	Coef. est.	ub[b]	SE	lb[b]	Coef. est.	ub[b]
Intercept	0.412	−4.087	−3.270	−2.453	0.476	−3.464	−2.520	−1.576	0.378	−2.920	−2.170	−1.420
bm	**0.004**	**0.015**	**0.023**	**0.031**	**0.005**	**0.006**	**0.016**	**0.026**	**0.011**	**0.009**	**0.032**	**0.054**
sex	0.237	−0.387	0.083	0.554	0.348	−0.356	0.334	1.024	0.299	−0.383	0.210	0.803
lact	**0.084**	**0.104**	**0.270**	**0.436**	**0.085**	**0.060**	**0.229**	**0.398**	**0.082**	**0.112**	**0.274**	**0.436**
bf	**0.160**	**−0.679**	**−0.362**	**−0.045**	**0.156**	**−0.665**	**−0.355**	**−0.045**	**0.155**	**−0.652**	**−0.344**	**−0.036**
yr	**0.064**	**0.307**	**0.434**	**0.561**	**0.068**	**0.209**	**0.344**	**0.479**	**0.064**	**0.048**	**0.174**	**0.300**
age F	0.008	−0.017	−0.001	0.014	0.008	−0.029	−0.014	0.001	0.008	−0.026	−0.011	0.004
age SA	0.598	−2.054	−0.868	0.318	0.503	−1.836	−0.838	0.160	0.432	−1.650	−0.793	0.064
kt	0.660	−2.074	−0.765	0.544	0.302	−0.881	−0.282	0.317	0.322	−0.966	−0.327	0.312
wt : age F	0.054	−0.087	0.019	0.126	0.055	−0.050	0.059	0.168	0.053	−0.066	0.039	0.144
wt : age SA	**0.019**	**0.002**	**0.040**	**0.078**	0.020	−0.021	0.018	0.056	0.019	−0.016	0.021	0.058
wt : sex	0.009	−0.029	−0.011	0.007	**0.009**	**−0.037**	**−0.019**	**−0.001**	0.009	−0.033	−0.015	0.002

[a] Note: bm, body mass; lact, lactation; bf, ln(back fat+1); yr, year; age F, fawns; age SA, subadults (reference category adult); kt, time of kill; wt : age F, interaction between body mass and age (fawn); wt : age SA, interaction between body mass and age (subadult); and wt : sex, interaction between body mass and sex.
[b] Coefficient estimates are given with lower (lb) and upper bounds (ub) of 95% confidence intervals. Covariates are statistically significant if confidence intervals exclude 0.

can either be absorbed across the rumen wall or utilized within the rumen–reticulum (Van Soest 1994). When consuming high-quality forage (high nitrogen content), recycling urea nitrogen back to nonessential amino acids is low.

By utilizing digesta samples for our CP measurements, the contribution of microbial protein, urea, and endogenous secretions were not differentiated from dietary proteins. To better quantify differences in protein intake,
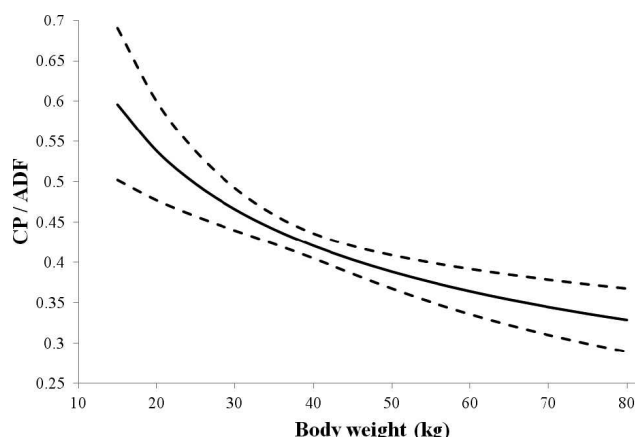
Figure 1. Ratio of CP : ADF across a spectrum of body masses with 95% confidence intervals. Ratios were derived from back-transformed predicted values of crude protein (CP [g]) divided by back-transformed predicted values of acid detergent fiber (ADF [g]) of white-tailed deer *Odocoileus virginianus* sampled during September, November, and December 2009 and 2010 in a 2,628-ha enclosure at Kerr Wildlife Management Area, Kerr County, Texas, USA. This ratio in relation to body mass indicated that smaller white-tailed deer possessed a greater amount of CP in relation to ADF in the rumen–reticulum.

microbial protein within the rumen–reticulum should be distinguished from dietary protein, as well as the amount of dietary protein fermented in the rumen–reticulum (Van Soest 1994). It has been noted that bacteria numbers within the rumen–reticulum fluid are correlated with forage quality (Van Soest 1994; Cantalapiedra-Hijar et al. 2009) and follow seasonal patterns (Barboza et al. 2006). Also, urea concentrations in digesta are typically very low. Most of the endogenous nitrogen is probably associated with proteins from mucosal cells as well as salivary proteins (Barboza et al. 2009).

If small-bodied individuals are recently weaned juveniles, then these animals might be learning what to eat from the mother, which could negate the possibility of differential forage selection (Provenza and Balph 1987; Mirza and Provenza 1990, 1994; Thorhallsdottir et al. 1990). However, it is feasible that fawns and their adult counterparts can consume different forages within the same foraging area. Spalinger et al. (1997) noted that diet selection by juvenile white-tailed deer was largely an innate behavior rather than a learned response.

Forage selectivity by small-bodied individuals is likely a means to efficiently meet their greater mass-specific metabolic demands, which can also influence the duration and frequency of foraging bouts and forage selection (Irvine et al. 2000; Aikman et al. 2008; Laca et al. 2010). There were notable differences between the covariates that influenced CP, ADF, and NDF in the rumen–reticulum. Our findings support previous studies that noted that animals adjust their forage intake in response to changing nutrient concentrations of the diet (Holand 1994; Gross et al. 1996).

In addition to consuming a greater amount of CP to more efficiently meet metabolic demands, forage selectivity by

small-bodied individuals also might have ramifications on forage niche partitioning. Because there were differences in the CP : ADF across a range of body masses, habitat use on the same forage patch might be mitigated, which could decrease competition. The decreased competition between deer of differing body masses within the same foraging area might be the result of either different-sized individuals selecting different forages, or possibly, different parts of the same forage. Also, the abundance of high-quality forage is likely to be rarer on the landscape compared with lower quality forage. Therefore, the base of the diet is likely composed of low-quality forage and supplemented with high-quality forage. The small-bodied individuals in our study might be acquiring a greater amount of CP by spending more time foraging in order to seek out the less abundant high-quality forage.

Large-bodied individuals require greater absolute dry-matter intake to meet greater absolute metabolic demands than do smaller bodied individuals (Van Soest 1994). Larger body masses consequently should have larger rumen–reticulums, which accommodate longer ruminal retention times, thereby increasing digesta exposure to rumen microbes to facilitate more efficient digestion of lower quality forage (Barboza and Bowyer 2000). Small-bodied individuals are likely to forage differently than their larger bodied counterparts to maximize intake of highly nutritious forage; this might result in quicker rumen turnover. Although large-bodied individuals will take advantage of high-quality forage, they are not as reliant on consuming forage with the highest nutrient content as are smaller bodied individuals. Therefore, individuals of varying body masses are likely able to partition foraging activities within the same foraging area.

Sex and reproductive status can influence forage intake (Barboza et al. 2009). We, surprisingly, did not detect differences based on sex. However, the influence of lactation might have overshadowed any influence attributed to sex due to our adult female data set being composed largely of lactating individuals (78%). With respect to lactation, we did detect higher CP values for lactating individuals. The increased CP intake of lactating females is likely attributable to increased metabolic demands associated with lactation (Barboza et al. 2009). Lactating females meet their high metabolic demands for energy and protein by selecting higher quality forage in addition to consuming greater amounts of forage compared with nonlactating females (Barboza and Bowyer 2000).

Typically, on an intraspecific level, adult males and females do not compete for forage when they are segregated spatially (McCullough 1979; Kie and Bowyer 1999). Large males select areas where they can best meet their nutritional demands, which frequently results in moving to areas where forage is more abundant but contains higher fiber content (Bowyer 1984; Clutton-Brock et al. 1987). The positive relationship between body mass and NDF we detected is consistent with the notion that larger animals feed in areas with more abundant and lower quality forage.

With respect to body condition, we noted a relationship between the amount of back fat and the amount of CP in the digesta. As fat stores are depleted, there is an increase in the rate of depletion of protein stores (Torbit et al. 1985; Cook et al. 2001). In our study, there was an inverse relationship between back fat and CP, ADF, and NDF; this indicated that individuals will likely be increasing food intake to replenish fat storages or to meet demands of growth.

Previous research has noted that lambs were capable of selecting forage that would maximize their growth (Cropper et al. 1986; Kyriazakis and Oldham 1993), and the proportion of protein in the diet decreased with increasing age (Cropper et al. 1985). Also, results of a controlled feeding experiment indicated that yearling white-tailed deer were selectively consuming forages that contained the greatest CP content (Dostaler et al. 2011). Gains in body mass resulting from consuming a high-quality diet increase the probability of survival for juvenile ungulates (Pettorelli et al. 2007). In order to increase their chances of survival, juveniles should maximize intake of high-quality forage. By primarily selecting high-quality forage (and thereby increasing CP intake), digestibility will increase as well as rumen turnover time (Oikawa et al. 2011), thereby maximizing nutrients available to meet demands of growth. Perhaps the amount of protein within the forage that causes satiety for an animal of young age could result in varying degrees of malaise in older individuals (Provenza 1995). If we use body mass as a proxy for age, our study followed the trend reported in domesticated sheep by Cropper et al. (1985), in that younger (lighter) animals consume a greater amount of protein than the older (heavier) animals.

Our study indicates that small-bodied individuals had a diet higher in CP than did their larger bodied counterparts. To increase their CP intake, small-bodied individuals might exhibit differential forage selection. By selectively choosing which forage items to consume, small-bodied individuals could increase rumen turnover, which would aid in meeting growth demands. Also, differential forage selection between small and large-bodied individuals would reduce competition and enable small-bodied individuals to efficiently meet their high mass-specific metabolic demands. Our study provides empirical evidence that foraging strategies probably differ across a body mass gradient within species. Therefore, forage partitioning is likely occurring, which would decrease dietary overlap and limit intraspecific competition.

Wildlife managers could use the information presented herein to better understand nutritional needs across body sizes. Additionally, by assessing landscapes, managers can use our information to determine how their property meets the forage needs of current populations. Depending on the age class of white-tailed deer populations and the quality and quantity of available forage, augmentations to the landscape may be required to increase high-quality forage. Augmentations to the landscape that increase forage quality would enable the young age classes to more efficiently meet their metabolic demands. This would potentially increase recruitment, as well as overall body condition of the population in general.

Supplemental Material

Please note: The *Journal of Fish and Wildlife Management* is not responsible for the content or functionality of any supplemental material. Queries should be directed to the corresponding author for the article.

Table S1. Kerr Wildlife Management Area white-tailed deer *Odocoileus virginianus* samples for November 2009 and 2010 and September 2010. Provided are the date the animal was harvested, sex, age category, time of kill, dressed weight, rump fat, lactation status, dry weight in grams of rumen crude protein, dry weight in grams of rumen–reticulum acid detergent fiber, and dry weight in grams of rumen–reticulum neutral detergent fiber. Table codes: CP (g) = dry weight in grams of crude protein in rumen–reticulum digesta; ADF (g) = dry weight in grams of acid detergent fiber from rumen–reticulum digesta; NDF (g) = dry weight in grams of neutral detergent fiber.

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Figure S1. Figure on three-dimensional plane with ADF, CP, and body mass to illustrate relationships between body mass, CP, and ADF. CP (g) = dry weight in grams of crude protein in rumen–reticulum digesta; ADF (g) = dry weight in grams of acid detergent fiber from rumen–reticulum digesta. Body mass was measured in kg. Nutritional values are in grams per rumen and were obtained from digesta samples collected from the rumen–reticulum of white-tailed deer *Odocoileus virginianus* sampled during September, November, and December 2009 and 2010 in a 2,628-ha enclosure at Kerr Wildlife Management Area, Kerr County, Texas, USA.

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Acknowledgements

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