

Daniel Fortin · John M. Fryxell · Lloyd O’Brodivich ·
Dan Frandsen

Foraging ecology of bison at the landscape and plant community levels: the applicability of energy maximization principles

Received: 7 May 2002 / Accepted: 3 October 2002 / Published online: 10 December 2002
© Springer-Verlag 2002

Abstract Predictions of animal distribution and resource use require multi-scale consideration because animals can use different sets of selection criteria at different scales. We investigated whether patterns of distribution and resource use by free-ranging bison (*Bison bison*) in Prince Albert National Park, Saskatchewan, follow rules of energy maximization that hold across multiple scales. Optimality theory predicts specialization on *Carex atherodes* and frequency-independent selection among plant species; that is, local variation in *C. atherodes* biomass should not influence diet choice but only the time spent in individual patches. The summer use of resources within meadows was closely related to energy maximization principles. *C. atherodes* dominated the diet of bison, was selected in all meadows, and diet choice was frequency-independent among meadows in the bison range. In winter, diet was still dominated by *C. atherodes*, but frequency-dependent selection of *Scolochloa festucacea* and the relative use of *Cirsium arvense* were inconsistent with theoretical predictions. At a larger spatial scale, however, the probability of meadow use was not positively related to the abundance of *Carex atherodes*. During summer and winter, general landscape features within the daily radius of bison (2 km in summer and 1.3 km in winter), together with abiotic characteristics of meadows, had the major influence on the probability of meadow utilization. Our study suggests

that bison distribution and resource use are influenced by abiotic and biotic factors which vary in importance at different spatio-temporal scales.

Keywords Energy maximization · Frequency-dependent diet selection · Large ungulate · Optimal foraging theory · Scale sensitivity

Introduction

Understanding what determines the distribution and abundance of organisms is fundamental to ecological studies. Adequate prediction of animal distribution patterns requires multi-scale consideration because diverse selection criteria are often used at different scales (Senft et al. 1987; Orians and Wittenberger 1991; Bergin 1992; Schaefer and Messier 1995; Wallace et al. 1995). Congruence in selection across scales has been reported for several animal species (Ward and Saltz 1994; Sedgwick and Knopf 1992; Carey et al. 1992; Hall and Mannan 1999). These conflicting observations emphasize the importance of multi-scale studies. Nonetheless, such studies are still rare compared to investigations at a single scale (Ward and Saltz 1994; Bergman et al. 2001).

Optimal foraging theory (Stephens and Krebs 1986) can formally test whether animal distribution can be explained by the spatial patterns of resources that maximize a given currency. Empirical investigations of optimal diet are generally performed at a single scale, often leaving unanswered the spatio-temporal consistency of optimal diet predictions (Bergman 2000; Fortin et al. 2002). Contingency models are the most frequently used optimal diet models. They predict which prey types should be eaten, and in what relative proportion (Stephens and Krebs 1986; Farnsworth and Illius 1998; Fortin 2001; Fortin et al. 2002). At the scale of an animal’s home range, positive frequency-dependence in prey selection is predicted from these models (Hubbard et al. 1982; Fryxell and Lundberg 1997). As the availability of highly profitable prey decreases, their encounter rate should

D. Fortin (✉) · J. M. Fryxell
Department of Zoology,
University of Guelph,
Guelph, Ontario, N1G 2W1 Canada
e-mail: dfortin@ualberta.ca
Tel.: +1-780-4927255
Fax: +1-780-4929224

L. O’Brodivich · D. Frandsen
Prince Albert National Park,
P.O. Box 100, Waskesiu Lake, Saskatchewan, S0 J 2Y0 Canada

D. Fortin
Department of Biological Sciences,
University of Alberta,
T6G 2E9 Alberta, Canada

decrease, eventually leading to diet expansion. Positive frequency-dependence may not hold at finer spatial scales. In heterogeneous environments, variation in prey availability among patches (or even resource depletion within patches) should not influence prey selection, but only patch residence time (McNamara et al. 1993). Therefore, selection among patches should be independent of the frequency of prey within patches (frequency-independent selection).

Resource distribution on the bison (*Bison bison*) range of Prince Albert National Park is patchy at multiple spatial scales: mosaics of plant species can be found in discrete meadows interspersed over the otherwise-forested landscape. In summer and winter, the bison of Prince Albert National Park can maximize short-term gains by specializing on *Carex atherodes*, an abundant sedge (Fortin et al. 2002). Consumption of less profitable plant species would reduce the potential intake rate of energy by causing a loss of opportunities for feeding on *C. atherodes* (Stephens and Krebs 1986). *C. atherodes* comprised the largest fraction of bison diets and was used more than expected based on availability measured over the entire bison range (Fortin et al. 2002). However, small-scale foraging patterns leading to this food selection observed at the landscape level remained unknown. Selection for *C. atherodes* may remain frequency-independent across meadows, as predicted from energy maximization principles (McNamara et al. 1993). Such information on food selection could then be used to determine whether fine-scale observations on foraging behavior can be used to infer animal distribution at large spatial scales.

Conflicting demands may lead to selection criteria that vary across scales. Water distribution has been considered to be the primary determinant of the grazing distribution patterns of many grazers (Bailey et al. 1996). Snow conditions can influence animal movement, energy costs of locomotion, feeding ability, probability of survival and susceptibility to predation in winter (Van Camp 1975; Telfer and Kelsall 1984; Turner et al. 1994). Bison appear particularly sensitive to the potentially negative effects of snow conditions compared to other North American ungulates (Telfer and Kelsall 1984).

We tested whether energy maximization principles, as predicted by optimal diet theory, predict patterns of bison spatial distribution and resource use across scales. Based on optimal diet predictions outlined by Fortin et al. (2002), we predict that bison should select *C. atherodes* during both summer and winter and in all meadows, irrespective of local abundance at the forage densities present in our study area. We also predict that the probability of using meadows should be positively related to local availability of *C. atherodes*. Predictions provided by our theoretical framework would hold if food availability were the major force driving bison distribution at all investigated scales.

Materials and methods

Study area

The bison population of Prince Albert National Park (53°44'N, 106°40'W) was studied during the winters (1 January–5 April) of 1997–1998 and summers (20 June–6 September) of 1997–1999. The estimated population of 220 bison (Fortin and Frandsen 1999) is established in the southwest corner of the park. This area of the park is composed of approximately 85% forest, 10% meadow, and 5% water. Bison are occasionally found in agricultural fields adjacent to the park, but cross-boundary movements were infrequent during our study. The forest is mainly deciduous in the southern part of the bison range and coniferous in the northern part. The number of plant species in individual meadows varied from 16 to 62, out of over 170 plant species recorded in the bison's range.

Plant availability and snow conditions

Plant phenology and snow conditions were estimated in 25 meadows distributed throughout the bison range, in the winter of 1997 and 1998 and in the summer of 1998. As many of these 25 meadows as possible were used in each statistical analysis. Depending on meadow area, plant characteristics were determined in 16–90 evenly spaced quadrats. These quadrats were 1 m² during the summer and 0.25 m² in winter. Total dry biomass (g/m²) of summer forage was determined by measuring the height (in centimeters) that a calibrated disk settled from the ground (Vartha and Matches 1977): $y=81.958+10.004x$ ($F_{1, 179}=162.99$; $r^2=0.48$; $P<0.0001$). In winter, forage abundance in each quadrat was visually estimated on a 0–5 categorical scale (Fortin et al. 2002). Evaluation of plant biomass was supplemented by visual estimation of the relative proportion of each plant species and, in summer, percent green biomass of each plant species.

Snow was characterized by its depth, density, softness, and the presence of crust. Snow density (g/cm³) 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. Snow softness was indexed by the sinking depth of a bottle (300 g; 8.5 cm in diameter) dropped 50 cm above the snow surface (Murray and Boutin 1991).

Bison diet was determined in all quadrats by visually estimating the percent of each plant species grazed (attack rate), and by measuring their grazed stratum (Fortin et al. 2002). We believe that forage consumption in meadows was primarily due to bison. White-tailed deer (*Odocoileus virginianus*), elk (*Cervus elaphus*) and moose (*Alces alces*) are present but were rarely seen in meadows during our aerial and ground surveys and bison represented >94% of all observed ungulates during any season (Fortin 2000). Fecal groups encountered 1 m each side of the

transect lines used for the plant and snow surveys were from bison 83% and 90% of the time in winter and summer, respectively. Likewise, over 99% of feeding craters in snow that were also recorded along the transects were made by bison.

Animal locations

During the study period (1997–1999), 10 female bison were equipped with Global Positioning System (GPS) collars (GPS 1000 collar from Lotek Engineering, Newmarket, Ontario, Canada). Some females wore GPS collars for more than one season. In 1997, we collared two individuals during the summer and four in winter; in 1998, four females were collared both in summer and in winter; four new individuals were followed in the summer of 1999. Animal locations were recorded at 0000 hours and every 2 h from 0600 to 1600 hours in winter of 1997. During the rest of the study period, animal locations were recorded every 3 h, starting at 0000 hours. Overall, 9,694 of the 12,259 GPS location attempts were successful (79%). Three-dimensional differential correction was successful in 6,177 locations, 2-dimensional differential correction in 3,326 locations, and 191 locations were not differentially corrected. The accuracy of 3-dimensional and 2-dimensional differentially corrected locations should be within about 25 m and 50 m 95% of time, respectively (Moen et al. 1996, 1997).

Geographic Information System

Aerial photographs (1:60,000) taken in 1995 and 1999 were digitized, geo-referenced, and imported into a Geographic Information System (GIS). Two meadows were excluded from our large-scale analysis of habitat selection because photographs were not available. Using ArcView GIS (Version 3.1), a buffer of 2 km in diameter was drawn from the edge of the 23 meadows. All distinguishable meadows, rivers, ponds and lakes within this large-scale study area were drawn and included as GIS layers of information.

Data analysis

Plant selection

Plant selection was investigated from surveys conducted during 1998. Three surveys were done in summer and four in winter. Before analyzing, the biomass used versus that available during a given season was averaged for each plant species found in each meadow. Compositional analysis (Aebischer et al. 1993) was then performed considering individual meadows as the sampling unit. Minimizing unused and unavailable plant types is desirable in compositional analyses. Consequently, we restricted our analysis to the eight most common plant types

(other plant types were pooled in a ninth category), and to the meadows frequented by bison where these plants were most abundant (12 meadows in summer and 11 in winter). Our plant surveys indicated that these eight plant species comprised 95% of the bison diet in summer (range among meadows: 70–100%) and 96% in winter (range: 63–100%). Some of these focal plant species remained unused or unavailable in certain meadows, and values of 0 cannot be directly included in the log-ratio computation used in compositional analysis. Consequently, plant types were replaced by an arbitrary value of 0.001%, whenever available but unused (Aebischer et al. 1993; Tufto et al. 1996; Pendleton et al. 1998). Also, if a plant species did not exist in a meadow, missing values were replaced by the mean of the non-missing values for that habitat class before calculating the likelihood ratio test (Aebischer et al. 1993; Pendleton et al. 1998).

Carex atherodes and *S. festucacea* have high short-term profitability (in kJ/min) (Fortin et al. 2002). Therefore, frequency-dependent selection by bison was tested between *C. atherodes*, *S. festucacea* and other plant types combined. Following Elton and Greenwood (1987) we evaluated frequency-dependence using the equation:

$$\log U_{i,j} = b_{i,j} \log V_{i,j} + b_{i,j} \log A_{i,j},$$

where $U_{i,j}$ = total biomass of plant type i grazed / total biomass of plant type j grazed; $A_{i,j}$ = total biomass of plant type i available / total biomass of plant type j available. $b_{i,j}$ is the slope of the relationship between $\log U_{i,j}$ and $\log A_{i,j}$, for which difference from unity indicates frequency-dependence. Finally, " $b_{i,j} \log V_{i,j}$ " is the intercept of the relationship for which a $V_{i,j}$ is a selectivity coefficient. An intercept different from 0 indicates plant selectivity. As for the compositional analysis, unused plant types were replaced by a usage of 0.001%, but unavailable resources corresponded to missing values. The significance of the estimated parameters was determined by t -test following Greenwood and Elton (1979). Because we considered three groupings of plants, three tests were done to cover all pair-wise comparisons. Significance level was set to 0.017 following Bonferroni adjustment (Sokal and Rohlf 1995).

Meadow selection

Habitat features influencing the probability of meadow use were investigated, for each season, with stepwise logistic regressions. Regression models included only variables with $P < 0.10$ that did not exhibit collinearity. The independent variables considered included meadow characteristics, as well as characteristics of the area covered by a 1- and 2-km radius starting at the meadow edge (see Tables 3 and 4 for a complete list of independent variables).

GPS locations associated with the selection of a given meadow included all locations recorded in that meadow, as well as in the meadow edge (≤ 25 m from meadows) because bison were often observed lying in edges between

Table 1 Percent of GPS locations within 100 m for pairs of female bison equipped with GPS-collars in summer and winter (*asterisk*). Pairwise comparisons were restricted to animals tracked simultaneously (blank cases occur when bison were not concurrently wearing collars). Sample size for each comparison ranged between 228 and 1,245 pairs of locations, with the exception of animal B vs animal E in winter where sample size was 34 pairs of locations

	Individuals									
	B	C	D	E	F	G	H	I	J	
C	5*		18	15	10	3				
D	0*	1*		13	10	6				
E	6*	8*	0*			5				
F	*	3*	81*	*		11				
K	*	*	*	*	*	*	35	15	23	
H	*	*	*	*	*	*		17	24	
J	*	*	*	*	*	*	*		30	

feeding bouts. Meadows with no bison GPS locations were assigned a value of 0 in the logistic regressions, whereas other meadows were assigned a value of 1. Years were pooled before analyzing the summer data, because not all habitat information was available annually.

Green (1992) considered that individual bison separated by more than 100 m belonged to different groups. Based on this criterion, pairs of female bison equipped with GPS-collars traveled in the same group for certain periods of time (Table 1). The median percent of fixes in which pairs of female bison with collars were within 100 m of each other was 11% in summer and 4% in winter. These low values suggest that marked individuals were rarely in a single group but neither was meadow selection by female bison completely independent. We performed logistic regression on individual animals, allowing direct comparison of the parameters influencing meadow selection among females, while knowing the proportion of time spent in the same group (Table 1).

Results

Plant selection

The relative biomass available varied among plant species (Fig. 1). Bison displayed strong selection among plant species (summer: $\chi^2=76$, $df=8$, $P<0.0001$; winter: $\chi^2=49$, $df=8$, $P<0.0001$). During both seasons, *Agropyron* spp., *Bromus ciliatus*, and *Calamagrostis inexpectans* were generally used less than expected on the basis of their availability (Fig. 2). Although *Carex atherodes* was one of the two most abundant species (Fig. 1), bison consumed this plant species even more than would be expected based on availability (Fig. 2). A similar trend in summer selection was found with the analysis of frequency-dependent selection (Table 2). Overall, the selection for *C. atherodes* was consistent across meadows (Fig. 2), and independent of its relative abundance (Table 2).

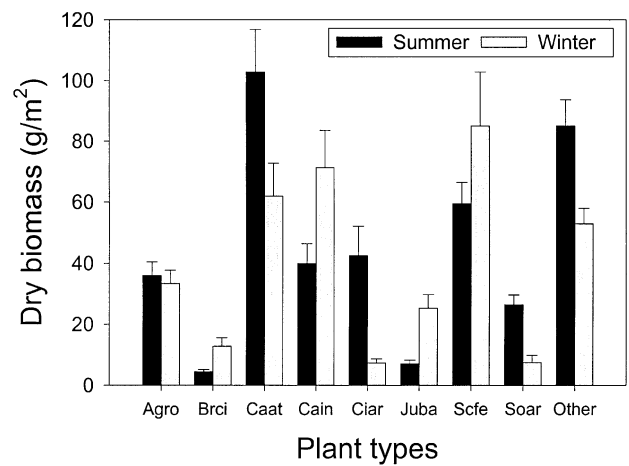


Fig. 1 Dry biomass of various plant species in Prince Albert National Park in 1998 ($n=12$ meadows in summer and $n=11$ meadows in winter). Acronyms for plant types are Agro, *Agropyron* spp.; Brci, *Bromus ciliatus*; Caat, *Carex atherodes*; Cain, *Calamagrostis inexpectans*; Ciar, *Cirsium arvense*; Hoju, *Hordeum jubatum*; Juba, *Juncus balticus*; Scfe, *Scolochloa festucacea*; Soar, *Sonchus arvensis*; and Other, all other species

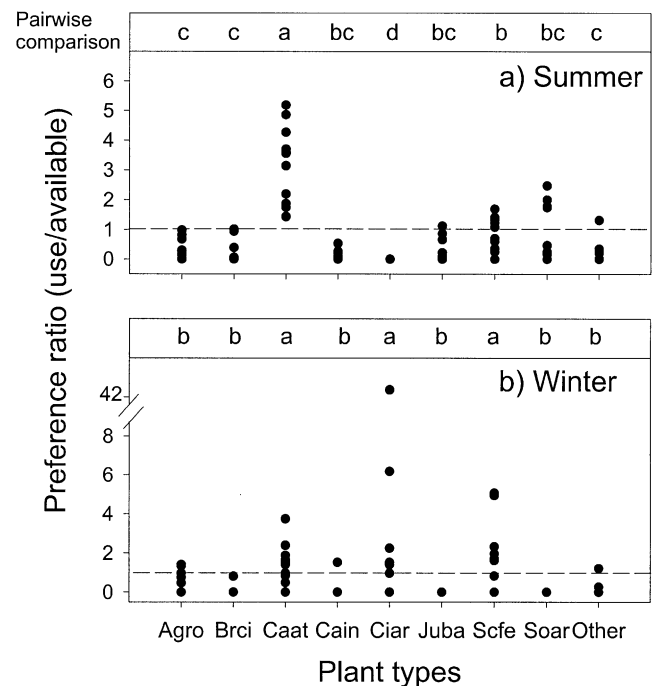


Fig. 2 Selection ratio of plant types found in 12 meadows of Prince Albert National Park during a) summer and b) winter in 1998. A selection ratio of 1 indicates that the resource was used in proportion to availability. A broken horizontal line displays this threshold. For a given season, selection of plant types with the same letter did not differ significantly following pairwise comparison ($P<0.05$). Acronyms for plant types are indicated in Fig. 1

In winter, *C. atherodes*, *S. festucacea* and *Cirsium arvense* were all selected equally (Fig. 2, Table 2). Although these species had the highest preference ratio, they were sometimes grazed more heavily than expected

Table 2 Bison selection of plant types in relation to the relative biomass of other plant types found in 25 meadows of Prince Albert National Park. Acronyms for plant types are *Caat*, *Carex atherodes*; *Scfe*, *Scolochloa festucacea* and *Other*, all other species

Comparison	Regression			H_0 : Intercept = 0			H_0 : Slope = 1		
	df	r^2	P	$b \log V$	t	P	b	t	P
Summer									
Caat-Scfe	10	0.51	0.009	1.59	2.09	0.06	1.59	1.21	0.25
Caat-Other	10	0.29	0.07	5.44	3.28	0.008	2.01	1.01	0.33
Scfe-Other	10	0.26	0.09	5.47	1.88	0.09	2.86	1.21	0.25
Winter									
Caat-Scfe	16	0.60	0.0002	1.47	1.68	0.11	2.34	2.79	0.013
Caat-Other	16	0.25	0.04	6.69	2.69	0.02	2.95	1.52	0.15
Scfe-Other	16	0.28	0.02	5.44	2.34	0.03	3.18	1.73	0.10

Table 3 Variables influencing the probability of use of 23 meadows in Prince Albert National Park during the summer of 1997–1998, as determined from stepwise logistic regressions. The independent variables that could have entered the model were: area of the meadow, area of water in the meadow, perimeter of water in the meadow, absence of water in the meadow (dicotomic variable),

combined. Non-significant intercept ($b \log V$) suggests that when the two contrasted plant types had equal availability, there was no selection between the two types. Non-significant slope (b) suggests frequency-independent selection among the contrasted plant types

biomass of *Agropyron* spp., *Carex aquatilis*, *C. atherodes*, presence of *Caat* (dicotomic variable), *Calamagrostis inexplansa*, *Juncus balticus*, *Hordeum jubatum* (biomass of Hoju) and *Scolochloa festucacea*, and percentage of an area of 2-km radius and 1-km radius covered by meadows, water areas and agricultural lands. Final models included only variables with $P < 0.10$

Animal id	Significant independent variable: $\beta \pm SE$			
	Intercept	Area (ha)	Water in a 2-km radius (%)	Biomass of Hoju (g/m^2)
C	-3.81±1.58*		0.56±0.22*	
D	-2.32±1.04*		0.38±0.15*	
E	-5.52±2.35*	0.19±0.11 ^φ	0.35±0.15*	
F	-1.70±0.90 ^φ		0.33±0.14*	
G	-3.84±1.47**		0.29±0.12*	
H	-2.54±0.95**	0.19±0.08*		
I	-4.39±1.98*		0.21±0.12 ^φ	1.45±0.67*
J	-7.29±3.81 ^φ		0.81±0.40*	
K	-2.54±0.95**	0.19±0.08*		

^φ $P < 0.10$, * $P < 0.05$, ** $P < 0.01$

and other times more lightly than expected from availability (Fig. 2). Such variation can be partly explained by bison switching behavior in food selection (Table 2). In contrast to the summer patterns, the relative consumption of *Carex atherodes* and *S. festucacea* in winter was positively frequency-dependent, i.e., bison selection of one species over another was a function of its local relative abundance. Further seasonal variation in species selection was evident from the use of *Cirsium arvense*, a species that often stands up above the snow cover. This species was unutilized in summer, but in winter, its selection equaled that of *Carex atherodes* and *S. festucacea* (Fig. 2).

Meadow selection

Female bison equipped with GPS-radio collars spent 81±8% (mean±SD; range: 62–89%; $n=10$ individuals) of their time on the 19% of the bison range that was inside of or within 25 m of the edge of meadows. During both the winter and summer, larger meadows were generally more likely to be visited than were smaller meadows (Tables 3,

4). Meadow utilization was also related to availability of resources within the average daily radius of individual animals. This daily radius, defined as the distance between locations recorded at 0000 hours on successive days, varied seasonally (three-way ANOVA: Factor “season”; $F_{1, 1,074}=49.2$, $P < 0.0001$). The daily radius was larger in summer (1,986±1,636 m, $n=538$) than in winter (1,297±1,236 m, $n=537$, Tukey’s studentized range test: $P < 0.01$). In summer, meadows with more land area covered by water within a 2-km radius were more likely to be visited by bison (Table 4). This pattern remained consistent among individuals spending little time with each other (Table 1).

Water availability in summer often overrides meadow size effects (Table 4). In these cases, the Nagelkerke r^2 increased by an average of 47% when the probability of meadow use was predicted by water availability within the daily radius instead of by meadow area. During the winter of 1997 when snow depth was 38±4 cm meadows with deeper snow were less likely to be visited by some bison (Table 4). In 1998 with less snow (27±4 cm, paired t -test; $t_{25} = 15.9$ $P < 0.0001$) meadow use was not influenced by snow depth. In three instances, regression

Table 4 Variables influencing the probability of use of 23 meadows in Prince Albert National Park in winter, as determined from stepwise logistic regressions. The independent variables that could have entered the model were: area of the meadow, snow depth, snow density, snow softness, presence of crusts in the snow column (dicotomic variable), biomass of *Agropyron* spp. (*Agro*), *Carex aquatilis*, *C. atherodes* (*Caat*), presence of *caat* (dicotomic variable), *Calamagrostis inexpansa*, *Hordeum jubatum*, *Juncus balticus* and *Scolochloa festucacea* (*Scfe*), and percentage of an area of 2-km radius and 1-km radius covered by meadows, water areas and agricultural lands. Final models included only variables with $P < 0.10$

Animal id	Significant independent variable: $\beta \pm SE$			
	Intercept	Area (ha)	Snow depth (cm)	Biomass of plants (g/m ²)
1997				
B	10.21±5.92 ^φ		-0.29±0.16 ^φ	
C	17.03±7.38*		-0.44±0.19*	
D	-2.04±0.82*	0.17±0.07*		
E	-3.12±1.10**	0.09±0.06*		
1998				
C	-0.81±0.83 ^{ns}			0.03±0.02 ^{φ, a} -0.02±0.009 ^{φ, b}
D	-1.50±0.72*	0.14±0.07*		
E	-0.26±1.32*			0.06±0.03 ^{φ, c}
F	-1.95±0.88*	0.27±0.14*		

^φ $P < 0.10$, * $P < 0.05$, ** $P < 0.01$, ^{ns} $P > 0.10$

^a Scfe

^b Caat

^c Agro

models included two independent variables with $P < 0.10$ (Tables 3, 4). Inclusion of the second variables improved by 4, 8, and 16% the concordance in classification of meadow use predicted by the logistic regression equations.

Plant biomass recorded within meadows had little influence on meadow selection by bison during any period of the year (Tables 3, 4). Even the biomass or presence of the species that dominated the diet of bison, *C. atherodes*, did not display a significant positive relationship in any of our multiple logistic regression models (Tables 3, 4). Simple logistic regression confirmed the lack of significant positive relationships between probability of meadow use and biomass of *C. atherodes* (summer: range of $\beta \pm SE = -0.006 \pm 0.005$, $P = 0.26$ to -0.01 ± 0.005 , $P = 0.04$; winter: range of $\beta \pm SE = -0.02 \pm 0.02$, $P = 0.15$ to 0.005 ± 0.007 , $P = 0.48$), or the presence of *C. atherodes* (summer: range of $\beta \pm SE = -0.81 \pm 0.95$, $P = 0.40$ to 0.81 ± 0.95 , $P = 0.40$; winter: range of $\beta \pm SE = -0.58 \pm 1.32$, $P = 0.19$ to 12.75 ± 223.6 , $P = 0.96$). Bison occasionally visited some dry meadows that did not offer any *C. atherodes*, and some individuals never visited other meadows that included some *C. atherodes*. Moreover, if *C. atherodes* influenced the summer selection of meadows, the eight meadows located in the northern part of the bison range should have been heavily used throughout the year because they offered higher biomass of *C. atherodes* than the other meadows (ANOVA on square root transformed values: $F_{1, 22} = 13.58$, $P = 0.001$). Instead, only 1 of 2,199 GPS locations in summer was in the northern meadows, while 117 of 1,492 GPS locations by four individuals were in northern meadows in winter. Southern meadows were five times larger than northern meadows ($F_{1, 22} = 5.94$, $P = 0.02$), which could explain why bison used northern meadows less than southern meadows. The difference between summer and winter use of

northern meadows where *C. atherodes* remained highly abundant supported the existence of environmental factors other than the abundance of *C. atherodes* that influenced the probability of meadow use by bison in summer (Table 3).

Discussion

Foraging decisions by bison maximize their short-term rate of energy intake (Fortin et al. 2002). However, the results presented here suggest that the predictive success of optimal diet models strongly depends on the spatio-temporal scale. Large-scale patterns of animal distribution can not be directly inferred based exclusively on small-scale information. The link between forage and animal distribution weakened as non-foraging objectives increased in importance at larger spatial scales.

Plant selection

During summer and winter, *Carex atherodes* held the highest rank in terms of plant selection by bison, and it predominated in their diet, consistent with bison diets elsewhere (Reynolds et al. 1978; Larter and Gates 1991; Bergman 2000) and expectations from foraging theory (Fortin et al. 2002). Here we showed that energy maximization principles can successfully predict resource use, but predictive ability varies with spatial and temporal scales of investigation. Optimal foraging predictions held up best during the summer. Bison selected *C. atherodes* in all meadows irrespective of its relative abundance. Such frequency independent selection for *C. atherodes* in summer was consistent with the predictions that diet selection should not change from patch to patch (McNa-

mara et al. 1993), as shown for moose (Danell and Ericson 1986; Lundberg et al. 1990). Frequency-independent diet selection should have a destabilizing effect on plant-herbivore dynamics compared to frequency-dependent selection (Hanski et al. 1991). The success of our predictions did not hold, however, throughout the year.

Winter diet of bison was still dominated by *C. atherodes*. However, in contrast to our predictions, *S. festucacea* and *Cirsium arvense* were also used more than would be expected by their abundance, and bison choice between *Carex atherodes* and *S. festucacea* was influenced by the relative local biomass of these plant species. Winter foraging decisions thus appeared to lead to sub-optimal diet for the maximization of short-term rate of gross energy intake. Several factors may contribute to the divergence from our prediction. Increased search costs can lead to broadening of the diet (Lifjeld and Slagsvold 1988). Given that the cost of digging a new crater (kJ/min) might conceivably surpass the difference in profitability (kJ/min) between plant species co-occurring at the feeding station, the maximization of net energy intake could lead to an increase in vegetation use in each crater, and thus to diet expansion.

The short-term profitability of plant species (digestible energy / handling time, Fortin 2001) would not change with the consideration of digging costs. Therefore, optimality principles based on the maximization of net energy intake would still predict preference for *C. atherodes*, but usage of some *S. festucacea* might also be predicted because this species often had the second highest short-term profitability (Fortin et al. 2002). Given that the optimal diet model could predict use of both *C. atherodes* and *S. festucacea*, the search strategy of bison might be responsible for the observed pattern of frequency-dependent selection. In winter, bison use area-restricted search to find their food when foraging within meadows (Fortin 2000). This strategy leads to increased search effort in areas where suitable food types are found. Spatial auto-correlation in plant distribution combined with area-restricted search should result in frequency-dependent selection of the most abundant plant species.

Meadow selection

Although simple optimal foraging models provided some success in predicting bison diets within meadows (this study) and across the landscape (Fortin et al. 2002), our results indicate that other factors may have an even stronger influence than abundance of preferred food types on the distribution of bison across the landscape. Large-scale patterns of animal distribution can be influenced by the movement capability of animals (Pearson et al. 1995). Female bison adjusted their movements to the presence of snow, with their daily displacement decreasing from 2 km in summer to 1.3 km in winter. The probability of meadow use by bison was also influenced by snow depth, a finding supported by observations on other bison populations (Larter and Gates 1991; Pearson et al.

1995). Meadows largely surrounded by water areas within a 2-km radius were more likely to be used in summer, when bison require daily access to surface water (McHugh 1958).

Even though meadows where *C. atherodes* occurred were not more likely to be used by bison, *C. atherodes* dominated bison diet (Fortin et al. 2002). The average number of bison locations (location/meadow) in meadows having *C. atherodes* was 12 times higher in summer and 16 times higher in winter than in meadows where this plant species was absent. In other words, although the presence of *C. atherodes* did not influence the selection of particular meadow, bison remained in meadows offering *C. atherodes* for longer periods of time and/or were more likely to revisit these locations, leading to a higher usage of this plant species than expected based on availability.

A small wolf (*Canis lupus*) population was present in the study area but bison predation appeared rare, presumably due to the abundance of alternative prey such as white-tailed deer. Wolf-bison interactions have never been observed during the 3 years (over 220 days from 1997 to 1999) that we conducted behavioral observations on bison herds (Fortin 2000; Fortin et al. 2002) or snow and plant surveys across the bison range. In contrast, there were 166 bison-wolf encounters during 102 days in the Wood Buffalo National Park (Carbyn and Trotter 1987). Therefore, wolf impact on bison selection of meadows was expected to be relatively small in Prince Albert National Park.

Integration across scales

The distribution of several ungulate species has been related to the spatial variation in forage quality (Albon and Langvatn 1992). Krasińska and Krasińska (1995) indicated that food selection is the major factor causing concentration of European bison in particular areas. Myrnerud et al. (1999) successfully predicted habitat selection by domestic sheep (*Ovis aries*) across spatial scales based on food availability. Ward and Saltz (1994) observed consistency in the foraging behavior of dorcas gazelles (*Gazella dorcas*) across spatial scales. Despite these observations, it appears that information on diet selection alone can not always be readily scaled up to explain animal distribution. The probability of a given meadow being used by bison was not related to the abundance or even presence of preferred plant species.

Maximization of gross energy intake is not the only currency that can influence reproduction and survival of ungulates. Individuals also have to consider other factors such as needs for other nutrients (McNaughton 1990) and for water (Bailey et al. 1996), energetic costs of foraging or raveling (Stephens and Krebs 1986), and predation risks (Edwards 1983). Given that large-scale decisions constrain the option available at smaller scales, the importance of considering each of these factors can change from one scale to the next (Senft et al. 1987), leading to scale-sensitivity in selection criteria. Our study

revealed that rules of energy intake maximization were insufficient to explain the distribution and resource use by plains bison across spatio-temporal scales. The relation between habitat use by wood bison (*B. b. athabascae*) and the distribution of *Carex atherodes* also varied among spatial scales (Bergman 2000). There were reversals of selection among forage species by muskoxen (*Ovibos moschatus*) at different spatial scales (Schaefer and Messier 1995), and woodland caribou (*Rangifer tarandus*) would not have a constant optimal foraging strategy across scales (Johnson et al. 2001). The scale-dependent selection observed in our study could be the reflection that maximization of bison fitness relies on trade-offs associated with non-dietary goals (Senft et al. 1987; Barton et al. 1992; Mysterud et al. 1999). In such instances, the complex nature of selection can reduce the utility of simple optimality principles in predicting habitat selection (Barton et al. 1992).

Our findings confirm Senft et al.'s (1987) contention that the relative importance of plant-herbivore interactions declines at larger scales, as abiotic factors become more important (Bailey et al. 1996). Bison distribution was influenced by the characteristics of meadows and by the characteristics of adjacent areas, an effect reported for ungulates and birds (Pearson et al. 1995, Fortin and Arnold 1997). The exact nature of relationships between resource characteristics and animal distribution is somewhat obscure (Barton et al. 1992), and our study underlines the existence of spatio-temporal variation in the relative influence of abiotic and biotic factors on bison distribution and resource use.

Acknowledgements The funding for this study was provided by Parks Canada, University of Guelph, NSERC, and scholarships from FCAR and OGS. We thank Mark Andruskiw, Régis Pilote and Sergio Juárez, as well as many volunteers for their help in the field and the laboratory. Ron Moen, Mark Andruskiw, Tom Nudds and Bart Nolet provided constructive comments on the manuscript. We are grateful to John McKenzie and Tracy Hillis for sharing their experience with ArcView. We acknowledge the Southern California Integrated GPS Network and its sponsors, the W.M. Keck Foundation, NASA, NSF, USGS, SCEC, for providing some of the data used in this study to perform the differential correction of bison locations.

References

- Aebischer NJ, Robertson PA, Kenward RE (1993) Compositional analysis of habitat use from animal radio-tracking data. *Ecology* 74:1313–1325
- Albon SD, Langvatn R (1992) Plant phenology and the benefits of migration in a temperate ungulate. *Oikos* 65:502–513
- Bailey DW, Gross JE, Laca EA, Rittenhouse LR, Coughenour MB, Swift DM, Sims PL (1996) Mechanisms that result in large herbivore grazing distribution patterns. *J Range Manage* 49:386–400
- Barton RA, Whiten A, Strum SC, Byrne RW, Simpson AJ (1992) Habitat use and resource availability in baboons. *Anim Behav* 43:831–844
- Bergin TM (1992) Habitat selection by the western kingbird in western Nebraska: a hierarchical analysis. *Condor* 94:903–911
- Bergman CM (2000) Behavioural responses to resource availability by northern ungulates. PhD thesis, University of Guelph
- Bergman CM, Fryxell JM, Gates CC, Fortin D. (2001) Ungulate foraging strategies: energy maximizing or time minimizing? *J Anim Ecol* 70:289–300
- Carbyn LN, Trottier T (1987) Responses of bison on their calving grounds to predation by wolves in Wood Buffalo National Park. *Can J Zool* 65:2072–2078
- Carey AB, Horton SP, Biswell BL (1992) Northern spotted owls: influence of prey base and landscape character. *Ecol Monogr* 62:223–250
- Danell K, Ericson L (1986) Foraging of moose on two species of birch when these occur in different proportions. *Holarct Ecol* 9:79–84
- Edwards J (1983) Diet shifts in moose due to predator avoidance. *Oecologia* 60:185–189
- Elton RA, Greenwood JJD (1987) Frequency-dependent selection by predators: comparison of parameter estimates. *Oikos* 48:268–272
- Farnsworth KD, Illius AW (1998) Optimal diet choice for large herbivores: an extended contingency model. *Funct Ecol* 12:74–81
- Fortin D (2000) Foraging decisions at multiple spatial and temporal scales: a bison perspective. PhD thesis, University of Guelph
- Fortin D (2001) An adjustment of the extended contingency model of Farnsworth and Illius (1998). *Funct Ecol* 15:138–139
- Fortin D, Arnold GW (1997) The influence of road verges on the use of nearby small shrubland remnants by birds in the central wheatbelt of Western Australia. *Wildl Res* 24:679–689
- Fortin D, Frandsen D (1999) Some preliminary results on the ecological hierarchy of foraging activities in bison. *Res Links* 7:13–15
- Fortin D, Fryxell JM, Pilote R (2002) The temporal scale of foraging decisions in bison. *Ecology* 83:970–982
- Fryxell JM, Lundberg P (1997) Individual behavior and community dynamics. Population and community biology series 20. Chapman and Hall, New York
- Green WCH (1992) Social influences on contact maintenance interactions of bison mothers and calves: group size and nearest-neighbour distance. *Anim Behav* 43:775–785
- Greenwood JJD, Elton RA (1979) Analysing experiments of frequency-dependent selection by predators. *J Anim Ecol* 48:721–737
- Hall LS, Mannan RW (1999) Multiscaled habitat selection by elegant trogons in Southeastern Arizona. *J Wildl Manage* 63:451–461
- Hanski I (1991) Single-species metapopulation dynamics: concepts, models and observations. In: Gilpin ME, Hanski I (eds) *Metapopulation dynamics: empirical and theoretical investigations*. Academic Press, London, pp 17–38
- Hubbard SF, Cook RM, Glover JG, Greenwood JJD (1982) Apostatic selection as an optimal foraging strategy. *J Anim Ecol* 51:625–633
- Johnson CJ, Parker KL, Heard DC (2001) Foraging across a variable landscape: behavioral decisions made by woodland caribou at multiple spatial scales. *Oecologia* 127:590–602
- Krasińska M, Krasiński ZA (1995) Composition, group size, and spatial distribution of European bison bulls in Białowieża Forest. *Acta Theriol* 40:1–21
- Larter NC, Gates CC (1991) Diet and habitat selection of wood bison in relation to seasonal changes in forage quantity and quality. *Can J Zool* 69:2677–2685
- Lifjeld JT, Slagsvold R (1988) Effects of energy costs on the optimal diet: an experiment with pied flycatchers *Ficedula hypoleuca* feeding nestlings. *Ornis Scand* 19:111–118
- Lundberg P, Åström M, Danell K (1990) An experimental test of frequency-dependent food selection: winter browsing by moose. *Holarct Ecol* 13:177–182
- McHugh T (1958) Social behaviour of the American Buffalo (*Bison bison bison*). *Zoologica* 43:1–40

- McNamara JM, Houston AI, Weisser WW (1993) Combining prey choice and patch use—what does rate-maximizing predict? *J Theor Biol* 164:219–238
- McNaughton SJ (1990) Mineral nutrition and seasonal movements of African migratory ungulates. *Nature* 345:613–615
- Moen R, Pastor J, Cohen Y, Schwartz CC (1996) Effects of moose movement and habitat use on GPS collar performance. *J Wildl Manage* 60:659–668
- Moen R, Pastor J, Cohen Y (1997) Accuracy of GPS telemetry collar locations with differential correction. *J Wildl Manage* 61:530–539
- Murray DL, Boutin S (1991) The influence of snow on lynx and coyote movements: does morphology affect behaviour? *Oecologia* 88:463–469
- Mysterud A, Larsen PK, Ims RA, østbye E (1999) Habitat selection by roe deer and sheep: does habitat ranking reflect resource availability? *Can J of Zool* 77:776–783
- Orians GH, Wittenberger JF (1991) Spatial and temporal scales in habitat selection. *Am Nat* 137:S29–S49
- Pearson SM, Turner MG, Wallace LL, Romme WH (1995) Winter habitat use by large ungulates following fire in Northern Yellowstone National Park. *Ecol Appl* 5:744–755
- Pendleton GW, Titus K, DeGayner E, Flatten CJ, Lowell RE (1998) Compositional analysis and GIS for study of habitat selection by goshawks in Southeast Alaska. *J Agric Biol Environ Stat* 3:280–295
- Reynolds HW, Hansen RM, Peden DG (1978) Diets of the Slave River lowland bison herd, Northwest Territories, Canada. *J Wildl Manage* 42:581–590
- Schaefer JA, Messier F (1995) Habitat selection as a hierarchy: the spatial scales of winter foraging by muskoxen. *Ecography* 18:333–344
- Sedgwick JA, Knopf FL (1992) Describing willow flycatcher habitats: scale perspectives and gender differences. *Condor* 94:720–733
- Senft RL, Coughenour MB, Bailey DW, Rittenhouse LR, Sala OE, Swift DM (1987) Large herbivore foraging and ecological hierarchies. *BioScience* 37:798–799
- Sokal RR, Rohlf FJ (1995) *Biometry: the principles and practice of statistics in biological research*, 3rd edn. Freeman, New York
- Stephens DW, Krebs JR (1986) *Foraging theory*. Princeton University Press, Princeton
- Telfer ES, Kelsall JP (1984) Adaptation of some large North American mammals for survival in snow. *Ecology* 65:1828–1834
- Tufto J, Andersen R, Linnell J (1996) Habitat use and ecological correlates of home range size in a small cervid: the roe deer. *J Anim Ecol* 65:715–724
- Turner MG, Wu Y, Wallace LL, Romme WH, Brenkert A (1994) Simulating winter interactions among ungulates, vegetation, and fire in Northern Yellowstone Park. *Ecol Appl* 4:472–496
- Van Camp J (1975) Snow conditions and the winter feeding behaviour of Bison bison in Elk Island National Park. Report CWS-53–75. Canadian Wildlife Service
- Vartha EW, Matches AG (1977) Use of a weighted-disk measure as an aid in sampling the herbage yield on tall fescue pastures grazed by cattle. *Agron J* 69:888–890
- Wallace LL, Turner MG, Romme WH, O'Neill RV, Wu Y (1995) Scale of heterogeneity of forage production and winter foraging by elk and bison. *Landscape Ecol* 10:75–83
- Ward D, Saltz D (1994) Foraging at different spatial scales: Dorcas gazelles foraging for lilies in the Negev desert. *Ecology* 75:48–58