

Group-size-mediated habitat selection and group fusion–fission dynamics of bison under predation risk

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Abstract. For gregarious animals the cost–benefit trade-offs that drive habitat selection may vary dynamically with group size, which plays an important role in foraging and predator avoidance strategies. We examined how habitat selection by bison (*Bison bison*) varied as a function of group size and interpreted these patterns by testing whether habitat selection was more strongly driven by the competing demands of forage intake vs. predator avoidance behavior. We developed an analytical framework that integrated group size into resource selection functions (RSFs). These group-size-dependent RSFs were based on a matched case–control design and were estimated using conditional logistic regression (mixed and population-averaged models). Fitting RSF models to bison revealed that bison groups responded to multiple aspects of landscape heterogeneity and that selection varied seasonally and as a function of group size. For example, roads were selected in summer, but not in winter. Bison groups avoided areas of high snow water equivalent in winter. They selected areas composed of a large proportion of meadow area within a 700-m radius, and within those areas, bison selected meadows. Importantly, the strength of selection for meadows varied as a function of group size, with stronger selection being observed in larger groups. Hence the bison–habitat relationship depended in part on the dynamics of group formation and division. Group formation was most likely in meadows. In contrast, risk of group fission increased when bison moved into the forest and was higher during the time of day when movements are generally longer and more variable among individuals. We also found that stronger selection for meadows by large rather than small bison groups was caused by longer residence time in individual meadows by larger groups and that departure from meadows appears unlikely to result from a depression in food intake rate. These group-size-dependent patterns were consistent with the hypothesis that avoidance of predation risk is the strongest driver of habitat selection.

Key words: *Bison bison; conditional logistic regression; exploitative competition; free-ranging plains bison; GPS radio collars; group size effects; habitat selection; predation risk; Prince Albert National Park, Saskatchewan, Canada; resource selection function.*

INTRODUCTION

The profound impact that organisms can have on their abiotic and biotic environment (e.g., Danell et al. 2006, Hastings et al. 2007) depends largely on their patterns of distribution and abundance. Animal distribution in heterogeneous landscapes is closely linked to habitat selection (Boyce and McDonald 1999, Boyce 2006), which involves behavioral decisions guided by the multiple needs and constraints faced by individuals. For example, large herbivores have been reported to make foraging choices consistent with energy maximization principles (Fortin et al. 2002), a selection that ultimately can shape their spatial distribution (Fryxell et al. 2004).

The search for resources by prey species, however, has to be done while considering predation risk (Focardi and Pecchioli 2005, Bowyer and Kie 2006). Animals can trade off food acquisition and safety by adjusting space use patterns to balance these often-conflicting demands. For example, elk (*Cervus elaphus*) respond to spatial patterns of wolf (*Canis lupus*) distribution by altering their relative preference for aspen stands and forest as a function of how risky they are (Creel et al. 2005, Fortin et al. 2005).

The rate of resource acquisition and the risk of predation generally change when an individual joins a group. Collective vigilance makes larger groups more effective at detecting predators (Dehn 1990). Each group member also has a relatively lower risk of being the victim of an attack because of cooperative defense, together with dilution and confusion effects (Dehn 1990, Bednekoff and Lima 1998, Isvaran 2007). Information gained through social foraging can decrease uncertainty

Manuscript received 18 February 2008; revised 20 November 2008; accepted 5 December 2008. Corresponding Editor: B. P. Kotler.

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about environmental quality, thereby increasing efficiency (Fernandez-Juricic et al. 2006). Such benefits provide an incentive to form a group and maintain its cohesion. Conversely, group members often have to share food, which can lead to a reduction in intake rate when food supplies are limited (Hobbs et al. 1996, Fortin et al. 2004). To remain in the group, individuals must synchronize their activities with other members, such as resting, foraging, and moving across the landscape (Conradt and Roper 2000). This synchronization can be costly when it forces, for example, an individual to interrupt a resting or foraging bout in order to maintain spatial cohesion with its conspecifics. All these costs should tend to reduce group stability.

Characteristics of the environment can vary over space and time, which can result in dynamic changes in the cost–benefit trade-offs of group living. For example, prey may reduce their probability of being detected by predators in forested environments by residing in smaller groups. Conversely, prey are likely to be detected when in open environments regardless of group size, so this should favor the formation of larger, hence relatively safer, groups (Jarman 1974, Pays et al. 2007). Spatial heterogeneity thus can lead to group instability, and spatial patterns of group fusion–fission allow us to identify the habitat characteristics that are driving the cost–benefit trade-offs of group living.

Habitat selection is recognized as a complex process (Jonzén et al. 2004, Fryxell et al. 2005, McLoughlin et al. 2006), but studies accounting for the response of animals to multiple habitat attributes generally overlook potential group size effects, even when dealing with gregarious animals (e.g., Johnson et al. 2001, 2004, Boyce et al. 2003). Our understanding of the role of group size in shaping distribution pattern in complex, natural environments therefore remains limited.

Our study investigates three elements of animal ecology that may drive the distribution dynamics of large gregarious herbivores. The first element pertains to how group size modifies resource selection behavior. We demonstrate how group size effects can be integrated into resource selection functions (RSFs) and then build group-size-dependent multivariable RSFs for free-ranging female plains bison (*Bison bison bison*) followed in winter and summer using global positioning system (GPS) collars. Resource selection functions are statistical tools that describe the relative probability of occurrence of animals based on their complex behavioral response to biotic and abiotic elements of their habitat (Boyce 2006, McLoughlin et al. 2006). Resource selection functions revealed that selection for meadows was stronger when bison were part of larger groups. Habitat selection thus appeared to be partly shaped by group size, which varies dynamically in bison, as in other ungulates (e.g., Conradt and Roper 2000, Focardi and Pecchioli 2005, Isvaran 2007). The next two elements of our research were therefore oriented toward a better

understanding of temporal changes in group size and the use of meadows by bison groups under predation risk.

Fusion–fission group dynamics are rarely studied for ungulates in their natural environment, presumably because of the difficulty of observing group dynamics (Pays et al. 2007). We addressed this challenge by investigating conditions under which pairs of radio-collared bison merged and split up. Given that those bison were captured in different groups found in all parts of the bison range and that individuals were otherwise a random sample of the female bison population, examination of bison pairs should provide general insights into group fusion–fission dynamics. Group cohesion entails activity synchronization among members (Conradt and Roper 2000), and circadian rhythms in movement rates are common in ungulates (Green and Bear 1990, Ager et al. 2003, Forester et al. 2007). On this basis, we predicted that fission of bison dyads (i.e., pairs of radio-collared bison that have grouped) would be more likely during parts of the day when distances moved are longer and more variable among individuals because there would be more opportunities for conflicts in activity synchronization. Group size is also expected to be larger in open areas than in forest (Pays et al. 2007), which implies that fusion of bison groups should be more likely in meadows and that the transition from meadow to forest should promote group fission.

Predation risk also may influence group dynamics (Jedrzejewski et al. 2006). We tested whether inter-meadow movements were better explained from a response to exploitative competition or to predation risk in a landscape composed of meadows interspersed in a forest matrix. If exploitative competition were driving inter-meadow movements, we would expect longer residence time when individuals were in small groups rather than in large groups because food would then be shared among fewer individuals and, therefore, should be depleted more slowly. Large herbivores should be able to maintain their intake rate until very little food remains in the food patch (Fortin et al. 2004) because food search can overlap with vegetation processing (Spalinger and Hobbs 1992). Such multi-tasking leads to gain functions that are virtually linear until the complete depletion of the vegetation patch (Illius et al. 2002, Fortin et al. 2004). We also examined whether most of the vegetation available at a given location had been consumed before the departure of bison, as could be expected if depression in intake rate triggered meadow departure. On the other hand, predation risk may precipitate departure from meadows. Mitchell and Lima (2002) suggested that frequent movements diminish predation risk by reducing the predictability of prey's location when predators have good spatial memory, such as wolves (Gude et al. 2006). Individuals most at risk might be inclined to make more frequent inter-meadow movements, resulting in more time spent in the forest matrix and thereby reducing the

strength of selection for meadows. The predation risk hypothesis predicts that bison should perceive higher risk when in small rather than in large groups, leading to shorter local residence time, more time spent in forests, and weaker selection for meadows when in smaller groups. We tested these hypotheses on the bison population of Prince Albert National Park, Saskatchewan, Canada.

METHODS

Study area

The study was conducted in the Prince Albert National Park, Canada, during the summers of 2005–2007 (20 May to 20 August 2005; 1 June to 16 August 2006; 31 May to 9 August 2007) and the winters of 2006 and 2007 (16 January to 12 March 2006, 18 January to 7 March 2007). The park harbors one of the few free-ranging populations of plains bison. The population was estimated at 385 individuals in 2006 (Parks Canada, unpublished data). The bison range is established in the southwest corner of the park, which is mostly composed of forests (85%), meadows (10%), and water bodies (5%; Fortin et al. 2003). The bison range includes few roads that are accessible to park's staff and researchers, but generally not to visitors. Wolf predation on bison was observed sporadically during the study.

Bison locations and group size

The distribution of bison groups was determined by following 15 female bison in summer and nine females in winter. The females were equipped with global positioning system collars (GPS collar 4400M; Lotek Engineering, Newmarket, Ontario, Canada) taking locations at 3-h intervals. They were captured across the entire bison range to insure broad sampling of the population. Group size (3 to >150) of each collared female was determined on average 15 times in summer (range = 5–28) and seven times (range = 2–20) in winter.

Individuals were considered in the same group when they were at a distance <100 m (Fortin et al. 2003). Group size displayed temporal variation, with the consequence that each time that group size was observed for a given radio-collared bison, we assumed that group cohesion would remain for 24 h. The GPS locations (i.e., eight locations per 24 h) of that individual on that day were thus associated with the observed group size for that day.

Habitat covariates

Land cover types at observed and random locations were characterized based on two classified Landsat Enhanced Thematic Mapper (ETM+) satellite images (path 38, rows 22 and 23; 28.5 m resolution; collected on 3 August 2001). The 18 landscape cover types originally recognized were combined to form five more general cover types: (1) meadow, including areas near lakes and rivers dominated by grasses, forbs, and sedges (MEADOW); (2) riparian areas largely comprised of shrubs and

located near streams and rivers (RIPARIAN); (3) forest consisting of deciduous, conifer, and mixed stands (FOREST); and (4) water bodies (WATER). All cells in this raster-based land cover map that contained a road or major hiking trail (determined using a vector GIS roads layer) were reclassified to form a fifth cover type (ROAD). To remain consistent with the resolution of the thematic mapper (TM) image, bison were considered on the road when <15 m away. Classification accuracy was 91.8% based on 110 random field locations (within 2 km from a road) in the various land cover types.

We also estimated snow water equivalent (SWE) for the bison range based on the snow model presented in Fortin (2007). The model relied on the sampling of 18 meadows distributed all across the bison range. An inverse distance weighting function (Schloeder et al. 2001) was used to extrapolate SWE from the 18 meadows to other locations across the study area. Snow water equivalent was adjusted for the influence of tree canopy on snow accumulation. The snow model was robust to cross-validation, with relationships between observed and predicted estimates having a mean $\bar{R} = 0.76$. The 18 meadows were sampled eight times (survey 06-1, 20–22 January 2006; survey 06-2, 2–3 February 2006; survey 06-3, 17–19 February 2006; survey 06-4, 7–10 March 2006; survey 07-1, 21–22 January 2007; survey 07-2, 31 January to 1 February 2007; survey 07-3, 13–14 February 2007; survey 07-4, 28 February to 1 March 2007), and the information from surveys 06-1 to 06-4 and 07-1 to 07-4 was used to estimate SWE over the following periods: 10–30 January 2006, 31 January to 13 February 2006, 14 February to 4 March 2006, 5–19 March 2006, 19–26 January 2007, 27 January to 6 February 2007, 7–20 February 2007, and 21 February to 7 March 2007, respectively.

Integrating group size effects into resource selection functions

In many gregarious species (e.g., Conradt and Roper 2000, Focardi and Pecchioli 2005, Isvaran 2007), including bison (Lott and Minta 1983), individuals experience frequent changes in group size and/or resource availability. In these dynamic systems, a matched case-control design should be used to integrate group size directly into RSFs. Indeed, group size must be associated with both observed and random locations. Each observed location (scored 1) needs to be linked to a set of random locations (scored 0) where the group could have been at that time, and the decision for a group to use a given location becomes contingent on local alternatives. For longitudinal data, random locations can be drawn within a limited domain corresponding to the distance to which the group could have traveled given the time interval between successive locations (Johnson et al. 2001, Boyce et al. 2003, Ciarniello et al. 2007). In our case, each observed location was associated with 10 random locations sampled within a 700-m radius circle of the GPS

location, a radius that encompassed >80% of the distances observed between two successive GPS locations (3-h time interval) during any season. Habitat characteristics at observed locations are compared to the characteristics at random locations while accounting for nonindependence between pairs of random and observed locations. Group size associated with focal individuals becomes an explanatory variable that takes a unique value for an observed location and its associated random locations. Group size thus remains constant within each choice set, but group size can change over time (between choice sets).

Assuming that we are interested in the relative probability of use of k independent variables (x_1, \dots, x_k), as well as in the potential influence of group size (G) on the selection for independent variable x_1 , the group-size-dependent RSF then takes the following structure:

$$w(\mathbf{x}) = \exp(\beta_1 x_1 + \beta_2 x_2 + \dots + \beta_k x_k + \beta_{k+1} x_1 G) \quad (1)$$

where β_{k+1} is the selection coefficient associated with the interaction term $x_1 G$. Because each observed location and its associated random locations are assigned the same group size, G cannot appear in the model as a main effect, but rather as an interaction term whose interpretation is that the link between bison distribution and habitat attribute x_1 changes with group size (Train 2003). The inclusion of G into RSFs (matched case-control models) is a fundamental aspect of the framework we propose here. A significant interaction $\beta_{k+1} x_1 G$ would indicate that the link between bison distribution and the habitat attribute x_1 changes as a function of group size.

Group-size-dependent resource selection functions for free-ranging bison

Group-size-dependent RSFs were estimated based on locations of the 15 radio-collared bison. Because of our interest in group size effects, the analysis only considered GPS locations during those 24-h periods for which group size was estimated, and other locations were omitted from the RSFs, leaving 1863 bison locations in summer for the 15 radio-collared females and 546 locations in winter for the nine bison. Habitat covariates considered in the analyses included a set of dummy variables representing four land cover types (i.e., ROAD, MEADOW, RIPARIAN, WATER), with FOREST being used as the reference category. We also considered the proportion of meadow area within a 700-m radius (p_{mead}) centered on observed or random locations (see Boyce et al. 2003 for a similar approach), as well as SWE in winter. Group size was included in RSFs through interaction with ROAD, MEADOW, and p_{mead} . Resource selection functions were assessed for multicollinearity, which became an issue when condition indices were >10 (Belsley et al. 1980). Multicollinearity arose when $\text{SWE} + \text{SWE}^2$ were included in RSFs, but once standardized (i.e., $\text{SWE}_i - \text{mean SWE}$), collinearity was absent from the models.

We consider two approaches of group-size-dependent RSF estimation. The first approach is based on mixed-effect conditional logistic regression, in which individual variation in habitat selection is modeled explicitly. This subject-specific approach relies on explicit modeling of the correlation structure between all locations for a given animal (Train 2003). We evaluated whether group-size-dependent habitat selection was similar among radio-collared bison by contrasting mixed-model Akaike Information Criterion (AIC) values of group-size-dependent RSFs, some of which included individual as random effects while others were their fixed RSF counterpart. (Given our objective to draw inference on group size effects, we used standard marginal AIC [Vaida and Blanchard 2005].) In our case, model parsimony decreased with the inclusion of random effects (see *Results*). We thus considered a population-averaged approach, which involved fixed-effect conditional logistic regression in conjunction with generalized estimating equations (GEE). This second approach allows for population-averaged inference and is robust to misspecification of the within-individual correlation structure (Fortin et al. 2005, Craiu et al. 2008). Robust variances (cf. Fortin et al. 2005) were calculated to ensure that the conclusions were not biased from potential temporal autocorrelation issues. As indicated previously, our analyses were based on a series of eight locations gathered during 24-h periods centered on the time that group size was determined for a particular female bison, with each series being considered as a cluster. Also, when females were together, we assumed that decisions were nonindependent, and we assigned their locations to the same cluster. Overall, analyses were based on 165 clusters in summer and 58 clusters in winter.

We used k -fold cross validation for case-control design to evaluate model robustness. An RSF was built using 80% of randomly selected strata. This RSF was then used to estimate $w(\mathbf{x})$ scores for the observed and random locations of the 20% withheld strata. The observed location of each stratum was ranked against its associated random locations from 1 to 11 (i.e., 11 potential ranks given that a stratum included 1 observed and 10 random locations) based on the $w(\mathbf{x})$ scores, where 1 was the lowest and 11 was the highest possible rank for that stratum. Ranks of observed locations were then tallied into the 11 potential bins. Spearman rank correlation (r_s) was performed between the bin's ranking (1–11) and its associated frequency. The process was repeated 100 times, and the mean and range of r_s were reported. The mean and range of expected r_s were also evaluated, assuming a completely random pattern of habitat selection by following the same steps, up to the use of the 20% withheld strata. Instead of ranking the observed locations against the random ones, we simply ranked one random location (selected randomly among the 10 random locations per stratum) against the other nine random locations (i.e., from 1 to 10). Ranks of the focal random locations were then tallied into the 10

potential bins. A Spearman rank correlation (r_S) was performed between the bin's ranking (1–10) and its associated frequency. The process was repeated 100 times.

Analysis of fusion–fission dynamics of bison pairs

Fusion–fission dynamics of bison groups was evaluated using all the radio-collared bison locations. We considered that two radio-collared bison had merged into a group when they were <100 m apart (Fortin et al. 2003), and we assumed that group cohesion remained as long as they traveled together (see Fig. 1 for an example of the dynamics of bison pairs). We defined a fission event as two or more consecutive locations separated by a distance of >100 m.

We evaluated whether pairs of radio-collared bison were more likely to merge in meadows than the forest. When two radio-collared bison first became part of the same group, the GPS location of one randomly chosen individual was associated with 10 random locations sampled within a 700 m radius buffer. Observed and random locations were then contrasted based on conditional logistic regression estimated by GEE, with robust SE calculated by grouping individual bison dyads into distinct clusters.

Once a group had formed, we used a mixed-effect Cox proportional hazards model, with pairs of bison as a random effect term, to assess temporal changes in the risk of fission, as well as to evaluate whether fission events were more likely when distance moved was greater and more variable (i.e., 09:00, 12:00, 15:00, 18:00 in winter and 06:00, 09:00, 18:00, 21:00 in summer; Appendix B) and when bison moved between land cover types.

Bison use of meadows

We used a mixed-effect Poisson regression model, in which the individual bison was considered a random term, to investigate whether the number of consecutive fixes spent in meadows varied as a function of group size. The number of consecutive fixes was proportional to meadow residence time. Linear mixed-effect models with normal distribution were used to test for a relationship between group size and meadow size, while considering individual bison as a random effect.

We also evaluated the amount of vegetation consumed and the biomass remaining following the visit of bison groups. In summer 2007, we surveyed the vegetation in meadow sections averaging 3 ± 1 ha (mean \pm SD; range = 0.4–5 ha, $n = 35$). Total dry biomass (B , in grams per square meter) was estimated in 16 ± 3.5 quadrats (range = 8–25 quadrats, depending on area), systematically located over the meadow sections, by measuring the height from the ground (in centimeters) that a calibrated plastic square (0.25 m^2) settled on the vegetation. The relationship followed: $B = -8.78 + 1.62 \times \text{height}$; $R^2 = 0.80$, $F_{1,105} = 426.45$, $P < 0.0001$, $n = 107$ (Fortin 2007). We then visually estimated the proportion of individual plants that had been consumed

(proportion “attacked,” A). Knowing that bison eat ~40% of each plant (Fortin et al. 2002), we calculated the percentage of dry biomass consumed as $A \times 0.40 \times 100$, and the plant biomass consumed as $B \times A \times 0.40$.

In winter 2007, vegetation was estimated in meadow sections of 9 ± 7 ha (range = 2–20 ha, $n = 11$) before the passage of bison (i.e., snow was undisturbed over the area). We used a 0–10 visual scale to evaluate total dry plant biomass (in grams per square meter) in 7–43 quadrats (24 ± 12 , depending on meadow section area) of 0.25 m^2 , systemically organized within the survey area. The visual scale was calibrated by clipping the aboveground vegetation in 0.25-m^2 quadrats, drying the samples at 60°C , and weighting plants after 48 h of drying. The calibrated scale followed $B = 6.58 + \text{visual estimation}^{1.81}$ ($R^2 = 0.94$, $F_{1,39} = 592.87$, $P < 0.0001$, $n = 41$). Following the passage of bison, we used a handheld GPS unit to delineate the foraging areas (i.e., areas with snow craters made by bison). We then visually estimated the proportion of vegetation consumed in the foraging areas by sampling 13 ± 10 quadrats (range = 5–35 quadrats, depending on the area). Percentage of biomass of dry vegetation consumed following the passage of bison was then estimated by considering the total biomass originally available in the whole meadow section minus the biomass removed from the foraging area.

RESULTS

Group-size-dependent resource selection functions

Behavioral responses to habitat attributes were similar among radio-collared female bison. Indeed, adding random slopes in RSFs generally reduced model parsimony (Appendix A). Further inferences on habitat selection thus were based on fixed-effect model RSFs estimated by GEE (Table 1).

Group size of radio-collared female bison averaged 46 ± 36 (mean \pm SD) individuals (range = 3–150 individuals, $n = 165$) in summer and 16 ± 8 individuals (range = 6–41 individuals, $n = 58$) in winter. Group-size-dependent RSFs revealed that bison distribution was the result of a behavioral response to multiple habitat attributes (Table 1). Cross-validation indicated that models were useful predictors of habitat selection in bison, as the distribution of observed r_S was higher than expected by chance alone (Table 1). Overall, RSFs indicated that bison avoided riparian areas during summer. In winter, bison were never in those areas and only once within 700 m of them, with the consequence that RIPARIAN could not even be considered in candidate winter RSFs (models would not converge). The probability of occurrence of bison groups increased with the proportion of meadows within a 700-m radius (Table 1). Water bodies were avoided in summer, but selected in winter. We also found that bison groups made selective use of the road network in summer (Table 1), but not in winter (-0.85 ± 1.02 [$\beta \pm \text{SE}$], $P = 0.67$). In winter, SWE had a quadratic

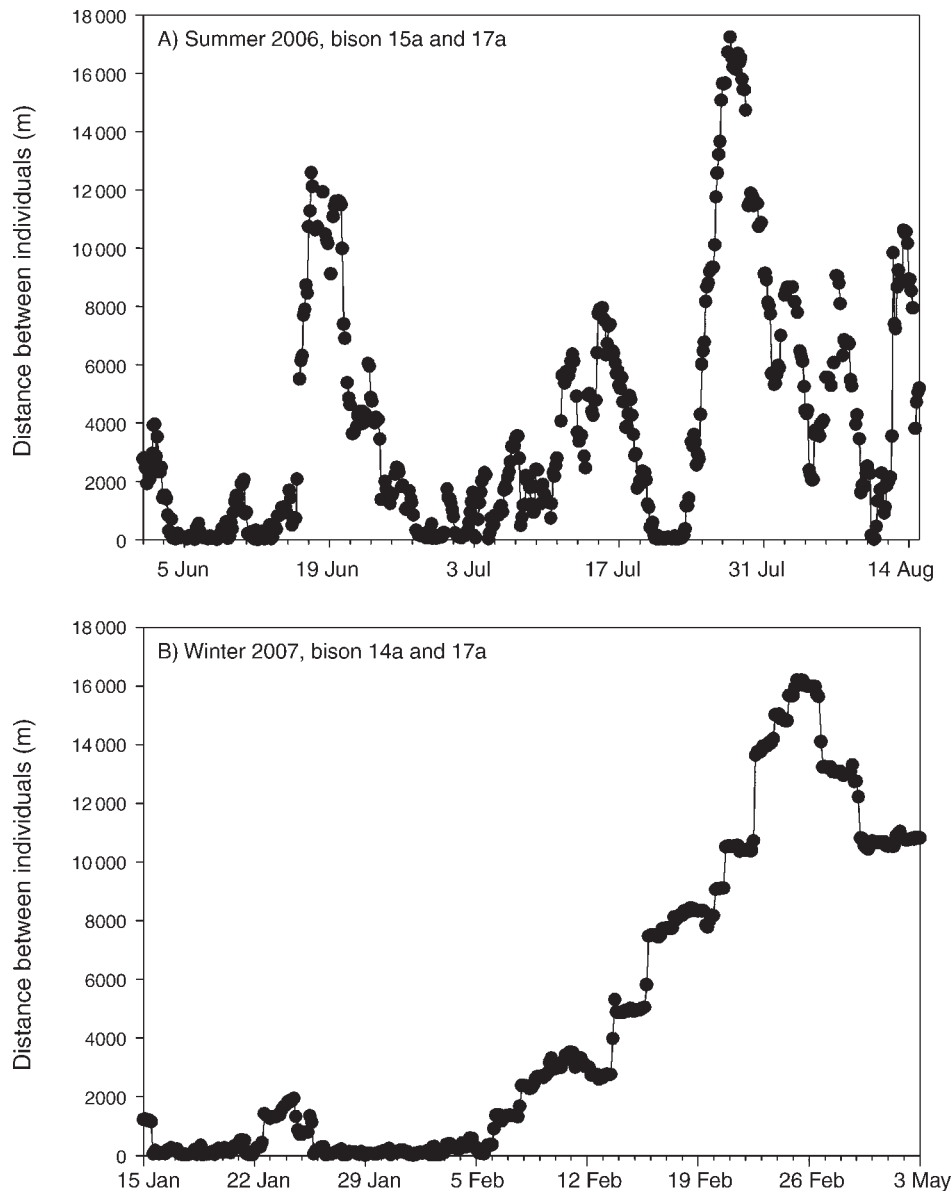


FIG. 1. Example of temporal changes in the distance between pairs of radio-collared female bison followed in (A) summer 2006 and (B) winter 2007 in Prince Albert National Park, Saskatchewan, Canada. Switch between sequences of short and large interindividual distances reveals the dynamics of the group fusion–fission process in bison dyads. Gaps in the sequence are due to missing locations from either of the individuals from the pair.

relationship with the probability of occurrence of bison, with negative effects only occurring when SWE > 1.9 cm (Fig. 2). Our analysis also revealed that the bison–habitat relationship varied as a function of group size. Bison groups generally selected meadows (Table 1), but the strength of meadow selection increased with group size in both summer and winter (positive interaction term, MEADOW \times G; Table 1). Because forest was the reference category, the increase in the selection for meadows with group size also implies that the probability of occurrence of bison in the forest decreases with increasing group size. To avoid multicollinearity, an RSF

could only include one interaction term involving group size. We thus built individual RSFs that, instead of including MEADOW \times G, were based on ROAD \times G, SWE_{std} \times G or p_{mead} \times G. In all cases, 95% CIs of interaction coefficients included zero. Therefore, our study only provides evidence for group-size-dependent association with meadows.

Fusion–fission dynamics of bison groups

Size of bison groups was highly variable over time. We observed 589 fusion–fission events in summers (median = 8 events per pair; range = 1–34 events per

TABLE 1. Resource selection function for bison (*Bison bison*) groups in Prince Albert National Park, Saskatchewan, Canada, in summer and winter.

Covariate	Summer		Winter	
	$\beta \pm SE$	<i>P</i>	$\beta \pm SE$	<i>P</i>
RIPARIAN	-2.20 ± 0.67	0.001
WATER	-1.25 ± 0.27	<0.001	1.66 ± 0.32	<0.001
ROAD	0.79 ± 0.18	<0.001	-0.85 ± 1.02	0.67
<i>p</i> _{mead}	1.09 ± 0.49	0.03	6.27 ± 1.64	<0.001
MEADOW	1.07 ± 0.26	<0.001	1.70 ± 0.40	<0.001
MEADOW × <i>G</i> †	0.15 ± 0.07	0.04	0.05 ± 0.02	0.03
SWE _{std}	-0.31 ± 0.10	0.002
SWE ² _{std}	-0.07 ± 0.03	0.01

Notes: Coefficients are presented with robust standard errors (SE) corrected for autocorrelation and associated *P* values. Model robustness was evaluated using *k*-fold cross-validation, which was based on observed \bar{r}_S and \bar{r}_S expected under random patterns (see *Methods* for details). The *k*-fold values (\bar{r}_S values and ranges), were: for summer, observed, 0.37 (0.26–0.50) and random, -0.04 (-0.35–0.21); for winter, observed, 0.90 (0.65–0.99) and random, -0.12 (-0.81–0.51).

† Group size, *G*, corresponds to *G* in winter and to ln(*G*) in summer.

pair) and 60 events in winters (median = 4 events per pair; range = 1–13 events per pair) among radio-collared bison pairs. Probability of occurrence of fusion events was higher in meadows than in the forest during both summer (conditional logistic regression, 1.88 ± 0.10 [$\beta \pm SE$], *P* < 0.001) and winter (1.71 ± 0.25, *P* < 0.001).

Following a fusion, bison dyads remained together for a median time of 21 h in summer and 30 h in winter. The probability of dyad cohesion decreased over time at a faster rate observed in summer than in winter (Fig. 3). Also, the risk of fission was 1.79 (i.e., exp[0.58]) times higher in summer and 2.05 (exp[0.72]) times higher in winter during the time of day when distance moved was longest and most variable (Table 2), which generally occurred during daylight hours (Appendix B). Fission risk, however, was not related to meadow size (Table 2). In summer, moving into the forest increased the risk of dyad fission by >1.65 (exp[0.50] or exp[0.67]) times compared to the absence of transition between cover types (Table 2). It might appear obvious that fission

would be more likely when bison transit between land cover types. However, moving into the forest was the only transition type influencing fission events (Table 2). Moreover, most fission events occurred in the absence of transition between land cover types (summer, 55.5%, *n* = 557; winter, 58.8%, *n* = 51).

Use of meadows by bison

Group-size-dependent RSFs detected stronger selection for meadows by larger bison groups (Table 1). This stronger selection can be explained by larger groups having longer residence time in individual meadows. Indeed, the number of consecutive locations within meadows increased with group size in summer (mixed-effect model with Poisson distribution; coefficient for group size, +0.019, *F*_{1,414} = 5.12, *P* = 0.02) and in winter (+0.151, *F*_{1,105} = 5.42, *P* = 0.02). On the other hand, meadow size was independent of group size in summer

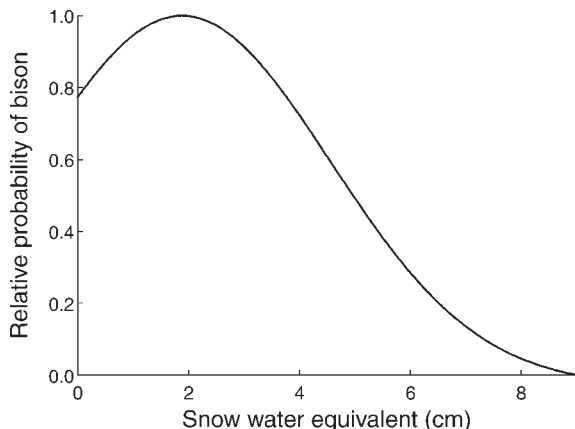


FIG. 2. Relative probability of occurrence by groups of plains bison in Prince Albert National Park, as a function of snow water equivalent (SWE). Relative probabilities were calculated based on the model displayed in Table 1 for winter.

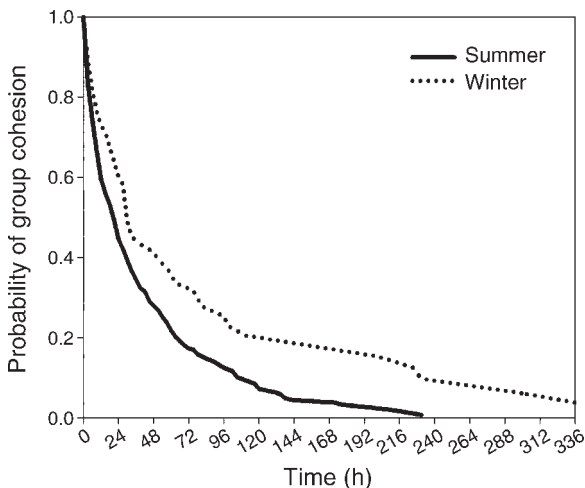


FIG. 3. Temporal changes in the probability of group cohesion for radio-collared bison dyads in summer and winter in Prince Albert National Park. Start time at 0 is the onset of group fusion.

TABLE 2. Mixed-effect Cox model investigating the risk of fission for bison dyads.

Covariate	Summer		Winter	
	$\beta \pm SE$	<i>P</i>	$\beta \pm SE$	<i>P</i>
MaxMov	0.58 ± 0.09	<0.001	0.72 ± 0.32	0.02
(Meadow size) ^{0.5}	-0.11 ± 0.11	0.30	0.05 ± 0.36	0.89
Transition				
Forest to meadow	0.18 ± 0.14	0.19	0.62 ± 0.51	0.23
Meadow to forest	0.50 ± 0.11	<0.001	0.64 ± 0.47	0.17
Forest to other	-0.21 ± 0.33	0.53
Other to forest	0.67 ± 0.27	0.01	0.68 ± 0.66	0.30
Meadow to other	0.08 ± 0.33	0.81	-0.40 ± 1.03	0.70
Other to meadow	0.42 ± 0.30	0.17	0.33 ± 0.78	0.67
Random effect	0.78 ± 0.71	0.27	0.00 ± 0.00	0.95

Notes: The investigation was undertaken to determine whether the risk of fission for bison dyads increased during the time of day when the distance bison moved was greatest (MaxMov: 06:00, 08:00, 18:00, or 21:00 in summer and 09:00, 12:00, 15:00, or 18:00 in winter; Appendix B) and when there was a transition between land cover types from the current and the next location.

(mixed-effect model with normal distribution; coefficient for meadow area, $+0.0003$, $F_{1,414} = 0.21$, $P = 0.65$) and in winter ($+0.001$; $F_{1,105} = 1.95$, $P = 0.17$).

Finally, bison groups consumed only a small proportion of the vegetation before leaving an area. In summer, a total of 176 ± 84 g/m² ($n = 35$) of dry vegetation remained in meadows following the passage of bison, and $6\% \pm 4\%$ of the available vegetation had been eaten. In winter, a total of 98 ± 58 g/m² ($n = 11$) remained following a visit by a bison group, during which only $2\% \pm 2\%$ of the vegetation was consumed.

DISCUSSION

Group-size-dependent resource selection function

Group-size-dependent RSFs revealed that bison make stronger selection for meadows when they are part of a large group than when they are part of a small group. The use of RSFs has increased in recent years (Johnson et al. 2004, Boyce 2006, Lele and Keim 2006) and, although commonly applied to gregarious animals (e.g., Johnson et al. 2001, 2004, Boyce et al. 2003), RSFs have yet to directly integrate group size. This omission may be problematic given that our understanding of animal-habitat relationships is becoming increasingly shaped by RSFs and that group dynamics can influence habitat selection. We demonstrate that a case-control design can be used to build multivariable RSFs in which the response to habitat varies as a function of group size. Group-size-dependent RSFs revealed that habitat selection in bison is a complex process that involves a behavioral response to multiple habitat elements, the nature of which can vary seasonally and with group size.

We found that bison avoided water bodies in summer, which probably reflects their sporadic and brief use (relative to our 3-h relocation interval) for drinking. In contrast, bison made selective use of water bodies in winter. The vegetation emerging from rather deep water becomes available in winter, once the water has frozen and can support bison. Snow water equivalent had little

effect until a threshold of SWE was reached, at which point snow had an adverse effect on probability of bison occurrence. Snow can influence animal movement, travel costs, feeding ability, probability of survival, and susceptibility to predation (Telfer and Kelsall 1984, Mech et al. 2001, Fortin et al. 2003). Bison appear particularly sensitive to the potentially negative effects of snow conditions compared to other large herbivores (Telfer and Kelsall 1984).

The use of roads by large herbivores may imply the need for management actions (Bruggeman et al. 2006). The importance of negative impacts, such as traffic disturbance and collision with vehicles, should be related to the frequency of use by animals. Bison selected roads for traveling in summer, but not in winter. Bison seem opportunistic in their use of roads (Bruggeman et al. 2007), using them when they are conveniently located to move between meadows. A network of unpaved roads and human trails provides links among several meadows in the bison summer range, but not in the more northern winter range where roads and trails are uncommon. Moreover, only a small portion (~ 1 km) of the road network is plowed in winter; hence the use of roads might not facilitate movement.

Bison generally selected areas largely comprised of meadows, and within those areas, they selected meadows. This selection for meadows was stronger for large than for small groups. Bison-habitat relationships thus depended on whether individuals were in a large or a small group. Habitat selection analyses were based on the assumption that group cohesion lasted 24 h. Our evaluation of fusion-fission dynamics of bison dyads confirms this is a reasonable assumption. The likelihood of observing a given group should be proportional to the length of time this group remains as a unit. For example, a group that remains together 8 h would be twice as likely to be observed in the field as a group that had only remained 4 h together. Based on this principle and on the observed distribution of cohesion time for radio-collared bison dyads, we evaluated that the assumption

that group unity lasted at least 24 h should have been correct >75% of the time in summer and >85% in winter. Our finding that habitat selection in bison depends on group size thus should be robust to this assumption. We thus found that spatial distribution of bison depended on fission–fusion dynamics that govern group structure, as also suggested for other ungulate species (Haydon et al. 2008).

Fusion–fission dynamics of bison groups

Group formation and breakdown were related to habitat structure and to circadian rhythm in movement patterns. Fusion of bison groups was most likely in open meadows. In open areas, conspecifics can see each other at relatively far distances, which should favor group formation in gregarious herbivores with unstable group dynamics (Pays et al. 2007). Once a group has formed, its cohesion implies that members must remain in the same place at the same time and must synchronize their activities (Conradt and Roper 2000). Synchronization of activity budget among group members may entail costs, which should promote group fission. Consistently, fission events of bison dyads were most likely during the period of the day when displacements were largest and most variable among individuals. Thus, we found that circadian rhythms in movement patterns, which are frequently observed in ungulates (e.g., Ager et al. 2003, Forester et al. 2007), seem to encourage group instability.

Fission risk was further influenced in summer by movements leading into the forest. Such reaction should lead to larger groups in meadows than in forests. This, however, should not be the mechanism behind our finding of stronger selection for meadows by large than by small bison groups. Independently of their size, bison groups were almost exclusively determined in meadows because accurate counts are difficult in the forest. Variation in group size used in habitat selection analyses was therefore not the result of a transition from meadow to forest. Instead, meadow selection was stronger for large than for small groups because large bison groups had longer residence time and thus spent less time in the forest matrix.

Group-size-dependent habitat use under predation risk

Bison have evolved in the presence of wolves. Their behavioral response to habitat structure has thus likely been shaped by cost–benefit trade-offs of antipredator strategies. Creel and Winnie (2005) suggested that prey may respond to risk by one of two “pure” strategies: they can (1) behave in a manner that would be optimal in the absence of predators or (2) minimize risk while accepting the costs of antipredator strategies. Of course, animals are likely to use a mixture of both strategies. According to optimality principles (Brown and Kotler 2004), social foraging by bison may be such that individuals deplete meadows until the energy intake rate drops to the point at which foraging costs from risk and

energy expenditures are not being covered. In this sense, both risk and resources should matter. Nevertheless, it is informative to evaluate the relative influence of bottom-up and top-down forces on space use patterns of animals.

In absence of predation, bison could maximize energy gains via optimal patch residency/occupancy times. We found little evidence, however, that this pure strategy was used by bison groups. If exploitative competition were driving inter-meadow movements, longer residence time would be expected when individuals were in small rather than in large groups because small groups should deplete food relatively slowly. We observed exactly the opposite, i.e., shorter residence time for smaller groups. Moreover, little vegetation (<6%) was consumed before bison left a meadow. Meadow departure thus appears unlikely to be triggered solely by depression in intake rate, even for large groups (Fortin et al. 2004). Exploitative competition alone appears to be insufficient to explain differences in meadow residence time between large and small groups.

So why are bison groups constantly on the move? Perhaps small groups are looking for conspecifics to form larger groups. But if this were the case, why would group cohesion be so weak in the first place? Minimizing predation risk is considered the most general and important benefit of grouping in large herbivores (Isvaran 2007), and we may have observed a behavioral response to changes in risk with group size (i.e., related to Creel and Winnie’s [2005] second strategy). Bison are certainly at risk in Prince Albert National Park: four of the 20 radio-collared female bison followed from 2005 to 2008 (total sampling effort = 8356 days × individuals) died from wolf predation (D. H. Frandsen, *unpublished data*). Regardless of predation risk, bison forage mostly in open areas (Hernández and Laundré 2005). Bison can nonetheless reduce risk by adjusting distribution patterns, depending on group size. First, grouping provides greater advantages in open areas (Isvaran 2007). In the forest, predation risk would be more closely related to the probability of detection, which may favor the formation of small groups (Jarman 1974). Such evolutionary pressure might explain why we observed increased risk of group fission as individuals moved into the forest. Second, frequent movements diminish predation risk by reducing the predictability of prey location (Mitchell and Lima 2002, Gude et al. 2006). Individuals most at risk might be inclined to make more frequent inter-meadow movements, which implies more time spent in the forest matrix, thereby reducing the strength of selection for meadows. Given that little variation in the group composition (female : calf ratio) was found to be linked to group size for the focal radio-collared females (Fortin 2007), individuals in smaller groups should have faced greater per capita risk following an encounter with wolves (Dehn 1990; see also *Introduction*). On this basis, and contrary to the food competition hypothesis, the predation risk hypoth-

esis predicts that individuals should perceive risk as relatively higher when in small groups rather than in large groups, leading to a shorter residence time, more time spent in the forest, and a weaker selection for meadows by individuals in smaller groups. This trend should be reinforced by the fact that forest areas appear safer than meadows for ungulates (Creel et al. 2005, Fortin et al. 2005, Kauffman et al. 2007), including bison (Hernández and Laundré 2005). For both summer and winter, our field observations supported all the predictions related to the predation risk hypothesis. Group size differences in trade-offs between food availability and predation risk thus can explain variations in the strength of meadow selection by small and large bison groups.

ACKNOWLEDGMENTS

Funding for this study was provided by Parks Canada Species at Risks Recovery Action and Education Fund, a program supported by the National Strategy for the Protection of Species at Risk, Natural Sciences and Engineering Research Council of Canada, Foundation for Innovation, and l'Université Laval. We are grateful to L. O'Brodovich and D. Frandsen for providing logistic support in Prince Albert National Park and to M. Delorme, E. Dastou, J. Benoît, É. Rioux-Paquette, and G. Bastille-Rousseau for their help in the field. We thank S. Nadeau, A. Jodoin-Nicole, N. Courbin, and M.-C. Paquin for help in assembling the database.

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APPENDIX A

List of candidate resource selection functions for groups associated with female plains bison in Prince Albert National Park, Saskatchewan, Canada (*Ecological Archives* E090-174-A2).

APPENDIX B

Temporal variations in median distance moved during a three-hour interval by female plains bison in Prince Albert National Park, Saskatchewan, Canada (*Ecological Archives* E090-174-A1).