



## Group-size-dependent association between food profitability, predation risk and distribution of free-ranging bison

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Predation risk and competition can impose foraging costs, whereas social information acquired from conspecifics may lead to foraging gains. By altering cost–benefit trade-offs of foraging, variations in group size and predation risk can influence plant selection by herbivores. This influence may vary seasonally, depending on how foraging constraints vary throughout the year. Empirical evidence of these combined effects remains limited, especially in natural settings. We evaluated the spatial association between wheat sedge, *Carex atherodes*, and bison, *Bison bison*, foraging under predation risk during summer and winter. To maximize their energy intake rate, bison should feed on *Carex atherodes*. We found that the strength of selection for foraging sites with *C. atherodes* decreased with increasing risk of wolf, *Canis lupus*, encounter in winter, but not in summer. Bison faced greater risk in winter than in summer. Selection for *C. atherodes* was further influenced by group size. Larger bison groups displayed stronger selection for *C. atherodes* in winter but weaker selection in summer. Seasonal variations in group-size effects can be explained by changes in the relative costs and benefits of social foraging. Bison groups are much larger in summer than winter, implying potentially stronger competition among bison foraging on *C. atherodes* in summer. *Carex atherodes* is more inconspicuous in winter than in summer, thereby increasing the value of social information during winter months. We suggest that predation risk and spatial heterogeneity of highly profitable food influence the foraging decisions of bison differently in summer and winter because of seasonal differences in cost–benefit trade-offs.

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Group living is an adaptive strategy observed in many animal species. Group members may benefit from dilution effects and cooperative defence against predators (Dehn 1990; Fortin et al. 2004b; Isvaran 2007). Foragers may reduce predation risk by scanning their surroundings, an activity that conflicts with food selection (Illius & FitzGibbon 1994). High predation risk may lead to strong apprehension (Hochman & Kotler 2007), whereby foragers reduce the attention devoted to foraging by reallocating attention to predator detection. By joining a group, members benefit from collective vigilance, which should allow each of them to spend less time scanning and more time selecting food items. Group members also profit from social information, which decreases uncertainty about environmental quality (Giraldeau & Caraco 2000; Danchin et al. 2004; Fernández-Juricic et al. 2006). Observing the behaviour of conspecifics can improve the ability of an individual to find suitable food patches (Thompson et al. 1974; Seppänen et al. 2007). Social information thus can decrease the diet breadth of optimal foragers (Beauchamp et al. 1997) by providing better knowledge

about the location of highly profitable food patches. This effect should be stronger in large groups than in small groups because social information becomes more reliable (King & Cowlshaw 2007).

Group living also entails costs. Prey are more conspicuous to predators when they are in large versus small groups (Lindström 1989; Hebblewhite & Pletscher 2002). Group members may also compete for resources. Exploitative competition decreases per capita food availability, while interference competition affects food accessibility (Hobbs et al. 1996; Shrader et al. 2007). Larger groups may be characterized by more intense competitive interactions (Molvar & Bowyer 1994; Ruxton et al. 1995; Kausrud et al. 2006), and foragers may be expected to pay the price of reduced food intake rate (Ruxton et al. 1995; Hobbs et al. 1996; Fraser et al. 2006). Optimality principles predict an increase in diet breadth with increasing exploitative or interference competition because either reduces encounter rates with highly profitable food items (Stephens & Krebs 1986). Cost–benefit trade-offs of group living should also be shaped by seasonal effects. The presence of snow, for example, may impose additional constraints to social foraging that can alter decisions of group members. Snow conditions can influence local foraging efforts (Collins & Smith 1991; Fortin et al. 2005), and foragers may rely on short-term sampling information to assess food quality (Fortin

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2003). Few studies of group-size effects on food selection have been conducted over more than a single season, weakening our appraisal of temporal variation in the determinants of foraging decisions.

Free-ranging bison, *Bison bison*, are large social grazers well suited to investigate how group size influences the relationship between spatial patterns of highly profitable food items and animal distribution under natural conditions. Bison face wolf, *Canis lupus*, predation (Larter et al. 1994; Smith et al. 2000), which can influence their space use patterns (Fortin et al. 2009) and foraging activity (Laundré et al. 2001). Bison generally forage in open meadows (Hernández & Laundré 2005) where they can be observed remotely. Individuals form groups of variable size (Lott & Minta 1983) and are exposed to exploitative and interference competition (Fortin et al. 2004b). Bison display strong selection for food that maximizes their energy gains (Bergman et al. 2001). During both summer and winter, energy maximization principles predict that the bison of Prince Albert National Park (Saskatchewan, Canada) should specialize on *Carex atherodes* (Fortin et al. 2002), a tall sedge species. This plant offers the most advantageous ratio between digestible energy content and handling time (i.e. cropping, chewing and swallowing). Throughout the year, bison select *C. atherodes* (Fortin et al. 2003), which makes up more than half of their diet in the mesic and wet meadows of Prince Albert Park (Fortin et al. 2002). The importance of *C. atherodes* in the diet of bison has been reported in other populations (Reynolds et al. 1978; Larter & Gates 1991), but the influence of predation risk and group size on selection of this highly profitable plant remains unknown.

Our objective was to assess the influence of group size and predation risk on the selection for the highly profitable *C. atherodes* by bison during summer and winter. Under these natural conditions, predation risk, social information and competitive interactions should all influence bison. If wolf predation influences foraging decisions, we predicted that selection for *C. atherodes* would decrease with increasing risk of wolf encounters. This is because greater apprehension should decrease food selection (Illius & FitzGibbon 1994), a response that should be stronger for small groups than for large groups because risk generally declines with group size. Furthermore, if foraging among an increasing number of conspecifics enhances benefits through richer or more reliable social information, then selection for *C. atherodes* during foraging should get stronger with increasing group size. Conversely, selection for *C. atherodes* should decrease with increasing group size if bison foraging in large groups incur stronger competition.

## METHODS

### Study Area

The study was conducted in Prince Albert National Park. The park supports one of the few free-ranging populations of bison. The population was estimated at 385 individuals in 2006. The bison range is established in the southwest corner of the park, an area composed mostly of forests (85%), water (5%) and meadows (10%). Over 170 plant species can be found in meadows, with *C. atherodes* common in wet and mesic areas. The bison range includes a few roads that are accessible to park staff and researchers. Elk, *Cervus elaphus*, white-tailed deer, *Odocoileus virginianus*, and moose, *Alces alces*, are also present in the bison range, but resource competition with bison appears weak (Fortin et al. 2003). Multiple wolf packs are also present in the park, and predation on bison is observed occasionally.

### Behavioural Observations and Habitat Sampling

Bison observations were conducted in summer 2005 (20 May–20 August) and winter 2006 (16 January–12 March). Scan

samplings were conducted with a spotting scope in various meadows located across the bison range. During the scan, we used landmarks to locate bison ( $\geq 2$  year old) that were randomly chosen among those foraging. Group size (interindividual distance  $< 100$  m, cf. Green 1992; Fortin et al. 2003) was estimated for each focal animal. The day following behavioural observations, we quantified habitat covariates (i.e. plant biomass and snow conditions or water depth) at all observed bison locations. Habitat sampling varied between summer and winter. In summer, three quadrats of  $0.25 \text{ m}^2$  were sampled for each animal location ( $< 2$  m from the landmark location), and the mean value was used in subsequent analysis. In winter, snow tracks increased location accuracy of used sites, and habitat covariates were evaluated within a single  $0.25 \text{ m}^2$  quadrat. Habitat covariates at used sites were compared to those at random sites located within the same meadow. The number of random sites sampled for habitat characteristics was proportional to meadow area and varied between 15 and 40 quadrats. We used a paired design, with quadrats at observed locations representing the animal's choice, whereas random quadrats described resource availability within that meadow. In other words, a given stratum (i.e. a set of observed and random locations) comprised quadrats for all individuals located during a particular observation session, together with the related random locations surveyed in the meadow where this session took place.

In summer, we measured water depth (cm) with a ruler in the centre of the quadrats at used and random locations. We also estimated total biomass ( $\text{g/m}^2$ ) of dry vegetation by measuring the height (cm) at which a calibrated plastic square placed on the vegetation settled from the ground (Vartha & Matches 1977). The relationship followed: total dry biomass =  $-8.78 + 1.62 \times \text{height}$  ( $R^2 = 0.80$ ,  $F_{1,106} = 426.45$ ,  $P < 0.0001$ ). This relationship was established by collecting, drying (at  $60^\circ \text{C}$  for 48–60 h) and weighing all above-ground vegetation present in 107 quadrats. Plant samples were then sorted by species and used to calibrate a visual estimation of the percentage of total dry biomass composed of different plant species. Distinct calibrations were done for each of the two observers as follows: percentage of biomass =  $0.077 + 0.74 \times \text{visual estimate}_{\text{observer1}}$  ( $R^2 = 0.84$ ,  $F_{1,135} = 711.26$ ,  $P < 0.0001$ ) and percentage of biomass =  $2.15 + 0.88 \times \text{visual estimate}_{\text{observer2}}$  ( $R^2 = 0.89$ ,  $F_{1,64} = 525.45$ ,  $P < 0.0001$ ). Based on these calibrations, we estimated the dry biomass of *C. atherodes* ( $b_{\text{Cath}}$ ) at used and random locations.

In winter, snow water equivalent ( $S$ ) was estimated at used and random locations. Measurements were taken 30 cm from observed locations (Fortin 2003; Fortin et al. 2005) because animals disturbed snow directly at foraging and resting sites. Care was taken to ensure that there was no change in the vegetation community over the 30 cm. Snow water equivalent was calculated as the product of snow depth and snow density. Snow depth (cm) was measured with a ruler, whereas snow density ( $\text{g/cm}^3$ ) was determined by weighing, with a spring scale, a sample of the snow column collected with a metal tube (diameter = 18.0 cm) inserted vertically into the snow, and by dividing the mass by the volume of snow gathered. Throughout the winter, each of the two observers estimated total dry biomass ( $\text{g/m}^2$ ) of vegetation on a 0–10 visual scale (Fortin 2003), which followed: dry biomass =  $-42.67 + 53.19 \times \text{visual estimation}_{\text{observer1}}$  ( $R^2 = 0.78$ ,  $F_{1,100} = 363.15$ ,  $P < 0.0001$ ), dry biomass =  $-94.76 + 116.12 \times \text{visual estimation}_{\text{observer2}}$  ( $R^2 = 0.89$ ,  $F_{1,86} = 706.98$ ,  $P < 0.0001$ ). Visual estimations of the percentage of total dry biomass of plant species were also calibrated for each observer: percentage of biomass =  $8.42 + 0.70 \times \text{visual estimate}_{\text{observer1}}$  ( $R^2 = 0.82$ ,  $F_{1,125} = 554.71$ ,  $P < 0.0001$ ), and percentage of biomass =  $3.63 + 0.89 \times \text{visual estimate}_{\text{observer2}}$  ( $R^2 = 0.77$ ,  $F_{1,38} = 124.17$ ,  $P < 0.0001$ ). The calibrations were done by clipping the above-ground vegetation in  $0.25 \text{ m}^2$

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