Conspecific body weight, food intake, and rumination time affect food processing and forage behavior

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Much research has been directed at the chemical characteristics of plants that influence forage digestibility but there is less investigation into relationships between chewing and foraging in herbivores. The role of body size on forage processing, via chewing, and ingestive behavior is poorly understood in spite of associations between conspecific body size of ruminants and botanical and nutritional composition of their diets. I examined the implications from a relationship between body weight and absolute forage intake (kg/day) and no relationship between body weight and rumination time (h/day) on chewing behavior and feeding time (h/day). Cattle were selected as the model species because the diets presented offered benefits to digestion from increased chewing and because of the number of studies that measured body weight, daily food intake, dietary nutritional characteristics, feeding time, and rumination characteristics on the same individuals. Data were extracted from 24 studies of cattle (n ≤ 74). Absolute food intake scaled allometrically (0.75) with body weight but rumination time was unrelated to body weight, meaning smaller animals had more rumination time for a unit weight of ingesta. Correspondingly, small cattle chewed the weight-specific ingesta more and fed longer than large animals, probably because of a reduction in time of rumen turnover. These findings might be revealing as to how differences in digestion and foraging are associated with body size among conspecific animals of wild ruminant species.

Key words: chewing, diet, feeding time, Jarman–Bell principle, ruminants

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In herbivores, food intake and digestion are most often limited by the chewing, digestion, and passage of ingesta, and not by the detection and capture of food (Barboza et al. 2009). There are 2 general ways to alter forage digestibility in herbivores: change the fraction of readily digestible matter through forage selection or alter chewing behavior, which affects the rate of particle breakdown (Van Soest 1994). Much research has been directed at the chemical characteristics of plants that influence forage digestibility but there has been less investigation into relationships between chewing, forage intake, and rumination time.

Rumination, the process of repeatedly chewing ingesta that has been regurgitated from the rumen, is the primary means of reducing forage particle size (Maulfair et al. 2010; Robbins 1993; Spaling and Robbins 1986). The comminuting of forage particles increases the ratio of surface area to volume of particles, which allows gut microorganisms greater access to cell wall carbohydrates (Robbins 1993). Also, smaller particles pass more readily through the reticulo-omasal orifice and into the hind gut than large-sized particles. Thus, the rate of particle size degradation affects rate of digestion and rumen turnover (Van Soest 1994). Because rumen turnover encompasses the rate of ingesta disappearance through digestion and passage of remaining matter to the hindgut, rumen turnover influences food intake (Short 1975).

The time that animals ruminate is part of the daily (24-h) activity budget of every ruminant (Van Soest 1994). The maximum amount of time that animals ruminate is 9–11 h/day (Welch 1982), but animals can invest less time ruminating per day when the diet is low in concentrations of cell wall carbohydrates and forage particle sizes are small (Maulfair et al. 2010; Robbins 1993). What has been unexplored is how rumination time might influence feeding time while considering variation in absolute food intake (kg dry matter/day) across conspecific body sizes.

There is not a satisfactory model to examine associations among rumination, body size, and foraging patterns of conspecific animals, which is unfortunate because different-
sized conspecific animals often vary in feeding behavior (Beier and McCullough 1990; Kie and Bowyer 1999; Short et al. 1969; Staines et al. 1982). Many examinations of the role of conspecific body size on trophic interactions and food selection are founded in the Jarman–Bell principle (Bell 1970, 1971; Jarman 1974). This principle predicts that larger animals have a digestive advantage when consuming diets high in concentrations of cell wall carbohydrates because, in theory, digesta is retained long enough to allow gut microorganisms the time to ferment cell wall components that are recalcitrant to digestion (Steuer et al. 2011). However, the Jarman–Bell principle is not supported when explaining dietary patterns among conspecific animals (Gross et al. 1996; Munn and Barboza 2008; Pérez-Barbería et al. 2008). Moreover, a key assumption of this principle is isometric scaling between body weight and gut capacity, which might not occur within species (Weckerly 2010). Consequently, the Jarman–Bell principle is unsatisfactory for explaining conspecific foraging patterns.

The role of conspecific body size on foraging and digestion might benefit from understanding the implications between 2 relationships, body weight–food intake (i.e., metabolizable energy intake) and body weight–rumination time. Absolute food intake should scale allometrically (0.75) with body weight (Brody et al. 1934; Clauss et al. 2009; Kleiber 1932; Shipley et al. 1994). As such, the digesta loads (kg digesta/kg body weight) of small animals should be greater than those of large animals to meet metabolic demands. Increased chewing could increase intake of metabolizable energy; however, body weight does not have to be related to rumination time. When rumination time is independent of body weight and absolute food intake is positively related to body weight, smaller animals have more time, per unit of ingesta, to chew material (rumination time/kg food intake). If small animals have the benefit of more time, compared to large animals, to process a unit weight of food, their chews during rumination in relation to absolute food intake (relative rumination chews) should be greater and rumen turnover should be quicker. It is unclear, however, whether increased chewing by small animals is due to relative rumination chewing rate or an increased rumination chewing rate (chews during rumination/rumination time) (Storer and Williams 2011). Nonetheless, small animals should then ingest more food per unit of body weight, on a daily basis, by increasing feeding time to maximize energy intake. Devoting more time to feeding requires that rumination time is not strongly competing with feeding time. Competition between feeding time and rumination time is more likely when the required time to ruminate and forage approaches the total amount of time that animals can devote to the 2 processes.

I am calling the relationships articulated above the rumination time hypothesis. The hypothesis assumes that absolute food intake scales to the 0.75 power of body weight, that rumination time is independent of body weight, and that animals are maximizing energy intake. Predictions of the hypothesis are: relative rumination time (daily rumination time/absolute food intake) is inversely related to body weight, relative rumination chews (chews during rumination/absolute food intake) are inversely related to body weight, and daily feeding time is inversely related to body weight.

Herein I tested the assumptions about body weight relationships with absolute food intake and rumination time and predictions of the rumination time hypothesis for cattle. Also, I estimated the relationship between body weight and rumination chewing rate. Cattle are unparalleled among ruminant species in the number of studies measuring body weight, daily food intake, dietary nutritional characteristics, feeding time, and rumination characteristics of the same individuals. These studies also fed cattle prepared diets that were relatively easy to comminute and rich in digestible nutrients compared to many forages available to free-ranging cattle and other species of ruminants (Dias et al. 2011; Holand 1994; Spalinger and Robbins 1986; Van Soest 1994). If increased relative rumination time and chews are going to benefit ruminants via rate of particle breakdown then the particles should not have high concentrations of antinutritional compounds such as lignin (Holand 1994; Spalinger and Robbins 1986). Hence, the data gathered from studies on cattle provided an opportunity to test whether the rumination time hypothesis is plausible and a candidate for testing with populations of wild species of ruminants.

**Materials and Methods**

Data on live body weight, absolute food intake, hours of daily rumination, chews when ruminating, and hours of feeding were gathered from studies where these variables were measured on the same cattle. Hours of daily rumination and feeding in these studies were measured from visual observation or using devices that recorded the time animals ingested food and ruminated (regurgitated and chewed boll). Animals ranged in size from young, recently weaned, and reproductively intact (84-kg) animals; to growing females (heifers) and castrated males (steers); to full-grown and lactating females that weighed as much as 701 kg (Aikman et al. 2008; Alende et al. 2009; Beauchemin et al. 2003; Coudere et al. 2006; Dias et al. 2011; Faleiro et al. 2011; Kononoff and Heinrichs 2003; Kononoff et al. 2003; Krause et al. 2002a, 2002b; Le Liboux and Peyraud 1998; Lugtenbuhl et al. 2000; Maulfair et al. 2010; Nishida et al. 2007; Penner et al. 2009; Robles et al. 2007; Rustas et al. 2010; Schwab et al. 2002; Tager and Krause 2011; van Ackeren et al. 2009; Yang and Beauchemin 2007; Yang et al. 2001a, 2001b; Zhang et al. 2010). In these studies animals consumed a diet of hay (alfalfa or grass), silaged corn or hay, or a specially formulated ration (i.e., total mixed rations) that was offered ad libitum in a receptacle. Diets were not identical in forage particle lengths or in nutritional characteristics. To account for at least some of the variation in forage characteristics I also recorded dietary neutral detergent fiber (NDF) concentration because dietary NDF has been shown to influence food intake (Van Soest 1994). The sample sizes and number of studies for each response variable are listed in Table 1. Across the studies the
The reference category was lactating.

Sex was not considered in the fixed effects to reduce the number of parameter estimates and because initial analyses indicated that sex did not influence any response variable (95% confidence intervals of sex coefficients included 0). To estimate nonlinear relationships and to satisfy the assumption of homoscedasticity, body weight and response variables of absolute food intake, relative rumination time, relative rumination chews, and rumination time chews were given a natural logarithm transformation. Relative rumination time, relative rumination chews, and rumination chewing rate were the respective ratios of rumination time/absolute food intake, chews during rumination/absolute food intake, and chews during rumination/rumination time.

RESULTS

Rumination time was not influenced by body weight and dietary NDF but lactating individuals had less rumination time (Table 1; Fig. 1). Rumination time averaged 7.2 h (SD = 1.4 h) across the distribution of body sizes. Absolute food intake scaled to the 0.77 power of body weight and food intake was greater in lactating animals and when cattle were consuming a diet lower in NDF. Relative rumination time was inversely related to body weight and was greater in nonlactating individuals and when dietary NDF was greater. The smallest animals had more than 2 h time to ruminate, per kilogram of ingesta, compared to the largest animals (Fig. 2). Not only did smaller individuals have more rumination time per kilogram of food intake that they consumed (relative rumination time), but they also chewed a kilogram of ingesta (relative rumination chews) more times than did large cattle (Fig. 3A). Relative rumination chews also was positively influenced by dietary NDF. The greater relative chews by small cattle was not because they chewed more quickly than larger animals but because they had lower absolute food intake relative to the rumination time (Fig. 3B). I detected no relationship between body weight and rumination chew rate.

Feeding hours was inversely related to body weight (Fig. 4). The smallest animals fed almost 3 h longer than the largest cattle. Feeding hours declined when cows were not lactating but feeding time increased when individuals consumed greater dietary NDF.

DISCUSSION

The findings of my analyses indicate that the rumination time hypothesis appears plausible. Rumination time per day

![Fig. 1](image_url) — Scatterplot showing the data between body weight and rumination time (hours ruminating in 24 h) for cattle. No relationship was detected between these 2 variables.
was not related to body weight but absolute food intake scaled to the 0.75 power of body weight. The allometric scaling of food intake matches the presumed allometric scaling of metabolic demands. Consequently, rumination time was independent of body weight and smaller animals had more time to chew and took more chews, relative to food intake, than larger animals at the timescale of a day. Smaller animals also had longer feeding times than larger animals, which presumably resulted from quicker rumen turnover.

Large ruminants have been described as more efficient ruminators because they chew more ingesta in a day than smaller ruminants (Bae et al. 1983). Whether or not large animals are more efficient at rumination depends, perhaps, on how you define efficient rumination. Is efficient rumination defined by amount of ingesta chewed per unit time or by the number of chews per unit of ingesta? An interpretation of my findings is that small animals probably comminuted forage particles more quickly because they chewed ingesta more thoroughly and had a quicker rumen turnover, which provides a means for small animals to meet their greater weight-specific energetic demands than large animals. This conclusion is consistent with findings in other studies where conspecific, size-dimorphic ruminants were fed the same diet. Gross et al. (1996) found that lactating female ibex (Capra ibex) spent more time ruminating ingesta than larger adult males. The increased chewing time resulted in females digesting forage to a similar extent as males but with a quicker rumen turnover. The passage time of particles through the gastrointestinal tracts of females ranged from 1 to 14 h less than particles in the gastrointestinal tracts of males. Munn and Barboza (2008) showed that juvenile and adult nonlactating female muskoxen (Ovibos moschatus) digested forage to a similar extent but that juveniles passed forage particles through the gut more quickly (about 5.5 h). Pérez-Barbería et al. (2008) reported that nonlactating female Soay sheep (Ovis aries) had slightly quicker gut passage of forage particles (2 h less, albeit the difference was statistically nonsignificant) and higher weight-specific food intake than larger adult male sheep.

How young, weaned herbivores accommodate and process a greater weight-specific food intake is poorly understood. Understanding how herbivores accommodate and process forage is vital for understanding animal growth and how growth varies with environmental settings (Parker et al. 2009). There are 4 ways to accommodate and process a greater weight-specific food intake, although these 4 ways are not necessarily mutually exclusive (Barboza et al. 2009; Spalinger et al. 1993): select a diet that has a greater fraction of digestible matter, possess a large gut capacity to accommodate more forage, process forage quickly by accelerating rate of particle breakdown, and increase the liquid passage rate of the rumen fluid. Wild ruminants do not always have access to highly
digestible forage and so small herbivores should have adequate gut capacity and the capability to process diets to meet metabolic demands. Small ruminants probably do have greater weight-specific gut capacity than their larger conspecific counterparts (Weckerly 2010). The rumination time hypothesis is the 1st hypothesis to provide a mechanism for how small animals can comminute forage more quickly than larger animals.

A shortcoming of this study is the use of data gathered from studies where animals were provided diets in a trough. If, instead, cattle grazed pastures the foraging times would undoubtedly be longer than what is reported herein (Prendiville et al. 2010). Grazing animals have travel costs and bite sizes are probably smaller than when animals consume a prepared diet presented in a trough. Yet, 2 of the assumptions of the rumination constraint model should not be violated. Rumination time will still be unrelated to body size and there will be an allometric relationship between body size and absolute food intake. Whether animals are maximizing energy intake will be influenced by the extent to which feeding time competes with rumination time. In this study, the average time to ruminate (7.2 h) was below the maximum number of hours that cattle ruminate (~11 h—Welch 1982). It was likely then that the animals in my analysis had rumination and feeding times that were not strongly competing. Animals had the benefit of being flexible in feeding times.

Many diets in this analysis were low in NDF, which means that animals can reduce the amount of chewing to comminute forage (Spalinger and Robbins 1986). But the diets were prepared in such a way as to stimulate chewing to increase salivary secretion of sodium bicarbonate to buffer rumen pH and reduce ruminal acidosis (Maulfair et al. 2010). Because of the diets fed to cattle, chewing effectiveness was probably high. Chewing effectiveness can be defined as the rate of particle breakdown. A surrogate of chewing effectiveness is the scaling of chewing effort (chews during rumination, feeding, or both per unit weight of ingesta) with body weight. Across species of mammalian herbivores that varied by 3 orders of magnitude in body weight the chewing effort scalar was -0.85 (Shipley et al. 1994), whereas the scalar was much steeper (-1.46) in my analysis where body weight varied by less than 1 order of magnitude. The much greater chewing effort by small cattle implies these animals can comminute forage rapidly and reduce rumen turnover time. Small cattle can then devote more time to feeding to meet their weight-specific metabolic demands. The question then is do small animals in free-ranging populations of wild ruminants also have greater rumen turnover, which can allow these animals to feed longer than large animals? The answer is probably conditional on at least 2 factors, the concentration of digestible matter in forage and feeding type. If animals are consuming forage with high concentrations of antinutritional compounds such as lignin there will be few benefits to rapid particle breakdown to facilitate digestion. Also, comminution time of particles is longer and might compete with feeding time. In a variety of ruminant species, however, small animals often do feed longer or are more active than larger conspecific animals (Beier and McCullough 1990; Li and Jinag 2007; Michelena et al. 2004; Shi et al. 2003; Wichrowski et al. 2005). Usually, the dominant activity of active animals is feeding (Mooring et al. 2003, 2005; Weckerly 1993). It appears that a smaller animal feeding longer than a larger animal is evident in wild species of ruminants that were exposed to a variety of environmental and nutritional settings. The feeding type (browser, grazer, or intermediate between the 2) also might influence feeding time, which could result in competition with rumination time (Mysterud 1998). Species with the intermediate feeding type might spend more time feeding because they take a longer time selecting forage from a broader foraging niche than the other 2 feeding types.

The time that animals devote to chewing can have pronounced influences on rate of forage particle breakdown, extent that forage is digested, and rumen turnover. How processing time should covary with attributes of conspecific animals has not been explored in much detail. Most attention in the past has been directed to the digestive and foraging implications of the scaling relationships of body size to metabolic rate and gut capacity, scaling relationships that are the foundation of the Jarman–Bell principle (Bowyer 2004). Unfortunately the Jarman–Bell principle is unable to account for processing patterns of forage that have been documented in conspecific ruminants (Barboza et al. 2009; Gross et al. 1995; Holand 1994). The rumination time hypothesis might facilitate an understanding of how differences in digestion and foraging are associated with body size in conspecific ruminants.

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LITERATURE CITED


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