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THE TEMPORAL SCALE OF FORAGING DECISIONS IN BISON

DANIEL FORTIN,^{1,3} JOHN M. FRYXELL,¹ AND RÉGIS PILOTE²

¹Department of Zoology, University of Guelph, Guelph, Ontario, Canada N1G 2W1

²Département de Biologie, Université Laval, Cité Universitaire, Québec, Canada G1K 7P4

Abstract. Assessing the temporal scale under which gain is maximized is critical for the understanding of diet choice by animals. Classical foraging theory assumes that animals maximize long-term rates. Few studies have considered several temporal scales concurrently, however, weakening tests of rate-maximizing models. We used contingency models based on maximization of short-term vs. long-term energy intake by bison (*Bison bison*). Model predictions were tested against field observations conducted during six periods of 1998: two periods in the winter, one in the spring, and three in the summer. During most of the year, foraging characteristics and plant attributes suggested that intake rate of bison should be limited by ingestion time over short periods of time, and by digestive constraints over long periods of time. Diet predictions varied across temporal scales for four of the six sampling periods. Selecting *Agropyron* spp., rather than *Carex atherodes*, during these periods would result in an increase of daily energy intake by as much as 15 565 kJ (i.e., 7.4% of daily gains) but would necessitate a longer daily foraging time. We observed, instead, that bison preferred *C. atherodes* to *Agropyron* spp., suggesting that patterns of diet selection by bison were more consistent with maximization of short-term than of long-term energy intake. We thus provide some evidence that, contrary to established principles of classic optimality models, the foraging decisions of bison reduce potential long-term gains by maximizing short-term gains.

Key words: *Agropyron* spp.; bison; *Bison bison*; *Carex atherodes*; contingency model; digestive constraints; energy maximization; foraging decision; intake rate; large grazers; optimal diet; temporal scales.

INTRODUCTION

There is a growing awareness of the importance of choosing the most appropriate time scale in foraging studies (Lucas 1983, 1990, Gross et al. 1993, Wallis de Vries and Daleboudt 1994, Wilmshurst and Fryxell 1995). According to classical foraging theory, animals are expected to maximize the long-term rate of energy intake (Stephens and Krebs 1986). There is no clear guideline, however, indicating which temporal scales should be considered. Investigators usually use their biological intuition to select temporal scales (Gass and Roberts 1992) and they commonly choose a single one (Owen-Smith and Novellie 1982, Langvatn and Hanley 1993, Wilmshurst et al. 1995, van Wieren 1996).

Under some conditions, predictions are insensitive to time frame. For example, the original contingency model predicts that animals would maximize both their short-term and long-term rates of intake by making the same diet choice (Stephens and Krebs 1986). Consideration of other constraints, however, can lead to different optimal diets at different temporal scales (Barkan and Withiam 1989, Gass and Roberts 1992).

Manuscript received 11 September 2000; revised 22 March 2001; accepted 10 May 2001; final version received 11 June 2001.

³ Present address: Department of Biological Sciences, University of Alberta, Edmonton, Alberta, Canada T6G 2P6. E-mail: dfortin@ualberta.ca

Large mammalian herbivores face constraints not considered by the classical diet model. Field evidence suggests that the rate of digestion is sometimes the predominant factor limiting the daily intake rate by large herbivores (Mould and Robbins 1982, Wilmshurst et al. 1995), and can influence the optimal choice of diet (Verlinden and Wiley 1989, but see Hirakawa 1997). The maximum daily food consumption resulting from one or several feeding bouts under ad libitum conditions (referred to as daily voluntary intake; Wilmshurst et al. 1999) is commonly used to represent such constraint imposed by digestive processes (Van Soest 1994, Wilmshurst et al. 1995, 1999, Bergman et al. 2001). The need to spend time in other activities or to maintain thermal balance can also constrain feeding time, setting an upper limit on the daily food intake (Arnold 1985, Belovsky and Slade 1986). Consideration of these constraints can lead to predictions of optimal diet that are sensitive to temporal scale (Bergman et al. 2001).

Farnsworth and Illius (1996, 1998) indicated that, over short time scales, intake rate of large herbivores can be restricted either by the encounter rate with plants or, when resources are highly abundant, by the time required to crop and chew food (ingestion time). Over long time scales, the consideration of these short-term constraints, together with digestive and time constraints, leads to four foraging situations (Fig. 1). Foraging situations I and II represent cases in

	Daily intake not limited by digestive constraints	Daily intake limited by digestive constraints
Short-term intake limited by encounter rate	Foraging situation I	Foraging situation III
Short-term intake limited by ingestion rate	Foraging situation II	Foraging situation IV

FIG. 1. The four mutually exclusive foraging situations that can be encountered, depending on (1) whether the short-term intake of resource is limited by the rates of encounter or ingestion and (2) whether this intake will allow the animal to fulfill its daily voluntary intake during the maximum time that can be allocated to feeding in a day.

which animals would be physically able to eat a greater amount of resources during the day, but their food is not abundant enough and/or it takes too long to ingest. In these cases, daily voluntary intake cannot be fulfilled in the maximum time that can be allocated to foraging activity during a day (T), and the optimal diet is scale insensitive because the best foraging behavior always consists of ingesting energy as quickly as possible.

In contrast, when digestive constraints limit the daily forage intake (situations III and IV), the diet can become scale sensitive. For example, taller (or higher biomass) plants often allow for larger bites and higher instantaneous intake rate (Laca et al. 1992, Wallis de Vries and Daleboudt 1994, Gordon et al. 1996, Bergman et al. 2000), and are faster to ingest. At the same time, taller (or higher biomass) plants generally provide less digestible energy per mass unit than do smaller plants because of maturational changes in quality (Van Soest 1994, Wilmshurst et al. 1999), which also tend to reduce daily voluntary intake (Bergman et al. 2001). These opposite trends can create a scale-sensitive optimal diet: rather than eating the plant species that provide the fastest short-term intake rate, an animal can extend its daily feeding time by selecting more digestible resources, thereby increasing its long-term intake rate.

Here, we use contingency models based on short-term vs. daily rates of energy intake. We then test which temporal modeling scale is most consistent with the observed diet of free-ranging plains bison (*Bison bison* L.) in western Canada (see Plate 1).

CONTINGENCY MODELS

Short-term model

We determined the diet that maximizes the short-term energy intake rate (in kiloJoules per minute) of bison, based on the work of Farnsworth and Illius (1998: Eqs. 1–17), with some modifications (Fortin 2001). All parameters were estimated as a function of dry matter mass rather than individual prey.

Long-term model

The diet that maximizes daily energy intake rate was determined by including the constraints imposed by time and daily voluntary intake in a contingency model

that also considers the overlap between searching and ingesting observed in large herbivores.

A feeding time of 642 min/d has been reported for bison (Hudson and Frank 1987), which we assumed to be the maximum daily activity time (T). Bergman et al. (2001) have shown that the daily voluntary intake of bison (G , in grams per day) shares a positive linear relationship with dry matter digestibility, as commonly observed in other species (Mould and Robbins 1982, Van Soest 1994, Wilmshurst et al. 1999). Based on the common assumption (Owen-Smith and Novellie 1982, Stephens and Krebs 1986, Fryxell and Doucet 1993) that the prey types constituting the animal's diet are accepted in proportion to their encountered rate (λ , in grams per minute), the linear relationship between G and the dry matter digestibility (d , as a percentage) can be expressed as

$$G_m = \frac{\sum_{i=1}^m d_i \lambda_i}{\sum_{i=1}^m \lambda_i} \gamma + \theta \quad (1)$$

where i represents individual prey types in a diet including m types. The fitted constants γ and θ are, respectively, equal to 0.224 and 10.804 g·kg body mass⁻¹·d⁻¹ in bison (Bergman et al. 2001).

Foraging is limited by prey encounter rate whenever $\sum_{i=1}^m \lambda_i (1 - \eta_i) h_i < 1$, where h (in minutes per gram) is ingestion time and η is the proportion of h that does not overlap with searching activity (Fortin 2001). During encounter-limited foraging (enc), the time needed to reach the daily voluntary intake ($T[\text{enc}]_m$, in minutes per day) is given by $T[\text{enc}]_m = G_m H_m$. Here, H_m (in minutes per gram) is the expected time required to encounter and to crop 1 g of the m prey types included in the diet, and is found by

$$H_m = \frac{1 + \sum_{i=1}^m \eta_i h_i \lambda_i}{\sum_{i=1}^m \lambda_i} \quad (2)$$

When, in contrast, the next bite is available for cropping as soon as the current bite has been chewed, foraging is limited by ingestion time. During ingestion-limited foraging (or handling-limited foraging, sensu



PLATE 1. Free-ranging plains bison in Prince Albert National Park, Saskatchewan, Canada. Photograph by Daniel Fortin.

Farnsworth and Illius [1998]), the time needed to reach the daily voluntary intake ($T[\text{hand}]_m$, in minutes per day) is given by

$$T[\text{hand}]_m = G_m \frac{\sum_{i=1}^m h_i \lambda_i}{\sum_{i=1}^m \lambda_i}. \quad (3)$$

Considering the time constraint, the daily voluntary intake cannot be reached when $T[\text{enc}]_m > T$ or $T[\text{hand}]_m > T$.

Situation I.—When the resource does not allow fulfillment of the daily voluntary intake during T and foraging is limited by encounter rate (situation I), the daily energy intake rate (I_m) is simply given by Eq. 5 of Farnsworth and Illius (1998) multiplied by T :

$$I_m = \frac{\sum_{i=1}^{m-1} \lambda_i e_i}{1 + \sum_{i=1}^{m-1} \lambda_i \eta_i h_i} T \quad (4)$$

where e_i is the digestible energy of prey types i (in kilojoules per gram of dry matter). To determine the optimal diet, prey types are ranked according to their short-term profitability (e/h , in kilojoules per minute), and the diet is expanded as long as Inequality 8 of Farnsworth and Illius (1998) is met.

Situation II.—When resources do not allow animals to meet their daily voluntary intake during T and foraging is limited by ingestion time (situation II), determination of the optimal diet also requires ranking prey types according to their short-term profitability (e/h), and adding them to the diet until foraging becomes ingestion limited.

When more than one type of prey is required to make the diet ingestion limited, the last type (m) should be

accepted in a proportion (p_m) that is relative to the $m - 1$ prey already included in the diet and that would just make the diet ingestion limited (see Fortin 2001: Eq. 3):

$$p_m = \frac{\frac{1}{\sum_{i=1}^{m-1} \lambda_i} - \frac{\sum_{i=1}^{m-1} \lambda_i (1 - \eta_i) h_i}{\sum_{i=1}^{m-1} \lambda_i}}{(1 - \eta_m) h_m}. \quad (5)$$

Intake rate under situation II is then given by

$$I_m = \frac{\sum_{i=1}^{m-1} \frac{\lambda_i e_i}{h_i} + \frac{\left(\sum_{i=1}^{m-1} \lambda_i\right) p_m e_m}{h_m}}{\sum_{i=1}^{m-1} \lambda_i (1 + p_m)} T. \quad (6)$$

Note that if only one prey is required to make the diet ingestion limited, $p_m = 0$ and intake rate is simply given by $e/h \times T$.

Situation III.—When the resource allows fulfillment of the daily voluntary intake during a period $< T$, and foraging is limited by encounter rate (situation III), determining the optimal diet requires one to rank the prey types according to their potential daily profitability (eG , in kilojoules per day), and then to add them sequentially to the diet until the daily voluntary intake can be achieved. If this requires more than one type of prey, the last type should be accepted at a rate (ϕ_m) that is relative to the $m - 1$ prey already included in the diet and that would just fulfill the animal's daily voluntary intake during T . This implies that $T[\text{enc}]_m = T = G'_m H'_m$. The daily voluntary intake that includes the partial acceptance of prey m (G'_m) is given by

$$G'_m = \frac{\sum_{i=1}^{m-1} \lambda_i d_i + \left(\sum_{i=1}^{m-1} \lambda_i\right) \phi_m d_m}{\sum_{i=1}^{m-1} \lambda_i (1 + \phi_m)} \gamma + \theta. \quad (7)$$

The expected time required to encounter and crop 1 g of a diet that now includes partial acceptance of prey type m (H'_m) is

$$H'_m = \frac{1 + \sum_{i=1}^{m-1} \eta_i h_i \lambda_i + \left(\sum_{i=1}^{m-1} \lambda_i\right) \phi_m \eta_m h_m}{\sum_{i=1}^{m-1} \lambda_i (1 + \phi_m)}. \quad (8)$$

The equality $T = G'_m H'_m$ can be expanded and rearranged in the form of a polynomial: $0 = a_m \phi_m^2 + b_m \phi_m + c_m$, where

$$a_m = \left(\sum_{i=1}^{m-1} \lambda_i\right)^2 [(\eta_m h_m)(d_m \gamma + \theta) - T] \quad (9)$$

$$b_m = \left(\sum_{i=1}^{m-1} \lambda_i\right) \left[\left(\sum_{i=1}^{m-1} \lambda_i \eta_i h_i\right) (d_m \gamma + \theta) + (\eta_m h_m) \left[\left(\sum_{i=1}^{m-1} d_i \lambda_i\right) \gamma + \left(\sum_{i=1}^{m-1} \lambda_i\right) \theta \right] + \left(\sum_{i=1}^{m-1} \lambda_i\right) \left[d_m \gamma + \theta - 2 \left(\sum_{i=1}^{m-1} \lambda_i\right) T \right] \right] \quad (10)$$

$$c_m = \left(\sum_{i=1}^{m-1} \lambda_i\right) \left[\left(\sum_{i=1}^{m-1} \lambda_i \eta_i h_i\right) \theta + \theta - \left(\sum_{i=1}^{m-1} \lambda_i\right) T \right] + \left(\sum_{i=1}^{m-1} d_i \lambda_i\right) \left[\left(\sum_{i=1}^{m-1} \lambda_i \eta_i h_i\right) \gamma + 1 \right]. \quad (11)$$

We can then find ϕ_m as the lowest positive value given by $\phi_m = (-b_m \pm \sqrt{b_m^2 - 4a_m c_m}) / (2a_m)$. The intake rate for a situation III of foraging becomes

$$I_m = \frac{\sum_{i=1}^{m-1} \lambda_i e_i + \left(\sum_{i=1}^{m-1} \lambda_i\right) \phi_m e_m}{1 + \sum_{i=1}^{m-1} \lambda_i \eta_i h_i + \left(\sum_{i=1}^{m-1} \lambda_i\right) \phi_m \eta_m h_m} T. \quad (12)$$

Situation IV.—Finally, when the resource allows fulfillment of the daily voluntary intake during T and foraging is ingestion limited (situation IV), determining the optimal diet also requires the prey types to be ranked according to their potential daily profitability (eG) and to be included in the diet, sequentially, until the daily voluntary intake can be achieved. If the prey type with the highest daily profitability were ingestion limited on its own, the optimal diet would predict specialization on this type of prey. When more than one prey type is required to make the diet ingestion limited, the last type (m) should be included in a proportion p_m ,

which is determined by Eq. 5. The daily energy intake rate in situation IV is found by Eq. 6, in which T is substituted by the $T[\text{hand}]'_m$ given by

$$T[\text{hand}]'_m = \frac{\sum_{i=1}^{m-1} \lambda_i h_i + \left(\sum_{i=1}^{m-1} \lambda_i\right) p_m h_m}{\sum_{i=1}^{m-1} \lambda_i (1 + p_m)} \times \left[\frac{\sum_{i=1}^{m-1} \lambda_i d_i + \left(\sum_{i=1}^{m-1} \lambda_i\right) p_m d_m}{\sum_{i=1}^{m-1} \lambda_i (1 + p_m)} \gamma + \theta \right]. \quad (13)$$

Whenever more than one prey is required for ingestion-limited foraging, $T[\text{hand}]'_m$ has to exactly equal T to be treated as a situation IV of foraging. Faster fulfillment (i.e., $T[\text{hand}]'_m < T$) indicates that the animal could have foraged for a longer period of time, and thus that the opportunity for foraging on the more digestible prey type had been lost. This case should then be treated as a situation III, with a partial acceptance ϕ_m of the prey type m (where $\phi_m < p_m$).

METHODS

The field study took place in Prince Albert National Park (Saskatchewan, Canada), which has a population of ~220 plains bison. Optimal and observed diets of bison were determined for six periods during 1998: 5 January–16 February, 17 February–4 April, 23 May–19 June, 20 June–12 July, 13 July–7 August, and 8 August–3 September. Information on plant phenology was collected in 25 meadows located throughout the bison range. Although >170 plant species were recorded, for logistic reasons, we focused on seven of the most abundant plant groups: *Carex atherodes* Spreng. and *C. aquatilis* Wahlenb. (two sedge species); *Agropyron* spp., *Calamagrostis inexpansa* A. Gray, *Hordeum jubatum* L., and *Scolochloa festucacea* (Willd.) Link. (four types of grass); and *Juncus balticus* Willd. (one rush species). Throughout the year, these species represented 50–72% of the total biomass available and 81–99% of the bison diet.

During the spring, summer, and winter of 1997 and 1998, foraging behavior of bison (excluding yearlings and calves) was recorded using focal animal sampling (Altmann 1974) during 5-min periods. Using a spotting scope, we followed any bison <100 m. We recorded into a tape recorder every bite, displacement of the front feet, head raising and lowering movement, and pawing and head sweeping motion for snow clearing. Data were later transcribed using a stopwatch to measure the time between movements (as in Wilmschurst et al. 1999), the frequency of behaviors per 5-min period, and the number of feeding stations determined from front feet displacement (Bailey et al. 1996).

Following an observation session, forage character-

istics and snow conditions were averaged over 3–5 quadrats spread over the foraging area. Quadrats were 1 m² during the spring and summer (referred to as the growing season), and 0.25 m² in winter. During the growing season, the total dry biomass (in grams per square meter) was determined by the distance (in centimeters) that a plastic disk settled from the ground (Vartha and Matches 1977), according to the regression: $y = 81.958 + 10.004x$ ($F_{1,179} = 162.99$, $r^2 = 0.48$, $P < 0.0001$). In winter, forage biomass was based on a 0–9 visual scale, according to $y = 82.229e^{0.29x}$ ($F_{1,38} = 366.27$, $r^2 = 0.91$, $P < 0.0001$). Evaluation of plant biomass was supplemented by estimation of the percentage of the quadrat visually covered by a given plant species when looking from above (percent cover) and, during the growing season, the percentage of green biomass of each plant species. Snow conditions consisted of density and depth. Snow density (in grams per cubic centimeter) was determined by weighing, with a spring scale, a sample of the snow column collected with a metal tube inserted vertically into the snow and dividing the mass by the volume of the snow gathered.

Prey encounter rate (λ)

Estimation of λ requires knowledge of the average effective plant biomass, stepping rate while searching, distance between steps, and the width of the animal's foraging path. Plant characteristics were determined in 16–90 evenly spaced quadrats, depending on the area of each of the 25 meadows surveyed. During winter, plant biomass was visually estimated on a 0–5 scale, according to: $y = 67.876e^{0.641x}$ ($F_{1,42} = 295.11$, $r^2 = 0.88$, $P < 0.0001$). This equation differed from the previous one because a different observer performed the meadow surveys.

Grazers do not consume plants completely (Ungar and Noy-Meir 1988, Burlison et al. 1991, Bergman et al. 2000), suggesting that the vegetation cannot be considered entirely available to the animal. Following Owen-Smith and Novellie (1982) and Owen-Smith (1993), we considered that the resource actually available was the fraction of a given plant species consumed by the animal. Grazed depth was determined for each focal species during the growing season of 1998. Sampling units consisted of the average height of 15 grazed and 15 adjacent ungrazed plants. Approximately 40 g of ungrazed individual plants were collected, at the grazed depth of nearby plants. Samples were weighed with a spring-scale following drying at 50°C for 72 h. We established the relationship between the percentage of the plant mass consumed (P) and plant height. Although it was only estimated during the growing season, we assumed that P had a similar relationship to species height in winter. For each of the six sampling periods, height of each plant species was also measured at randomly selected stations among the 25 meadows, with each sample consisting of 15 measurements. From

this information, P was established for each sampling period based on the regression analyses. The effective dry biomass of a species was calculated for winter as effective biomass = total biomass \times cover \times grazed depth, and for the growing season as effective green biomass = effective biomass \times percentage of green tissue.

Step rate was calculated by measuring the time required for the bison to accomplish 4–20 steps when moving between feeding stations. This sequence excluded the animal's first step because its initiation was often difficult to determine accurately, which could lead to a slight overestimate of searching speed (Shipley et al. 1996). In winter, the distance between footprints in the snow was directly measured and averaged over five replicates for each animal path. During the growing season, distance between steps was established, based on animals 15–25 m away from a blind, by counting the total number of steps between landmarks divided by the distance traveled. The search speed consisted of the product of step rate and step size.

We estimated the effective foraging path width (W) during the behavioral observations. We considered that a foraging animal moves its head from side to side in a semicircle of diameter W (in meters). We first estimated the total biomass grazed in the visited area (in grams per square meter) by summing visual estimates of the percentage of cover of the species grazed by bison. For each observed feeding bout, we then estimated the amount of forage grazed per station (in grams) from the product of the observed average number of bites per station and the expected mass of these bites. Expected bite mass (S , in grams per bite) was determined by reanalyzing the data displayed in Bergman et al. (2000: Fig. 4). Dry mass of bites increased in a decelerating manner with increasing total dry biomass (V , in grams per square meter), according to $S = 2.57 V/(290.84 + V)$. On the basis of the estimated parameters and from the assumption that a feeding station represents half a circle, W was estimated from

$$W = \sqrt{\frac{8(\text{biomass grazed per station})}{\pi(\text{total biomass grazed})}}. \quad (14)$$

Finally, using all of the estimated parameters, we determined the encounter rate (in grams per minute) of each species for winter as encounter rate = effective biomass \times search speed \times effective path width, and for spring and summer as encounter rate = effective green biomass \times search speed \times effective path width.

Ingestion time (h) and proportion of ingestion time exclusive to searching time (η)

The intake rate of dry matter in patches of concentrated food is limited by ingestion time (Spalinger and Hobbs 1992). Therefore, we used functional responses estimated in food-concentrated patches to determine the ingestion time of each of the seven focal species.

Following Bradbury et al. (1996), we determined dry matter intake rate (F) by multiplying the bite rate (D) observed in the field by bite mass (S). Forage intake rate was then related to forage biomass using the Michaelis-Menten (Michaelis and Menten 1913) form of the functional response:

$$F = \frac{\psi V}{\beta + V} \quad (15)$$

where ψ is the maximum feeding rate (in grams per minute) and β is the half-saturation constant (in grams per square meter) (Wilmshurst et al. 1999, Bergman et al. 2000). Two functional responses were determined: one for spring and summer and one for winter.

Assessment of the expected intake rate for a given plant species requires field estimates of biomass at a relevant scale. According to Bergman et al. (2000), the area of a bite represents the scale of relevance in foraging processes. In many instances, species occurred in mixed swards and their aggregation was smaller than the area of the disk (0.3 m^2) used to estimate biomass during the growing season. For this reason, the relationship between plant height and disk biomass was determined during the growing season of 1997 in stands largely dominated (cover >70%) by each of the focal species. Positive relationships between height and biomass were observed for all of the seven focal species ($P < 0.005$ in all cases). Using these regression relationships, we transformed the average height of each species observed during each of the six sampling periods into dry matter biomass. When foraging is ingestion limited (process-3 foraging, sensu Spalinger and Hobbs [1992]), ingestion time simply equals the inverse of intake rate (see Farnsworth and Illius 1996: Eq. 16). Therefore, we estimated the average time required to crop and chew 1 g of a given plant type (h , in minutes per gram of dry matter) from the inverse of its average intake rate as calculated with our functional responses.

Ingestion time can be partitioned into cropping time (ηh), during which the animal cannot search for food, and chewing time ($[1 - \eta]h$), during which the animal can finish ingesting the prey while searching for the next bite (Farnsworth and Illius 1996, 1998). Thus, η represents the proportion of ingestion time spent cropping. Following the modeling approach of Spalinger and Hobbs (1992), we calculated the time required to crop a bite from the relationship between bite rate (D , in bites per minute) and bite mass (S , in grams per bite):

$$D = \frac{R_{\max}}{R_{\max} \bar{h}' + S} \quad (16)$$

where R_{\max} is the rate of food processing in the absence of cropping (in grams per minute) and \bar{h}' is the average time required to crop a bite (minutes per bite). The distinct values of \bar{h}' found during the growing season

and in winter were divided by the average bite mass of species i to determine the time required to crop 1 g of plant species i (\bar{h}_i , in minutes per gram). Then η_i was found from the ratio of \bar{h}_i (cropping time) and h_i (cropping + chewing time).

Dry matter digestibility (d) and digestible energy (e)

Samples of aboveground tissue of each of the seven focal plant species were collected at random locations throughout the bison range, separated by tissue (stems and leaves), and dried at 50°C for 72 h. Dry matter digestibility and digestible energy of the samples were then determined following Bergman et al. (2001). Only the digestible energy of the tissue consumed by bison was considered in the contingency models. Tissue selectivity was determined during the assessment of grazing depth, as well as during other plant surveys.

The relationship between daily voluntary intake and plant digestibility was calculated by assuming a bison body mass of 636 kg (Belovsky 1986), because all other model parameters reflected adult animals.

Observed diet

Bison diet was determined by estimating the total biomass grazed per unit of area in each quadrat, averaging over 25 meadows for each of the seven focal species, as well as for nontarget plant species. Grazing intensity of white-tailed deer (*Odocoileus virginianus* Zimmermann), elk (*Cervus elaphus* L.), and moose (*Alces alces* L.) was relatively small in these meadows (Fortin 2000).

RESULTS

We first describe our field evaluation of the parameters used in the contingency models and then present our predictions of optimal diet for different temporal scales, comparing these predictions to the observed diet of bison.

Model parameters

Grazed depth increased with plant height for most species ($P < 0.002$), except for *Hordeum jubatum* ($F_{1,21} = 0.002$, $P = 0.97$) and *Carex aquatilis* ($F_{1,9} = 1.18$, $P = 0.31$). The percentage of biomass grazed declined with increasing plant height for *Agropyron* spp., *Calamagrostis inexplansa*, and *Scolochloa festuacea*, ($P < 0.05$; Fig. 2A), whereas no significant relationships were observed in other species ($P > 0.18$; Fig. 2B). Based on this information, and considering the average species height measured during each of the sampling periods (Table 1), we determined that, on average, bison consumed less than half of the aboveground biomass during any period of the year (Table 1). In late spring (period 3, 23 May–19 June), the biomass of most plant species was still low, and bison generally grazed stems together with leaves. *Carex atherodes* and *S. festuacea* were the only exception, with leaves only consumed. During the other periods of the year, grazing

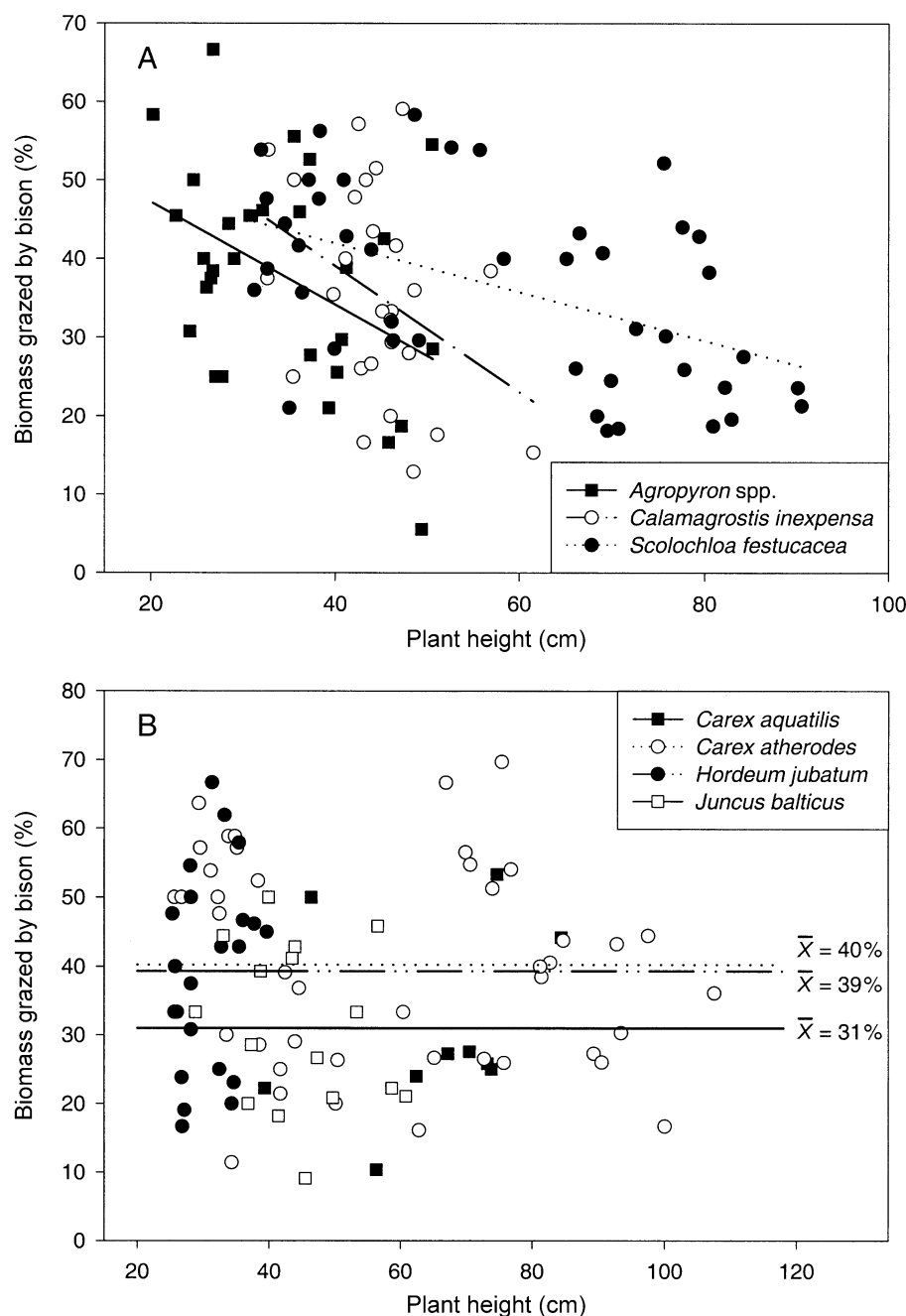


FIG. 2. Percentage of plant biomass consumed by bison as a function of plant height. The fraction grazed declined significantly with height for three species (panel A), whereas there was no relationship for the last four focal species, and their averages are displayed in panel (B). Note that *Carex aquatilis* and *Juncus balticus* both averaged 31% of biomass grazed.

activity was limited to leaves for *Agropyron* spp., *C. atherodes*, *C. aquatilis*, *Calamagrostis inexpectata*, and *S. festuacea*. Dry matter digestibility varied between 40% and 75% throughout the year, tending to be higher for *Agropyron* spp. and *C. atherodes* than for the other species (Table 1).

Bison traveled between feeding stations at a stepping rate of 58.9 ± 6.2 steps/min (mean ± 1 SD, $n = 21$)

in spring and summer, and 48.3 ± 8.7 steps/min ($n = 23$) in winter, whereas the distance between these steps was 0.55 ± 0.09 m ($n = 13$) in spring and summer and 0.34 ± 0.06 m ($n = 10$) in winter. Hence, searching speed was, on average, twice as fast during the growing season than in winter. Bison path width averaged 1.78 ± 1.03 m ($n = 101$) during the growing season and 1.91 ± 1.27 m ($n = 210$) in winter, leading to a searched

TABLE 1. Foraging parameters and characteristics used to determine the optimal diet of bison during six sampling periods in 1998 in Prince Albert National Park, Saskatchewan, Canada.

Sampling period†	Plant species‡						
	agro	caaq	caat	cain	hoju	juba	scfe
A) Elongated height (cm), $n = 8-59$							
1	33.74	74.21	101.30	63.26	32.76	49.66	104.04
2	34.01	68.89	96.19	57.03	30.69	51.06	100.40
3	23.34	38.67	35.52	27.11	16.74	27.94	34.54
4	28.23	48.11	47.95	35.73	27.58	44.22	49.36
5	40.40	65.41	81.39	45.17	31.94	45.63	74.35
6	48.31	72.00	87.06	48.89	30.54	52.41	81.83
B) Total biomass (g/m ²), $n = 752-964$							
1	16.00	21.01	65.42	54.76	1.11	8.54	88.95
2	15.17	23.19	64.94	53.34	1.10	8.28	86.85
3	6.75	5.08	17.41	13.68	0.51	7.25	11.02
4	12.03	6.86	66.72	27.26	1.00	8.08	34.58
5	19.23	19.76	121.65	46.34	3.93	5.34	63.71
6	36.64	23.27	135.52	44.61	7.07	4.67	80.59
C) Biomass grazed individual plant (%), $n = 10-44$							
1	38.25	30.98	40.23	20.48	39.30	31.06	22.15
2	38.07	30.98	40.23	25.47	39.30	31.06	23.28
3	45.03	30.98	40.23	49.41	39.30	31.06	43.68
4	41.84	30.98	40.23	42.51	39.30	31.06	39.09
5	33.91	30.98	40.23	34.96	39.30	31.06	31.35
6	28.76	30.98	40.23	31.98	39.30	31.06	29.03
D) Encounter rate (g/min)							
1	194.13	206.45	834.84	355.77	13.89	84.12	624.97
2	183.18	227.88	828.73	430.98	13.77	81.60	641.26
3	175.88	91.027	405.28	391.15	11.58	130.30	278.64
4	291.25	123.02	1552.98	670.42	22.70	145.22	782.05
5	377.31	354.06	2831.63	937.49	89.46	95.94	1155.60
6	609.63	417.11	3154.48	825.61	160.72	83.93	1353.77
E) Ingestion time (min/g)							
1	0.0203	0.0175	0.0162	0.0178	0.0188	0.0191	0.0161
2	0.0203	0.0177	0.0163	0.0182	0.0188	0.0190	0.0162
3	0.0181	0.0171	0.0176	0.0185	0.0164	0.0183	0.0180
4	0.0178	0.0165	0.0164	0.0174	0.0164	0.0170	0.0164
5	0.0172	0.0157	0.0149	0.0166	0.0164	0.0169	0.0151
6	0.0169	0.0155	0.0148	0.0164	0.0164	0.0165	0.0149
F) Proportion of ingestion time exclusive to searching activity							
1	0.68	0.62	0.58	0.63	0.65	0.65	0.58
2	0.67	0.62	0.59	0.63	0.65	0.65	0.58
3	0.45	0.43	0.44	0.46	0.41	0.46	0.45
4	0.44	0.42	0.41	0.44	0.41	0.43	0.41
5	0.43	0.40	0.38	0.42	0.41	0.43	0.38
6	0.43	0.39	0.37	0.42	0.41	0.42	0.38
G) Dry matter digestibility (%), $n = 6-10$, with the exception § $n = 3$, $n = 5$;							
1	54.40	40.17	56.11	44.12	48.06	45.64	48.49
2	53.97	41.31	51.98	40.36	47.01	46.67	48.95
3	75.79	62.58	71.24	61.96	76.06	68.85§	70.95
4	68.56	58.09	65.30	53.06	55.38	53.76	65.18
5	65.96	54.83	64.53	54.15	60.21	56.22	58.41
6	56.55	52.66	60.16	43.74	58.88	53.83	53.00
H) Digestible energy content (kJ/g of dry matter)							
1	10.01	7.39	10.33	8.12	8.85	8.40	8.93
2	9.94	7.60	9.57	7.43	8.65	8.59	9.01
3	13.95	11.52	13.12	11.41	14.00	12.67	13.06
4	12.62	10.69	12.02	9.77	10.20	9.90	12.00
5	12.14	10.09	11.88	9.97	11.09	10.35	10.75
6	10.41	9.70	11.08	8.05	10.84	9.91	9.76

† Sampling periods: 1, 5 January–16 February; 2, 17 February–4 April; 3, 23 May–19 June; 4, 20 June–12 July; 5, 13 July–7 August; and 6, 8 August–3 September.

‡ Abbreviations for the plant species considered: agro, *Agropyron* spp.; caaq, *Carex aquatilis*; caat, *C. atherodes*; cain, *Calamagrostis inexpectans*; hoju, *Hordeum jubatum*; juba, *Juncus balticus*; and scfe, *Scolochloa festuacea*.

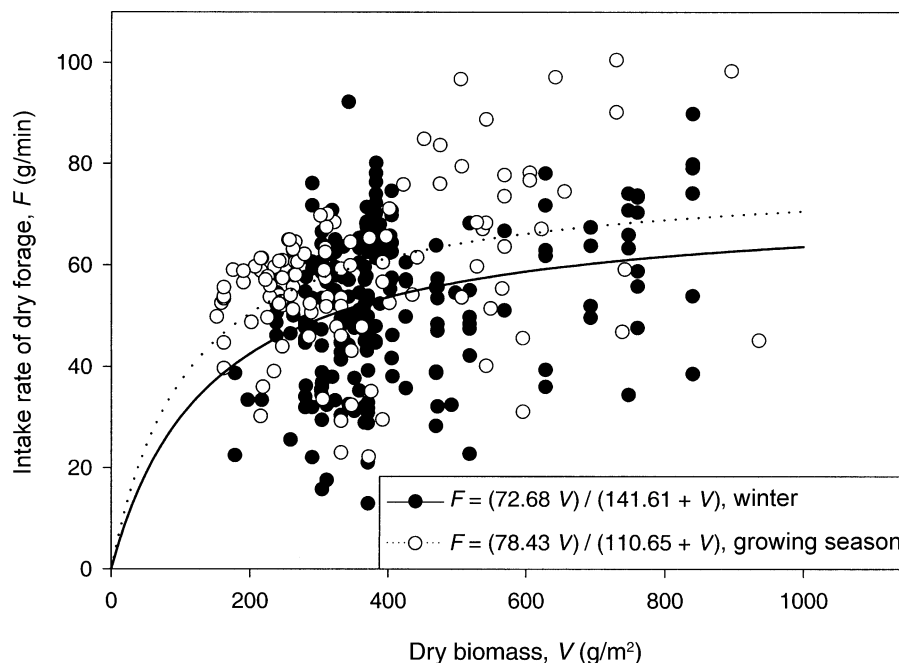


FIG. 3. Relation between bison intake rate and sward biomass in winter and during the growing season (late spring and summer). Intake rate was calculated from the product of bite rate and bite mass, which came from behavioral observations and from the literature, respectively.

area of 57.9 m²/min and 31.7 m²/min, respectively. Similar to cattle (Illius and O'Connor 2000), bison tended to graze only green biomass during the growing season. During winter, however, all of the accumulated biomass was used. High biomass during winter partly compensated for low searching speed, providing an intermediate encounter rate in winter (Table 1). The higher forage biomass of *C. atherodes* conferred to this species the highest encounter rate throughout the year (Table 1).

Forage intake rate in mixed swards increased with biomass toward an asymptote of 78.43 g/min during the growing season and 72.68 g/min in winter (Fig. 3). These functional responses represented process-3 foraging. First, behavioral observations were performed over short periods of time (5 min), requiring visits to only a few feeding stations. Second, we found weak, but significant, negative relationships between bite rate and biomass (for winter, $F_{1,224} = 5.90$, $r^2 = 0.03$, $P = 0.016$; for the growing season, $F_{1,112} = 14.58$, $r^2 = 0.12$, $P = 0.0002$), which is only characteristic of process-3 foraging (Bradbury et al. 1996). Our functional responses thus reflect a situation in which intake rate was restricted by ingestion rate (i.e., cropping and chewing) rather than by encounter rate.

Using these functional responses and the average seasonal biomass, we calculated that it took a bison 0.015–0.020 min to ingest 1 g of forage during any period of the year (Table 1). The larger bites that can be cropped in species with high local abundance reduce the ingestion time per unit mass because less time is

spent cropping relative to chewing. Rapid ingestion time was consistently noticeable for tall species such as *C. atherodes* and *S. festuacea*. The proportion of ingestion time exclusive to searching time (η) varied between 0.37 and 0.68, being more important during winter (Table 1). Tall species like *C. atherodes* and *S. festuacea* tended to have more overlap between searching and ingesting because of the longer chewing time associated with the larger bites they offered.

Model predictions and observed diet

Our field measurements indicated that resources were abundant enough to allow bison to meet their daily voluntary intake throughout the year. Hence, bison foraging fell into categories III and IV, conditions under which the optimal diet is potentially scale sensitive. During most of the year, both short- and long-term models suggest that intake rate would be maximized by specializing on a single plant type, but the most profitable type changed seasonally. During the winter and summer, bison diet should be ingestion limited over short periods of time, leading to foraging situation IV (Fig. 1). For several of the sampling periods, predictions of the optimal plant type differed between models because of differences in short-term vs. daily profitability. During three periods (2, 4, 5), specializing on *C. atherodes* would maximize animals' short-term energy intake rate (in kilojoules per minute), because the high energy content and rapid ingestion time lead to high short-term profitability (in kilojoules per minute). On the other hand, *Agropyron* spp. had the highest dry

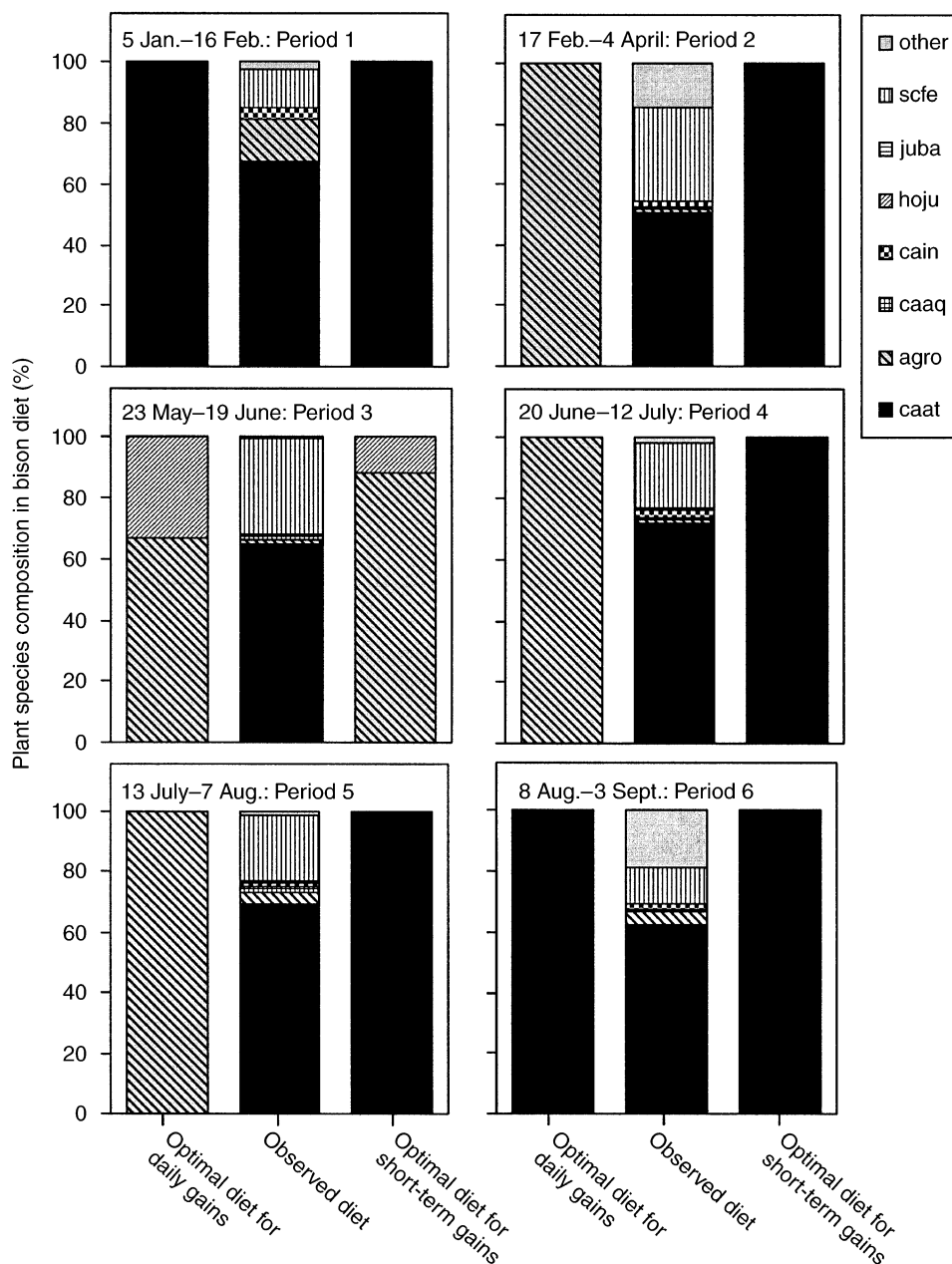


FIG. 4. Comparison between the observed diet of bison in Prince Albert National Park and the optimal diet predicted for maximization of short-term and daily intake rate during six periods in 1998. Species abbreviations and dates of the investigation periods are indicated in Table 1 footnotes.

matter digestibility and highest daily voluntary intake, accordingly offering the highest daily profitability (in kiloJoules per day). Consequently, an individual specializing on *Agropyron* spp. would forage 31–63 min longer than one specializing on *C. atherodes*, ending up with 5.5% more energy at the end of the day (i.e., an additional 6677–15 565 kJ/d). Specialization on *Agropyron* spp. should also result in higher *net* daily energy intake rate, despite the higher activity costs in-

volved with longer periods of foraging (see Fortin 2000).

Carex atherodes constituted most of the bison diet throughout the year (Fig. 4). Positive Ivlev electivity indices indicate a use of this species disproportionate to its availability (Table 2). In contrast, *Agropyron* spp. made up only a small amount of the diet, tending to be avoided during most of the year. The preference for *C. atherodes* and avoidance of *Agropyron* spp. suggest

TABLE 2. Ivlev's electivity index indicating preference or avoidance of plant species grazed by bison in Prince Albert National Park, Saskatchewan, Canada. Preference for *Carex atherodes* and *Scolochloa festucacea* is suggested by positive indices, shown in boldface.

Sam pling period	Plant species							
	agro	caa	caat	cain	hoju	juba	scfe	others
1	0.41	-1.00	0.46	-0.53	-1.00	-1.00	-0.18	-0.87
2	-0.51	-0.96	0.35	-0.69	-1.00	-1.00	0.25	-0.34
3	-0.62	-0.35	0.65	-0.99	-1.00	-0.69	0.54	-0.98
4	-0.55	-0.64	0.46	-0.66	-0.98	-0.57	0.24	-0.93
5	-0.14	-0.28	0.37	-0.76	-0.95	-0.51	0.24	-0.91
6	-0.23	-0.64	0.29	-0.74	-0.98	-0.99	-0.10	-0.19

Note: Sampling periods and species abbreviations are as in Table 1.

that bison foraging decisions maximize short-term energy intake.

Mixed diets were predicted to be optimal during the late spring (period 3). Both models suggested that *Hordeum jubatum* should be eaten whenever it is encountered in the late spring, whereas only a fraction of the *Agropyron* spp. encountered should be included in the diet. Bison did not follow this prediction, instead foraging largely on *C. atherodes* (Fig. 4, Table 2).

DISCUSSION

Our study demonstrates the potential dependence of optimal diet predictions on temporal scale. At both temporal scales considered, the optimal diet for bison should usually consist of a single plant type, but the identity of that type depends on the time scale under consideration. Several factors contribute to the prediction of narrow diets in bison. First, the extensive overlap between chewing and searching reduces the proportion of time spent in exclusive search, making the diet more likely to become ingestion limited with inclusion of only few prey types. Second, bison display fast ingestion rates even on swards of low biomass (Bergman et al. 2000). Third, the most profitable plant species (in kilojoules per minute or day) were highly abundant in our study system (Table 1).

The observed diet was most consistent with short-term rather than long-term goals. For half of the sampling periods, short-term gains occurred at the expense of long-term gains. Bison "avoided" *Agropyron* spp., which would have enhanced daily intake, preferring instead *Carex atherodes*. Such findings are important because they constitute evidence that foraging decisions by bison reduce their potential long-term energy gain, contrary to established principles of classic optimality models (Barkan and Withiam 1989).

Although few studies have considered the question, it appears that the relevant temporal scale could vary among herbivore species. Wallis de Vries and Daleboudt (1994) observed that foraging decisions by cattle were more consistent with long-term than short-term energy maximization. In contrast, Illius et al. (1999) observed that goats (*Capra hircus* L.) selected a diet that maximized short-term forage intake, which coin-

cided closely with short-term energy intake. Maximization of daily energy gains was unlikely in the study of Illius et al. (1999) because of poor correlation between short-term energy intake rate and forage digestibility among plant species.

Probably the most striking support for our interpretation comes from a wood bison (*Bison bison athabasca* Rhoads) study by Bergman et al. (2001). Optimality modeling was used to determine whether selection of short vs. tall swards of *C. atherodes* led to the maximization of either short- or long-term energy gains. Wood bison displayed patch preferences most consistent with the maximization of short-term goals. We suggest that bison make consistent foraging decisions at different hierarchical levels: first maximizing short-term energy intake rate by choosing *C. atherodes*, and then selecting sward height on the basis of short-term gain.

Several factors could contribute to short-term energy maximization by bison. First, bison may need to get relief from insect harassment, to scan for predators, or to maintain thermal balance or social status (Bergman et al. 2001). The time saved by selecting a diet that maximizes short-term intake appears to be rather small (31–63 min), but we have no idea of its potential fitness importance. Kagel et al. (1986) predicted that interruptions of foraging activity should lead to discounting of future rewards. Herd movements are determined by a small number of individuals (McHugh 1958), making feeding opportunities somewhat unpredictable for other individuals. Disturbance by predators or humans can prematurely terminate foraging bouts. We suggest that such interruptions might push bison toward the maximization of short-term, rather than long-term, goals.

Despite good agreement during most of the year, the diet that we observed during spring did not correspond to predictions given by either of our models. Spring was actually the only period during which *C. atherodes* would not maximize short-term energy intake. Maximizing gains would have required a switch to *H. jubatum* and *Agropyron* spp., but bison did not perform such a dietary change. Changes in diet impose adjustments in the microbial species of the rumen, as well as new rates of fermentation and rumen turnover, which

may take from one to several weeks and may cause rumen upset (Van Soest 1994). Perhaps, bison simply kept foraging on *C. atherodes* to avoid the need for adjustments of digestive processes during a period when all food types were of high quality (Table 1).

This hypothesis provides an alternative interpretation for the observed patterns of diet selection. *Agropyron* spp. is commonly grazed by many ungulate species (McInnis and Vavra 1987, Painter et al. 1993, Merrill et al. 1994, Ganskopp and Cruz 1999), and thus constitutes a potentially suitable resource. However, *C. atherodes* is more digestible than *Agropyron* spp. during some critical periods of the year, such as in late summer. Keeping the rumen microbial system primed to maximize gains during critical times of the year may be advantageous, and may require minimizing diet switches. From this perspective, rather than maximizing short-term gains, bison may simply optimize their energy balance over the annual seasonal cycle.

The importance of *C. atherodes* in the diet of bison has been reported in other landscapes with similar plant availability (Reynolds et al. 1978, Larter and Gates 1991). As in these other studies, however, bison did not specialize solely on *C. atherodes*, consuming other species, particularly *S. festuacea*. This species often had the second highest short-term profitability (in kiloJoules per minute). Broader diets than predicted are commonly observed in large herbivores (Owen-Smith and Novellie 1982, Wilmshurst et al. 1995, Illius et al. 1999). Factors such as animal variation, discrimination errors, and sampling update information can be used to explain such partial preferences (Wilmshurst et al. 1995, Illius et al. 1999). Herbivores require nutrients other than energy (Belovsky 1978, Van Soest 1994), which also may lead to broader diets and may potentially explain the observed use of *C. atherodes* instead of *Agropyron* spp. during certain periods of the year.

Overall, our results suggest that dietary decisions of bison can be largely explained by simple rules of energy maximization, and that bison prefer rapid energy acquisition, even at the expense of long-term gains.

ACKNOWLEDGMENTS

Funding for this work was provided by Parks Canada, NSERC (Natural Sciences and Engineering Research Council of Canada), and scholarships from FCAR (Fonds pour la formation de Chercheurs d'Aide à la Recherche) and OGS (Ontario Graduate Scholarships) to D. Fortin. I thank M. Andruskiw and S. Juárez, as well as many volunteers, for their help in the field and the laboratory. Park wardens L. O'Brodovich, D. Frandsen, and N. Stolle made the fieldwork possible. J. S. Brown, N. Owen-Smith, J. F. Wilmshurst, T. D. Nudds, and B. A. Nolet provided constructive comments on this paper.

LITERATURE CITED

- Altmann, J. 1974. Observational study of behavior: sampling methods. *Behaviour* **49**:227–267.
- Arnold, G. W. 1985. Regulation of food intake. Pages 81–

- 101 in R. J. Hudson and R. G. White, editors. *Bioenergetics of wild herbivores*. CRC Press, Boca Raton, Florida, USA.
- Bailey, D. W., J. E. Gross, E. A. Laca, L. R. Rittenhouse, M. B. Coughenour, D. M. Swift, and P. L. Sims. 1996. Mechanisms that result in large herbivore grazing distribution patterns. *Journal of Range Management* **49**:386–400.
- Barkan, C. P. L., and M. L. Withiam. 1989. Profitability, rate maximization, and reward delay: a test of the simultaneous-encounter model of prey choice with *Parus atricapillus*. *American Naturalist* **134**:254–272.
- 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., and J. B. Slade. 1986. The importance of body size and thermal environment in the time budgets of some grassland herbivores. *Oecologia* **70**:53–62.
- Bergman, C. M., J. M. Fryxell, and C. C. Gates. 2000. The effect of tissue complexity and sward height on the functional response of wood bison. *Functional Ecology* **14**:61–69.
- Bergman, C. M., J. M. Fryxell, C. C. Gates, and D. Fortin. 2001. Ungulate foraging strategies: energy maximizing or time minimizing? *Journal of Animal Ecology* **70**:289–300.
- Bradbury, J. W., S. L. Vehrencamp, K. E. Clifton, and L. M. Clifton. 1996. The relationship between bite rate and local forage abundance in wild Thomson's gazelles. *Ecology* **77**:2237–2255.
- Burlison, A. J., J. Hodgson, and A. W. Illius. 1991. Sward canopy structure and the bite dimensions and bite weight of grazing sheep. *Grass and Forage Science* **46**:29–38.
- Farnsworth, K. D., and A. W. Illius. 1996. Large grazers back in the fold: generalizing the prey model to incorporate mammalian herbivores. *Functional Ecology* **10**:678–680.
- Farnsworth, K. D., and A. W. Illius. 1998. Optimal diet choice for large herbivores: an extended contingency model. *Functional Ecology* **12**:74–81.
- Fortin, D. 2000. Foraging decisions at multiple spatial and temporal scales: a bison perspective. Dissertation. University of Guelph, Guelph, Canada.
- Fortin, D. 2001. An adjustment of the extended contingency model of Farnsworth and Illius (1998). *Functional Ecology* **15**:138–139.
- Fryxell, J. M., and C. M. Doucet. 1993. Diet choice and the functional response of beavers. *Ecology* **74**:1297–1306.
- Ganskopp, D., and R. Cruz. 1999. Selective differences between naive and experienced cattle foraging among eight grasses. *Applied Animal Behaviour Science* **62**:293–303.
- Gass, C. L., and W. M. Roberts. 1992. The problem of temporal scale in optimization: three contrasting views of hummingbird visits to flowers. *American Naturalist* **140**:829–853.
- Gordon, I. J., A. W. Illius, and J. D. Milne. 1996. Sources of variation in the foraging efficiency of grazing ruminants. *Functional Ecology* **10**:219–226.
- Gross, J. E., L. A. Shipley, N. T. Hobbs, D. E. Spalinger, and B. A. Wunder. 1993. Functional response of herbivores in food-concentrated patches: tests of a mechanistic model. *Ecology* **74**:778–791.
- Hirakawa, H. 1997. How important is digestive quality? A correction of Verlinden and Wiley's digestive rate model. *Evolutionary Ecology* **11**:249–252.
- Hudson, R. J., and S. Frank. 1987. Foraging ecology of bison in aspen boreal habitats. *Journal of Range Management* **40**:71–75.
- Illius, A. W., I. J. Gordon, D. A. Elston, and J. D. Milne. 1999. Diet selection in goats: a test of intake-rate maximization. *Ecology* **80**:1008–1018.

- Illius, A. W., and T. G. O'Connor. 2000. Resource heterogeneity and ungulate population dynamics. *Oikos* **89**:283–294.
- Kagel, J. H., L. Green, and T. Caraco. 1986. When foragers discount the future: constraint or adaptation? *Animal Behaviour* **34**:271–283.
- Laca, E. A., E. D. Ungar, N. Seligman, and M. W. Demment. 1992. Effects of sward height and bulk density on bite dimensions of cattle grazing homogeneous swards. *Grass and Forage Science* **47**:91–102.
- Langvatn, R., and T. A. Hanley. 1993. Feeding-patch choice by red deer in relation to foraging efficiency: an experiment. *Oecologia* **95**:164–170.
- Larter, N. C., and C. C. Gates. 1991. Diet and habitat selection of wood bison in relation to seasonal changes in forage quantity and quality. *Canadian Journal of Zoology* **69**:2677–2685.
- Lucas, J. R. 1983. The role of foraging time constraints and variable prey encounter in optimal diet choice. *American Naturalist* **122**:191–209.
- Lucas, J. R. 1990. Time scale and diet decisions. Pages 165–184 in R. N. Hughes, editor. *Behavioural mechanisms of food selection*. NATO ASI series G. Volume 20. Springer-Verlag, Berlin, Germany.
- McHugh, T. 1958. Social behaviour of the American buffalo (*Bison bison bison*). *Zoologica* **43**:1–40.
- McInnis, M. L., and M. Vavra. 1987. Dietary relationships among feral horses, cattle, and pronghorn in southeastern Oregon (USA). *Journal of Range Management* **40**:60–66.
- Merrill, E. H., N. L. Stanton, and J. C. Hak. 1994. Responses of bluebunch wheatgrass, Idaho fescue, and nematodes to ungulate grazing in Yellowstone National Park. *Oikos* **69**:231–240.
- Michaelis, L., and M. L. Menten. 1913. Kinetics of invertase action. *Biochemische Zeitschrift* **49**:333–369.
- Mould, E. D., and C. T. Robbins. 1982. Digestive capabilities in elk compared to white-tailed deer. *Journal of Wildlife Management* **46**:22–29.
- 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., and P. Novellie. 1982. What should a clever ungulate eat? *American Naturalist* **119**:151–178.
- Painter, E. L., J. K. Detling, and D. A. Steingraeber. 1993. Plant morphology and grazing history: relationships between native grasses and herbivores. *Vegetatio* **106**:37–62.
- Reynolds, H. W., R. M. Hansen, and D. G. Peden. 1978. Diets of the Slave River lowland bison herd, Northwest Territories, Canada. *Journal of Wildlife Management* **42**:581–590.
- Shipley, L. A., D. E. Spalinger, J. E. Gross, N. T. Hobbs, and B. A. Wunder. 1996. The dynamics and scaling of foraging velocity and encounter rate in mammalian herbivores. *Functional Ecology* **10**:234–244.
- Spalinger, D. E., and N. T. Hobbs. 1992. Mechanisms of foraging in mammalian herbivores: new models of functional response. *American Naturalist* **140**:325–348.
- Stephens, D. W., and J. R. Krebs. 1986. *Foraging theory*. Princeton University Press, Princeton, New Jersey, USA.
- Ungar, E. D., and I. Noy-Meir. 1988. Herbage intake in relation to availability and sward structure: grazing processes and optimal foraging. *Journal of Applied Ecology* **25**:1045–1062.
- Van Soest, P. J. 1994. *Nutritional ecology of the ruminant*. Second edition. Cornell University Press, Ithaca, New York, USA.
- 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.
- Vartha, E. W., and A. G. Matches. 1977. Use of a weighted-disk measure as an aid in sampling the herbage yield on tall fescue pastures grazed by cattle. *Agronomy Journal* **69**:888–890.
- Verlinden, C., and R. H. Wiley. 1989. The constraints of digestive rate: an alternative model of diet selection. *Evolutionary Ecology* **3**:264–272.
- Wallis de Vries, M. F., and C. Daleboudt. 1994. Foraging strategy of cattle in patchy grassland. *Oecologia* **100**:98–106.
- Wilmschurst, J. F., and J. M. Fryxell. 1995. Patch selection by red deer in relation to energy and protein intake: a re-evaluation of Langvatn and Hanley's (1993) results. *Oecologia* **104**:297–300.
- Wilmschurst, J. F., J. M. Fryxell, and P. E. Colucci. 1999. What constrains daily intake in Thomson's gazelles? *Ecology* **80**:2338–2347.
- Wilmschurst, J. F., J. M. Fryxell, and R. J. Hudson. 1995. Forage quality and patch choice by wapiti (*Cervus elaphus*). *Behavioural Ecology* **6**:209–217.