

SCALING RELATIONSHIPS BETWEEN BODY WEIGHT AND
FERMENTATION GUT CAPACITY IN *CERVUS AXIS*
AND *CERVUS ELAPHUS NANNODES*

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by

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ABSTRACT

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The scaling relationship between body weight and fermentation gut capacity impacts dietary patterns of ruminants. Interspecific scaling relationships between body weight and fermentation gut capacity were reported to have a slope of 1.0 (isometric scaler) when body weights ranged between 3-5 orders of magnitude. The implications of an isometric scaling relationship between body weight and fermentation gut capacity

have been extended to explain dietary patterns within species. Whether or not scaling relationships are isometric within a single species or when body weight differences between species are small is unresolved. The goals of my study were to determine if the intraspecific scaling relationship between body weight and fermentation gut capacity was isometric, assess any potential influence from reproductive status of females on the scaling relationship, and determine if the interspecific scaling relationship between two species differing in weight by roughly 200 kg was isometric. I collected 29 adult male ($n = 8$) and female ($n = 21$) axis deer (*Cervus axis*) from January 2004 to April 2005 at a private ranch in Bastrop County, Texas. Capacity of the rumen-reticulum, cecum, and colon, organs where fermentation occurs, was estimated by calculating wet weight and volume capacity. Forage samples were taken from the rumen-reticulum of each specimen to assess variation in forage quality across the collection period. Forage quality and gender did not influence scaling relationships for axis deer. Regressions for axis deer had isometric scalars for fermentation gut capacity. Female axis-deer were analyzed for a relationship between reproductive status and fermentation gut capacity. A trend was identified with pregnant females having lowest fermentation gut capacity. Tule elk (*C. elaphus*) data ($n = 25$), collected using methods identical to mine, was combined with axis deer data to conduct an interspecific comparison between body weight and rumen-reticulum capacity. Regression analysis estimated scalars that were similar for both axis deer and Tule elk but the scalars were not isometric. The scaling relationship between body weight and fermentation gut capacity is isometric for axis deer. However, scaling relationships between body weight and fermentation gut capacity are stronger between species than within a single species.

INTRODUCTION

The Bell-Jarman Principle states that smaller sized herbivore species feed on higher quality, more digestible, forages while larger herbivores can survive on lower quality, less digestible, forages (Bell 1970, Jarman 1974). Larger species extract more nutrients from low quality forage than smaller species because of a longer retention time of forage within fermentation chambers. Because fermentation rates are a function of food quality, higher quality forage requires less fermentation time to extract nutrients (Bell 1970, Jarman and Sinclair 1979, Van Soest 1982, Demment and Van Soest 1985). Consequently, the shorter retention time of digesta in smaller herbivores may limit nutrients available to them in forage of poor quality (Van Soest 1982). Since decreased body size is associated with lower nutrient extraction from forage, smaller herbivores should be more selective foragers.

The mechanism accounting for longer retention of forage in larger body sizes is based on two scaling relationships. Kleiber (1975) determined that metabolic requirement increases to the 0.75 power of body weight. Larger herbivores, therefore, have slower metabolic rates than smaller herbivores in relation to body weight. Because gut capacity scales isometrically (slope equal to 1.0) with body weight across species of ruminant and non-ruminant herbivores, the mean retention time of digesta should scale to the 0.25 power of body weight ($1.0 - 0.75 = 0.25$) (Parra 1978, Illius and Gordon 1992).

The Bell-Jarman Principle applies directly to interspecific comparisons, but it has been extended to intraspecific comparisons. Barboza and Bowyer (2000) used

interspecific scaling relationships between body weight, metabolic rate, and gut capacity to explain, in part, dietary patterns among individuals within populations of sexually dimorphic cervids. Larger males should have increased retention time of digesta in the gut that would result in greater extraction of nutrients from high fiber forage. However, if the scaler in intraspecific comparisons is not isometric, then the Bell-Jarman Principle may not be applicable. Weckerly et al. (2003) compared body weight to capacity of the rumen-reticulum in Tule elk (*Cervus elaphus nannodes*) and female mule deer (*Odocoileus hemionus*). Their results were inconclusive as to whether the scaler was 1.0.

Several studies have examined the effects of lactation on energy demands in mammalian species (Smith and Baldwin 1974, Lochmiller et al. 1982, Hammond and Diamond 1992, Jenks et al. 1994, Derting and Austin 1998). A trend of heavier, or larger, gastrointestinal tracts in lactating females over not pregnant or lactating (non-reproductive) females has been reported in dairy cattle maintained on high quality forages (Smith and Baldwin 1974). Jenks et al. (1994) found shortest intestinal lengths in pregnant white-tailed deer (*Odocoileus virginianus*), intermediate intestinal lengths in not-reproductive females, and longest intestinal lengths in lactating females. This trend also existed for weight of intestinal contents. Weight of rumen contents, however, was greater in lactating females than in pregnant females, but similar between not-reproductive females and lactating females. There are currently no studies that assess fermentation gut capacity relative to whether females are pregnant, lactating, or not-reproductive.

If the scaling relationship between body weight and gut capacity is isometric for interspecific comparisons across a wide weight distribution of mammalian herbivores, it

should also be isometric for a narrower weight range (Jarman 1974, Parra 1978, Demment 1982, Barboza and Bowyer 2000). I used data for Tule elk collected by Weckerly et al. (2003) to test whether the scaling relationship between body weight and rumen-reticulum capacity was isometric between two grazing species that differ in body weight by approximately 200 kg. This weight range was considerably smaller than the 3-5 orders of magnitude in weight range reported by Parra (1978) and Demment (1982).

I measured body weight and fermentation gut capacity in axis deer and used the data for Tule elk reported by Weckerly et al. (2003) to address three areas of the Bell-Jarman Principle. First, is the scaling relationship between body weight and fermentation gut capacity isometric in a single population of axis deer? Currently, there are no studies that address the application of the Bell-Jarman Principle to an intraspecific analysis that includes all organs where fermentation occurs. Second, does reproductive status affect fermentation gut capacity of females? I expect lower capacity in pregnant females due to the constraints imposed by a developing fetus, intermediate capacity in non-reproductive females, and largest capacity in lactating females (Smith and Baldwin 1974, Jenks et al. 1994). Third, is the scaling relationship between body weight and rumen-reticulum capacity isometric between species with a range in weights smaller than that used in previous interspecific studies? Scaling relationships for rumen-reticulum capacity were estimated because it was the only organ measured by Weckerly et al. (2003).

MATERIALS AND METHODS

Study area.—My study was conducted at a private ranch in Bastrop County, Texas (29°52'30"N, 97°17'24"W). The ranch included oak savannah, loblolly pine (*Pinus taeda*) stands, and pastures. Oak savannahs were dominated by post oak (*Quercus stellata*) and blackjack oak (*Q. marilandica*) and contained eastern red cedar (*Juniperus virginiana*) and black hickory (*Carya texana*). Common shrubs in loblolly pine stands were yaupon (*Ilex vomitoria*), possumhaw holly (*I. decidua*), and American beauty berry (*Callicarpa americana*). Pastures were dominated by coastal Bermuda grass (*Cynodon dactylon*) and Willman lovegrass (*Eragrostis superba*). Mean daily temperatures reached a minimum of 4 °C in January and a maximum of 36 °C in July. The annual mean precipitation was 89 cm.

Exotic ungulates received approximately 1364 kg of a pellet supplemental feed three times a week. The pellet consisted of 20% crude protein, 12.5% crude fiber, 1.25% calcium, and 1.25% phosphorous. Between 3,600 and 4,050 kg of alfalfa were provided per week (approximately 7 tons per year). During late fall and early winter, between 202 and 243 ha of food plots were planted with rye grass and oats.

Specimen collection occurred within a 1618 ha fenced area of the ranch that included approximately 1000 total individuals of axis deer (*Cervus axis*), sika deer (*C. nippon*), elk (*C. elaphus*), fallow deer (*Dama dama*), Père David's deer (*Elaphurus davidianus*), white-tailed deer (*Odocoileus virginianus*), addax (*Addax nasomaculatus*), black buck antelope (*Antelope cervacapra*), springbok (*Antidorcas marsupialis*),

American bison (*Bison bison*), red lechwe (*Kobus leche*), scimitar-horned oryx (*Oryx dammah*), eland (*Taurotragus oryx*), aoudad sheep (*Ammotragus lervia*), Chilton markhor (*Capra falconeri*), Corsican sheep (*Ovis gmelini musimon*, variety *corsicana*), white sheep (*O. dalli*), and mouflon sheep (*O. musimon*).

Specimen and data collection.—I randomly selected adult males ($n = 8$) and females ($n = 19$) for collection from January 2004 to May 2005. All specimens were shot in the head or neck with a 280 rifle, with dissection initiated within 30 minutes of time of kill. Whole weights, minus blood loss, were taken to the nearest kilogram. Internal organs were removed through a mid-ventral incision with an anterior cut made through the esophagus, trachea, and aorta and a posterior cut around the anus. All organs and tissues were excised from the alimentary tract, which I separated from the rumen-reticulum, omasum, abomasum, small intestine, cecum, and colon. The small intestine and colon were severed from the cecum at the ileocecal junction. The omasum and abomasum were removed from the rumen-reticulum at the reticulo-omasal sphincter. The esophageal opening of the rumen-reticulum was sown shut with dental floss. The colon was sewn shut at the cecal end after digesta was removed.

I measured total fermentation gut capacity by individually determining capacity of the rumen-reticulum, cecum, and colon in two ways: wet weight and volume (Krausman et al. 1993, Weckerly et al. 2003). Calculations for wet weight were made to the nearest 0.1 kg by subtracting the weight of the organ after digesta was removed and the organ flushed clean, from the weight of the organ plus digesta. Any perforations in organ walls were stitched closed with dental floss. I measured volume capacity by placing each organ in a 208 liter drum filled with tepid water, and pouring water into each organ using

a 1 liter container marked at 100 ml increments. Organs were considered "full" when water began to flow from the opening. Volume was recorded as the amount of water held by each organ. I measured volume in triplicate and used the mean volume for the rumen-reticulum, cecum, and colon in analyses.

Fiber Analysis.—Since axis deer were collected over 16 months, I measured nutritional composition of the diet by assaying 1 liter digesta samples collected from the rumen-reticulum for crude protein, neutral detergent fiber, and acid detergent fiber. Digesta samples were frozen until assays were conducted by A&L Laboratories in Lubbock, Texas. Crude protein was measured using the Kjeldahl procedure and the two fibers were assayed with a detergent analysis (Robbins 1993). The detergent analysis was used to partition the plant sample into its basic parts, cell wall and cell soluble components. Neutral detergent fiber measures the percentage of a plant cell comprised of cell wall (cellulose, hemicellulose, lignin, and cutin-suberin). Acid detergent fiber measures percentage of neutral detergent fiber comprised of cellulose, lignin, and cutin-suberin. I assumed forage was more digestible when crude protein content was higher and neutral detergent and acid detergent fiber was lower (Weckerly and Nelson 1990, Robbins 1993).

Data analysis.—I calculated all possible pair-wise correlations between neutral detergent fiber, acid detergent fiber, and crude protein for each sample of digesta to assess whether each variable provided independent information. Correlations between forage variables (r) were considered weak if they were between -0.5 and 0.5 (Kleinbaum et al. 1998). Pairs of forage variables with weak correlation coefficients were included in the regression analysis for axis deer. I calculated the coefficient of variation for volume

capacities for each specimen and organ to assess precision of my volume measurements. Coefficients of variation were summarized by calculating the quartiles (Kleinbaum et al. 1998). I also calculated the proportion of the total fermentation capacity accounted for by each organ for wet weight and volume.

Dummy variables were designated for gender in order to determine if gender-based regressions between the natural logarithm of axis deer body weight and natural logarithm of fermentation gut capacity differed in intercepts, slopes, or both. An extra sums of squares test was used to determine the significant variables for the regression equations (Kleinbaum et al. 1998). Multiple regression equations for wet weight and volume were analyzed for significance of forage variables. I used a t-test to determine if the slopes of regression equations for wet weight and volume differed from 1.0 (Kleinbaum et al. 1998).

Crown to rump lengths were taken for each fetus (Saunders 1955). Residuals from axis deer body weight-fermentation capacity regressions were analyzed to determine if fermentation gut capacity varied by reproductive state among females. I used a single factor analysis of variance (Kleinbaum et al. 1998) to determine if fermentation gut capacity was lowest in pregnant females, intermediate in non-reproductive females, and highest in lactating females. If the analysis of variance indicated differences among means of residuals for the three reproductive states, I conducted an orthogonal polynomial contrast analysis (Kleinbaum et al. 1998) to determine if the variation among the means fit my prediction.

Weckerly et al. (2003) measured wet weight and volume of Tule elk rumen-reticulums with the same methodology used herein. I coded dummy variables for species

to determine if species-based regression equations between the natural logarithm of body weight and natural logarithm of rumen-reticulum capacity for axis deer and Tule elk differed in intercepts, slopes, or both. An extra sums of squares test was used to determine significant variables for regression analysis. A t-test was used to determine whether the regression slopes differed from 1.0 (Kleinbaum et al. 1998). All regression analyses were performed using S-PLUS (Lucent Technologies, Inc. 2002).

RESULTS

Acid detergent fiber and neutral detergent fiber had a positive correlation ($r = 0.73$, $d.f. = 25$, $P < 0.001$). Crude protein was negatively correlated to both neutral detergent fiber ($r = -0.50$, $d.f. = 25$, $P = 0.007$) and acid detergent fiber ($r = -0.23$, $d.f. = 25$, $P = 0.254$). Since crude protein ($\bar{x} = 21.26$, $s = 2.54$, minimum = 16.25, maximum = 25.50) had a weak correlation with both acid detergent fiber and neutral detergent fiber, it was included in the regression equation analysis for axis deer. Because neutral detergent fiber ($\bar{x} = 55.22$, $s = 2.92$, minimum = 48.22, maximum = 60.98) and acid detergent fiber ($\bar{x} = 34.81$, $s = 2.98$, minimum = 29.25, maximum = 40.81) had a strong correlation, I included neutral detergent fiber in the regression analysis for axis deer.

The variation in volume measurements was smallest for rumen-reticulum ($Q_1 = 0.02$, $Q_2 = 0.03$, $Q_3 = 0.05$), intermediate for colon ($Q_1 = 0.03$, $Q_2 = 0.06$, $Q_3 = 0.10$), and largest for cecum ($Q_1 = 0.06$, $Q_2 = 0.10$, $Q_3 = 0.15$). For wet weight of the fermentation gut capacity, the rumen-reticulum accounted for, on average, 85.94% ($s = 0.059$), the cecum 6.50% ($s = 0.019$), and the colon 7.56% ($s = 0.059$) (Table 1). For volume capacity of the fermentation chambers, the rumen-reticulum accounted for, on average, 55.17% ($s = 0.032$), the cecum 28.71% ($s = 0.019$), and the colon 15.89% ($s = 0.044$).

The extra sums of squares test indicated that gender and the interaction between gender and body weight were not significant variables for either wet weight (gender: $F = 0.03$, $d.f. = 1, 24$, $P = 0.872$; interaction: $F = 2.39$, $d.f. = 1, 23$, $P = 0.136$) or volume (gender: $F = 0.8008$, $d.f. = 1, 24$, $P = 0.3801$; interaction: $F = 1.037$, $d.f. = 1, 23$, $P =$

0.319). Slopes and intercepts were similar for males and females for both wet weight and volume regressions. Crude protein and neutral detergent fiber concentrations did not influence the regression between body weight and wet weight (crude protein: $t = -0.18$, $d.f. = 21$, $P = 0.858$; neutral detergent fiber: $t = -0.27$, $d.f. = 21$, $P = 0.792$) or volume (crude protein: $t = 1.41$, $d.f. = 21$, $P = 0.173$; neutral detergent fiber: $t = 0.01$, $d.f. = 21$, $P = 0.993$). The regressions for wet weight and volume were $\hat{Y}_{\text{wet}} = 0.237X^{0.718}$ ($r^2 = 0.33$, $F = 12.13$, $d.f. = 1, 25$, $P = 0.002$) and $\hat{Y}_{\text{vol}} = 0.6429X^{0.64}$ ($r^2 = 0.27$, $F = 9.40$, $d.f. = 1, 25$, $P = 0.005$) (Fig. 1). For both regression equations the scaler for fermentation gut capacity was not statistically different from 1.0 (wet weight: $t = -1.36$, $d.f. = 25$, $P = 0.184$; volume: $t = -1.70$, $d.f. = 25$, $P = 0.101$).

Of the females collected, five were pregnant, one with twins, seven were non-reproductive, and seven were lactating. The six fetuses average 480.7 mm (minimum 152.4 mm, maximum 620 mm) in length, and 2.57 kg (minimum 0.11 kg, maximum 4.5 kg) in weight. The single factor analysis of variance on residuals from the body weight-wet weight regression indicated differences in mean fermentation gut capacity among pregnant, lactating, non-reproductive ($F = 5.82$, $d.f. = 2, 16$, $P = 0.013$) females. The means of the residuals for wet weight were: pregnant = -0.31, non-reproductive = 0.08, and lactating = 0.14. The orthogonal polynomial analysis indicated that 81% of the variation in reproductive status was explained by a linear contrast with pregnant females having the lowest capacity and lactating females having the greatest capacity ($F = 9.46$, $d.f. = 1, 16$, $P = 0.007$). The quadratic contrast was not statistically significant ($F = 2.17$, $d.f. = 1, 16$, $P = 0.160$). For volume, the single factor analysis of variance indicated differences in fermentation gut capacity related to reproductive status ($F = 3.31$, $d.f. = 2$,

16, $P = 0.063$). The means of the residuals for volume were pregnant = -0.200, non-reproductive = 0.197, and lactating = -0.006. Orthogonal polynomial analysis indicated 84.5% of the variation in the means among reproductive status was accounted for by the quadratic contrast ($F = 5.60$, $d.f. = 1, 16$, $P = 0.030$). The linear contrast was not statistically significant ($F = 1.02$, $d.f. = 1, 16$, $P = 0.327$).

For the relationship between body weight and rumen-reticulum wet weight, the extra sums of squares test indicated that species differed in intercepts ($F = 40.75$, $d.f. = 1, 49$, $P < 0.001$) but not slopes ($F = 0.28$, $d.f. = 1, 48$, $P = 0.597$). The relationship for Tule elk was $\hat{Y} = 0.85X^{0.6673}$ and axis deer, $\hat{Y} = 0.29X^{0.6673}$ ($r^2 = 0.9457$, $F = 426.8$, $d.f. = 2, 49$, $P < 0.001$) (Fig. 2). The regression slopes were statistically less than 1.0 ($t = -2.40$, $d.f. = 50$, $P = 0.010$). For rumen-reticulum volume as the response variable, the extra sums of squares test indicated that y-intercepts differed between regressions for each species ($F = 30.05$, $d.f. = 1, 49$, $P < 0.001$) but the slopes did not ($F = 0.02$, $d.f. = 1, 48$, $P = 0.881$). The regression between body weight and rumen-reticulum volume capacity for Tule elk was $\hat{Y} = 1.61X^{0.6588}$ and $\hat{Y} = 0.60X^{0.6588}$ for axis deer ($r^2 = 0.93$, $F = 335.9$, $d.f. = 2, 49$, $P < 0.001$). The regression slopes were less than 1.0 ($t = -2.30$, $d.f. = 50$, $P = 0.013$).

DISCUSSION

Volume measurements were precise for the rumen-reticulum, cecum, and colon, because the median coefficients of variation were ≤ 0.10 . Since the variation of volume measurements was low, each organ filled in a similar fashion indicating pressure from the water in the drum created constant static pressure (Krausman et al. 1993, Weckerly et al. 2003). Because it may not be possible to directly measure fermentation capacity unbiasedly, I measured capacity in two ways. All organs had volume capacities greater than wet weight capacity. This indicates that volume measures over-estimated organ capacity and wet weight underestimated organ capacity (Demment 1982). Therefore, wet weight and volume set the lower and upper bounds, respectively, for the fermentation gut capacity (Demment 1982).

For axis deer, fermentation gut capacity was dependent, to some extent, upon body weight of the individual. Similar to Tule elk, the dependence of fermentation gut capacity upon body weight was not influenced by gender (Weckerly et al. 2003). Barboza and Bowyer (2000) used the Bell-Jarman Principle to partly explain dietary patterns among sexually dimorphic cervids by assuming that if the scaling relationship between body weight and gut capacity was isometric and strong across species, it would also be isometric and strong among individuals within a single population. They did not have evidence to support such an assumption. For both volume and wet weight measures, slopes of regressions between axis deer body weight and fermentation gut capacity indicate an isometric relationship. Yet, the relationships are not strong ($r^2 \leq$

0.33). I conclude that the scaling relationship between body weight and fermentation gut capacity is isometric although the relationship is not strong ($r^2 \leq 0.33$, Barboza and Bowyer's 2000).

Fermentation gut capacity was influenced by reproductive status among female axis deer. This source of variation may help explain why the intraspecific relationships I detected were not as strong as the interspecific relationships reported by Parra (1978) and Demment (1982). Pregnant females had the lowest fermentation gut capacity with both volume and wet weight measures. It was unclear whether non-reproductive females had intermediate fermentation gut capacity and lactating females the largest fermentation gut capacity because results differed between volume and wet weight measures. Elevated energy demands from a developing fetus are presumably counteracted by gut capacity restrictions due to limited space within the body cavity (Clauss et al. 2003). Randolph et al. (1977) found that in cotton rats (*Sigmodon hispidus*), pregnant females showed a 25% increase in ingestion over non-reproductive females, while lactating females showed a 66% increase. In *Mus musculus*, food intake rates were 2.7-3.4 times greater in lactating mice than in mice prior to breeding, at time of parturition, and post-weaning (Hammond and Diamond 1992). Wet weight of the gut also increased through pregnancy and parturition, and began to decline after peak lactation had been reached. Increased ingestion rates have been linked to the increased energy demands associated with late-stage pregnancy and lactation over non-reproductive states in *Microtus pinetorum* (Lochmiller et al. 1982, Derting and Austin 1998). Lactating females have a higher energy demand than pregnant females and meeting these demands may be facilitated by a larger gut that can accommodate more ingesta (Randolph et al. 1977, Hammond and

Diamond 1992, Derting and Austin 1998). Energy requirements associated with lactation have been linked to increases in stomach, cecum, and colon capacity for small mammals (Hammond and Diamond 1992, Derting and Austin 1998).

The rumen-reticulum is the initial site for fermentation of forage. There is a greater extraction of nutrients per unit of forage intake in the rumen-reticulum than in either the cecum or colon because of the selective delay of forage within the rumen-reticulum (Demment and Van Soest 1985). Clauss et al. (2003) proposed that as selective forage retention within the rumen-reticulum ultimately limits the intake of forage, the capacity of the rumen-reticulum is large to counteract intake limitations so energy demands can be met. For axis deer, the rumen-reticulum comprised 85.94% of the fermentation gut wet weight capacity and 55.17% of the volume capacity. In accordance with Clauss et al. (2003), it can be assumed that the rumen-reticulum also accounts for the same proportion of fermentation gut capacity in Tule elk.

Regressions between body weight and rumen-reticulum capacity for Tule elk and axis deer had scalars < 1.0 for both volume and wet weight measurements. Since the scalars of regressions for body weight and total fermentation gut capacity (all four fermentation chambers) for axis deer were isometric for both volume and wet weight, it can be argued that the rumen-reticulum alone is not sufficient for estimating scaling relationships indicating fermentation gut capacity. To determine if the Bell-Jarman Principle is applicable across a smaller weight range than that investigated by Parra (1978) and Demment (1982), all four fermentation chambers should be measured. However, the ambiguous conclusions of Weckerly et al. (2003) may be due to weak relationships. The one pattern that emerges from both studies estimating intraspecific gut

capacity regressions is that intraspecific scaling relationships are not as strong as interspecific scaling regressions (Parra 1978, Demment 1982).

Gut tissue is metabolically expensive to maintain (Parra 1978, Demment 1982, Demment and Van Soest 1985). The relationship between body weight and fermentation gut capacity should scale equal to, or greater than, the scaler between body weight and metabolic rate in order to meet maintenance energy demands (Kleiber 1975). The greater the difference in the scalers between body weight and fermentation gut capacity and body weight and metabolic rate, the longer forage should be retained (Demment and Van Soest 1985).

The intraspecific scaling relationship for axis deer has two important implications. The scaler was not different from 1.0. Therefore, the Bell-Jarman Principle has the potential to explain dietary patterns within a single population of axis deer (Bell 1970, Jarman 1974). When forage is limited yet variable in quality, I expect smaller bodied females to seek out higher quality forages than the larger-bodied males due to the constraint of a shorter retention time of forage within the gut (Weckerly and Nelson 1990, Jenks et al. 1994, Kamler et al. 2003). Also, the need for high quality forage by females should be greatest during the last trimester of pregnancy when gut capacity is least due to physical constraints imposed by a rapidly growing fetus.

LITERATURE CITED

- Barboza, P. S. and R. T. Bowyer. 2000. Sexual segregation in dimorphic deer: a new gastrocentric hypothesis. *Journal of Mammalogy* 81: 473-489.
- Bell, R. H. V. 1970. The use of the herb layer by grazing ungulates in the Serengeti. In Watson, A. (ed.). *Animal population in relation to their food resources*. Blackwell Scientific, New York.
- Clauss, M., R. Frey, B. Kiefer, M. Lechner-Doll, W. Loehlein, C. Polster, G. E. Rössner, and W. J. Streich. 2003. The maximum attainable body size of herbivorous mammals: morphophysiological constraints on foregut, and adaptations of hindgut fermenters. *Oecologia* 136: 14-27.
- Demment, M. W. 1982. The scaling of ruminoreticulum size with body weight in East African ungulates. *African Journal of Ecology* 20: 43-47.
- Demment, M. W. and P. J. Van Soest. 1985. A nutritional explanation for body-size patterns of ruminant and nonruminant herbivores. *American Naturalist* 125: 641-672.
- Derting, T. L. and M. W. Austin. 1998. Changes in gut capacity with lactation and cold exposure in a species with low rates of energy use, the Pine Vole (*Microtus pinetorum*). *Physiological Zoology* 71: 611-623.
- Hammond, K. A. and J. Diamond. 1992. An experimental test for a ceiling on sustained metabolic rate in lactating mice. *Physiological Zoology* 65: 952-977.

- Illius, A.W. and I. J. Gordon. 1992. Modeling the nutritional ecology of ungulate herbivores: evolution of body size and competitive interactions. *Oecologia* 89: 428-434.
- Jarman, F. J. 1974. The social organization of antelope in relation to their ecology. *Behaviour* 48: 215-266.
- Jarman, F. J. and A. R. F. Sinclair. 1979. Feeding strategy and the pattern of resource partitioning in ungulates. Pages 130-163 in A. R. E. Sinclair and M. Norton-Griffiths, editors. *Serengeti: dynamics of an ecosystem*. University of Chicago Press, Chicago, Illinois.
- Jenks, J. A., D. M. Leslie Jr., R. L. Lochmiller, and M. A. Melchior. 1994. Variation in gastrointestinal characteristics of male and female white-tailed deer: implications for resource partitioning. *Journal of Mammalogy* 75: 1045-1053.
- Kamler, J., J. Dvořák, and K. Kamlerová. 2003. Differences in relative volume and weight of stomach among four free living ruminants. *Acta Veterinaria* 72: 33-39.
- Kleiber, M. 1975. *The fire of life: an introduction to animal energetics*. Krieger, Huntington, New York.
- Kleinbaum, D. G., L. L. Kupper, K. E. Muller, and A. Nizam. 1998. *Applied regression analysis and other multivariate methods*. 3rd ed. Duxbury Press, Pacific Grove, California.
- Krausman, P. R., J. D. Wehausen, M. C. Wallace, and R. C. Etchberger. 1993. Rumen characteristics of desert races of mountain sheep and desert mule deer. *Southwestern Naturalist* 38: 172-174.

- Lochmiller, R. L., J. B. Whelan, and R. L. Kirkpatrick. 1982. Energetic cost of lactation in *Microtus pinetorum*. *Journal of Mammalogy* 63: 475-481.
- Lucent Technologies, Inc. 2002. S-PLUS v. 6.1 for Windows. Insightful Corp.
- Parra, R. 1978. Comparison of foregut and hindgut fermentation in herbivores. Pages 205-230 in G. G. Montgomery, ed. *The ecology of arboreal folivores*. Smithsonian institute, Washington, D. C.
- Randolph, P. A., J. C. Randolph, K. Mattingly, and M. M. Foster. 1977. Energy costs of reproduction in the Cotton Rat, *Sigmodon hispidus*. *Ecology* 58: 31-45.
- Robbins, C. T. 1993. *Wildlife feeding and nutrition*. Academic Press, Inc. New York.
- Saunders, J. K. 1955. Fetus in yearling cow elk, *Cervus canadensis*. *Journal of Mammalogy* 36: 145.
- Smith, N. E. and R. L. Baldwin. 1974. Effects of breed, pregnancy, and lactation on weight of organs and tissues in dairy cattle. *Journal of Dairy Science* 57: 1055-1060.
- Van Soest, P. J. 1982. *Nutritional ecology of the ruminant*. O & B Books, Corvallis. In
- Smith, F. A. 1995. Scaling of digestive efficiency with body mass in neotoma. *Functional Ecology* 9: 299-305.
- Weckerly, F. W. and J. P. Nelson. 1990. Age and sex-differences of white-tailed deer diet composition, quality, and calcium. *Journal of Wildlife Management* 54: 532-538.
- Weckerly, F. W., V. C. Bleich, C. B. Chetkiewicz, and M. A. Ricca. 2003. Body weight and rumen-reticulum capacity in Tule elk and Mule deer. *Journal of Mammalogy* 84(2): 659-664.

Table 1.—Proportion ($\bar{x} \pm s$) of fermentation gut capacity accounted for by organ in axis deer collected at a ranch in Bastrop County, Texas (2004-2005).

Measure	Rumen-Reticulum	Cecum	Colon	<i>n</i>
Wet Weight	0.859 ± 0.06	0.065 ± 0.02	0.076 ± 0.06	27
Volume	0.552 ± 0.03	0.287 ± 0.02	0.159 ± 0.04	27

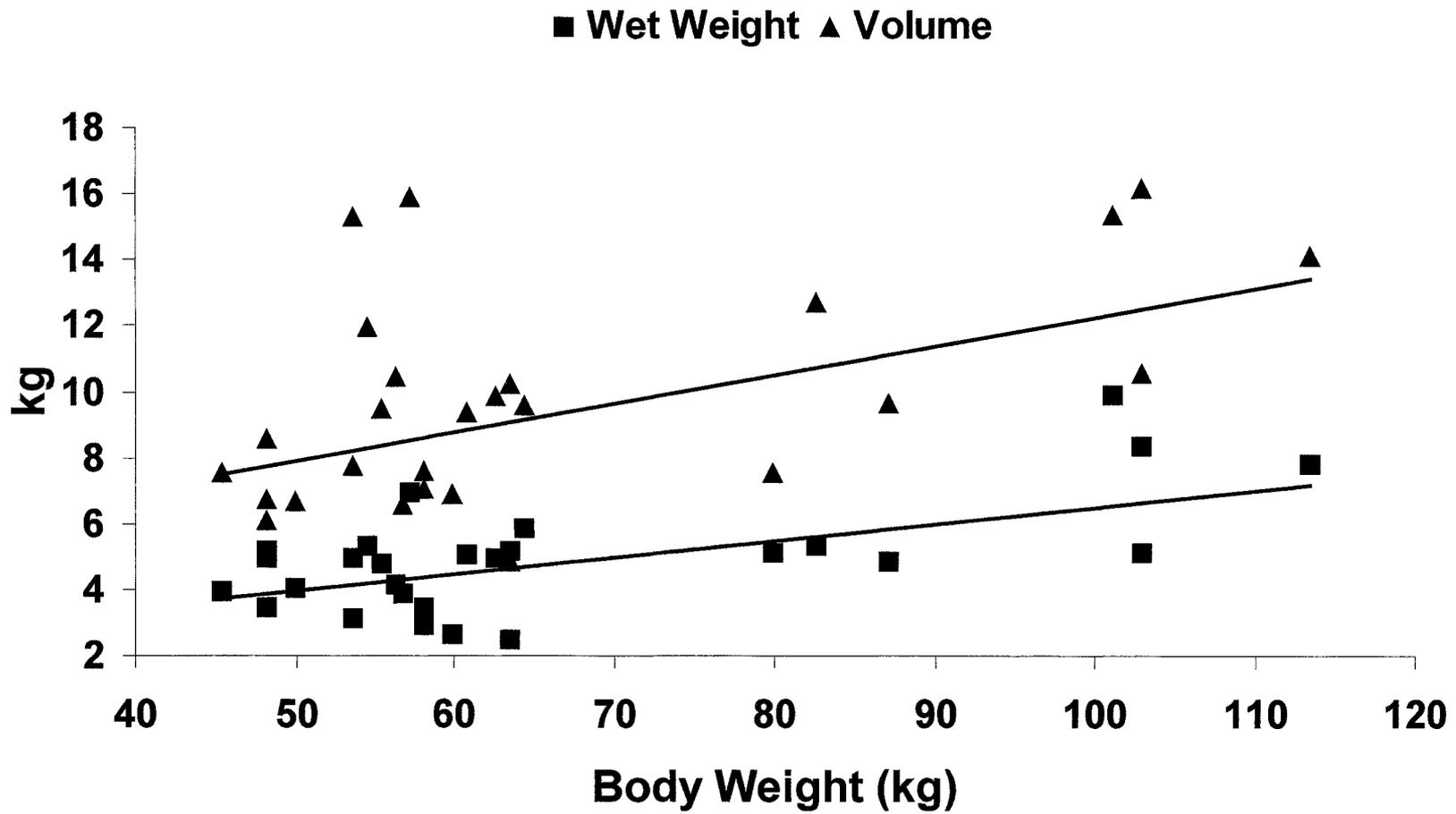


Figure 1. Wet weight and volume regression between body weight and fermentation gut capacity in axis deer collected at a ranch in Bastrop County, Texas (2004-2005). Fermentation gut capacity is given in kg since 1 liter of water equals 1 kg.

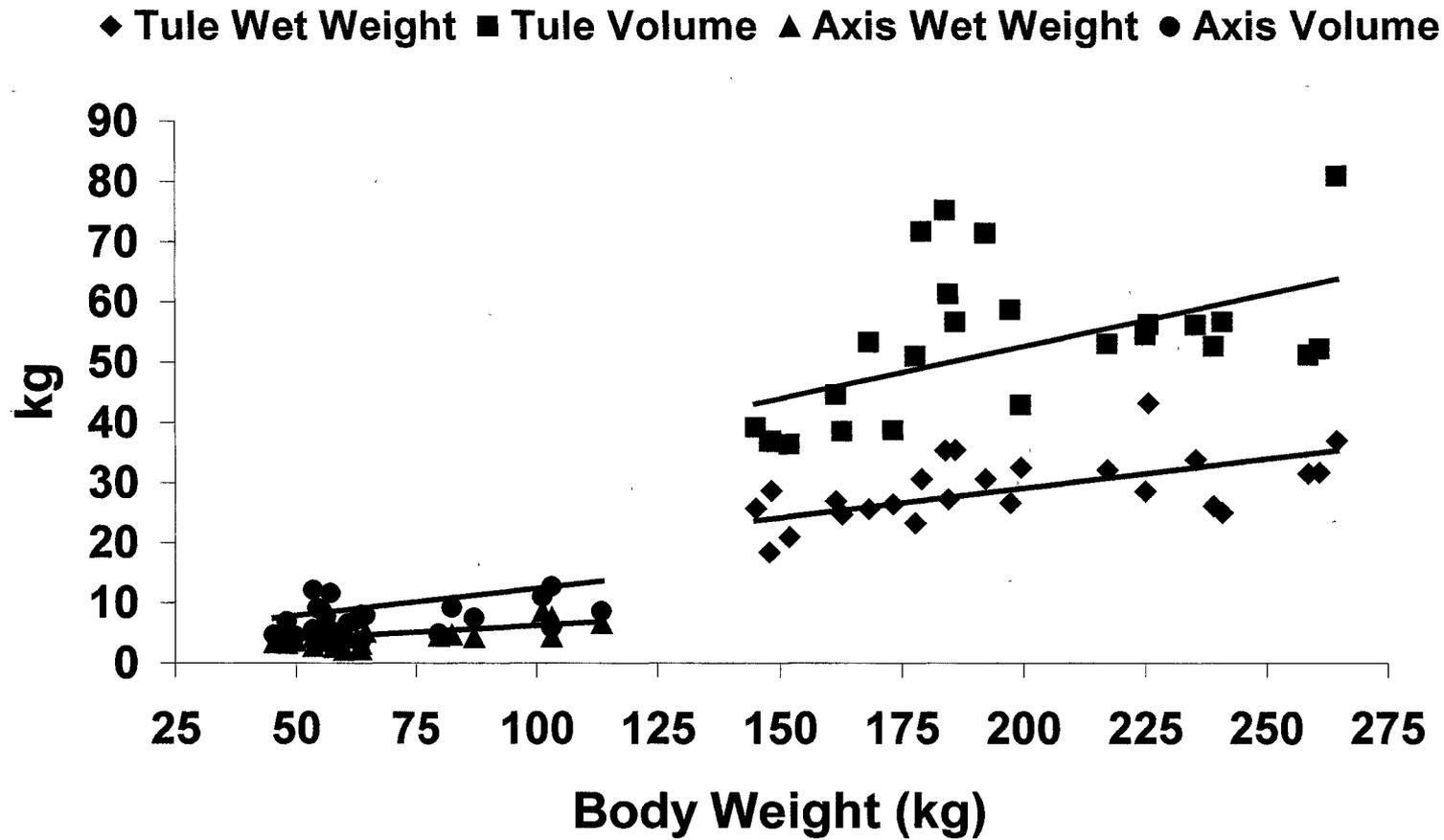


Figure 2. Wet weight and volume regression between body weight and rumen-reticulum capacity in Tule elk and axis deer. Tule elk data was collected and reported by Weckerly et al. (2003). Axis deer data was collected at a ranch in Bastrop County, Texas (2004-2005). Separate regression lines are given for wet weight and volume for axis deer and Tule elk. Rumen-reticulum capacity is given in kg since 1 liter of water equals 1 kg.

VITA

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