
Searching Behavior and Use of Sampling Information by Free-Ranging Bison (*Bos bison*)

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Searching behavior and use of sampling information by free-ranging bison (*Bos bison*)

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Abstract I examined the searching behavior of free-ranging plains bison (*Bos bison bison*) in their natural habitat, and determined whether their assessment of food patch quality was influenced by the short-term sampling information acquired during search. Bison used area-concentrated search during their winter foraging activity. Their movements between areas of suitable food patches were influenced by local environmental conditions, being sometimes less sinuous, and at other times more sinuous, than expected from a correlated random walk model. Bison also systematically avoided digging in areas where plants of low profitability lay under the snow. Where they dug, there was evidence that a bison's perception of food quality varied during a foraging bout, and was therefore influenced by short-term sampling information. After controlling for forage quality, I found that small feeding craters were more likely to be preceded by samples of high quality food patches. My observations suggest that bison take advantage of the structural characteristics of their environment during searching activity, and base foraging decisions on local rather than global availability.

Keywords Area-concentrated search · Bison · Correlated random walk · Intensive and extensive search modes · Reference windows

Introduction

Foragers can take advantage of the spatial autocorrelation in the distribution of their food by using area-concentrated search to find food resources (Haskell 1997; Smith 1974). This strategy generally leads to higher efficiency than do random search patterns (Benhamou 1992). Area-concentrated search involves the use of intensive and extensive search modes (Benhamou 1992; Cézilly and Benhamou 1996). During the intensive search mode, animals intensify their search effort near areas where suitable food types have been found by having low travel speed and highly sinuous paths (Cézilly and Benhamou 1996). In contrast, during extensive search mode, animals leave an area offering poor quality food by traveling rapidly and moving with a rather straight path. The perception of food quality thus directly dictates which mode of area-concentrated search should be used to find the next prey item, thereby having an important influence on foraging patterns (Fortin 2002; Krakauer and Rodríguez-Gironés 1995).

A central issue in foraging ecology is to determine how long an animal should stay in a food patch (McNamara et al. 1993), which relates to the question: when is it time for a forager to abandon its intensive search mode and leave the area by adopting an extensive search mode? Classical foraging models have shown that, when food is distributed in discrete patches, patch departure decisions should be based on a comparison between the current gain and the expected gains over the entire environment (Charnov 1976; Stephens and Krebs 1986). Focardi et al. (1996) demonstrated that ungulates foraging in non-patchy habitats should also adopt a leaving rule based on a fixed threshold level that is related to global expectations. Optimality models further suggest that the reference point used to assess food quality should not change within and among food patches (Charnov 1976; McNamara et al. 1993), and should therefore remain constant over short periods of time. If animals assess food quality based on global expectations for the entire environment (i.e., based on a specific threshold value), it can be predicted that

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different areas of similar food value encountered on a search path should be exploited with the same intensity, because they will be perceived similarly.

It appears, however, that recent information collected while foraging can influence subsequent decisions made by animals. For example, sheep become more selective after having recently consumed high quality food (Jung and Koong 1985). Such an observation indicates that patch departure rules could be based on a value of expected gains that, rather than being fixed, fluctuates with the animals' recent sampling experience. When recent experience influences foraging decisions, two areas offering similar food could be exploited with different intensities, providing that different experience was gained prior to arrival at each area. Accordingly, it can be predicted that, given two areas with similar food value, the one where an animal arrived with the highest expectation (e.g., recent encounter with several high quality patches) should be exploited less intensively. This prediction arises because the threshold value that triggers area departure will be relatively higher in that area, leading to a less intensive exploitation despite the presence of similar food.

In this study, I investigate factors influencing winter search patterns of free-ranging plains bison (*Bos bison bison*) in their natural habitat. In winter, bison obtain food by digging through the snow with sweeping motions of the head, which results in snow craters of different sizes located along their searching/feeding path. These paths have been associated with area-concentrated search (Fortin 2000). The size of most craters (averaging 3 m²; Fortin 2000) indicates that they are comprised of several adjacent sampling/feeding stations, which reflects the use of an intensive search mode (i.e., movements that are made within a single cratering area) to find a food patch of similar quality. The discrete nature of craters also indicates the use of an extensive search mode (i.e., inter-crater movements) to leave an area of poor quality food.

I investigated attributes of both modes of area-concentrated search. Firstly, I focused on the extensive search mode by determining whether movements of free-ranging plains bison are non-random during inter-crater movements. To this end, bison movements from crater to crater were compared to predictions from correlated random walks. Additionally, food and snow characteristics of areas located between craters were compared with characteristics observed within craters. Secondly, I investigated whether assessment of food patch quality was influenced by short-term sampling experience. This investigation, based on bison behavior during intensive search mode, was done through the comparison of sequential craters found along searching/feeding paths.

Methods

Searching path characteristics

The field study took place in Prince Albert National Park (Saskatchewan, Canada), where approximately 220 free-ranging bison spend most of their time feeding in grass and sedge meadows interspersed in a boreal forest (Fortin and Frandsen 1999). Bison searching activity was studied in the winter of 1998 by recording information on ten paths of subsequent snow craters found in six meadows located as far as 20 km apart. I investigated the longest section of each search path that met the following criteria: (1) the focal bison had remained in the meadow, (2) the bison had not lain down, insuring that the section included a single foraging bout, and (3) its snow pattern had not been obscured by tracks of other individuals. Search paths were first described by recording the angle and the number of steps between successive craters, as well as the average distance between steps. Foot print size and the distance between steps suggested that adult individuals made all paths studied. The average path comprised 15 consecutive craters (range: 11–17), with individual crater covering an average area of 3 m² of disturbed snow (range: <1–17 m², $n=203$). The area of each feeding crater was estimated assuming simple geometric shapes associated with the crater, rectangles in most cases. Changes in crater size indicated variation in searching intensity, and thus reflected changes in animals' perception of food patch quality, with larger craters being indicative of higher quality.

Snow characteristics

Snow depth, density and softness were evaluated at a distance of 30 cm next to each crater in an area of undisturbed snow. Snow characteristics were averaged from one to four locations for each crater, with more observations taken for larger crater areas. For each search path, snow conditions were also determined in 5–16 areas located halfway between subsequent craters. Measurements were assumed to reflect conditions at the time the foraging activities occurred. From my frequent surveys, I estimated that searching/feeding paths were less than 2 days old when surveyed. Snow density (g/cm³) was estimated by weighing with a spring scale a sample of the snow column collected using a metal tube, and dividing the mass by the volume of snow gathered. Snow softness was measured as the sinking depth of a bottle (300 g, 8.5 cm of diameter) dropped 50 cm above the snow surface (Murray and Boutin 1991).

Forage characteristics

Food quality can be defined in the context of the maximization of a currency. For example, some large grazers maximize their rate of food intake (Illius et al. 1999), short-term gain of protein (Langvatn and Hanley 1993), or daily gain of energy (Wilmschurst and Fryxell 1995; Wilmschurst et al. 1995). Bison foraging decisions in Prince Albert National Park are most consistent with the maximization of short-term rate of energy intake (Fortin et al. 2002, 2003). Individuals thus respond to variation in short-term profitability (kJ/min) of food patches.

Consequently, I characterized vegetation along search paths by considering parameters related to plant profitability. I estimated food biomass (g/m²) and digestibility (%), and evaluated the potential intake rate of dry matter (g/min) and digestible energy (kJ/min) that bison would obtain by feeding on these plants. My empirical approach was first to create equations allowing estimation of these attributes of bison food from behavioral observations and plant samples taken all across the bison range, and then to use these equations to characterize food along the ten search paths. Along these paths, forage characteristics were evaluated in one (for craters ≤ 1 m²) to four 0.25-m² quadrats for each of the craters, and average values were used in subsequent analyses. Plant characteristics were also quantified in quadrats located halfway between

successive craters. Below, I provide details of the design used to characterize food encountered along the search paths, as well as describing the development of equations for estimation of food characteristics.

Dry matter intake rate

Forage abundance was estimated at a distance of 30 cm from each crater, in 0.25-m² quadrats where the plant community was visually similar to that found in the crater. A large amount of the vegetation found in craters remained generally ungrazed (approximately 70% from visual estimation), allowing the corroboration of vegetation abundance estimates. Forage abundance in each quadrat was visually related to a value ranging from 0 to 9, i.e. from small to large amounts of vegetation, respectively. The relationship between forage biomass and the visual evaluation of forage abundance on the 0–9 categorical scale was established after clipping above-ground vegetation in 39 random quadrats (0.25 m²), and weighing the samples after 60 h of drying at 50°C. The resulting non-linear relationship followed: dry biomass (g/m²) = $82.229e^{0.29(\text{visual estimate})}$, $R^2=0.91$.

Finally, forage intake rate was determined using biomass estimates together with the functional response developed by Fortin et al. (2002). This type II functional response does not account for the time required to move between snow crater areas because only few steps generally separated these areas (median = 5 steps, corresponding to a distance of 2 m that can be traveled in 6 s, Fortin et al. 2002) and, as is commonly observed for large herbivores (Bradbury et al. 1996; Illius et al. 2002), a bison's short-term rate of food intake was generally limited by processes of food handling rather than food encounter (Fortin et al. 2002). In such cases, travel time should not be part of the gain function because it does not influence food intake rate (Spalinger and Hobbs 1992; Illius et al. 2002).

Digestibility

Dry matter digestibility of forage types was determined from 481 plant samples of known species composition collected in 25 meadows during the winter of 1997. Samples of the tissue grazed were taken following the procedure of Hudson and Frank (1987), and the percent cover of each species comprising the sample was visually estimated. Samples were dried at 50°C for 60 h, and their in vitro digestibility was estimated using Tilley and Terry's (1963) method with cattle rumen fluid. Forage digestibility was then related to species cover using stepwise multiple regressions, with separate analyses for samples of species growing in "dry" and "wet" areas. Dry areas were generally located on hillsides where soil drainage was rapid, whereas wet areas were found in depressions where soil drainage was relatively slow. Dry and wet areas were also distinguishable by their plant assemblages: *Bromus inermis*, *Epilobium angustifolium*, *Galium boreale*, *Ranunculus acris*, *Rosa acicularis* were commonly found in dry areas, whereas *Carex aquatilis*, *C. atherodes*, *Calamagrostis inexpansa*, *Scolochloa festucacea* and *Sonchus arvensis* were generally encountered in wet areas. The regression model for dry area forage explained 36.3% of the variation in forage digestibility on the basis of percent cover of six plant species ($F_{6,70}=6.07$, $P<0.0001$). For wet area forage, eight plant species explained 36.6% of the variation in forage digestibility ($F_{8,411}=29.08$, $P<0.0001$). Because digestibility was established using cattle rumen fluid, these equations were converted to reflect bison digestibility following Bergman et al. (2001). Field estimates of plant cover within and between the craters found along the 10 search paths were then transformed to forage digestibility for bison using the two corrected regression models.

Intake rate of digestible energy and food patch profitability

I determined the digestible energy content of plant samples (kJ/g) from the product of their dry matter digestibility and the gross energy content of 18.4096 kJ/g (National Research Council 1996). The intake rate of energy (kJ/min) expected within and between craters found along the ten search paths was calculated from the product of digestible energy (kJ/g) and expected forage intake rate (g/min). When, as for these bison, the rate of food intake is limited by handling time rather than encounter rate, the rate of energy intake corresponds directly to the profitability of a food patch (see Fortin et al. 2002).

Although the evaluation of food profitability includes many steps and is derived from many field estimates, general patterns became apparent. Craters comprised of highly profitable food species were mostly those offering high forage biomass predominantly comprised of *Carex atherodes* and *Sonchus arvensis*. Alternatively, areas with forage of low profitability generally had relatively low plant biomass, and were often largely comprised of *Calamagrostis inexpansa* and *Carex aquatilis*.

Reference windows and their field estimates

Investigating the amount of sampling information used to assess food quality requires keeping track of the animal's search history. This can be done using the concept of a memory window (Cowie 1977), which constitutes a running average that is constantly updated as the searching/foraging bout progresses. Thus, as time passes, new information is added to the animal's memory window while an equivalent amount of the oldest information is discarded. Here, rather than considering the amount of information gathered during certain periods of time (Cowie 1977; Mackney and Hughes 1995; Valone 1992), I followed the approach outlined in Fortin (2002) by considering the information acquired during the sampling of given spatial amounts of habitat (referred to as reference windows).

From the sequence of craters along a search path, it was possible to quantify different *short-term* reference windows that might be used to assess food patch quality during search using the equation:

$$W_L = \sum_{i=1}^{n-1} \frac{A_i \times E_i}{L} + \frac{L - \sum_{i=1}^{n-1} A_i}{L} \times E_n$$

where W_L is the expected energy intake rate averaged over the reference window L m² of past sampling experience, i.e., L m² of the previous snow craters. A_i is the area of crater i , with $i=1$ being the first previous crater, n is the number of previous craters needed to reach L , E_i is the food profitability in craters i , and E_n is the profitability in crater n . Using this equation, I estimated W_2 , W_4 , W_6 , W_8 , W_{10} and W_{12} along each of the ten studied search paths. The reference window based on the past 12 m² of discrete craters made by the animal was the largest of the six reference windows considered to assess food patch quality because most paths did not meet the required criteria (see Searching path characteristics) over a long enough area to allow consideration of larger short-term reference windows.

Data analysis

Correlated random walk between feeding craters

The net squared displacement ($\overline{R^2}$) was calculated for each of the paths, and compared to the R^2 predicted from a correlated random walk as calculated from equation 2 of Kareiva and Shigesada (1983). A path is comprised of several sequential inter-crater movements (S), and the expected and observed R^2 were calculated for each path for up to 15 S (the maximum recorded in the field for most paths). As suggested by Turchin (1998), a bootstrapped test of significance was used to determine whether the difference between

the observed and expected squared displacements was statistically significant. I first generated a distribution of inter-crater angles (θ) and distances (l) based on the ten observed bison paths. The expected R^2 was calculated using $\cos \theta$ and l averaged over 15 values (most of the observed paths were composed of 15 S) randomly taken from their respective distributions. For each S , mean and confidence intervals were estimated from 10,000 bootstrap simulations of R^2 . Any observed R^2 falling outside of this interval was considered to be significantly different than expected from a correlated random walk. I also tested whether the average of R^2 for all ten paths was significantly different from that expected from a correlated random walk. Confidence limits (90 and 95%) were calculated from 1,000 averages made of 6–10 R^2 values that were randomly selected from the 10,000 R^2 simulated. The number of R^2 values reflected the number of observed paths with that total number of S (cf. Turchin 1998). More specifically, all ten paths were comprised of 10 S , nine paths had 11 S , eight had 14 S and six were comprised of 15 S .

Food quality between craters

Snow and forage characteristics were determined at all 11–17 consecutive craters (average: 15 craters) of each search paths, as well as at 5–16 areas (average: 11 inter-crater areas) located halfway between successive craters. Food and snow characteristics measured within and between subsequent craters were compared using 2-way repeated-measures ANOVAs for each environmental condition (i.e. snow softness, depth and density, as well as forage biomass, dry matter digestibility and food profitability), with individual path and the temporal sequence of visited areas (first crater, inter-crater area and second crater) as factors.

Groups of craters offering food of similar profitability

I investigated whether short-term sampling experience influenced a bison's assessment of food patch quality based on the following alternative predictions (see also introduction). If bison assess food patch quality based on their expected gains for the entire habitat (i.e., a fixed threshold value), search intensity should be similar in areas offering food of the same profitability, resulting in craters of similar size. In contrast, if bison use short-term sampling information (i.e., any of W_2 – W_{12}) to evaluate food patch quality, the smaller craters within a group of craters offering similar food should be the ones preceded by richer food patch profitability (i.e., by higher W -values).

I tested this latter prediction by identifying, for each path, groups of craters (generally pairs) that were comprised of identical estimates of food profitability. Then, I calculated the average crater size for each of these groups, and identified the craters above this average as relatively large craters (value of 1) and the others as small craters (value of 0). Using conditional logistic regressions (Breslow 1996), I investigated factors influencing the odds of bison creating a relatively large crater. Unlike the traditional unconditional logistic regression, the conditional logistic regression can analyze factors potentially influencing crater size while accounting for variation among individual paths and groups of craters. Individual paths and crater groups thus were considered as strata in the analyses.

Analyses were done with reference window size (L : 2–12 m^2) and snow depth, density, and hardness as independent variables. The rate of forage intake may depend on the animal's state of hunger (Laca and Demment 1996), which should decrease as the foraging bout progresses. Therefore, I also considered the chronological sequence of craters as an independent variable. For each group of m craters offering the same food profitability, I assigned a value of 1 to the first crater to be made within the group and a value of m to the last one. Finally, although global analyses (Fortin et al. 2002; Fortin et al., unpublished data) indicated that the rate of food intake by bison is generally limited by processes of food handling instead of food encounter, intake rate might have been encounter-

limited in some occasions (Illius et al. 2002). Consequently, the number of steps made from the previous crater was also considered as an independent variable in analyses of search intensity. Multiple statistical models were investigated, and the most parsimonious model was identified based on Akaike Information Criteria adjusted for sample size (AIC_c; Morris and Doak 2002).

Results

Correlated random walk between feeding craters

Using the conventional approach of pooling search paths in a single analysis (Turchin 1998), I found that, overall, the R^2 tended to be longer than expected from the prediction of the correlated random walk model (Fig. 1). Based on the 95% confidence limits, over half of inter-crater movements differed significantly from expectations under a correlated random walk. However, variation among paths might be expected if animals are “navigating” based on local food patch distribution, even for animals that are all foraging in similar habitat types. The classical approach of path pooling would mask such variation, and it should therefore be followed by examination of individual paths. Indeed, such an examination revealed little consistency among paths (Fig. 2). Three of the ten paths were comprised of at least half of their inter-crater movements that differed significantly (under 95% confidence limits) from what would be expected for a correlated random walk. Two of those paths were over-estimated and one was under-estimated by a correlated

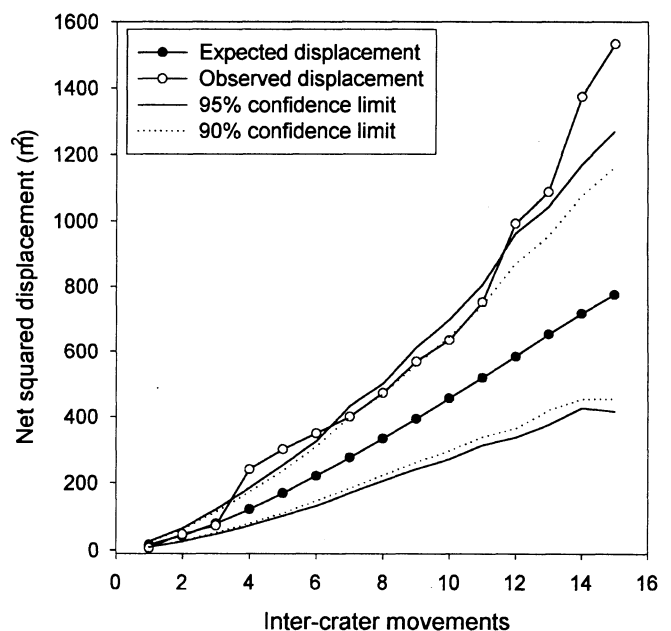
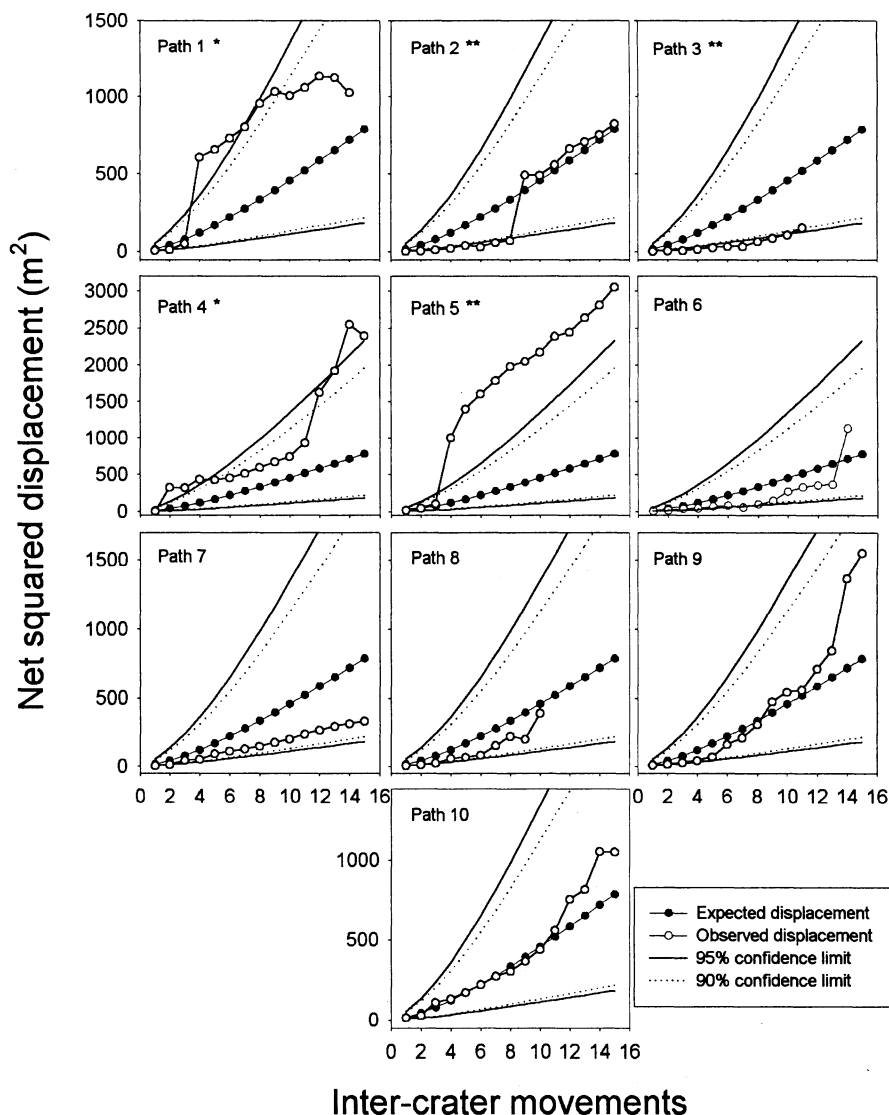


Fig. 1 Relationship between the predicted and observed average net squared displacement, and the number of consecutive inter-crater movements by plains bison (*Bos bison bison*). The average and 90–95% confidence limits for the expected net squared displacement were calculated from 1,000 simulation of six–ten average bison searching paths, depending on the number of observed paths for each inter-crater movement

Fig. 2 Relationship between the predicted and observed average net squared displacement and the number of consecutive inter-crater movements for each observed path. The average and 90–95% confidence limits for the expected net squared displacement were calculated from 10,000 simulations of expected searching paths. Paths for which at least half of their inter-crater movements were outside of the 90 or 95% confidence limits are indicated with * and **, respectively



random walk. Under 90% confidence limits, five of the ten paths had at least half their inter-crater movements differing from the correlated random walk's predictions, with two paths being over-estimated and three under-estimated. Longer or shorter paths indicate that they included one or several inter-crater movements that are disproportional to expectations by chance alone. Overall, it appears that bison movements are flexible to local food patch distribution, being sometimes random and, at other times, either less sinuous or more sinuous than expected randomly.

An increase in spatial heterogeneity should translate into greater opportunity for adjustment of search behavior. The variance to mean ratio for plant biomass varied from 7 to 109, and for plant profitability from 0.7 to 9 (Fig. 3), indicating important spatial heterogeneity among the craters found along most paths. The ratios appeared comparably high for paths that did not differ significantly from a correlated random walk, and those that did (Fig. 3). Difference in path length (range of net displacement: 12–

55 m, Fig. 2) did not influence the variance to mean ratio of food biomass ($r_s=0.30$, $P=0.40$, $n=10$), or profitability ($r_s=-0.17$, $P=0.63$, $n=10$).

Divergence of net square displacement from random expectations could also reflect an adjustment of movements to the vegetation that emerged from the snow ($\bar{x} \pm \text{SE}$, $10 \pm 3\%$ cover of above-snow vegetation, $n=10$ paths). There was, however, no significant difference in the percentage of snow covered by emerging vegetation between areas where movement patterns met expectations of correlated random walk (13.5% cover, $n=5$) and where they did not (8.9% cover, $n=5$; Wilcoxon 2-sample test, $Z=0.42$, $P=0.68$, $n=10$).

Food quality between craters

Bison were able to avoid poor feeding areas by adjusting their searching path to the local conditions (Fig. 4). Over all sites, snow softness associated with successive craters

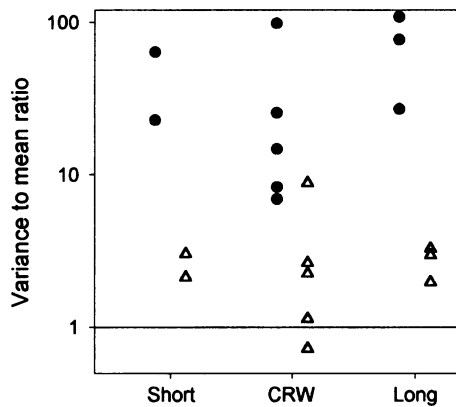
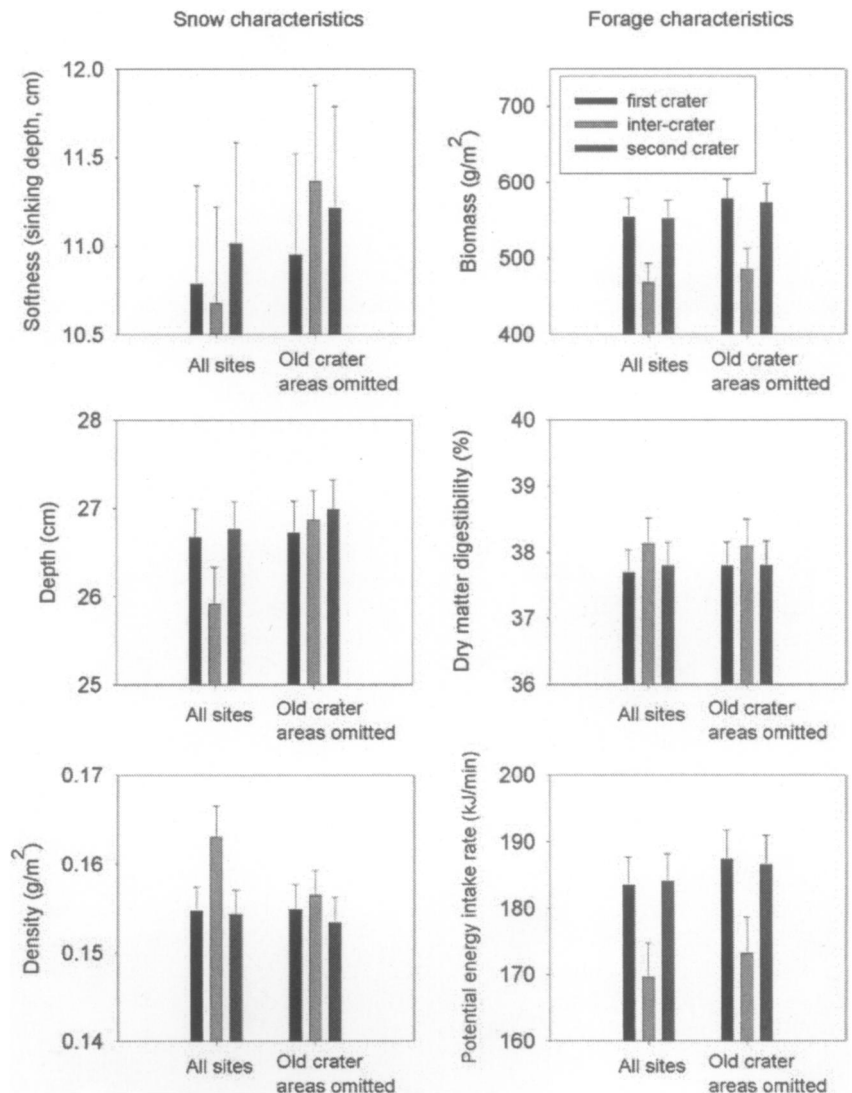


Fig. 3 Variance to mean ratio of food biomass (●) and food profitability (Δ) encountered along search paths that did not differ from expectations of a correlated random walk (CRW) model, and paths that tended to be shorter (*Short*) or longer (*Long*) than random expectations. A ratio was calculated for each of the ten studied bison paths considering the vegetation available at cratering areas. Ratios are displayed on a log-scale, and a vertical line indicates where the variance equals the mean

Fig. 4 Average variation in snow and forage characteristics ($\bar{X} \pm \text{SE}$) for pairs of successive craters along a searching path and the area separating them (inter-crater), as calculated for all sites and only for sites that were not old crater areas covered by fresh snow



did not differ from softness in inter-crater areas ($F_{2,96}=0.91$, $P=0.41$). However, differences were observed in both snow depth ($F_{2,96}=3.78$, $P=0.03$) and density ($F_{2,96}=3.48$, $P=0.03$). Snow was shallower (post hoc test: $F_{1,97}>4.45$, $P<0.04$ for both comparisons, i.e. previous crater vs. inter-crater and following crater vs. inter-crater) and denser in the area between craters (post hoc test: $F_{1,97}>4.89$, $P<0.03$ for both comparisons). For all sites (Fig. 4, all sites), successive snow craters were separated by an area with lower plant biomass than that associated with either crater (post hoc test: $F_{1,97}>23.70$, $P<0.0001$ for both comparisons). Forage digestibility did not vary among sites ($F_{2,96}=1.21$, $P=0.30$), but the difference in biomass led to the encounter of lower food patch profitability (as estimated from the expected energy intake rate) between craters than within craters (post hoc test: $F_{1,97}>28.83$, $P<0.0001$ for both comparisons). These differences could simply reflect prior foraging, as some of the areas between craters had been used before being recovered with fresh snow. I therefore extended the

analysis by excluding craters separated by previous foraging activity.

When old cratered areas were excluded (Fig. 4, see "old crater areas omitted"), no significant difference was found in snow softness ($F_{2,82}=0.29$, $P=0.75$), depth ($F_{2,82}=0.62$, $P=0.54$) or density ($F_{2,82}=1.01$, $P=0.37$) between the first craters, inter-crater areas and second craters. However, the same trends remained for forage characteristics when previously foraged areas were omitted. Biomass was still lower between successive craters than within them (post hoc test: $F_{1,83}>19.17$, $P<0.0001$ for both comparisons), with the consequence that, despite the absence of important differences in forage digestibility ($F_{2,82}=2.27$, $P=0.11$), food profitability was lower between craters than within craters (post hoc test: $F_{1,83}>17.95$, $P<0.0001$ for both comparisons). These findings suggest that the distance traveled between craters was neither random nor simply dictated by obvious visual cues to past foraging activity.

Groups of craters offering similar food profitability

Bison search behavior was further influenced by past sampling experience recently acquired. The odds that bison create a larger than average crater in areas offering similar food profitability were higher following the encounter with food of relatively poor profitability. Among the short-term reference windows investigated, W_2 – W_6 had $P\leq 0.10$, whereas W_8 – W_{12} had $P>0.20$. The relative influence of W_2 – W_6 on search intensity was further evaluated. Not as much past sampling experience was quantified for craters encountered early along the path than the ones encountered late (e.g., first crater of a path has no quantifiable past experience). Consequently, the number of crater groups decreased as greater extent of sampling information was considered (i.e., $n=51$ for W_2 versus $n=47$ for W_6), which may influence P -values and AIC_c -estimates. I reviewed the analysis by considering only the 47 observations available for the three shortest reference windows. W_2 still fit the data better ($P=0.04$; $AIC_c=27.06$) than W_4 ($P=0.06$; $AIC_c=29.18$) or W_6 ($P=0.07$; $AIC_c=29.80$). Akaike weights (Morris and Doak 2002) indicate that W_2 was at least 2.9 times as likely to provide the best description of the data than were W_4 or W_6 . Overall, these results indicate that bison search intensity was influenced by their short-term experience, especially the experience gained over the last 2 m² of searching activity.

Past sampling experience provided a better explanation to the observed variation in search intensity between areas offering similar food profitability (W_2 , model 1; Table 1) than did the chronological sequence of crater formation during a foraging bout (model 2), the number of steps traveled before reaching crater locations (model 3) or the snow conditions at crater locations (model 4). In fact, Akaike weights indicate that model 1 (W_2) was 8.9 times as likely to be the best model as were models 2–4. Moreover, the most parsimonious model considered only

W_2 ; adding independent variables to the model only increased complexity without significantly adding to the model fit (Table 1).

Discussion

Free-ranging bison in Prince Albert National Park used area-concentrated search during their winter foraging activity. My analysis of bison search strategy indicates that individuals find suitable food items by adjusting their movements to habitat structure. This has also been reported in many other ungulate species. Dorcas gazelles (*Gazella dorcas*) adjust their move length to resource distribution consistently with area-concentrated search (Ward and Saltz 1994). Characteristics of area-concentrated search also have been reported in foraging African antelope (Underwood 1982). Area-concentrated search appears particularly valuable in patchy environments (Laca and Ortega 1996), where adjustment of travel speed and rate of turning should enable animals to remain inside patches of suitable resources (Cézilly and Benhamou 1996; Lima and Zollner 1996).

Navigation during searching activity

Bovet and Benhamou (1991) demonstrated that the efficiency of area-concentrated search can be increased by adjusting the search path to local conditions. For this reason, it becomes important to determine whether animals are capable of such adjustments. Departure from a correlated random walk is a sign of non-random movement in the landscape (Root and Kareiva 1984), and can be used to investigate whether environmental cues influence searching activity. I found that some of the observed search paths did not differ from predictions of correlated-random walk, whereas others were less sinuous or more sinuous than random expectations. Such flexibility during the extensive search mode of area-concentrated search is to be expected if animals adjust their movements to the local food patch distribution and if this distribution varies among sampling locations. I was not able to identify site differences that could explain the departure from predictions of correlated random walk in certain areas. Nevertheless, the comparison of observed movement paths to correlated random walk provides indication that bison movements are not simply random and might therefore be sensitive to local habitat characteristics.

Comparison of characteristics of areas within and between craters was also used to investigate whether bison make non-random movements during their extensive search mode (Fig. 4). The adjustment of search path by bison appeared to be partly dictated by the spatial distribution of poor quality food patches. Discrimination between food patches requires a minimum difference of quality between foraging options (Illius et al. 1999). For example, sheep make more appropriate foraging decisions

Table 1 Comparison between models used to explain variations in the odds of plains bison (*Bos bison bison*) creating a larger than average crater among groups of craters found in areas offering the same food profitability, as determined from conditional logistic regression with individual paths and crater groups as strata. Independent variables considered in the models were sampling experience gained over the past 2 m² of foraging/searching activity (W_2), chronological sequence of crater formation (*sequ*), number of steps made before arrive to a given cratering area (*step*), and snow depth (S_{depth}), density (S_{density}) and hardness (S_{hardness}) at crater locations. Sign of β -values is indicated before each independent variable; positive and negative β -values reflect an increase and a decrease in odds, respectively AIC_c of the most parsimonious model is displayed in bold

Model id: independent variables included	Wald χ^2	P-value	AIC_c
1: $-W_2^*$	3.90	0.05	33.41
2: $+sequ^{ns}$	0.35	0.55	38.68
3: $-step^{ns}$	0.97	0.33	37.78
4: $-S_{\text{depth}}^{ns}-S_{\text{density}}^{ns}+S_{\text{hardness}}^{ns}$	3.23	0.36	39.59
5: $-W_2^*+sequ^{ns}$	4.05	0.13	35.26
6: $-W_2^\phi-step^{ns}$	3.98	0.14	35.49
7: $-W_2^\phi-(sequ \times W_2)^{ns}$	4.25	0.12	34.53
8: $-W_2^{ns}+(step \times W_2)^{ns}$	3.91	0.14	35.57
9: $-W_2^\phi+(step \times sequ)^{ns}$	3.86	0.15	35.45
10: $-W_2^\phi-S_{\text{depth}}^{ns}-S_{\text{density}}^{ns}+S_{\text{hardness}}^{ns}$	4.01	0.40	37.26
11: $-W_2^{ns}-S_{\text{depth}}^{ns}-S_{\text{density}}^{ns}+S_{\text{hardness}}^{ns}-step^{ns}+sequ^{ns}$	4.03	0.67	42.17

* $P < 0.05$, $\phi P \leq 0.10$, $^{ns}P > 0.10$

when the energy gain difference between foraging options exceeds 30 kJ/min (Dumont et al. 1998). The difference between the maximum and the minimum food patch profitability recorded along foraging/searching paths ranged from 52 to 178 kJ/min ($n=10$), indicating significant opportunities for selection. I found that bison avoided digging in areas where their rate of energy intake would have been lower by an average of 14 kJ/min (Fig. 4, consideration of all sites). Bison were able to avoid areas where they would have experienced slow energy intake, by simply walking on without even sampling food by digging through the snow. Although snow-digging costs have yet to be quantified for bison, observations on other ungulate species suggest that these costs should be important compared to the costs traveling between patches (Fortin 2002). Bison should thus benefit from the observed reduction in digging activity in areas offering poor quality vegetation. On the other hand, the difference of 14 kJ/min appears small given the important variation in resource profitability encountered along search paths. This rather small difference may reflect some limitation in a bison's ability to distinguish high- from low-quality food patches without digging, discrimination errors, and/or imperfect knowledge of local resource distribution.

Spatial memory can be used to help avoid or locate food patches in heterogeneous landscapes (Dumont and Petit 1998; Edwards et al. 1996; Gillingham and Bunnell 1989; Laca 1998). Large herbivores can remember the locations and relative availability of food for at least 20 days (Bailey et al. 1996). The advantages of using

spatial memory decrease, however, with increasing environmental complexity (Dumont and Hill 2001). Spatial memory thus might have low adaptive value for small-scale decisions of herbivores foraging in their natural environments, such as bison in Prince Albert National Park. Indeed, vegetation displayed important spatial variation in abundance and profitability. Moreover, exploitative competition should make the future status of potentially good foraging sites rather unpredictable.

Many cues can also be used to navigate in the environment. Animals may adjust their search path to increase searching efficiency in response to olfactory (Benhamou 1989) or visual (Laca and Ortega 1996) signals. For example, reindeer could distinguish good and poor lichen sources by smell through 91 cm of soft snow (Helle 1984). The seed heads and stems of some plant species remain above the snow cover for most of the Saskatchewan winter, offering a visual indication of the vegetation lying underneath the snow (Fortin and Frandsen 1999). Even though bison may have selected crater locations using such visual cues, I found no evidence that the amount of above-snow vegetation was responsible for the departures of bison search paths from expectations of correlated random walk.

The use of sampling information

Searching behavior of bison was also adjusted to the sampling information gained by individuals while foraging. Indeed, the area covered during a single continuous episode of intensive search mode varied depending on the profitability of the food recently encountered in other locations. I found that areas of similar food quality were searched with different intensities depending on short-term past sampling experience, resulting in craters of different sizes.

Factors other than differences in past experience could also induce variations in the size of crater groups. Hunger can increase forage intake rate by animals (reviewed in Laca and Demment 1996), which might have resulted in the larger crater of groups offering similar food profitability being located earlier along foraging paths, i.e. sooner during the foraging bout, when the animal's hunger should be higher. My analyses, however, ruled out this hypothesis. My evaluation of bison searching paths also refuted the hypothesis that differences in the size of these crater groups was related to the distance traveled before reaching the areas. This finding contrasts with those of Cuthill et al. (1990, 1994) on starlings (*Sturnus vulgaris*) and Todd and Kacelnik (1993) on pigeons (*Columba livia*), who found that the last travel distance covered by the animal influenced its patch exploitation. In grazers and browsers, the rate of vegetation intake is independent from the time spent traveling traveled between resource patches when chewing time does not exceed travel time (Hobbs et al. 2003; Illius et al. 2002). The inter-crater distance appeared generally too short (median: 2 m) to impact a bison's rate of food intake,

which could explain why no effects of traveled distance were detected in my study. In contrast, distances of 23 or 46 m seem sufficient to influence foraging decisions by sheep (Dumont et al. 1998). In summary, the most parsimonious explanation for the difference in search intensity in areas offering similar food profitability was that bison assess food patch quality using a reference point that fluctuates with their short-term experience.

The observed plasticity of bison in their perception of food quality during a searching bout suggests quality assessment through reference windows of fairly small size (mostly the past 2 m² of sampling). Similarly, bumblebees (*Bombus appositus*, *Delphinium nelsonii*) were found to use an intermediate amount of habitat sampling information to adjust their foraging activity (Pleasants 1989). Long-tongued bees (*Anthophora* spp. and *Eucera* spp.) use a probabilistic departure rule from flowers that is influenced by their foraging experience at the two last-visited flowers (Kadmon and Shmida 1992). These observations contrast with the assumption of most optimality models. The marginal value theorem and the contingency model of optimal diet assume that animals assess food patch quality relative to a reference point that is independent of small-scale spatial variation in food characteristics (Charnov 1976; McNamara et al. 1993; Stephens and Krebs 1986). A simple model of area-concentrated search indicates that the benefits of this search strategy increase in a decelerating fashion with the expansion of reference windows, and rapidly levels off following the consideration of only 60 m² of past sampling (Fortin 2002). However, considering information gathered over only the past 2 m² of sampling information, as observed in these free-ranging bison, should decrease the search efficiency. In this case, a bison's decision of whether to adopt an intensive or extensive search mode to find the next food patch would be overly affected by the local distribution of vegetation quality (Fortin 2002).

Bison movement paths revealed an adjustment of search decisions to small-scale plant distribution. However, this does not imply, that foraging bison do not also use long-term information when foraging. Large herbivores can remember and use different types of information at different temporal scales (Bailey et al. 1996; Laca and Ortega 1996), which may lead to divergence in foraging decisions at different scales (Schafer and Messier 1995). Presumably because of the use of information at multiple scales, bison diet quantified at the landscape level ended up being largely comprised of a few plant species (Fortin et al. 2003). The observed food selection led to the maximization of a bison's short-term rate of energy intake (Fortin et al. 2002).

My study is one of few that have looked at the use of sampling information by free-ranging animals searching for food in their natural habitat. I found that bison adjust their searching behavior to the local distribution of food, and use this local information to assess food patch quality. I conclude that bison take advantage of the structural characteristics of their environment during searching

activity, and base their decisions on local rather than global availability.

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