Journal of Animal Ecology 2001
70, 289–300

Ungulate foraging strategies: energy maximizing or time minimizing?

CARITA M. BERGMAN*, JOHN M. FRYXELL*, C. CORMACK GATES† and DANIEL FORTIN*

**Department of Zoology, University of Guelph, Guelph, Ontario N1G 2W1 Canada; and †Faculty of Environmental Design, University of Calgary, 2500 University Drive NW, Calgary, Alberta T2N 1N4, Canada*

Summary

1. Many classical models of ungulate foraging are premised on energy maximization, yet limited empirical evidence and untested currency assumptions make the choice of currency a non-trivial issue. The primary constraints on forage intake of ungulates are forage quality and availability. Using a model that incorporates these two constraints, we predicted the optimal biomass of forage patches for ungulate grazers using an energy maximizing vs. a time minimizing strategy.

2. We tested these predictions on wood bison (*Bison bison athabascae* Rhoads) grazing naturally occurring sedge (*Carex atherodes* Spreng). The digestive constraint was determined by a series of *ad libitum* feeding trials using sedge at different stages of growth. Sedge digestibility declined with biomass. *Ad libitum* intake of sedge by bison declined with sedge digestibility and thus decreased with sedge biomass. On the other hand, short-term sedge intake rates of wood bison increased with biomass.

3. Incorporation of these constraints resulted in the prediction that daily energy gain of bison should be maximized by grazing patches with a biomass of 10 g m^{-2}, whereas a bison could minimize daily foraging time needed to fulfil its energy requirement by cropping patches with a biomass of 279 g m^{-2}.

4. To test these quantitative predictions, we used a staggered mowing regime to convert even-aged stands of sedge to a mosaic of patches varying in quality and quantity. Observations of bison grazing these mosaics indicated that patches of biomass below 120 g m^{-2} were avoided, while patches of biomass 156 and 219 g m^{-2} were highly preferred, with the greatest preference for the latter.

5. These results indicate that bison were behaving as time minimizers rather than energy maximizers. Daily cropping times of free-ranging bison from the literature corroborate our results.

Key-words: *Bison bison*, energy maximization, food intake constraint, foraging strategy, time minimization.

Journal of Animal Ecology (2001) **70**, 289–300

Introduction

Constraints are crucial to foraging models (Pyke 1984; Illius & Gordon 1990), and have been used explicitly to model forage intake in large ungulates (Belovsky 1978; Illius & Gordon 1991; Fryxell 1991; Newman *et al.* 1995; Wilmshurst, Fryxell & Bergman 2000). For ruminant ungulates, the primary constraints on energy intake result from the interplay between morphological and physiological limitations of the ungulate and characteristics of the plant resource under exploitation (Arnold 1985). There is general consensus that daily food intake is limited by either the short-term rate of intake (Short 1985; Spalinger, Hanley & Robbins 1988; Andersen & Saether 1992; Spalinger & Hobbs 1992; Gross *et al.* 1993; Laca, Ungar & Demment 1994; Shipley & Spalinger 1995; Prache 1997; Woodward 1997) or the turnover rate in the gut (Westoby 1974; Hodgson, Rodrigues Capriles & Fenlon 1977; Belovsky 1978; Poppi, Minson & Ternouth 1980; Owen-Smith & Novellie 1982; Mertens 1987; Illius & Gordon 1991; Meissner & Paulsmeier 1995). Much debate has ensued, however, over which of these constraints contributes

Correspondence: Carita M. Bergman, Alberta Environment, Natural Resources Service, P.O. Box 1420, 2nd Floor Provincial Building, Pincher Creek, Alberta TOK 1W0 Canada. Tel: 403-627-1151. Fax: 403-627-4316. E-mail: dr.carey@doctor.com

most substantially to intake limitation and under which conditions they act, hence the large number of studies listed herein. Gradually, however, ecologists are recognizing that the roles of these two constraints are not mutually exclusive, but rather operate under different forage availabilities and at different time scales (Langvatn & Hanley 1993; Illius 1997).

Whereas short-term food intake often increases with plant biomass according to a type 2 functional response (Spalinger & Hobbs 1992; Gross *et al.* 1993; Wilmshurst, Fryxell & Colucci 1999), *ad libitum* intake declines with biomass due to a reduction in digesta passage rate associated with the digestion of low quality forage of senescent plants (Spalinger, Robbins & Hanley 1986; Mertens 1987; Wilmshurst *et al.* 1999). The opposing nature of these functional relationships leads to the prediction that daily energy intake should be maximized at intermediate biomass, termed the forage maturation hypothesis (McNaughton 1984, 1986; Hobbs & Swift 1988; Fryxell 1991). This model reconciles the persistent debate over the respective roles that short- and long-term intake play in controlling energy consumption. Data on biomass preferences of grazing ungulates support qualitative predictions of the forage maturation hypothesis (Hodgson 1985; Chestnutt 1992; Morris *et al.* 1993; Pfeiffer & Hartnett 1995). However, quantitative predictions have been difficult to test experimentally (Wilmshurst, Fryxell & Hudson 1995; Wilmshurst *et al.* 1999), due largely to the inherent problem of accurately measuring functional responses and passage rates of free-living ungulates in natural habitats (Langvatn & Hanley 1993).

This and many other classical models of ungulate foraging (Westoby 1974; Owen-Smith & Novellie 1982; Belovsky 1986) are premised on the strategy of energy maximization, i.e. that the assumed goal of foraging is to maximize the long-term rate of energy intake (Stephens & Krebs 1986). Yet both energy maximization and its counterpart, time minimization [a strategy in which an animal forages only long enough to obtain energy requirements, thus freeing time to partake in non-foraging activities that yield increased fitness (Schoener 1971; Hixon 1982; Ward 1992; Nonacs 1993)], represent the endpoints of a continuum of foraging behaviour (Hixon 1982) shaped by the contribution of foraging to fitness. Numerous observations based on theory and observation support such a continuum. First, recent theory suggests that simple changes in physiological state may cause foraging behaviour to vary along this continuum over time periods of less than 1 day (Newman *et al.* 1995). Secondly, habitat complexity and heterogeneity of resource abundance in time and space further imply that foraging strategies may not be constant, but also vary through time and in space. Ungulate grazers clearly face such heterogeneity (Gordon 1989; Wallis de Vries & Daleboudt 1994; Van de Koppel *et al.* 1996).

Thirdly, pure energy maximizing models based on fixed constraints (e.g. Fryxell 1991; Wilmshurst *et al.* 2000) cannot explain why ungulates with increased energy requirements are capable of increasing their energy intake in compensatory fashion. If a foraging animal is a true energy maximizer, it is not possible for that individual to increase energy intake in response to increased requirements, unless the constraints on foraging also change (i.e. constraints are flexible rather than fixed). There does appear to be some evidence for flexible digestive constraints (Van Soest 1982; Ørskov & Ryle 1990). In lactating females, the rumen expands to increase the exchange rate of metabolites with the blood, resulting in an increased efficiency in the absorption of nutritional components. Such physiological changes allow increased food intake by lactating ungulates, both domestic (Arnold 1975) and wild (Clutton-Brock *et al.* 1982; Bunnell & Gillingham 1985). Ruminants experiencing increased energy requirements due to reduced ambient temperature may experience increases in their rate of digestion, resulting in reduced retention time and thus lowered fibre digestibility, but allowing for the absorption of energy from concentrate material (cell contents) to increase.

While both these instances of flexible constraints may result in increased rates of energy absorption, the extent to which these physiological changes are capable of compensating for the increase in energy requirements is unclear. Moreover, regardless of whether the constraints are fixed or flexible, in both cases one would predict from a dual constraint model based on the influences of plant availability and quality (Fryxell 1991), that individuals experiencing such flexibility in constraints should select patches of higher biomass than they would when requirements are lower. Clearly, this is not the case. Rather, it has been observed that lactating female ungulates tend to select patches lower in biomass and graze for longer portions of the day compared to non-lactating individuals (Clutton-Brock *et al.* 1982). This paradox might be readily explained by time minimizing, a strategy in which an animal may increase foraging time and thus energy intake, to accommodate elevated energy demands at the expense of time devoted to other activities.

A fourth reason underlining the continuity of foraging strategies is the effect that changing nutritional requirements are proposed to have on the hypothetical, sigmoidal relationship between nutritional gain and fitness (Newman *et al.* 1995). Clearly, the disparity between survival of those with high vs. low energy requirements, indicates that individuals experiencing increased requirements (perhaps due to lactation, low temperature or increased activity) must re-allocate time from non-foraging activity that contributes to fitness to foraging if they are simply to survive (Newman *et al.* 1995). In other words, the proportional contribution of non-foraging activities to fitness decreases when animals experience increased nutritional requirements, resulting in a shift in foraging strategy along the continuum from time minimizing to energy maximizing.

Both models that explore the continuum between time minimizing and energy maximizing, and empirical evidence for time minimizing are, however, limited. Possibly the most extensive test of whether animals behave as time minimizers or energy maximizers was undertaken by Belovsky (1986), who examined the foraging strategies of 14 herbivorous species ranging in body mass over five orders of magnitude. Using a linear programming model based on nutritional, physiological and time constraints, he predicted herbivore diet composition. From comparison with observed diets, he concluded that all 14 species behaved as energy maximizers, despite an inability to distinguish statistically between the two strategies for two herbivore species, one of which was *Bison bison*. Moreover, Belovsky's linear programming model of optimal diet selection has since been criticized for being biologically unrealistic (Hobbs 1990), for producing results that are statistically unlikely (Hobbs 1990; Huggard 1994), and for being circular (Owen-Smith 1993, 1994, 1996). Such criticism at least raises the potential that time minimizing has not been ruled out by previous work.

Our objective is to present a generalized model of patch selection by ungulates that yields both energy maximizing and time minimizing solutions, and to illustrate mechanistically the continuum between these theoretical endpoints. To generate predictions of optimal patch selection under both scenarios, we use a quantitative formulation of the forage maturation hypothesis (Fryxell 1991), and apply it to bison grazing native forage. Bison represent an ideal test species because (1) they graze graminoid plants whose quality is low enough to constrain consumption, and (2) a previous attempt to determine whether bison behaved as energy maximizers or time minimizers produced equivocal results (Belovsky 1986). To test our predictions, we measure patch selection of bison grazing among a mosaic of patch types varying in quality and quantity of natural forage.

Methods

MODEL DESCRIPTION

The quantitative model of the forage maturation hypothesis (Fryxell 1991) is predicated on the idea that forage intake of ruminant ungulates is constrained by forage availability at low forage biomass, and by forage digestibility at high forage biomass. The availability constraint is derived as:

$$I_1 = \left(\frac{aV}{b+V}\right) T_{potential}\, Q \qquad \text{eqn 1}$$

where I_1 is daily energy intake in the absence of a digestive constraint, a and b are functional response parameters using a Michaelis–Menten formulation (maximum instantaneous forage consumption rate and the forage biomass at which consumption is one-half the maximum, respectively), V is forage biomass, $T_{potential}$ is the maximum time that could be spent cropping per day, and Q is the digestible energy content of forage.

The digestive constraint is derived as:

$$I_2 = LQ \qquad \text{eqn 2}$$

where I_2 is daily energy intake in the absence of an availability constraint, and L is *ad libitum* forage intake per day. L is expected to decline with forage biomass because Q usually declines with forage biomass (Van Soest 1982).

Applying both constraints to foraging individuals, gross energy gain (G) is derived as:

$$G = \min(I_1, I_2) \qquad \text{eqn 3}$$

The energy maximizing solution is determined as the forage biomass at which gross energy intake is highest, which occurs at the intersection of the two constraints.

Using these same constraints, we define the time minimizing solution as the numerical minimum of the relationship between daily cropping time and forage biomass. Daily cropping time ($T_{cropping}$) is computed by:

$$T_{cropping} = R/I_1 \qquad \text{eqn 4}$$

where R is the daily energy requirement. It is necessary to assume that when an animal is foraging at the optimum daily time (i.e. the minimum daily foraging time), the daily requirement lies below the digestive constraint, because by definition a constraint cannot be physically surpassed. Should this not hold true, the solution becomes the forage biomass at which the daily energy requirement intersects the digestive constraint.

STUDY SITE

This study was conducted in the Slave River Lowlands, 20 km north of Fort Smith, Northwest Territories, Canada. Research was conducted from 1 May to 31 August 1994 at the Hanging Ice Bison Facility, a government-operated, 8 km^2 enclosure containing a breeding herd of 170 wood bison. This setting gave access to animals living in a semi-wild state that were accommodated to natural patterns of feeding behaviour. Handling facilities permitted close observation of individuals during feeding experiments. The main enclosure contained vegetation natural to the area, primarily characterized by wet, sedge and dry, grassy meadows predominated by *C. atherodes*, and several *Calamagrostis* spp., respectively. Rowe (1972) and Reynolds (1987) describe the physiography and vegetation of the study area, and Reynolds, Hansen & Peden (1978) give a detailed description of meadow communities, the primary habitats used by foraging bison. Demography, food habits, and habitat use of local free-ranging bison populations are elaborated in Reynolds & Hawley (1987).

VEGETATION SAMPLING

Forage biomass of wet meadows dominated by *C. atherodes* was estimated over the growing season in each of 15 grazing exclosures measuring 5 × 7 m. Exclosures were constructed at random locations in the study area before the start of the growing season. Samples consisted of all vegetation clipped 3 cm above ground from a circular 0.3 m^2 quadrat chosen randomly without replacement in each exclosure. Samples were collected weekly in 1993, and every 2 weeks in 1994, beginning in late May at the first green flush and ending 30 August. Clipped samples were sorted into sedges, grasses and forbs. Vegetation samples were dried in a forced air drying oven at 70 °C to a constant mass and stored in sealed plastic bags. Samples were ground in a Wiley Mill to pass through a 20-mesh (1 mm) screen. Dry matter digestibility was determined following the two-stage *in vitro* procedures of Tilley & Terry (1963). Rumen liquor for the procedure was obtained from a fistulated polled Hereford cow, the much-lauded Chucky. To correct bias introduced by using cattle, rather than bison rumen liquor, we used linear least-squares regression to derive a correction factor from literature values of simultaneous estimation of cattle and bison dry matter digestion of 34 forages at early and late stages of maturity (Hawley *et al.* 1981; Plumb & Dodd 1993; $r^2 = 0{\cdot}82$, $P < 0{\cdot}001$):

$$\begin{array}{l}\text{\%Digestibility}\\ \text{by bison}\end{array} = 16{\cdot}04 + 0{\cdot}789\,(\text{\%Digestibility by cattle}) \qquad \text{eqn 5}$$

Finally, we constructed a linear least-squares regression model to relate forage digestibility to forage biomass.

AD LIBITUM FEEDING TRIALS

To assess the effect of forage quality on long-term (daily) intake of wood bison, we conducted five *ad libitum* feeding trials during the growth period of natural vegetation. Trial periods lasted 4 days and were spaced at 2-week intervals, beginning 22 June and ending 30 August 1994. This design allowed us to utilize natural changes in forage quality due to plant senescence, to produce diets spanning a full summer range of energy content. Although ideally one should conduct all feeding trials simultaneously, or randomize diet quality through time, logistical limitations prevented us from doing so, leaving open the possibility for confounding effects of other factors that vary over time. However, we had no reason to suspect that such factors influenced animal food intake in this study. Once daily during trial periods, forage was harvested from ungrazed sedge meadows composed of > 90% *C. atherodes*. A gasoline-powered brush cutter (Stihl™; London, Ontario, Canada; model FS 200) with grass blade attachment was used to mow sedge approximately 5 cm from ground level. Harvested forage was transported back to the experimental area and kept in a cool location, wrapped in a tarpaulin to prevent desiccation.

In each trial, three yearling bison were individually isolated in adjacent, 30 × 6 m paddocks separated by high visibility electric fencing. Animals were fed preweighed amounts of forage twice daily, at which time the orts were cleared from individual feeding areas and weighed. Subsamples (200 g) of forage on offer and of orts were dried at 70 °C to a constant mass and retained for determination of dry matter content and of digestibility. The amount of forage on offer was maintained approximately 10% above consumption level to assure free choice and minimal selection. Salt blocks and water were available *ad libitum*. Between experimental trials bison were not fed supplementally, but were allowed access to sedge meadows similar in composition to those mowed for experimental diets. This ensured that the effects of rumen microbe adaptation on trial results were minimal.

CALCULATION OF CONSTRAINTS

Dry matter consumption was determined as the difference between the dry matter content of forage on offer and of the orts. To compare individuals of different size, we standardized consumption on a per kilogram basis. Body mass of experimental animals was determined at the end of August from girth measurements, using the regression model of Kelsall, Telfer & Kingsley (1978). Then, using a growth rate of yearling bison of 0.44 kg day^{-1} (Berger & Peacock 1988; Renecker, Blyth & Gates 1989), we estimated body mass of individuals during each feeding trial. Dry matter intake was converted to digestible energy intake from the equation:

$$1\ \text{kg TDN} = 18{\cdot}4096\ \text{MJ DE} \qquad \text{eqn 6}$$

where TDN (total digestible nutrients) was determined as the product of the dry matter mass and digestibility of the forage consumed (National Research Council 1996). Using the regression model relating forage digestibility to forage biomass, we determined the field biomass of forage on offer in the *ad libitum* feeding trials. Using a repeated-measures analysis of variance, we looked for an effect of sedge digestibility on dry matter intake rates. Measurements of intake were repeated on three individuals at five different levels of sedge digestibility. Similarly, we examined the effect of sedge biomass on energy intake of bison in *ad libitum* feeding trials.

The availability constraint was derived from functional response data estimated in a concurrent experiment (Bergman, Fryxell & Gates 2000), and from field estimates of daily foraging time (Hudson & Frank 1987). Short-term rates of dry matter intake were converted to daily energy intake using equation 1, by multiplying them by the energy content of the forage (Q), and by the potential daily time available for cropping food ($T_{potential}$), estimated to be a maximum of 10·7 h (Hudson & Frank 1987).

Table 1. Patch characteristics of treatment blocks in experimental paddocks

Treatment	Date of mowing	Weeks of re-growth	Green biomass at start of experiment (g m^{-2})	95% confidence interval of biomass (g m^{-2})
1	3 August	2	107	11
2	27 July	3	120	21
3	20 July	4	157	25
4	13 July	5	219	25
5	Unmown	14	419	30

The daily energy requirement, *R*, used in calculation of the time minimizing solution, was determined from literature values. Christopherson, Hudson & Christopherson (1979) estimated the resting metabolic rate of yearling bison closely approximating the age and mass of bison in this study (12–15 months of age, weighing 200–230 kg), reporting 721 kJ kg$^{-0·75}$. A correction factor of 1·5 was applied to this value to allow for activity expenses incurred by free-living animals (Moen 1973).

PATCH CHOICE TRIALS

To test predictions of the foraging model, we observed patch choice of animals under controlled conditions. We used high visibility, solar-powered electric fencing to demarcate three replicate paddocks measuring 25 × 50 m, in an ungrazed sedge meadow at the beginning of the growing season. Using a Latin square design to eliminate possible bias caused by environmental gradients within paddocks, we divided each paddock into 25 blocks in a 5 × 5 design. Each week for 4 consecutive weeks, five unmown blocks were cut to approximately 15 cm with a brush cutter, the cut forage removed from the paddock, and the forage allowed to re-grow. The highest biomass treatment blocks remained unmown (Table 1). It should be recognized the cutting procedure used to manipulate patches of sedge biomass resulted in structural changes (i.e. a short stubble of possibly lower digestibility) in the sward that may have affected the foraging behaviour of bison grazing these patches. None the less, the height of grazing of bison in meadows of *C. atherodes*, both natural and mown, was observed to usually be much higher than the level of stubble (about 10–15 cm), so we assumed that possible bias was negligible.

After 6 weeks from the start of mowing, vegetation biomass was estimated in each of the 75 blocks. One destructive measure (0·3 m^2 circular clipped plot), and two non-destructive measures (vertical height of a 250-g, 0·3-m^2, circular cardboard disk; Bransby, Matches & Krause 1977; Santillan, Ocumpaugh & Mott 1979) of biomass were collected, for a total of 45 biomass estimates for each of the five treatments. Clipped forage was dried and weighed, as above. Disk height was calibrated to biomass by correlating disk height of clipped plots prior to sampling against biomass of the clipped plot. There was a strong correlation between disk height and biomass ($r^2 = 0·72$, $P < 0·001$). Disk measures of biomass were averaged with those obtained from destructive sampling for each block, and these biomass estimates were then averaged across treatments.

Six yearling wood bison maintained on ungrazed sedge meadow identical to experimental paddocks were used in the experimental trials. Animals had continuous grazing access to natural areas adjacent to the paddocks daily for 1 month prior to the trial to accommodate them to the area and to human observation. To initiate a trial, two bison were allowed to graze a paddock for 2 h, during which time we used continuous recording (Martin & Bateson 1986) to measure the time spent resident (standing, walking or lying) and grazing (head down biting forage) in each of the five mowing treatments. The order of introduction of grazing pairs was rotated between paddocks to expose each to similar forage depletion levels. While there is some controversy regarding group effects and the non-independence of group members, we assumed that interference due to group foraging (Manseau 1996) was negligible due to the limited pairing of individuals. Moreover, it was not practical to isolate individuals for such an experiment since these herd animals became obviously uncomfortable when separated from all others. Observations of patch choice were made by two observers seated on a 2·5-m raised platform located centrally on the edge of the long paddock axis. Once observations were complete, an identical second round of observations (a repeat of the experiment) was made for statistical comparison to examine whether depletion of patches was occurring. This was a concern since depletion of patches would alter patch choice over time.

Grazing times were analysed with a four-way factorial ANOVA, with treatment, individual, paddock and round as main effects. To preserve degrees of freedom, the four-way interaction was omitted. Three-way interactions were also omitted when they were found to be non-significant, and the model was run with only the lower order interactions (Cochran & Cox 1950). Because grazing time was measured as a proportion with numerous values below 0·3, data were transformed with an arcsine-square root transformation (Zar 1984). Preference was assessed using Ivlev's electivity index (Krebs 1989, p. 394). A significance level of 0·05 was used in all tests.

Results

Spring growth of *C. atherodes* meadows began in late May, with the standing crop increasing until late July

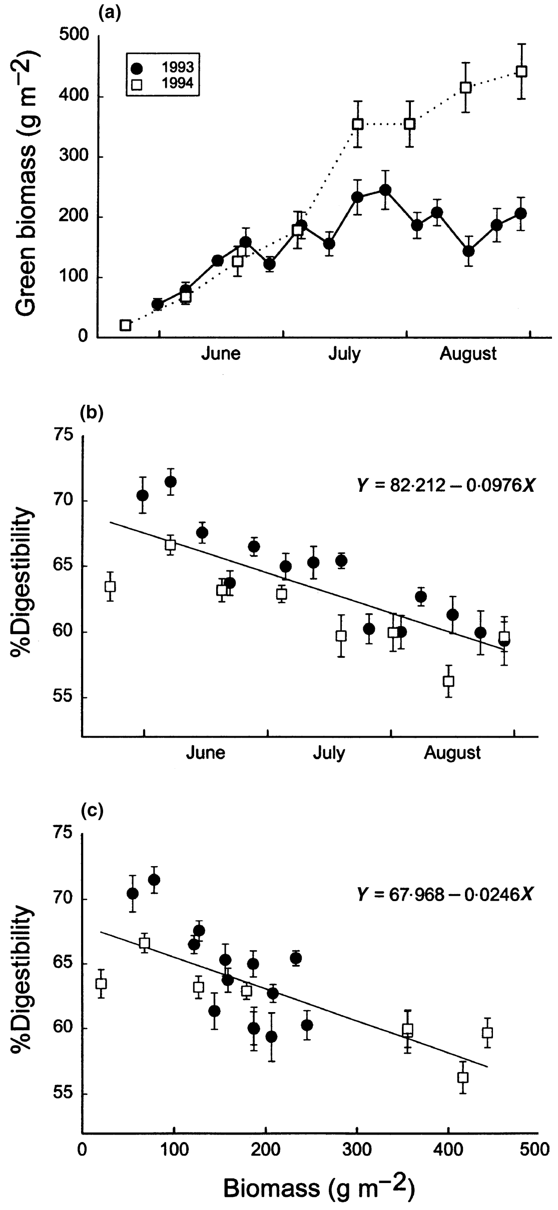

Fig. 1. (a) The change in biomass through the growing season of wet meadows dominated by *Carex atherodes*. (b) The change in digestibility of sedge meadows over the growing season. (c) The relation between sedge digestibility and biomass.

(Fig. 1a). Least-squares regression of per capita growth rate (per g dry matter per week) on biomass revealed density-dependence ($Y = 0{\cdot}65 - 0{\cdot}0034X$; $r^2 = 0{\cdot}48$, $P < 0{\cdot}01$ in 1993; $Y = 0{\cdot}46 - 0{\cdot}0012X$; $r^2 = 0{\cdot}79$, $P < 0{\cdot}01$ in 1994), and a mean August standing crop of 189 g m^{-2} and 400 g m^{-2} in 1993 and 1994, respectively. The mean depth of standing water in sample plots was 14·5 ± 3·4 cm on June 7, declining to 5·6 ± 2·8 cm on August 29 in 1993, and 43·6 ± 3·1 cm, declining to 12·5 ± 3·4 cm on the same dates in 1994. *In vitro* digestibility of *C. atherodes* was approximately 70% in late May, declining nearly 10% over the growing season to 60% at the end of August ($r^2 = 0{\cdot}62$, $P < 0{\cdot}01$; Fig. 1b). This was mirrored in the significant negative relationship between forage digestibility and forage biomass ($r^2 = 0{\cdot}53$, $P < 0{\cdot}01$; Fig. 1c).

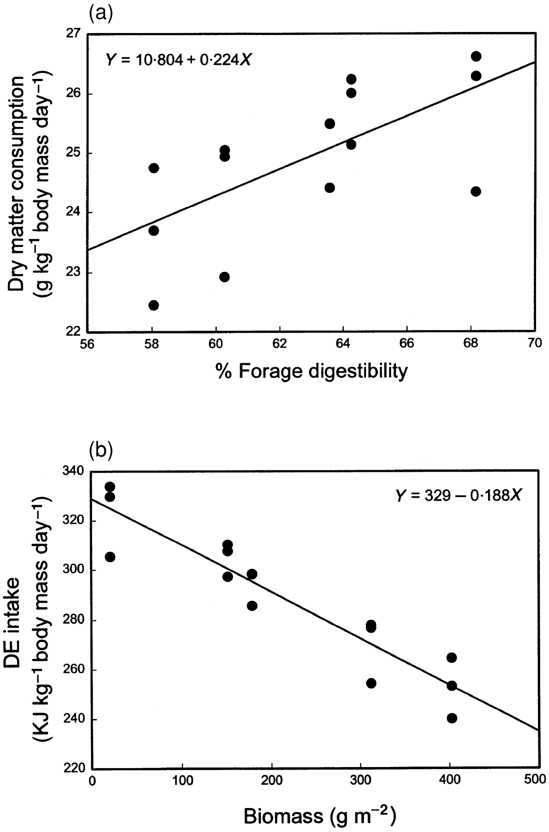

Fig. 2. (a) The relation between dry matter consumption by bison and forage digestibility in *ad libitum* feeding trials. (b) The relation between digestible energy intake of bison and forage biomass (the digestive constraint).

In the absence of an availability constraint, daily consumption of *C. atherodes* by bison was positively associated with digestibility ($r^2 = 0{\cdot}44$, $F = 5{\cdot}9$, $P = 0{\cdot}016$; Fig. 2a), and therefore negatively associated with forage biomass ($F = 3{\cdot}7$, $P = 0{\cdot}050$). Digestible energy intake by bison declined significantly from 325 kJ day^{-1} kg^{-1} body mass at a forage biomass of 20 g m^{-2}, to 250 kJ day^{-1} kg^{-1} body mass at a biomass of 400 g m^{-2} ($r^2 = 0{\cdot}87$, $F = 17{\cdot}2$, $P = 0{\cdot}001$; Fig. 2b).

Whereas short-term food intake was a monotonically saturating function of sedge biomass (Fig. 3), energy consumption actually declined at high biomass, due to the maturational decline in forage digestibility, an effect that is swamped at low biomass due to the rapid type 2 increase in forage consumption (Fig. 4). Thus, the availability constraint (instantaneous energy consumption) was a hump-shaped function of biomass (Fig. 4).

The energy maximizing model predicted that maximum daily energy intake occurs at a forage biomass of 10 g m^{-2}, assuming a daily cropping time of 10·7 h (Fig. 4). In contrast, the time minimizing model predicted that a minimum daily cropping time of approximately 3 h, while simultaneously meeting energy requirements, would be achieved at a forage biomass of 279 g m^{-2} (Fig. 5). Thus, we predicted that bison behaving as time minimizers would select food patches with a biomass nearly 30 times higher than would those

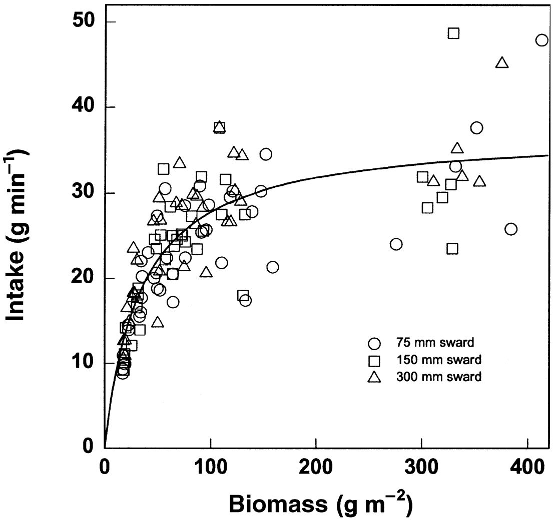

Fig. 3. The functional response obtained from observations of food intake rates of six yearling bison grazing hand-constructed, variable height swards of *C. atherodes* leaf tissue (from Bergman *et al.* 2000). The functional response was parameterized according to the Michaelis–Menten formulation. The parameters a, the maximum intake rate, and b, the half-saturation constant, were estimated with non-linear least squares methods to be 37·8 ± 6·5 g min^{-1} and 35·4 ± 12·2 g (means ± 95% confidence intervals). The non-linear regression coefficient was 0·92.

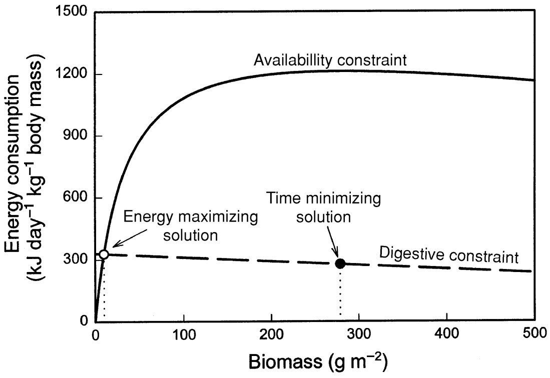

Fig. 4. Short-term intake increases with forage biomass leading to a monotonically decelerating availability constraint (solid line). Passage rate declines with biomass due to concomitant decline in forage quality, resulting in a negative relationship between long-term intake and biomass (dashed line). Net energy gain follows the minimum of the two constraints; thus, the biomass (10 g m^{-2}) at which energy intake is maximized corresponds to the peak (open circle) of the net gain function. The time minimizing solution (derived in Fig. 5) is indicated by the filled circle for comparison.

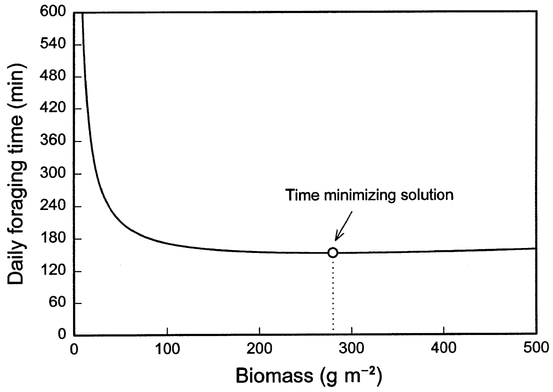

Fig. 5. Prediction of daily foraging time of a time minimizing bison as a function of biomass. Daily foraging time takes a minimum value (open circle) when patch biomass is 279 g m^{-2}.

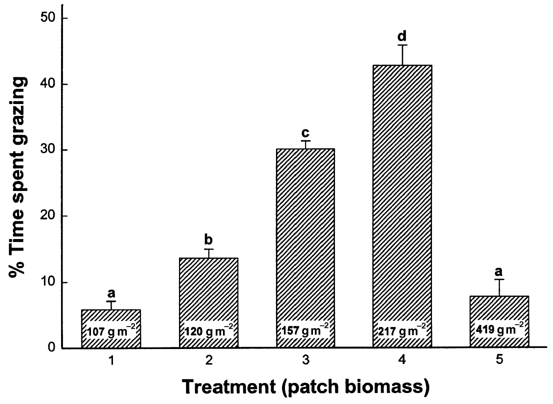

Fig. 6. Allocation of grazing time by bison in patches of sedge according to resource abundance. Treatments on the x-axis are ranked in order of increasing mean patch biomass, as indicated in bold on each bar (see Table 1). Differing letters above each bar indicate significant differences according to *post hoc* tests.

behaving as energy maximizers. In addition, a time minimizer would be expected to crop bites for only 3 h per day, contrasting with 10·7 h per day for an energy maximizer, a saving of nearly 8 h.

Observations of patch selection by bison suggested that they behaved according to a time minimizing strategy. Estimates of patch biomass in experimental treatments ranged between 107 and 419 g m^{-2} (Table 1). Treatment 1, with a biomass of 107 g m^{-2}, was closest to the energy maximizing solution. Treatment 4, with a biomass of 219 g m^{-2}, was closest to the time minimizing solution. Treatment (i.e. patch biomass) was the only factor to significantly affect grazing time of bison ($F_{4,118}$ = 74·76, P < 0·001; Table 2).

That the factor round was non-significant ($F_{1,118}$ = 0·01, P = 0·908; Table 2) indicated that depletion due to grazing was minor and did not affect the patch preference of grazing bison over the trial interval. *Post hoc* Tukey tests (α = 0·05) indicated that grazing time in all treatments except for the shortest treatment 1 and tallest treatment 5 significantly differed from one another. Bison spent the most time grazing in patches with 5 weeks of re-growth, corresponding to a biomass of 219 g m^{-2}, and significantly lesser amounts of time grazing patches of higher and lower biomass (Fig. 6). An analysis of preference using Ivlev's electivity index revealed that Treatments 3 and 4 corresponding to patch biomass of 157 and 219 g m^{-2} were preferred (Fig. 7). Of the five treatments used in our study, treatments 1 and 2 comprised patch biomass that could potentially be associated with the energy maximizing solution. However, these two treatments were avoided by grazing bison (Fig. 7).

Table 2. Statistical results of four-way ANOVA on grazing time of bison

Source of variation	Sum of squares	Degrees of freedom	Mean square	*F*-ratio	*P*-value
Treatment	6·534	4	1·634	74·761	0·000
Animal	0·021	5	0·004	0·191	0·964
Paddock	0·005	2	0·002	0·107	0·899
Round	0·000	1	0·000	0·013	0·908
Paddock × round	0·000	2	0·000	0·003	0·996
Animal × paddock	0·020	10	0·002	0·104	0·999
Animal × round	0·004	5	0·001	0·045	0·999
Treatment × round	0·200	4	0·051	2·258	0·040
Treatment × paddock	0·266	8	0·033	1·178	0·101
Treatment × animal	1·004	20	0·050	2·596	0·001
Error	2·284	118	0·019		

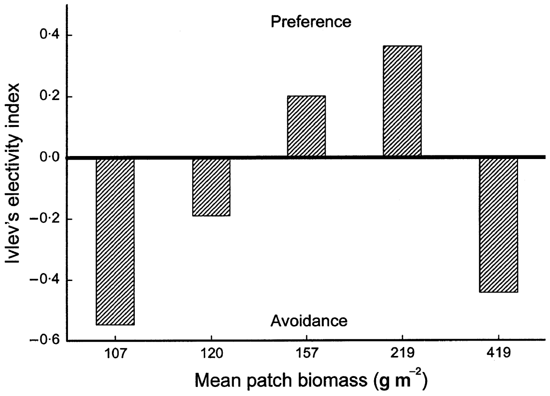

Fig. 7. In grazing trials, bison preferred grazing patches with mean biomass 157 and 219 g m^{-2}, and avoided grazing patches with higher or lower biomass. Preference was determined using Ivlev's electivity index.

Discussion

Our results indicate that bison behaved as time minimizers. They showed strong preference for patches of intermediate biomass greater than that expected for energy maximizers. It should be noted, however, that there are two time scales implied by the nature of the constraints incorporated into the model presented here: the availability constraint utilizes the functional response, a measure of instantaneous intake, whereas the digestive constraint embodies forage intake measured over several days. The importance of temporal scale in optimization studies has been emphasized previously (Templeton & Lawlor 1981; Gass & Roberts 1992), and it is generally agreed that averages of net energy accumulation should be calculated over an extended period (Stephens & Krebs 1986). Thus, we have identified bison as time minimizers on the longest temporal scale, while they implicitly behave as energy maximizers over short periods by foraging at maximum instantaneous rates. Obviously, if one's goal is to minimize daily foraging time, it is conceivable that one should feed at a maximum short-term rate. It is rare that both long- and short-term intake are measured simultaneously for ungulates, and such data are especially scarce for non-domesticated ungulates grazing natural plant species. Thus, the results of this study represent a novel contribution to our knowledge of ungulate foraging.

In contrast to our results, classical models of ungulate foraging favour energy maximization as the currency of choice, and there appears to be some empirical evidence that this is so (sheep: Black & Kenney 1984; red deer and cattle: van Wieren 1996; goats: Illius *et al.* 1999). Closer examination reveals, however, that observations of energy intake in these studies were made over short time periods in the order of minutes, corresponding to instantaneous intake rates. Thus, there is no conflict with our results: these studies simply confirm the validity of our assumption that bison are foraging at a maximum instantaneous rate. While time minimizing and energy maximizing are often viewed as endpoints of a continuum, it is not commonly recognized that the continuum also represents a gradient of temporal scales over which energy intake is measured. The widespread recognition of many animals as energy maximizers (Belovsky, Fryxell & Schmitz 1999) is an empty truth, since at some time scale it is inevitable that this is so. The wide range of temporal scales characterizing studies that draw energy maximizing conclusions provides strong support for this observation.

However, one recent study suggests that foraging ungulates might not always maximize their short-term intake. Iason *et al.* (1999) found that sheep with a daily foraging time constraint were able to increase their instantaneous intake rate compared with those given unlimited time to graze. If this were true for bison, for instance because of reduced cropping rates due to foraging on complex swards (Bergman *et al.* 2000), it is possible bison are still behaving as time minimizers, but that the minimum time to reach satiety is increased due to the depressed instantaneous rate of intake. This explanation accounts for the disparity between observed daily cropping times of bison (3 h; Belovsky & Slade 1986) and the much longer daily foraging time inclusive of other foraging behaviour such as chewing and walking between patches observed in other studies of bison foraging (10·7 h; Hudson & Frank 1987). Interestingly, the model of daily cropping time presented here (Fig. 5) is well supported by empirical evidence in the literature (Trudell & White 1981), and the predicted minimum value for bison (slightly less than 3 h) corresponds almost exactly to that observed by Belovsky & Slade (1986) for bison foraging on pastures of intermediate to high biomass (2·97 h). Thus, our simple model of daily foraging time may be useful for predicting daily cropping times of free-ranging ungulates on patches of different biomass.

Using diet composition as a choice criterion in his model of herbivore foraging, Belovsky (1986) tested energy maximizing and time minimizing hypotheses for 14 species of herbivores. While the majority of species examined appeared to be energy maximizers, the results for several species were ambiguous. For bison grazing pastures with mean biomass of 189 g m^{-2}, he found the observed diet, composed almost exclusively of monocot species, was not significantly different from that expected from either time minimizing or energy maximizing strategies. Our study examines the same hypothesis on a finer scale: assuming that the diet is composed of monocot plants, we are able to clarify that the foraging strategy of bison corresponds to that of a time minimizer.

In consideration of the shallow slope of a large portion of the daily foraging time curve, it is interesting to examine the effect of variation in parameter values on the optimal solution. An increase in R, the daily energy requirement, would result in a shift of the daily foraging time curve (Fig. 5) upwards (and vice versa for a decrease in R); the optimal solution (i.e. the minimum daily foraging time), however, remains constant. On the other hand, changes in I_1, the rate of short-term intake, have the potential to influence the location of the optimal solution along the daily foraging time curve. None the less, it is unlikely that overlap occurs between the shallow portion of the daily foraging time curve and the energy maximizing solution which lies far to the left. The fact remains that patch choice by bison resulted in a clear rejection of the energy maximizing hypothesis (Fig. 7), but was consistent with the time minimizing hypothesis. Should we have expected such a close match between prediction and observation given the shallowness of the predictive curve? Natural selection always favours a gradient, no matter how slight; the evolutionary time required to reach a gradient extreme is simply a function of the gradient steepness. Moreover, shallowness of the observed gradient allows for large short-term plasticity in foraging behaviour with relatively little cost to the individual, a phenomenon that is still poorly understood. Indeed, Belovsky (1990) underlines the importance of sensitivity in optimal foraging models, stating that they should be capable of describing why we observe such drastic behavioural variability in natural systems. Our model provides an explanation for this plasticity and pinpoints which parameters should be more closely examined for more detailed mechanistic explanation.

Given that energy maximization is the favoured paradigm incorporated by ungulate foraging models, it is useful to examine the numerous intrinsic or extrinsic factors that might favour time minimization. First, biting flies are notorious for harassment of northern ungulates during the summer (bison: Melton *et al.* 1989; caribou: Toupin, Huot & Manseau 1996; Morschel & Klein 1997). At high levels of black fly (*Simuliidae*) infestation, wood bison decrease their daily foraging time by up to 15% (Melton *et al.* 1989). Caribou also show significant reductions in foraging time due to insect harassment (Toupin *et al.* 1996). This would favour both the short-term maximization of energy intake as well as a long-term minimization of foraging time.

Similarly, foraging time decreases during the breeding season for both male and female bison, and increases beyond normal levels at the conclusion of breeding (Melton *et al.* 1989). Not only does the decrease at breeding support a time minimizing strategy, but the increase during the post-breeding period suggests that bison are not long-term energy maximizers outside the breeding period, since daily foraging time would then already be at a maximum. Thirdly, the thermal physiology of ungulates also favours time minimizing (Schmitz 1991). There is a strong negative relation between activity/feeding time and temperature for ungulates (moose: Belovsky 1978; bighorn sheep, bison, elk, pronghorn, white-tailed deer, mule deer: Belovsky & Slade 1986; bison: Melton *et al.* 1989).

Fourthly, social behaviour can be a prominent feature of gregarious wild ungulates, much more so than in cattle (Soper 1941). Dominance rank is crucial to the breeding success of mature male bison, since the highest ranked bulls breed with the majority of receptive cows (Lott 1979; Komers, Messier & Gates 1992, 1994; Wolff 1998). For female bison, foraging success is related to dominance status (Lott & Galland 1987). Thus, the time necessary for individual bison to obtain and maintain status within social groups may be a wise investment in maximizing fitness. Fifthly, although large-bodied ungulates are less vigilant than smaller ungulates (Berger & Cunningham 1988), predation is a significant limiting factor of their populations (Oosenberg & Carbyn 1985; Bergerud 1988). The probability of being preyed upon decreases with body mass, such that calves experience the highest rates of predation, cows an intermediate level, and bulls the lowest (Soper 1941; Carbyn 1997). Thus, one might predict that larger-bodied animals would forage on patches of lower biomass for longer times, since the risk of predation is lower. In sum, these numerous examples of time-consuming activities in which ungulates participate to increase their fitness are supportive of our finding that bison appear to behave as time minimizers during foraging.

While it is possible to model direct energetic costs as a function of biomass (Fryxell 1991), it is somewhat more difficult to estimate the costs of non-foraging activities such as vigilance, reproduction, social interaction or insect harassment. These activities are associated with a certain unit cost, but this cost may change disproportionately with the amount of time spent foraging. For example, while foraging on patches of high biomass, vigilance (i.e. lifting the head to scan for predators) may be carried out in the time utilized to chew bites that have already been cropped (Illius & Fitzgibbon 1994). In contrast, while foraging on patches of low biomass where cropping and chewing may be simultaneous (Laca *et al.* 1994), foraging may have to be slowed or stopped completely in order to lift the head and scan for predators. In essence, vigilance may be free of cost at high biomass, but not at low biomass (Illius & Fitzgibbon 1994). The same may also be true for insect harassment and for some forms of social interaction, such as patch defence. While the difficulty of calculating these costs in equivalent currencies currently precludes their use in optimization models, it highlights the possibility that costs of many activities may be much greater when grazing plant patches of low biomass. Thus, in some circumstances the true energy maximizing solution may be somewhat higher than estimated here, making it possible that it may coincide with the time minimizing solution (Hixon 1982).

Our model makes additional predictions that are relevant to patch selection of grazing ungulates. For instance, the inclusion of costs of non-foraging activities that increase greatly at low biomass are likely to decrease the variance around the time minimizing optimal biomass. While our presentation of this model shows a relatively flat slope around the optimum, the inclusion of such activities would mean much greater costs and/or less benefits if optimum patch biomass is not adhered to. Such would also be the case on hot summer days, since daily grazing time of ungulates can be severely affected by thermoregulatory limits (Schmitz 1991). Further, ungulates with increased energy requirements should graze in patches of lower biomass. This is an important prediction, because there is some evidence of spatial partitioning of animals on the basis of sex (Bowyer 1984; Main & Coblentz 1990; Conradt 1998; Ruckstuhl 1998). Moreover, our model explains the apparent paradox that animals with increased energetic demands may compensate by increasing energy intake. While lactating animals could theoretically adhere to a time minimizing strategy and obtain their higher requirements by foraging for a longer time, this is not actually possible, since they become limited by digestive capacity almost immediately (Fig. 4). Thus, they are forced to select patches of lower biomass that are more easily digested and therefore show a concomitant increase in daily foraging time. This prediction is supported by comparisons of habitat selection of lactating and non-lactating female ungulates (Clutton-Brock *et al.* 1982; Crête, Huot & Gauthier 1990).

In sum, our results call into question the widely favoured paradigm of energy maximization for ungulate foragers. Such a paradigm has developed through a focus on digestive and availability constraints and their role in predicting energy intake, whereas time constraints have largely been overlooked. We speculate that bison may have evolved in an environment where foraging time competes directly with other activities affecting total fitness, and explains why we found that bison behave as time minimizers, even outside their breeding period.

Acknowledgements

Many thanks to Rita Antoniak, Nadele Flynn, Indrani Ghosh, Derek Haley, Jonathan Kenny, Emma White, Karla Williamson and Anita Young for their laborious hours in the field, and to Troy Ellsworth and the staff at the Department of Renewable Resources in Fort Smith, Northwest Territories for logistical assistance, guidance and steadfast support. John Frederick Wilmshurst was an instrumental critic of this work at all stages. Thanks also to Cheryl Campbell and the numerous volunteers who assisted with *in vitro* analyses. Our research was supported by grants from the Natural Sciences and Engineering Research Council of Canada, the Department of Renewable Resources for the Northwest Territories, the Association of Canadian Universities for Northern Studies, the Canadian Wildlife Service and the Sigma Xi Scientific Society.

References

Andersen, R. & Saether, B.E. (1992) Functional response during winter of a herbivore, the moose, in relation to age and size. *Ecology*, **73**, 542–550.

Arnold, G.W. (1975) Herbage intake and grazing behaviour in cows of four breeds at different physiological states. *Australian Journal of Agricultural Research*, **21**, 755–766.

Arnold, G.W. (1985) Regulation of forage intake. *Bioenergetics of Wild Herbivores* (eds R.J. Hudson & R.G. White), pp. 81–101. CRC Press, Boca Raton, Florida, USA.

Belovsky, G.E. (1978) Diet optimization in a generalist herbivore: the moose. *Theoretical Population Biology*, **14**, 105–134.

Belovsky, G.E. (1986) Optimal foraging and community structure: implications for a guild of generalist grassland herbivores. *Oecologia*, **70**, 35–52.

Belovsky, G.E. (1990) A reply to Hobbs. *Behavioural Mechanisms of Food Selection* (ed. R.N. Hughes), pp. 415–422. NATO ASI Series. Springer-Verlag, New York, USA.

Belovsky, G.E., Fryxell, J.M. & Schmitz, O.J. (1999) Natural selection and herbivore nutrition: optimal foraging theory and what it tells us about the structure of ecological communities. *Nutritional Ecology of Herbivores: Proceedings of the Vth International Symposium on the Nutrition of Herbivores* (eds H.-J. Jung & G. Fahey), pp. 1–70. American Society of Animal Science, Savoy, Illinois, USA.

Belovsky, G.E. & Slade, J.B. (1986) Time budgets of grassland herbivores: body size similarities. *Oecologia*, **70**, 53–62.

Berger, J. & Cunningham, C. (1988) Size-related effects on search times in North American grassland female ungulates. *Ecology*, **69**, 177–186.

Berger, J. & Peacock, M. (1988) Variability in size–weight relationships of *Bison bison*. *Journal of Mammalogy*, **69**, 618–624.

Bergerud, A.T. (1988) Caribou, wolves and man. *Trends in Ecology and Evolution*, **3**, 68–72.

Bergman, C.M., Fryxell, J.M. & Gates, C.C. (2000) The effect of tissue complexity and sward height on the functional response of wood bison. *Functional Ecology*, **14**, 61–69.

Black, J.L. & Kenney, P.A. (1984) Factors affecting diet selection by sheep. II. Height and density of pasture. *Australian Journal of Agricultural Research*, **35**, 551–563.

Bowyer, R.T. (1984) Sexual segregation in southern mule deer. *Journal of Mammalogy*, **65**, 410–417.

Bransby, D.I., Matches, A.G. & Krause, G.F. (1977) Disk meter for rapid estimation of herbage yield in grazing trials. *Agronomy Journal*, **69**, 393–396.

Bunnell, F.L. & Gillingham, M.P. (1985) Foraging behaviour: dynamics of dining out. *Bioenergetics of Wild Herbivores* (eds R.J. Hudson & R.G. White), pp. 53–79. CRC Press, Boca Raton, Florida, USA.

Carbyn, L.N. (1997) Some aspects regarding wolf predation on bison in Wood Buffalo National Park. *Proceedings of the International Symposium on Bison Ecology and Management in North America*, pp. 92–95. Bozeman, Montana, USA.

Chestnutt, D.M.B. (1992) Effect of sward surface height on the performance of ewes and lambs continuously grazed on grass/clover and nitrogen-fertilized grass swards. *Grass and Forage Science*, **47**, 70–80.

Christopherson, R.J., Hudson, R.J. & Christopherson, M.K. (1979) Seasonal energy expenditures and thermoregulatory responses of bison and cattle. *Canadian Journal of Animal Science*, **59**, 611–617.

Clutton-Brock, T.H., Iason, G.R., Albon, S.D. & Guinness, F.E. (1982) The effects of lactation on feeding behaviour and habitat use of wild red deer hinds. *Journal of Zoology*, **198**, 227–236.

Cochran, W.G. & Cox, G.M. (1950) *Experimental Design*. Chapman & Hall, London, UK.

Conradt, L. (1998) Could asynchrony in activity between the sexes cause intersexual social segregation in ruminants? *Proceedings of the Royal Society of London, Series B*, **265**, 1359–1363.

Crête, M., Huot, J. & Gauthier, L. (1990) Food selection during early lactation by caribou calving on the tundra in Québec. *Arctic*, **43**, 60–65.

Fryxell, J.M. (1991) Forage quality and aggregation by large herbivores. *American Naturalist*, **138**, 478–498.

Gass, L.C. & Roberts, W.M. (1992) The problem of temporal scale in optimization: three contrasting views of hummingbird visits to flowers. *American Naturalist*, **140**, 829–853.

Gordon, I.J. (1989) Vegetation community selection by ungulates on the Isle of Rhum. III. Determinants of vegetation community selection. *Journal of Applied Ecology*, **26**, 65–79.

Gross, J.E., Shipley, L.A., Hobbs, N.T., Spalinger, D.E. & Wunder, B.A. (1993) Functional response of herbivores in food-concentrated patches: tests of a mechanistic model. *Ecology*, **74**, 778–791.

Hawley, A.W.L., Peden, D.G., Reynolds, H.W. & Stricklin, W.R. (1981) Bison and cattle digestion of forages from the Slave River Lowlands, Northwest Territories, Canada. *Journal of Range Management*, **34**, 136–130.

Hixon, M.A. (1982) Energy maximizers and time minimizers: theory and reality. *American Naturalist*, **119**, 596–599.

Hobbs, N.T. (1990) Diet selection by generalist herbivores: a test of the linear programming model. *Behavioural Mechanisms of Food Selection* (ed. R.N. Hughes), pp. 395–413. NATO ASI Series. Springer-Verlag, New York, USA.

Hobbs, N.T. & Swift, D.M. (1988) Grazing in herds: when are nutritional benefits realized? *American Naturalist*, **131**, 760–764.

Hodgson, J. (1985) The control of herbage intake in the grazing ruminant. *Proceedings of the Nutrition Society*, **44**, 339–346.

Hodgson, J., Rodrigues Capriles, J.M. & Fenlon, J.S. (1977) The influence of sward characteristics in the herbage intake of grazing cattle. *Journal of Agricultural Science*, **89**, 743–750.

Hudson, R.J. & Frank, S. (1987) Foraging ecology of bison in aspen boreal habitats. *Journal of Range Management*, **40**, 71–75.

Huggard, D.J. (1994) A linear programming model of herbivore foraging: imprecise, yet successful? *Oecologia*, **100**, 470–474.

Iason, G.R., Mantecon, A.R., Sim, D.A., Gonzalez, J., Foreman, E., Bermudez, F.F. & Elston, D.A. (1999) Can grazing sheep compensate for a daily foraging time constraint? *Journal of Animal Ecology*, **68**, 87–93.

Illius, A.W. (1997) Advances and retreats in specifying the constraints on intake in grazing ruminants. XVIII International Grasslands Congress, Saskatoon, Saskatchewan.

Illius, A.W. & Fitzgibbon, C. (1994) Costs of vigilance in foraging ungulates. *Animal Behavior*, **47**, 481–484.

Illius, A.W. & Gordon, I.J. (1990) Constraints on diet selection and foraging behaviour in mammalian herbivores. *Behavioural Mechanisms of Food Selection* (ed. R.N. Hughes), pp. 369–393. NATO ASI Series. Springer-Verlag, New York, USA.

Illius, A.W. & Gordon, I.J. (1991) Prediction of intake and digestion in ruminants by a model of rumen kinetics integrating animal size and plant characteristics. *Journal of Agricultural Science*, **116**, 145–157.

Illius, A.W., Gordon, I.J., Elston, D.A. & Milne, J.D. (1999) Diet selection in goats: a test of intake-rate maximization. *Ecology*, **80**, 1008–1018.

Kelsall, J.P., Telfer, E.S. & Kingsley, M. (1978) Relationship of bison weight to chest girth. *Journal of Wildlife Management*, **42**, 659–661.

Komers, P.E. (1994) Plasticity of reproductive behaviour in wood bison bulls: when subadults are given a chance. *Ethology, Ecology and Evolution*, **6**, 313–330.

Komers, P.E., Messier, F. & Gates, C.C. (1992) Search or relax: the case of bachelor wood bison. *Behavioral Ecology and Sociobiology*, **31**, 195–203.

Krebs, C.J. (1989) *Ecological Methodology*. HarperCollins, New York, USA.

Laca, E.A., Ungar, E.D. & Demment, M.W. (1994) Mechanisms of handling time and intake rate of a large mammalian grazer. *Applied Animal and Behaviour Science*, **39**, 3–19.

Langvatn, R. & Hanley, T.A. (1993) Feeding-patch choice by red deer in relation to foraging efficiency: an experiment. *Oecologia*, **95**, 164–170.

Lott, D.F. (1979) Dominance relations and breeding rate in mature male American bison. *Zoologica Tierpsychologica*, **49**, 418–432.

Lott, D.F. & Galland, J.C. (1987) Body mass as a factor influencing social status in American bison cows. *Journal of Mammalogy*, **68**, 683–685.

Main, M.B. & Coblentz, B.E. (1990) Sexual segregation among ungulates: a critique. *Wildlife Society Bulletin*, **18**, 204–210.

Manseau, M. (1996) *Relation réciproque entre les caribous et la végétation des aires d'estivage: le cas du troupeau de caribous de la rivère George*. PhD Thesis, Université Laval, Québec.

Martin, P. & Bateson, P. (1986) *Measuring Behaviour: an introductory guide*. Cambridge University Press, Cambridge, UK.

McNaughton, S.J. (1984) Grazing lawns: animals in herds, plant form, and coevolution. *American Naturalist*, **124**, 863–886.

McNaughton, S.J. (1986) Grazing lawns: on domesticated and wild grazers. *American Naturalist*, **128**, 937–939.

Meissner, H.H. & Paulsmeier, D.V. (1995) Plant compositional constituents affecting between-plant and animal species prediction of forage intake. *Journal of Animal Science*, **73**, 2447–2457.

Melton, D.A., Larter, N.C., Gates, C.C. & Virgal, J.A. (1989) The influence of rut and environmental factors on the behaviour of wood bison. *Acta Theriologica*, **34**, 179–193.

Mertens, D.R. (1987) Predicting intake and digestibility using mathematical models of ruminal function. *Journal of Animal Science*, **64**, 1548–1558.

Moen, A.N. (1973) *Wildlife Ecology: an analytical approach*. W.H. Freeman, San Francisco, California, USA.

Morris, S.T., Hirschberg, S.W., Michel, A., Parker, W.J. & McCutcheon, S.N. (1993) Herbage intake and liveweight gain of bulls and steers continuously stocked at fixed sward heights during autumn and spring. *Grass and Forage Science*, **48**, 109–117.

Morschel, F.M. & Klein, D.R. (1997) Effects of weather and parasitic insects on behavior and group dynamics of caribou of the Delta herd, Alaska. *Canadian Journal of Zoology*, **75**, 1659–1670.

National Research Council (Subcommittee on Beef Cattle Nutrition) (1996) *Nutrient Requirements of Beef Cattle*. National Academy Press, Washington.

Newman, J.A., Parsons, A.J., Thornley, J.H.M., Penning, P.D. & Krebs, J.R. (1995) Optimal diet selection by a generalist grazing herbivore. *Functional Ecology*, **9**, 255–268.

Nonacs, P. (1993) Is satisficing an alternative to optimal foraging theory? *Oikos*, **67**, 371–375.

Oosenberg, S. & Carbyn, L.N. (1985) *Wolf Predation on Bison in Wood Buffalo National Park*. Canadian Wildlife Service Report, Edmonton, Alberta, Canada.

Ørskov, E.R. & Ryle, M. (1990) *Energy Nutrition in Ruminants*. Elsevier Applied Science, London, UK.

Owen-Smith, N. (1993) Evaluating optimal diet models for an African browsing ruminant, the kudu: how constraining are the assumed constraints? *Evolutionary Ecology*, **7**, 499–524.

Owen-Smith, N. (1994) Foraging responses of kudus to seasonal changes in food resources: elasticity in constraints. *Ecology*, **75**, 1050–1062.

Owen-Smith, N. (1996) Circularity in linear programming models of optimal diet. *Oecologia*, **108**, 259–261.

Owen-Smith, N. & Novellie, P. (1982) What should a clever ungulate eat? *American Naturalist*, **19**, 151–178.

Pfeiffer, K.E. & Hartnett, D.C. (1995) Bison selectivity and grazing response of little bluestem in tallgrass prairie. *Journal of Range Management*, **48**, 26–41.

Plumb, G.E. & Dodd, J.L. (1993) Foraging ecology of bison and cattle on a mixed prairie: implications for natural area management. *Ecological Applications*, **3**, 631–643.

Poppi, D.P., Minson, D.J. & Ternouth, J.H. (1980) Studies of cattle and sheep eating leaf and stem fractions of grasses. The voluntary intake, digestibility and retention time in the reticulo-rumen. *Australian Journal of Agricultural Research*, **32**, 99–108.

Prache, S. (1997) Intake rate, intake per bite and time per bite of lactating ewes on vegetative and reproductive swards. *Applied Animal and Behaviour Science*, **52**, 53–64.

Pyke, G.H. (1984) Optimal foraging theory: a critical review. *Annual Review of Ecology and Systematics*, **15**, 523–575.

Renecker, L.A., Blyth, C.B. & Gates, C.C. (1989) Game production in western Canada. *Wildlife Production Systems*, Chapter 13 (eds R.J. Hudson, K.R. Drew & L.M. Baskin). Cambridge University Press, Cambridge, UK.

Reynolds, H.W. (1987) Description of the Slave River lowlands. *Bison Ecology in Relation to Agricultural Development in the Slave River Lowlands, N.W.T* (eds H.W. Reynolds & A.W.L. Hawley). Occasional Paper no. 63. Canadian Wildlife Service, Edmonton, Alberta, Canada.

Reynolds, H.W., Hansen, R.M. & Peden, D.G. (1978) Diets of Slave River Lowland bison herd, Northwest Territories, Canada. *Journal of Wildlife Management*, **42**, 581–590.

Reynolds, H.W. & Hawley, A.W.L. (1987) Seasonal variation in forage quality. *Bison Ecology in Relation to Agricultural Development in the Slave River Lowlands, N.W.T.* (eds H.W. Reynolds & A.W.L. Hawley). Occasional Paper No. 63. Canadian Wildlife Service, Edmonton, Alberta, Canada.

Rowe, J.S. (1972) *Forest Regions of Canada*. Publication No. 1300. Department of the Environment, Canadian Forestry Service, Ottawa.

Ruckstuhl, K.E. (1998) Foraging behaviour and sexual segregation in bighorn sheep. *Animal Behaviour*, **56**, 99–106.

Santillan, R.A., Ocumpaugh, W.R. & Mott, G.O. (1979) Estimating forage yield with a disk meter. *Agronomy Journal*, **71**, 71–74.

Schmitz, O.J. (1991) Thermal constraints and optimization of winter feeding and habitat choice in white-tailed deer. *Holarctic Ecology*, **14**, 104–111.

Schoener, T.W. (1971) Theory of feeding strategies. *Annual Review of Ecology and Systematics*, **2**, 369–404.

Shipley, L.A. & Spalinger, D.E. (1995) Influence of size and density of browse patches on intake rates and foraging decisions of young moose and white-tailed deer. *Oecologia*, **104**, 112–121.

Short, J. (1985) The functional response of sheep, kangaroos and rabbits in an arid grazing system. *Journal of Applied Ecology*, **22**, 435–447.

Soper, J.D. (1941) History, range, and home life of the northern bison. *Ecological Monographs*, **11**, 347–412.

Spalinger, D.E., Hanley, T.A. & Robbins, C.T. (1988) Analysis of the functional response in foraging in the Sitka black-tailed deer. *Ecology*, **69**, 166–1175.

Spalinger, D.E. & Hobbs, N.T. (1992) Mechanisms of foraging in mammalian herbivores: new models of functional response. *American Naturalist*, **140**, 325–348.

Spalinger, D.E., Robbins, C.T. & Hanley, T.A. (1986) The assessment of handling time in ruminants: the effect of plant chemical and physical structure on the rate of breakdown of plant particles in the rumen of mule deer and elk. *Canadian Journal of Zoology*, **64**, 312–321.

Stephens, D.W. & Krebs, J.R. (1986) *Foraging Theory*. Princeton University Press, Princeton, New Jersey, USA.

Templeton, A.R. & Lawlor, L.R. (1981) The fallacy of averages in ecological optimization theory. *American Naturalist*, **117**, 390–393.

Tilley, J.M.A. & Terry, R.A. (1963) A two-stage technique for the *in vitro* digestion of forage crops. *Journal of the British Grassland Society*, **18**, 104–111.

Toupin, B., Huot, J. & Manseau, M. (1996) Effect of insect harassment on the behavior of the Riviere George caribou. *Arctic*, **49**, 375–382.

Trudell, J. & White, R.G. (1981) The effect of forage structure and availability on food intake, biting rate and daily eating time of reindeer. *Journal of Applied Ecology*, **18**, 63–81.

Van de Koppel, J., Huisman, J., Van der Wal, R. & Olff, H. (1996) Patterns of herbivory along a productivity gradient: an empirical and theoretical investigation. *Ecology*, **77**, 736–745.

Van Soest, P.J. (1982) *Nutritional Ecology of the Ruminant*. Cornell University Press, Ithaca, New York, USA.

Wallis de Vries, M.F. & Daleboudt, C. (1994) Foraging strategy of cattle in patchy grassland. *Oecologia*, **100**, 98–106.

Ward, D. (1992) The role of satisficing in foraging theory. *Oikos*, **63**, 312–317.

Westoby, M. (1974) An analysis of diet selection by large generalist herbivores. *American Naturalist*, **108**, 290–303.

van Wieren, S.E. (1996) Do large herbivores select a diet that maximizes short-term energy intake rate? *Forest Ecology and Management*, **88**, 149–156.

Wilmshurst, J.F., Fryxell, J.M. & Bergman, C.M. (2000) The allometry of patch selection in ruminants. *Proceedings of the Royal Society of London, Series B*, **267**, 345–349.

Wilmshurst, J.F., Fryxell, J.M. & Colucci, P.E. (1999) What constrains daily intake in Thomson's gazelles? *Ecology*, **80**, 2338–2347.

Wilmshurst, J.F., Fryxell, J.M. & Hudson, R.J. (1995) Forage quality and patch choice by wapiti. *Behavioural Ecology*, **6**, 209–217.

Wolff, J.O. (1998) Breeding strategies, mate choice, and reproductive success in American bison. *Oikos*, **83**, 529–544.

Woodward, S.J.R. (1997) Formulae for predicting animals' daily intake of pasture and grazing time from bite weight and composition. *Livestock Production Science*, **52**, 1–10.

Zar, J.H. (1984) *Biostatistical Analysis*. Prentice Hall Inc., Englewood Cliffs, New Jersey, USA.

Received 13 April 2000; revision received 7 November 2000