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BODY WEIGHT AND RUMEN–RETICULUM CAPACITY IN TULE ELK AND MULE DEER

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The relationship between body size and rumen–reticulum capacity among conspecific individuals is predicted to be isometric. We examined whether the relationship between body weight and rumen–reticulum capacity was isometric in adult male and female tule elk (*Cervus elaphus nannodes*) and in adult female mule deer (*Odocoileus hemionus*). We detected no effect of sex on this relationship in elk, and the slope of the regression was 1.0 for one measure of rumen–reticulum capacity and <1.0 for another. Among deer, the slope of the relationship was <1.0 in one measure of rumen–reticulum capacity, and we detected no relationship with the other.

Key words: body weight, *Cervus elaphus nannodes*, gut scaling, *Odocoileus hemionus*, rumen–reticulum capacity

Small and large ruminants differ in their ability to digest forage high in structural carbohydrates (Robbins 1993). The isometric relationship between body weight and capacity of the rumen–reticulum is part of the theoretical explanation for this difference: small ruminants possess a small fermentation capacity with respect to their metabolic needs and, consequently, do not retain digesta long enough for gut microorganisms to break down structural carbohydrates (Demment 1982; Demment and van Soest 1985). The isometric relationship between body weight and rumen–reticulum capacity among ruminant species is also integral to a gastrocentric explanation of resource partitioning within populations of ruminants that are sexually dimorphic in size (Barboza and Bowyer 2000; Bleich et al. 1997). This theory (Barboza and Bowyer 2000) suggests that retention time of digesta scales to about the 0.25 power of body weight (the quotient of the scalars of gut capacity [1.0] and metabolic rate [0.75]—Robbins 1993).

Although evidence supporting a gastrocentric role in intersexual resource partitioning by sexually dimorphic ruminants is increasing (Gross et al. 1996; Perez-Barberia and Gordon 1999; Post et al. 2001), there are few empirical studies examining body weight and rumen–reticulum capacity within species (Freudenberger 1992). In this study, we estimated body weight and rumen–reticulum capacities of male and female tule elk and of female mule deer. Our objectives were to determine whether the scaling relationship between body weight and rumen–reticulum capacity differed between sexes of tule elk and to determine

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whether rumen–reticulum capacity scaled to the 1.0 power of body weight in both species. We expected no differences between the sexes because gut capacity is presumably a constraint that forces males and females to feed on differing resources (Miquelle et al. 1992). We examined body weight and rumen–reticulum scaling relationships in deer and elk because these species occur in the same geographic area but differ in their diet: deer are concentrate selectors, and elk tend to be bulk and roughage eaters (Hofmann 1989).

Materials and Methods

We obtained samples from tule elk and mule deer inhabiting the Owens Valley (37°15′N, 118°22′W), Inyo County, California. Elk occurred primarily on the valley floor and occupied desert scrub, riparian areas, irrigated pastures, and, occasionally, alfalfa fields (Bleich et al. 2001). Mule deer occupied the western part of the valley and occurred primarily in habitats dominated by bitterbrush (*Purshia tridentata*) and sagebrush (*Artemisia tridentata*—Pierce et al. 2000).

We obtained data on elk, from animals killed by hunters (17 males, 14 females), during November 1993 and 1994. Hunts took place approximately 1 month after cessation of the mating season. Before the opening of each season, we asked hunters to retain the intact viscera after field dressing the animal; they also recorded time of kill. Internal organs were placed in 200-liter plastic drum liners, and these organs, along with the otherwise intact carcass, were transported immediately to a check station. We summed eviscerated carcass weight and weight of internal organs (including ingesta), each to the nearest 0.5 kg, to estimate bled-carcass weight (hereafter body weight).

We ligated the esophagus immediately anterior to the rumen. Also, we tied off the omasum and then excised the rumen–reticulum. During this process we used dental floss to suture any cuts that were present in the rumen–reticulum. We weighed these organs to the nearest 0.5 kg, then emptied them of rumen fluid and ingesta, inverted and rinsed them, and weighed the empty organs. We determined wet weight of rumen–reticulum contents by subtraction. We estimated volume of the rumen–reticulum by using the suspension method (Krausman et al. 1993). The empty rumen–reticulum was placed in a 200-liter steel drum and filled with water; we recorded volume to the nearest 0.1 liter and replicated the process 3 times for each animal. Volume was converted from liters to kilograms to express wet weight and volume measurements of the rumen–reticulum in the same units.

We obtained data on female mule deer (n = 17) that were pregnant during March 1994 from animals collected for other purposes (Pierce et al. 2000). We determined bled-carcass weight (body weight) directly, excised the viscera, and determined wet weight of rumen–reticulum contents and their volume in a manner identical to that described for elk. The majority of deer were collected before noon. Methods used in this research were approved by the Institutional Animal Care and Use Committee at the University of Alaska–Fairbanks (Pierce et al. 2000).

We calculated the quartiles of the coefficient of variation among the 3 replicates to assess precision of measuring volume (Kleinbaum et al. 1998). In the course of assaying wet weight of rumen–reticulum contents of elk, one of us (VCB) observed that texture of digesta seemed to change with time of day an animal was killed. As a result, we first examined relationships between time of kill and the ratio of wet weight of rumen–reticulum contents to body weight in tule elk. If time of kill influenced the ratio of wet weight of rumen–reticulum contents to body weight, we then adjusted wet weight of rumen–reticulum contents to a constant time of day, 1200 h, and used time-adjusted wet weight of rumen–reticulum contents in subsequent regression analyses of elk. We chose the time of 1200 h to improve estimation because it was near the mean time of kill (11:47—Kleinbaum et al. 1998). Time-adjusted wet weight of rumen–reticulum contents was the product of body weight and the residual from the time-of-kill regression. We used ordinary least-squares regression to examine relationships between the natural logarithm of body weight and our 2 measures of rumen–reticulum capacity (natural logarithm of volume and natural logarithm of wet weight of rumen–reticulum contents). Data were expressed in untransformed values and regressions reported as power functions (rumen–reticulum = $a[\text{body weight}]^b$). Indicator variables were coded for sex, and we used an extra-sum-of-squares test to examine whether separate equations were

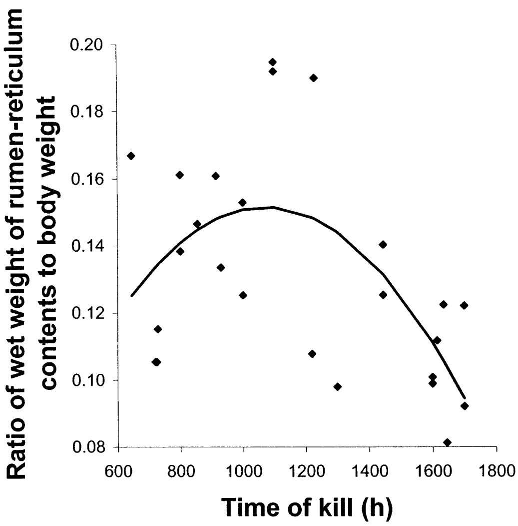

FIG. 1.—Relationship between time of kill and ratio of wet weight of rumen–reticulum contents to body weight for tule elk. Symbols show individual values, and curve is regression line.

needed for female and male tule elk (Kleinbaum et al. 1998). We used a 2-tailed *t*-test to determine whether slopes of regressions differed from 1.0. For all analyses, the criterion for statistical significance was $P < 0.05$. Regressions of body weight versus wet weight of rumen–reticulum contents and body weight versus volume often included data on the same individual; therefore, we reduced experiment-wise error by halving statistical significance ($P \leq 0.025$) for these analyses (Kleinbaum et al. 1998).

RESULTS

The coefficient of variation for volume was low; it ranged from 0 to 0.16 in elk and from 0 to 0.04 in mule deer. The 1st, 2nd, and 3rd quartiles of coefficients of variation were 0.02, 0.04, and 0.07 for tule elk and 0.006, 0.01, and 0.03 for deer, respectively. The coefficients of variation were lower for deer than for elk, yet, for both species, >75% of coefficients of variation for volume were ≤0.07.

In elk, wet weight of rumen–reticulum contents increased slightly through the morning, reached a plateau during midday, and then declined after noon (Fig. 1). A quadratic regression ($Y = -0.015 + 0.0003X - 0.0000001X^2$) fit the data ($F = 5.9$, *d.f.* = 2, 22, $P = 0.009$, multiple $r^2 = 0.29$), and the quadratic term was significant ($t = -2.45$, *d.f.* = 22, $P = 0.023$). Wet weight of rumen–reticulum contents was adjusted to the same time of kill (1200 h) in subsequent analyses for elk.

Among elk, we detected no effect of sex on the relationship between body weight and volume ($F = 2.01$, *d.f.* = 2, 27, $P = 0.155$) or between body weight and wet weight of rumen–reticulum contents ($F = 0.66$, *d.f.* = 2, 21, $P = 0.527$); hence, we disregarded sex in further analyses. We detected relationships between body weight and wet weight of rumen–reticulum contents ($1.502 \times \text{body weight}^{0.56}$, $F = 11.0$, *d.f.* = 1, 23, $P = 0.003$, $r^2 = 0.32$; Fig. 2) and between body weight and volume for elk ($0.443 \times \text{body weight}^{0.91}$, $F = 22.8$, *d.f.* = 1, 29, $P < 0.001$, $r^2 = 0.44$). Higher estimates of capacity were obtained from rumen–reticulum volume than from wet weight of rumen–reticulum contents. The slope of the equation was <1.0 for wet weight of rumen–reticulum contents ($t = -2.6$, *d.f.* = 23, $P = 0.016$), but the slope of the equation for volume did not differ from 1.0 ($t = -0.5$, *d.f.* = 29, $P = 0.623$).

In mule deer, the relationship between body weight and wet weight of rumen–reticulum contents was marginally nonsignificant ($0.158 \times \text{body weight}^{0.73}$, $F = 3.7$, *d.f.* = 1, 12, $P = 0.077$, $r^2 = 0.24$; Fig. 2), but the relationship between body weight and volume was statistically significant ($1.642 \times \text{body weight}^{0.47}$, $F = 10.7$, *d.f.* = 1, 9, $P = 0.010$, $r^2 = 0.54$). Like elk, volume estimates of rumen–reticulum capacity were higher than estimates of wet weight of rumen–reticulum contents. The slope of the equation using volume was <1.0 ($t = -3.6$, *d.f.* = 9, $P = 0.006$).

DISCUSSION

Our estimates of rumen–reticulum volume were precise. The rumen–reticulum organ has many folds and is contained in the airtight and pressurized peritoneal cavity in

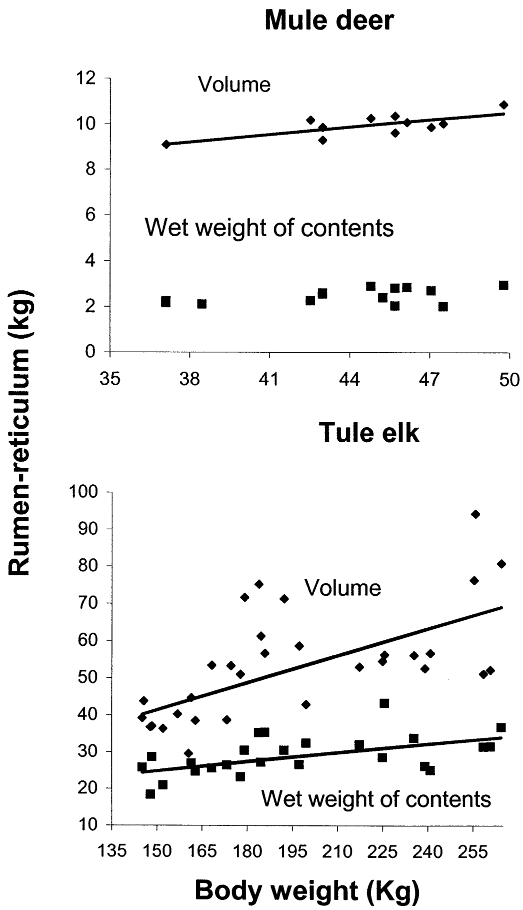

FIG. 2.—Relationship between body weight and capacity of rumen–reticulum as shown by volume (given as kilograms of water) and wet weight of contents in mule deer and tule elk. Squares are individual values for volume, diamonds are individual values for wet weight, and lines are regressions (regression of wet weight for mule deer was not statistically significant). Wet weight of contents for tule elk was standardized to the same time of day, 1200 h.

a live animal (Hofmann 1973). Consequently, when this organ is excised and filled with water, the repeatability of volume measurements among animals is suspect if the internal spaces of the rumen–reticulum do not unfold to a similar extent (Freehling and Moore 1987; Hofmann 1973; Krausman et al. 1993). The rumen–reticulum expanded when determining volume because capacity estimates were higher than wet weight estimates in both elk and mule deer, a common finding when estimating gut capacity (Demment 1982).

Wet weight of rumen–reticulum contents of elk was greater at midday, albeit the relationship between time of kill and rumen–reticulum contents had considerable variation. Elk that were killed throughout the day were assayed, and we apparently captured synchronized patterns of feeding, resting, and ruminating (Conradt 1998). Owing to rumination and microbial digestion of ingesta from a previous foraging bout, particle size of digesta in the rumen–reticulum may have been smaller, with much ingesta having already passed to the hindgut in morning and afternoon (Gross et al. 1996; Robbins 1993). At midday, elk may have been actively foraging or had fed recently but had not yet ruminated the ingested forage; consequently, digesta formed a larger part of rumen–reticulum contents, and weight of rumen–reticulum contents was higher (Robbins 1993).

For mule deer, rumen–reticulum capacity had a scalar <1.0, and for elk, only 1 measure had a scalar similar to 1.0. Although this evidence is not conclusive, it is plausible that the relationship between body weight and rumen–reticulum capacity may not be isometric. Among a sample of 12 male and female feral goats (*Capra hircus*), the scalar for wet weight of fermentation contents was 0.92, a scalar that probably did not differ from 1.0 (Fruedenberger 1992). Perhaps our sample of mule deer had a scalar <1.0 because we had no adult males in our sample (Weckerly 1998). The possibility that the scalar would change if we had included adult male mule deer seems unlikely because we found no effect due to sex among tule elk. Alternatively, we did not assay capacity of the cecum and large intestine, organs where some fermentation also occurs (Robbins 1993). Sampling the cecum and large intestine, however, may not substantially alter an estimate of the scalar of fermentation capacity because it is probable that $>60\%$ of that capacity occurs in the rumen–reticulum (Freudenberger 1992; Jenks et al. 1994; Parra 1978; Sibbald and Milne 1993).

Our findings also suggest that the scalar for body weight and gut capacity differs between the 2 species. For volume data, this possibility seems tenuous, however, because the 95% confidence intervals of the slopes (elk: 0.52–1.29; deer: 0–0.80) overlap considerably. For wet weight of rumen–reticulum contents, our findings should be tempered with the fact that elk were sampled in autumn and female deer were sampled in late winter. Sampling the 2 species in different seasons may confound direct interpretation of slopes because fill of rumen–reticulum with ingesta and rumen–reticulum capacity can vary with diet quality, photoperiod, and reproductive status (Jenks et al. 1994; Sibbald and Milne 1993; Staaland and White 1991).

Retention time of digesta scaling to the 0.25 power of body weight is a vital part of the gastrocentric hypothesis of Barboza and Bowyer (2000). Metabolic rate scales to the 0.67–0.75 power of body weight (Parker et al. 1996, 1999). To determine whether the relationship between body size and gut capacity has a scalar that is isometric or greater than metabolic rate scalars, estimates of the capacities of fermentative and nonfermentative organs are needed from a variety of ruminant populations under a variety of environmental conditions (Barboza and Bowyer 2000).

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