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EFFETS DE LA TAILLE DU GROUPE SUR LA SÉLECTION DE L'HABITAT À PLUSIEURS ÉCHELLES SPATIO-TEMPORELLES PAR LE BISON DES PLAINES (*BISON BISON BISON*)

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Résumé

L'objectif de cette étude consistait à déterminer dans quelle mesure des changements dans la taille du groupe influencent la sélection des ressources à plusieurs échelles spatio-temporelles chez le bison des plaines (*Bison bison bison*) du parc national de Prince Albert, Saskatchewan. Nous avons évalué la sélection de l'habitat à trois échelles spatiales au cours de l'été 2005 et de l'hiver 2006. Nos résultats ont révélé que la répartition spatiale du bison à chacune des échelles spatiales était influencée à la fois par des facteurs abiotiques (e.g., route, couvert de neige, pente) et biotiques (e.g., biomasse et espèce végétale), et que l'effet de ces facteurs variait en fonction de l'abondance des individus. Notre étude suggère que la sélection de l'habitat par le bison des plaines est un processus influencé par les compromis entre l'acquisition des ressources de haute qualité, les coûts associés aux déplacements et le risque de prédation, et ce, à différentes échelles spatiales. De plus, les résultats mettent en évidence que la nature de ces compromis change en fonction de la taille du groupe.

Abstract

This study had for objective to evaluate whether habitat selection by plains bison (*Bison bison bison*) in Prince Albert National Park (Saskatchewan) was influenced by group size at multiple spatio-temporal scales. We evaluated habitat selection at three spatial distinct scales during summer 2005 and winter 2006. Our results revealed that both abiotic (e.g., road, snow cover, slope) and biotic (e.g., biomass of plants, plant species) factors influenced the spatial distribution of bison at each of the three spatial scales, and that the effects of these factors on resource selection changed with the abundance of individuals. Our study suggests that pattern of habitat selection by bison is affected by trade-offs between the intake of high-quality resources, movement costs and predation risk at different spatial scales. Moreover, our results showed that the nature of the trade-offs varies with group size.

Avant-propos

Ce mémoire de maîtrise comprend trois parties, dont une introduction générale, un chapitre principal rédigé en anglais, et une conclusion générale. L'article inséré à l'intérieur du mémoire sera éventuellement soumis à une revue scientifique. Étant donné mon implication à chacune des étapes du projet, de l'élaboration à l'écriture du mémoire, je serai la première auteure de l'article. Daniel Fortin, en tant que directeur de recherche, a participé activement à la réalisation de ce projet ainsi qu'à la rédaction du mémoire de maîtrise et sera inscrit comme co-auteur de l'article.

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Introduction générale

Un aspect fondamental de l'écologie animale consiste à expliquer la répartition des espèces fauniques dans l'environnement. Les connaissances concernant le processus de sélection de l'habitat sont donc essentielles pour comprendre et prédire la dynamique spatio-temporelle des populations animales car elles font le lien entre la répartition des individus et celle des ressources (e.g., nourriture, eau, couvert) à l'intérieur d'un paysage hétérogène. La sélection de l'habitat par les grands herbivores est associée à une variété de facteurs abiotiques et biotiques, tels que l'organisation spatiale des routes et du couvert de neige, la disponibilité des communautés végétales, ainsi que l'intensité de la compétition et du risque de prédation. L'influence de ces facteurs sur le patron de répartition des individus a fait l'objet de nombreuses études (e.g., Alvenson et al., 1988; Morris, 1989; Brown et Theberge, 1990; Ramp et Coulson, 2002; McLoughlin et al., 2004; Amano et al., 2006a; Hancock et Milner-Gulland, 2006). Par contre, malgré toutes ces recherches, plusieurs aspects du processus de sélection de l'habitat restent toujours méconnus. La présente étude se penche sur une voie encore peu explorée de la sélection de l'habitat, soit l'effet de la taille du groupe sur la répartition des grands herbivores à plusieurs échelles spatiales.

La sélection de l'habitat, une question de compromis

Le processus de sélection de l'habitat reflète le compromis entre différents facteurs associés à l'utilisation des différentes composantes de l'environnement (e.g., coûts de déplacement, du risque de prédation, compétition, taux de consommation d'énergie) (Morris, 1987). Puisque les animaux sélectionnent les ressources de façon à maximiser leur aptitude phénotypique, le patron de répartition spatiale des individus devrait donc représenter le meilleur compromis. Toutefois, la nature des décisions qui offriront un compris avantageux n'est pas immuable et peut changer en fonction, par exemple, des caractéristiques du paysage, de l'abondance des individus et de l'échelle spatiale considérée.

Caractéristiques de l'habitat et coûts de déplacement

Afin de répondre à l'ensemble de leurs besoins, les animaux ont souvent à se déplacer entre les parcelles de ressources présentes dans l'environnement. Les coûts associés à ces déplacements influencent grandement la sélection de l'habitat par les individus (Fancy et White, 1987; Morris, 1989; Johnson et al., 2002b; Lin et Batzli, 2004). La répartition spatiale des animaux est donc affectée par les caractéristiques du paysage, comme la répartition des ressources limitantes (WallisDeVries, 1996; Shenbrot, 2004), la pente (Poole et Mowat, 2005; Liu et al., 2005; Fortin et al., 2005b), le couvert de neige (Fortin et al., 2003; Dussault et al., 2005; Fortin et al., 2005a; Poole et Mowat, 2005), et la présence de routes (Wielgus et al., 2002; Potvin et al., 2005; Bruggeman et al., 2006; Sawyer et al., 2006), puisque l'ensemble de ces attributs du paysage peuvent influencer les coûts de déplacement. Par exemple, les grands herbivores ont tendance à éviter les zones où le couvert de neige est important (Reynolds et Peden, 1987; Fortin et al., 2003; Dussault et al., 2005; Poole et Mowat, 2005), car en plus de diminuer l'accessibilité à la ressource alimentaire (VanCamp, 1975; Fortin et al., 2003; Fortin et al. 2005b), la densité et la profondeur du couvert de neige augmentent les coûts associés aux déplacements (Parker et al., 1984; Telfer et Kelsall, 1984).

La répartition spatiale des animaux est également modulée par la présence de route dans le paysage. L'effet des routes semble toutefois lié à leur intensité d'utilisation par l'humain (Richens et Lavingne, 1978; Eckstein et al., 1979; Kilgo et al., 1998; Wielgus et al., 2002; Potvin et al., 2005; Sawyer, 2006). Par exemple, les grands mammifères, tels que le grizzly (*Ursus arctos*), le loup (*Canis lupus*), le cerf mulet (*Odocoileus hemionus*) et le cerf élaphe (*Cervus elaphus*), évitent habituellement les routes achalandées, alors que les routes peu ou pas fréquentées par l'homme seront davantage utilisées (Rowland et al., 2000; Wielgus et al., 2002; Potvin et al., 2005; Sawer, 2006). Des routes dont l'accès est interdit peuvent toutefois devenir évitées par les grands mammifères si elles se trouvent à proximité de routes ouvertes à la circulation (Wielgus et al., 2002). La sélection pour différentes composantes de l'environnement doit donc être évaluée dans un contexte qui tient compte autant des facteurs abiotiques (e.g., densité des routes, profondeur du couvert de neige, pente, élévation), que des facteurs biotiques (e.g., proximité de l'homme, présence de prédateurs, abondance des conspécifiques), afin de mieux comprendre la répartition spatiale des individus.

Structure de l'habitat et risque de prédation

L'organisation spatio-temporelle du risque de prédation peut influencer la répartition spatiale des proies (Holbrook et Schmitt, 1988; Kunkel et Pletscher, 2000; Altendorf et al., 2001; Childress et Lung, 2003; Fortin et al., 2005a; Mao et al., 2005). Dans un environnement hétérogène, les animaux vont favoriser l'utilisation des parcelles de meilleure qualité (Morris, 1989; Sutherland, 1997). En général, les bénéfices d'utiliser une parcelle augmentent lorsque la quantité et la qualité des ressources alimentaires y sont élevées (MacArthur et Pianka, 1966; WallisDeVries, 1996) et diminuent lorsque le risque de prédation y est important (Cerri et Fraser, 1983; Holbrook et Schmit, 1988; Morris, 2005). La maximisation de l'aptitude phénotypique d'un individu requière donc un compromis entre l'acquisition de nourriture et l'évitement de la prédation (Moody et al., 1996; Houston et al., 1993; Brown et Kotler, 2004; Morris, 2005).

Afin de diminuer la probabilité d'être attaquées et capturées par un prédateur, les proies peuvent adopter certains comportements, comme la vigilance, la fuite et l'agrégation (Lima et Dill, 1990; Wrona et Dixon, 1991; McNamara et Houston, 1992; Cresswell, 1994; Hebblewhite et Pletscher, 2002). Mitchell et Lima (2002) ont aussi suggéré que l'augmentation de la fréquence des déplacements pouvait réduire le risque de prédation en diminuant la prédictibilité de la localisation des proies dans un système où le prédateur est doté d'une bonne mémoire spatiale. L'utilisation de structures de fuite, est un autre moyen adopté par les proies afin de diminuer le risque de prédation (Cassier et al., 1992; Bergman et al., 2006). En fait, différentes caractéristiques de l'habitat sont connues pour influencer la vulnérabilité des proies face aux prédateurs (Hebblewhite et al., 2005) et plusieurs études ont considéré les bordures entre deux types de couvert comme des structures pouvant influencer le risque de prédation chez les grands herbivores (Altendorf et al., 2001; Dussault et al., 2005; Hernàndez et al., 2005; Bergman et al., 2006).

Pour les individus s'alimentant à l'intérieur des milieux ouverts, la forêt offre souvent une meilleure protection contre les prédateurs (Blumstein et Daniel, 2002; While et McArthur, 2005), et les bordures formées par la transition entre ces milieux ouverts et la forêt représentent donc des structures de fuite pouvant être utilisées par les individus. En fait, pour plusieurs espèces de grands herbivores, tels que cerf élaphe, l'orignal (*Alces alces*) et le cerf mulet, le type de couvert offrant une grande disponibilité et qualité de nourriture sont rarement ceux procurant la meilleure protection contre les prédateurs (Altendorf et al., 2001; Dussault et al., 2005; Fortin et al., 2005; Bergman et al., 2006). L'augmentation de la distance par rapport à la bordure du couvert protecteur lors du comportement d'alimentation est donc souvent associée à une augmentation du risque de prédation (Blumstein et Daniel, 2003; While et McArthur, 2005). Afin de maximiser leurs gains d'énergie tout en diminuant le risque de prédation, plusieurs espèces d'herbivores, comme l'orignal (Edwards, 1983), le cobaye (*Cavia aperea*) (Cassini et Galante, 1992), le pademelon de Tasmanie *(Thylogale billiardieri)* (While et McArthur, 2005) et le wallaby tammar (*Macropus eugenii*) (Blumstein et Daniel, 2002), préfèrent donc s'alimenter près du milieu leur offrant une meilleure protection contre les prédateurs afin de s'assurer l'accessibilité à un corridor de fuite.

L'importance du risque de prédation est toutefois dépendants de l'abondance des individus (Wrona et Dixon, 1991; McNamara et Houston, 1992; Cresswell, 1994; Hebblewhite et Pletscher, 2002). Par exemple, il a été suggéré que les grands groupes de proies sont plus facilement détectables par un prédateur mobile que les petits groupes de proies (Taylor, 1979). D'un autre côté, une augmentation du nombre de conspécifiques accentue aussi le phénomène de dilution et les individus peuvent alors bénéficier de la vigilance des autres membres du groupe, diminuant ainsi le risque individuel de prédation (Abramson, 1979; Dehn, 1990; Lima, 1995; Roberts, 1996). En influençant ainsi le risque de prédation, la taille du groupe est donc susceptible de modifier le patron de sélection de l'habitat par les proies.

Compétition et taille de groupe

Dans un environnement hétérogène, la disponibilité et la qualité des ressources varient entre les différentes parcelles du paysage. Plus l'abondance des individus augmente dans l'environnement, plus la compétition intraspécifique pour certaines ressources favorables s'intensifie (Lin et Batzli, 2002; Stewart et al., 2005; Nicholson et al., 2006). La compétition peut résulter en une réduction de la disponibilité des ressources *per capita*, ou tout simplement à l'exclusion de certains individus des meilleures parcelles du paysage. En conséquence, certains individus sont contraints d'exploiter des ressources de moindre profitabilité (i.e., une ressource est peu profitable lorsque le ratio entre l'énergie consommée et le temps de manipulation est relativement faible). L'augmentation du nombre d'individus dans l'environnement pourrait donc être accompagnée d'une diversification des ressources utilisées (Morris, 1987; Sutherland, 1997; Kawata, 1997; Shepherd et Litvak, 2004).

Chez les grands herbivores, la disponibilité de la ressource alimentaire est un facteur déterminant dans le processus de sélection de l'habitat (WallisDeVries, 1996;

Shenbrot, 2004). Un aspect fondamental des modèles classiques d'approvisionnement optimal (Stephens et Krebs, 1986) prévoit que les individus devraient toujours consommer les ressources les plus profitables. De plus, les individus s'alimentant de manière optimale devraient augmenter le nombre d'items dans leur régime alimentaire lorsque leur taux de rencontre avec les ressources les plus profitables chute sous un certain seuil (Fortin et al., 2002). De cette façon, tous facteurs susceptibles de réduire le taux de rencontre entre l'animal et les ressources optimales devraient entraîner une diversification des ressources utilisées.

La compétition, soit par interférence ou par exploitation, est connue pour être un facteur pouvant réduire le taux de rencontre avec certaines ressources (Fryxell et Lundberg, 1998). La sélection des ressources les plus profitables pourrait donc avoir tendance à diminuer avec l'augmentation de l'abondance des individus. Des études ont ainsi montré que chez le cerf de Virginie (*Odocoileus virginianus*), le cerf mulet et le wapiti, une augmentation de la compétition pour les ressources alimentaires entraînait une sélection pour des plantes alternatives de moins bonne qualité (Kie, 1980; McLoughlin et al. 2006; Nicholson et al., 2006). Les compromis entre les différents facteurs de sélection (e.g., disponibilité de la nourriture, risque de prédation) peuvent donc être grandement influencés par l'abondance ou la densité locale des individus et affecter ainsi la répartition animale (McLoughlin et al., 2006). Afin de mieux comprendre le patron de répartition spatiale des animaux, il devient alors essentiel de considérer l'influence de l'abondance des individus sur la sélection de l'habitat.

La sélection de l'habitat, une question d'échelles spatiales

La répartition des ressources peut être hétérogène à plusieurs échelles spatio-temporelles. Les animaux peuvent ajuster leur utilisation de l'espace en réponse aux caractéristiques des ressources à ces différentes échelles, de telle sorte que la sélection de l'habitat est reconnue depuis longtemps comme un processus hiérarchique (Johnson, 1980; Addicott et al., 1987). L'influence des divers critères de sélection (e.g. répartition des ressources, coûts de déplacement, risque de prédation) sur les différents compromis peut donc varier selon l'échelle spatiale (Senft et al., 1987; Morris, 1992b; Mysterud et Ims, 1998; Johnson et al., 2002a; Boyce et al., 2003; McLoughlin et al., 2004; Dussault et al., 2005). Certaines études ont toutefois montré que la sélection de l'habitat pouvait être influencée par les mêmes facteurs de sélection à travers les différentes échelles spatiales (Carey et al., 1992; Ward et Saltz, 1994; Hall et Mannan, 1999). Ces observations contradictoires montrent donc l'importance de considérer plus d'une échelle lorsqu'on tente d'expliquer le patron de répartition des animaux à l'intérieur du paysage. Schaefer et Messier (1995a) pousse la réflexion encore plus loin en suggérant de considérer un minimum de trois échelles spatiales, puisqu'à une échelle donnée la sélection peut être influencée par les facteurs sélectionnés à échelles plus fines et contrainte par ceux sélectionnés à échelles plus vastes. Par contre, seulement une fraction des études faites jusqu'à maintenant (e.g., Johnson et al., 2002b; Boyce et al., 2003; Mosnier et al., 2003) ont tenu compte de plus de deux échelles spatiales dans leurs analyses, de telle sorte que la relation hiérarchique existant entre les caractéristiques de l'environnement et l'utilisation de l'habitat par les animaux demeure obscure.

Choix des échelles spatiales et analyse de sélection de l'habitat

La définition et le choix des échelles spatiales sont souvent basés sur des critères en relation directe avec la réponse des individus face à leur environnement. Par exemple, certains auteurs ont basé le choix de leurs échelles spatiales sur les mouvements des individus à travers le paysage (e.g., Arthur et al., 1996; Johnson et al., 2002a; Johnson et al., 2002b; Boyce et al., 2003), alors que d'autres ont préféré utiliser l'aire de répartition spatiale des individus (e.g., Rettie et Messier, 2000; Mosnier et al., 2003; McLoughlin et al., 2004; Dussault et al., 2005) ou leur comportement d'alimentation (e.g. Johnson et al., 2001, Fortin et al., 2003) pour définir leurs échelles d'analyse. Par exemple, Boyce et al. (2003) ont utilisé une échelle dont le domaine spatial correspondait à un cercle de taille variable centré sur chaque localisation GPS et dont le rayon était égal à la distance jusqu'à la prochaine localisation GPS. Cette échelle permettait ainsi de déterminer les ressources disponibles en fonction de la distance parcourue par l'animal.

Les études de la sélection de l'habitat par les animaux peuvent emprunter plusieurs voies d'analyse, mais une méthode statistique qui gagne en popularité est celle des fonctions de sélection des ressources (RSF). Les RSF permettent d'estimer la probabilité d'occurrence relative des individus à l'intérieur d'un paysage hétérogène (Manly et al., 2002). Cette méthode est basée sur une comparaison entre les caractéristiques de l'environnement aux endroits où l'animal a été localisé avec celles à des points aléatoires lancés dans l'environnement à l'intérieur d'un domaine spatial particulier (Boyce, 2006). Les RSF sont particulièrement utiles pour étudier le rôle de l'échelle spatiale dans le processus de sélection de l'habitat, car ils offrent un cadre d'analyse qui permet de faire le lien entre les différentes échelles spatio-temporelles utilisées (Boyce, 2006). Par contre, il est très important de bien identifier les échelles spatiales à considérer et de choisir celles qui sont le plus appropriées pour l'espèce étudiée, car le choix de l'échelle spatiale aura une grande influence sur la quantification des attributs de l'habitat (Boyce, 2006). Ainsi, les ressources considérées comme étant disponibles pour un individu varieront selon le domaine spatial considéré. L'étendue spatiale utilisée pour définir une échelle particulière aura donc une grande influence sur notre compréhension de la sélection de l'habitat par les animaux.

Plusieurs approches statistiques utilisées dans l'étude de la sélection des ressources considèrent souvent un nombre plutôt restreint de composantes de l'habitat (e.g., McClean et al., 1998; Morris, 1996; Aebischer et al., 1993). L'utilisation des RSF pour définir le rôle de l'échelle spatiale dans le processus de sélection de l'habitat permet de tenir compte de la complexité souvent inhérente aux habitats en milieu naturel (Boyce et McDonald, 1999; Boyce et al., 2003). En utilisant les RSF, il est possible de considérer l'effet simultané d'une multitude de variables environnementales (e.g., proportion de chaque type de couvert, densité des routes, pente, élévation, profondeur du couvert de neige, abondance de nourriture, taille de groupe), afin d'identifier celles permettant le mieux d'expliquer la répartition des individus à chacune des échelles spatiales. De plus, les RSF peuvent être utilisées avec un Système d'Information Géographique (GIS) pour cartographier la probabilité d'occurrence des individus à travers l'aire d'étude (Johnson et al., 2004b; Boyce et McDonald, 1999; Boyce et al., 2003; Nielsen et al., 2003) et, dans une certaine mesure, d'anticiper la répartition des animaux en fonction de la variation des variables de l'environnement (Carroll et al., 2003). Utilisées dans cette optique, les RSF représentent un outil intéressant pour la gestion et la conservation de la faune.

La hiérarchie de la sélection de l'habitat

La relation existant entre les différents facteurs de sélection à chacune des échelles spatiales a fait l'objet de nombreuses recherches (Senft et al., 1987; Morris, 1992b; Rettie et Messier, 2000; Johnson et al., 2002a; Fortin et al. 2003; McLoughlin et al., 2004). Certaines études ont tenté de montrer que le patron de sélection de l'habitat à travers les différentes échelles spatiales reflétait la hiérarchie existant entre les facteurs de sélection (Johnson et al., 2001; Mosnier et al., 2003; Dussault et al., 2005). Chez les grands herbivores, il a été suggéré que les facteurs abiotiques, telles que la pente, la distance à un point d'eau et la densité du couvert de neige, influencent davantage la sélection de l'habitat à vastes échelles spatiales, alors qu'à plus fines échelles, la répartition des individus dépend principalement de facteurs biotiques, comme la qualité et la quantité de végétation (Senft et al., 1987; Bailey et al., 1996). Ainsi, il semble que l'importance relative de l'interaction plante-herbivore dans le processus de sélection de l'habitat diminue de fines à vastes échelles spatiales (Fortin et al., 2003). Une étude a toutefois montré que, contrairement à ces prédictions, les facteurs abiotiques (e.g., le couvert de neige) et biotiques (e.g., la disponibilité de la nourriture et le risque de prédation) pouvaient avoir une influence majeure sur le processus de sélection à une variété d'échelles spatiales (Dussault et al., 2005).

Chez les espèces grégaires, l'étude de la sélection de l'habitat à plusieurs échelles spatiales est d'autant plus complexe car les variations dans l'abondance des individus peuvent influencer leur patron de répartition spatiale (McNamara et Houston, 1992; Cresswell, 1994; Hebblewhite et Pletscher, 2002). Plusieurs études se sont penchées sur l'effet de la compétition intraspécifique sur la sélection de l'habitat (e.g., Morris, 1989; Mitchell et al., 1990; Dolman et Sutherland, 1997; Mysterud et Ims, 1998; Shenbrot, 2004). Par contre, peu d'entre elles ont exploré ce sujet en tenant compte de la complexité structurale de l'environnement, c'est-à-dire en tenant compte à la fois de l'ensemble des composantes de l'environnement (e.g., routes, forêt de conifère, eau, pré) et de la disposition spatiale de ces dernières (e.g., densité, proportion). De plus, lorsqu'elles considéraient cette complexité, ces études omettaient souvent de voir la sélection de l'habitat comme un processus s'effectuant à plusieurs échelles spatiales (e.g., McLoughlin et al., 2006). L'influence des variations dans la taille du groupe sur la répartition des individus à différentes échelles reste donc méconnue.

Population à l'étude

Le parc national de Prince Albert (Saskatchewan, Canada) abrite l'une des rares populations sauvages de bisons des plaines. La population est aujourd'hui estimée à près de 400 individus (Parcs Canada, *données non publiées*), et est composée de plusieurs groupes de taille variable. Puisque le parc national de Prince Albert n'est pas délimité par des clôtures, il arrive parfois que les bisons sortent des frontières du parc pour aller sur les terres agricoles avoisinantes où ils créent plusieurs perturbations (e.g. bris de clôtures, dommages aux cultures). En côtoyant de si près les bisons et les bovins d'élevage, les bisons sauvages s'exposent aussi à la transmission de maladies. De plus, lorsqu'ils traversent les frontières du parc national, les bisons se trouvent confrontés à un risque de chasse élevé, car en dehors des limites du parc, les autochtones de la région peuvent chasser librement le bison. Ces problèmes risquent de s'intensifier avec l'augmentation des effectifs de cette population qui a plus que triplée au cours des 10 dernières années (Parcs Canada, *données non publiées*). Les biologistes et gestionnaires du parc national de Prince Albert désirent donc élaborer un plan d'aménagement qui permettra de diminuer les escapades des bisons au-delà de la frontière du parc, tout en préservant le plus possible l'intégrité du paysage. La mise en place de telles mesures prend d'autant plus d'importance depuis mai 2004, alors que le Comité sur la Situation des Espèces en Péril du Canada (COSEPAC) a suggéré que les populations sauvages de bisons des plaines, telles que celle du parc national de Prince Albert, étaient menacées au pays. Identifier les facteurs influençant la répartition des bisons des plaines à plusieurs échelles spatiales fournirait donc des connaissances essentielles à la mise en place d'un plan de gestion et permettrait d'identifier les zones principales où les actions sont plus susceptibles d'être efficaces.

Une étude a déjà été réalisée sur cette population de 1996 à 1999 (Fortin, 2000). Certains éléments concernant le comportement de sélection des ressources par le bison des plaines ont été mis en évidence grâce à ce projet, mais plusieurs aspects de l'écologie de l'espèce susceptibles d'expliquer la répartition spatiale des individus demeurent inexplorés. En fait, l'influence de l'abondance des individus sur les compromis à la base de la sélection de l'habitat à plusieurs échelles spatiales n'a toujours pas été étudiée. D'ailleurs, cet aspect de l'écologie animale demeure relativement peu étudié pour l'ensemble des grands mammifères.

Objectifs de l'étude

L'étude a pour but principal de déterminer dans quelle mesure des changements dans la taille du groupe influencent la sélection des ressources à plusieurs échelles spatiales chez le bison des plaines. Il a souvent été montré que la répartition spatiale des individus est le reflet des compromis entre les différents facteurs de l'environnement (Mysterud et Ims, 1998; Rettie et Messier, 2000; McLoughlin et al., 2004). L'approche utilisée se base donc sur les compromis entre les gains énergétiques, les dépenses énergétiques associées à l'acquisition des ressources et le risque de prédation, puisque ces facteurs sont connus pour influencer la sélection de l'habitat par les grands herbivores (Boyce et al., 2003; Dussault et al., 2005; Fortin et al., 2005a; Mao et al., 2005; McLoughlin et al., 2006). En plus d'identifier explicitement les variables affectant la répartition spatiale des bisons, cette étude vise surtout à clarifier dans quelle mesure l'abondance des individus influence les compromis à la base de la sélection de l'habitat à une variété d'échelles spatiales.

Pour atteindre cet objectif, la sélection de l'habitat par le bison des plaines a été analysée à l'aide de RSF à trois échelles spatiales, chacune étant associée à une étendue spatiale distincte. De l'étendue la plus vaste à la plus fine on reconnaît (1) le parc, (2) un cercle centré sur chaque localisation GPS et dont le rayon est de 700 mètres et (3) le pré. Afin d'étudier la sélection de l'habitat à vastes échelles spatiales (i.e., étendues 1 et 2), neuf bisons ont été capturés dans le parc national de Prince Albert et équipés de colliers GPS. La position de chaque animal était ainsi enregistrée à intervalle de trois heures et la taille du groupe de chacune de ces femelles a été déterminée en moyenne 10 fois au cours de l'été 2005 et sept fois à l'hiver 2006. Pour étudier la sélection à notre échelle la plus fine, la position des bisons à l'intérieur des prés a été déterminée à l'aide d'observations comportementales.

La population de bisons des plaines du parc national de Prince Albert est en croissance démographique depuis leur établissement dans le parc en 1969. En définissant le parc comme échelle spatiale, il est alors possible d'utiliser un GIS pour connaître les zones susceptibles d'être utilisées par une population en expansion. De plus, cette échelle permet de connaître les facteurs qui ont poussé les bisons à établir leur aire de répartition dans la partie sud-ouest du parc. Cette échelle spatiale est sans aucun doute essentielle à la compréhension de la sélection de l'habitat par le bison des plaines, ainsi qu'à la gestion de cette population. L'échelle définie par un cercle centré sur chaque localisation GPS a été déterminée à partir des mouvements effectués par les bisons équipés d'un collier GPS. Le rayon de 700 m correspond à 80% des distances observées entre deux localisations (i.e., intervalle de 3 heures) GPS successives au cours de la période estivale (Boyce et al., 2003). Les analyses effectuées à cette échelle permettent de comprendre les facteurs qui influencent le mouvement des animaux à travers l'habitat (Johnson et al., 2002a). Finalement, puisque les bisons s'alimentent principalement à l'intérieur des prés (Fortin et al., 2003), cette dernière échelle (i.e., le pré) permet d'identifier les communautés végétales influençant la répartition des bisons et de comprendre l'effet des caractéristiques abiotiques du pré sur la répartition des individus à fine échelle spatiale.

Chapitre principal

GROUP SIZE EFFECTS ON MULTI-SCALE HABITAT SELECTION BY PLAINS BISON

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Résumé

Les effets de la taille du groupe sont généralement négligés dans les études portant sur la sélection de l'habitat à plusieurs échelles spatiales par les grands herbivores. Au cours de cette étude nous avons évalué dans quelle mesure la sélection de l'habitat par le bison des plaines (*Bison bison bison*) du parc national de Prince Albert (Saskatchewan, Canada) était influencée par la taille du groupe à différentes échelles spatiales. Au cours de l'été 2005 et l'hiver 2006, nous avons étudié la sélection de l'habitat à trois échelles spatiales représentées par trois étendues spatiales distinctes (i.e., le parc, un cercle de 700 m de rayon centré sur chaque localisation de bison et le pré). Aux deux plus vastes échelles spatiales, la localisation de neuf femelles équipées de colliers GPS a été déterminée à toutes les trois heures, et l'habitat a été caractérisé à partir d'un Système d'Information Géographique. À la plus fine échelle spatiale, la localisation des bisons a été déterminée à l'aide d'observations visuelles, et les ressources ont été caractérisées à la suite d'inventaires aux sites utilisés par les bisons et à des sites localisés aléatoirement à l'intérieur des prés. La sélection de l'habitat par le bison à chacune de nos trois échelles spatiales a été étudiée à l'aide de fonctions de sélection des ressources. Nos résultats suggèrent que la répartition spatiale des bisons peut être largement expliquée par les compromis qui existent entre la disponibilité des ressources, les coûts de déplacement et le risque de prédation. Par exemple, à l'échelle du parc, les bisons sélectionnaient généralement les endroits composés d'une grande proportion de prés et d'une importante densité de bordures (celles-ci augmentent les possibilités de fuite contre les prédateurs), en plus d'éviter les secteurs fortement enneigés. La nature des compromis entre les différents facteurs de sélection peut toutefois varier en fonction de la taille du groupe, et les animaux peuvent répondre à ces changements en modifiant leur utilisation de l'habitat. Par exemple, plus la taille du groupe augmentait, moins la densité de bordures dans l'environnement devenait un facteur important dans le processus de sélection à vastes échelles spatiales, et plus la sélection sur la plante la plus profitable (i.e., *Carex atherodes*) diminuait lors de l'activité d'alimentation à l'intérieur du pré. La sélection des ressources est donc un processus dépendant de l'abondance des individus à plusieurs

échelles spatiales. Notre étude démontre ainsi l'importance de tenir compte à la fois de l'échelle spatiale et de la taille du groupe lors d'investigation sur la sélection de l'habitat.

Abstract

Group size effects are generally overlooked in the assessment of multi-scale habitat selection by large herbivores. We evaluated whether habitat selection by plains bison (*Bison bison bison*) in Prince Albert National Park (Saskatchewan, Canada) was influenced by group size at multiple spatial scales. During summer 2005 and winter 2006, we evaluated habitat selection at three spatial scales based on distinct spatial extents (i.e., from the broadest to the finest scale: park, buffer with a radius of 700 m centred on each bison location, and meadow). At the two broadest scales, bison distribution was determined by locating nine females equipped with GPS collars every 3 hours, and habitat was characterised from a Geographic Information System. At the finest scale, bison locations were determined from behavioural observations, and resources were characterised from field surveys. Habitat selection of bison was evaluated using resource selection functions. Our results showed that the spatial distribution of bison could be largely explained by trade-offs between resource accessibility, costs of locomotion and predation risk. For example, at the park scale, bison generally selected areas surrounded by a large proportion of meadows and a high density of edges (which are commonly used to flee predators), and they tended to avoid sites with more snow cover. The nature of the trade-offs between limiting factors should also vary with group size, and individuals should respond to such changes by altering patterns of habitat selection. Consistently, as group size increased, the selection for areas with high edge density decreased at broad scales, while the selection for the most profitable plant (i.e., *Carex atherodes*) decreased within meadows. Overall, we found that resource selection was a process that depended on group size at every scale. Our findings stress the importance of considering multiple spatial scales and group size effects in habitat selection studies.

Introduction

Resource selection is a central behavioural mechanism leading to animal distribution. Knowledge of resource selection is essential to understand the spatio-temporal dynamics of animal populations in heterogeneous landscapes. Habitat selection must be viewed as a hierarchical process that implies selection or avoidance of environmental components at different spatial scales (Johnson et al., 1980; Rettie and Messier, 2000; Johnson et al., 2002a; Boyce et al., 2003; Mosnier et al., 2003; Johnson et al., 2004b; McLoughlin et al., 2004). Consideration of scales is indeed essential for understanding resource selection because the response of animals to habitat attributes can vary among scales (Schaefer and Messier, 1995a; Dussault et al., 2005; Boyce, 2006). For example, abiotic factors (e.g., snow, slope and distance to water) are believed to be the primary determinants of the distribution patterns of large herbivores at broad scales (Bailey et al., 1996), whereas biotic factors (e.g., spatio-temporal patterns of plant distribution) have the greatest influence on herbivore distribution at fine scales (Senft et al., 1987; Fortin et al., 2003). On the other hand, the distribution of large herbivores may also be influenced by abiotic and biotic factors at many scales (Dussault et al., 2005). Despite an increasing number of studies on resource selection at multiple scales (e.g., Johnson et al., 2002b; Boyce et al., 2003; Chamberlain et al., 2003; Nikula et al., 2004; Marell and Edenius, 2006; Morin et al., 2006), the hierarchical nature of habitat selection remains unclear.

Animals may pursue different goals at different spatial scales (Senft et al., 1987; Bailey et al., 1996; Boyce et al., 2003), and the spatial distribution of animals at various scales should reflect trade-offs among several limiting factors (Mysterud and Ims, 1998; Rettie and Messier, 2000; McLoughlin et al., 2004). Energy gain and predation risk are two major considerations that influence habitat selection by animals (Gilliam and Fraser, 1987; Lima and Dill, 1990; McNamara and Houston, 1990). Foragers should select optimal food items or foraging sites that offer the highest energy gain (Bergman et al., 2001; Fortin et al., 2002). For example, the plains bison (*Bison bison bison*) of Prince Albert National Park select *Carex atherodes*, a selection that maximises their short-term rate of energy gains (Fortin et al., 2002). However, in response to predation risk, most foragers must balance food and safety by selecting landscape areas that not only provide high quality forage, but also good protection from predators (Brown and Kotler, 2004; Dussault et al., 2005). For many herbivores, cover types offering the highest availability of food are often relatively risky (Mysterud and Østbye, 1995; Mysterud and Ims, 1998; Altendorf et al., 2001; Fortin et al., 2005a). An increase in the distance to areas providing safety from predators is often associated with a gradual intensification of predation risk (Blumstein and Daniel, 2003; While and McArthur, 2005), with the consequence that, to diminish risk, moose (*Alces Alces*) (Edwards, 1983), guinea pigs (*Cavia aperea*) (Cassini and Galante, 1992), red-bellied pademelons (*Thylogale billiardieri*) (While and McArthur, 2005) and tammar wallabies (*Macropus eugenii*) (Blumstein and Daniel, 2002), tend to forage close to a protective cover. In fact, the transition zone between two cover types are commonly considered as a landscape feature where a change in predation risk occurs (Altendorf et al., 2001; Dussault et al., 2005; Hermàndez et al., 2005; Bergman et al., 2006). Escape possibility offered by the hard edges delimiting open and forest areas thus may represent a significant habitat attribute, particularly for herbivore species foraging within open areas (Hermàndez and Laundré, 2005; Ripple and Beschta, 2006), because forests are known to provide greater safety (Blumstein and Daniel, 2003; While and McArthur, 2005). Researches have also shown that ungulates may display anti-predator behaviours irrespective of whether the predator is present (Molvar and Bowyer, 1994; Hirth, 1997; Bleich, 1999). Thus, habitat selection by ungulates (e.g., plains bison) may reflect trade-off involving predation risk, even when predators are not present in the environment.

While balancing food intake and safety, large herbivores also have to account for energy costs of foraging (Dussault et al., 2005; Fortin et al., 2005b; Mao et al., 2005; Poole and Mowat, 2005). Landscape features such as road, slope and snow cover, are known to influence the travel and foraging costs of large herbivores (Parker et al., 1984;

Fortin et al., 2005; Mao et al., 2005; Bruggeman et al., 2006). For example, snow negatively affects the movements and feeding efficiency of herbivores (Parker et al., 1984; Telfer and Kelsall, 1984; Fancy and White, 1987; Fortin et al., 2005b), with the consequence that the avoidance of deep or dense snow has been reported for multiple herbivores species at various spatial scales (VanCamp 1975; Boyce et al., 2003; Fortin, 2003; Dussault et al., 2005; Mao et al., 2005). Individuals thus seek areas offering high food availability and favourable snow conditions (Fortin, 2003; Fortin et al., 2005b). The importance of a trade-off between resource accessibility and energy expenses has been further demonstrated through the selection of foraging areas near water by large herbivores (McHugh, 1958; Bailey et al., 1996; Fisher and Gates, 2005).

In addition to being a multi-variable and multi-scale phenomenon, habitat selection is also a process that depends on the presence of conspecifics (Fretwell and Lucas, 1970; Rosenzweig, 1980; WallisDeVries, 1996). Influential ecological theories such as ideal free distribution (Fretwell and Lucas, 1970) and isodars (Morris, 2003) are based on the principle that animals achieve their distribution by selecting habitats in a way that would maximize individual fitness, and that fitness decreases with competitor density. Field observations confirm the potential for density-dependent effects on fitness. For example, life time reproductive success of female elk (*Cervus elaphus*) is positively linked to food selection and negatively affected by competitor density (McLoughlin et al., 2006). Reproductive benefits of selecting high quality forage in *Agrostis/Festuca* grassland would decrease with increasing elk density (McLoughlin et al., 2006). The presence of conspecifics can not only influence foraging decisions (Sutherland, 1983), but it may also alter predation risk. Dilution effects and collective scanning provide higher protection from predators for large than small groups of prey (Abramson, 1979; Dehn, 1990; Lima, 1995; Roberts, 1996). Group size thus can have direct effects on the nature of the trade-off between acquiring food and avoiding predators. Under circumstances where there is spatial segregation between food-rich and safe locations, individuals in small groups should be most likely to select safe areas (e.g., with high escape possibilities) at the expense of rich areas, because they are more at risk than individuals in large groups.

Overall, habitat selection is often a complex process that involves decisions influenced by multiple scale-dependent needs and constraints. Therefore, studies that account for such complexity might be more efficient at gaining knowledge about the influence of habitat selection on animal distribution and population dynamics in heterogeneous landscapes. Fortunately, an increasing number of statistical methods and technological tools (e.g., global positioning system, GPS; geographic information system, GIS) now facilitate the integration of habitat complexity at multiple scales in resource selection analysis, while still explaining observed patterns with parsimony. Despite important advances in habitat selection analysis (Manly et al., 2002; Boyce, 2006), few studies have explored the effect of group size on multi-scale habitat selection in complex landscapes.

Here we investigated whether habitat selection by plains bison was influenced by group size at multiple spatio-temporal scales. To achieve this objective, nine female plains bison were captured in Prince Albert National Park (Saskatchewan, Canada), and equipped with GPS-collars. Group size of these females was regularly determined, and this information was considered when relating bison distribution to environmental covariates obtained from a GIS for both summer and winter. We also conducted field observations and meadow surveys to evaluate foraging and resting site selection by plains bison within meadows. Our overall intent was to evaluate whether group size effects on habitat selection could be explained by trade-offs between the needs and constraints faced by bison at various scales.

Methods

Study area

The study was conducted in summer 2005 (May 20th to August 20th) and winter 2006 (January 16th to March 12th) in the Prince Albert National Park (Saskatchewan, Canada), which covers an area of 3875 km^2. The park harbours one of the few free-ranging populations of plains bison. The population was estimated at 350 individuals in 2005 and 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 deciduous and boreal forests (85 %), water (5 %) and meadows (10 %) (Fortin et al., 2003). Over 170 plant species can be found within these meadows, with the most abundant plants being: *Carex atherodes*, *Carex aquatilis*, *Agropyron* spp., *Calamagrostis inexpansa, Hordeum jubatum*, *Scolochloa festucacea* and *Juncus balticus* (Fortin et al., 2002). The bison range includes few roads that are accessible to park's staff and researchers, but generally not to visitors. Elk, white-tailed deer (*Odocoileus virginianus*), moose and caribou (*Rangifer tarandus*) are also present in the park, but resource competition with bison does not seem important (Fortin et al., 2003). A wolf (*Canis lupus*) population is established in the park, and predation on bison was observed sporadically during our study.

GPS collared bison

The distribution of bison was determined by following nine adult females that were equipped with GPS-collars (GPS collar 4400M from Lotek Engineering, Newmarket, Ontario, Canada) taking locations at a 3-hour interval. In March 2005, bison were captured throughout the bison range using chemical immobilization administered using darts fired from a rifle by a shooter within a helicopter. GPS collars were equipped with a VHF beacon, which facilitated the relocation of individuals to determine group size.

Spatial scales

Habitat selection by plains bison was studied at three spatial scales for which changes in the trade-offs among limiting factors might occur for large herbivores (Boyce et al., 2003; Fortin et al., 2003). Each of these scales was associated with a specific spatial extent used to define resource availability (Boyce et al., 2003). From broadest to finest scale, we recognized: (1) the park scale, (2) the 700-m buffer scale, and (3) the meadow scale. The spatial extent associated with the park scale included the entire park together with an area going 5 km south and 5 km west of the park. The park scale should expose factors associated with bison establishment in the southwest portion of the park, as well as potential suitable areas for range expansion. The 700-m buffer scale was linked to a spatial extent that included the area covered by fixed-size circular plots (700 m radius) centered on each GPS location of collared bison. The 700-m radius encompassed 80 % of the distances observed between two successive GPS locations (3-hour time interval) in summer, and 92 % in winter. The circle thus included the locations where bison could have reasonably travelled to during the time interval between successive locations (Arthur et al., 1996; Johnson et al, 2002a; Boyce et al., 2003). Compared to the park scale, analyses carried out at the 700-m buffer scale should inform on finer scale decisions because they should reveal a selection for habitat attributes that is contingent to nearby habitat attributes (Boyce, 2006). Finally, the meadow scale was associated with a spatial extent restricted to the area covered by meadows, which constitute prime foraging areas for plains bison (Fortin et al., 2003; Hermàndez and Laundré, 2005; Ripple and Beschta, 2006). Analyses conducted at the meadow scale should inform on the local characteristics of resting or foraging sites selected within meadows.

Sampling design

Park and 700-m buffer scales

At the two broadest scales (i.e., Park and 700-m buffer scales) resources used by bison were represented by habitat characteristics at each GPS location, and available resources were identified at random locations throughout the spatial extent associated with each scale. We used a classified TM image (year: 2001) to characterise habitat attributes (30 m × 30 m pixels). We also used a GIS layer from the Prince Albert National Park to characterise the road and trail network (including majors hiking trails). Overall, 18 landscape cover types were identified and boiled down into: Meadow (including areas near lakes and rivers dominated by grasses, forbs and sedges), Riparian area (i.e., areas near rivers largely comprised of shrubs), Deciduous forest, Conifer forest, Mixed forest, Agricultural land, Open water, and Road.

Snow survey

Snow conditions were characterised across the landscape based on a snow model developed during winter 2006. The model enabled us to quantify local snow conditions throughout the Park's greater ecosystem from snow characteristics in sampled open areas (i.e., meadows) and the influence of forest type on snow accumulation. To build the snow model, we evaluated snow conditions in 18 meadows throughout the bison range. These open sites were used to evaluate local snow conditions. We also quantified how forest cover types influenced local snow characteristics. We sampled 28 forest areas clustered into three categories: deciduous forests (n = 11), mixed forests (n = 9) and conifer forests (n = 8). Open sites were sampled four times (i.e., survey 1: January 20th to January 22th, survey 2: February 2nd to February 3th, survey 3: February 17th to February 19th, survey 4: March 7th to 10th), and forest stations were sampled twice (i.e., survey 1: February 17th to February 19th, survey 2: March 7th to 10th). Two snow surveys in forest areas where sufficient to determine the influence of cover types on local snow conditions in the vicinity of open areas. At each open site, snow was sampled at eight locations along a 70-m transect. For each forest site, snow was sampled at five locations along a 40-m transect. Snow was characterised by its depth and density. Snow density (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 dividing the mass by the volume of snow gathered. Following Turner et al. (1994), we calculated the snow water equivalent (SWE) (cm) from the product of snow depth (cm) and density (proportion, where 1 g/cm^3 corresponded to a proportion of 1).

Snow conditions evaluated at the forest and open sites were used to create a predictive model for snow water equivalent across the landscape. We used a multiple regression model to relate snow water equivalent at forest sites to: (1) elevation, which was a continuous variable (m); (2) forest type, which consisted in two dummy variables (one for each of deciduous and mixed forest stands), with conifer stands being used as the reference category; (3) the period of forest site survey, which took the form of a dummy variable with the first survey serving as the reference category; and (4) the snow water equivalent averaged among all open sites (SWE_{stn}). SWE_{stn} (cm) is intended to reflect the local snow conditions during a given survey of open sites; SWE_{stn} is weighted based on the distance between the site where we wish to estimate snow water equivalent and all open sites:

$$SWE_{stn} = \frac{\sum_{i=1}^{18}\left(OSWE_i \times \frac{1}{\sqrt{dist\,(km)_i}}\right)}{\sum_{i=1}^{18}\left(\frac{1}{\sqrt{dist\,(km)_i}}\right)},$$

where $OSWE_i$ is the snow water equivalent (cm) at open site i, and $dist(km)_i$ is the distance (km) from open site i. Because the survey period (i.e., variable 3 above) was not significant in the multiple regression model ($P = 0.64$), we pooled the two forest survey periods to build a general snow model. We found that the local snow water equivalent at forest sites followed: $SWE = -8.72 + 4.03\times\text{deciduous} + 1.98\times\text{mixed} + 0.014\times\text{elevation} + 0.79\times SWE_{stn}$ ($R^2 = 0.74$). Each of these variables was significant at $P < 0.0015$. To assess the robustness of our snow modeling approach, we used a cross validation method where we built a regression model from 90 % of the original dataset, and then try to predict the SWE for the remaining dataset (Turney, 1993). This process was done 10 times, and the relationship between observed and predicted estimates had an overall $\overline{R^2} = 0.76$. Our snow model was thus used to estimate snow conditions throughout the park using each of our four surveys of open sites. SWE calculated based on surveys 1 to 4 were associated, respectively, to four periods: 10th January to 30th January, 31st January to 13th February, 14th February to 4th March, and 5th March to 19th March.

Meadow scale

Animal locations

At the meadow scale, bison locations were determined from visual observations of individuals foraging and resting within meadows. For each observed herd, we recorded group size, and identified the sex and the age (i.e., red calf, brown calf, yearling, sub-adult, and adult) of each bison within the group. Bison were considered in the same group when they were at a distance < 100 m (Green, 1992; Fortin et al., 2003). We randomly chose animals that were either resting or foraging and, with a spotting scope, we determined their location based on landmarks.

Habitat sampling

The day following behavioural observations, we sampled habitat covariates at animal locations. In summer, we sampled three quadrats of 0.25 m^2 at each observed location, and considered a mean value of local characteristics for that animal. The position of focal bison could be determined with greater accuracy in winter than in summer because of snow tracks in the snow at foraging and resting sites. Thus, local characteristics were determined in a single 0.25 m^2 quadrat, 30 cm away from the foraging or resting site (as Fortin et al., 2003). In winter, to estimate resource availability within the meadows where the observations took place, we surveyed 15 or 40 quadrats, depending on meadow area. For both seasons, we estimated the total dry biomass of vegetation and the percent of total dry biomass represented by various plant groups (i.e., *Carex atherodes*, *Carex* spp. [excluding *C. atherodes*], *Agropyron* spp., *Calamagrostis inexpansa, Scolochloa festucacea*, all other *Grasses,* all *Forbs*, and all other plants within the quadrat). In each quadrat, we also recorded slope and water depth or snow conditions, depending on the season.

Plant characteristics

In summer, total dry biomass (g/0.25 m^2) was estimated by measuring the height from the ground (cm) that a calibrated plastic square placed on the vegetation settled (Vartha and Matches, 1977). The relationship followed: $\textit{dry biomass} = -8.78 + 1.62 \times \textit{height}$, ($R^2 = 0.80$, $F = 426.45$, $P < 0.0001$, $n = 107$). This calibration was done by collecting and drying at 60°C for 48 to 60 hours all above-ground vegetation present in quadrats. These samples were then sorted by species, and used to calibrate a visual estimation of the percent of total dry biomass comprised of different groups of plants. The calibration of the visual estimation followed: $\textit{percent biomass} = 0.077 + 0.74 \times \textit{visual estimate}_{observer1}$ ($R^2 = 0.84$, $F = 711.26$, $P < 0.0001$, $n = 136$) for the first observer and

$percent\ biomass = 2.15 + 0.88 \times visual\ estimate_{observer2}$ ($R^2 = 0.89$, F = 525.45, $P < 0.0001$, n = 65) for the second observer.

In winter, because the focal animals disturbed snow directly at foraging and resting sites, snow was estimated 30 cm from the actual observed locations (as Fortin, 2003 and Fortin et al., 2003). From a visual assessment, we insured that the vegetation community was similar between the observed locations and where the measures were actually taken. Snow water equivalent was estimated based on the product of snow density and snow depth. Throughout the winter, each of the two observers estimated the total dry biomass (g/ 0.25m^2) of vegetation from a 0-10 visual scale, according to the regressions: $dry\ biomass = -10.669 + 13.297 \times visual\ estimation_{observer1}$ ($R^2 = 0.78$, F = 363.15, $P < 0.0001$, n = 101), $dry\ biomass = -23.69 + 27.03 \times visual\ estimation_{observer2}$ ($R^2 = 0.89$, F = 706.98, $P < 0.0001$, n = 86). Visual estimations of the percent of total dry biomass of each group of plants were also calibrated for each observer: $percent\ biomass = 8.42 + 0.70 \times visual\ estimate_{observer1}$ ($R^2 = 0.82$, F = 554.71, $P < 0.0001$, n = 126), and $percent\ biomass = 3.63 + 0.89 \times visual\ estimate_{\mathrm{observer2}}$ ($R^2 = 0.77$, F = 124.17, $P < 0.0001$, n = 38). These calibrations were done by clipping the above-ground vegetation in 0.25 m^2 quadrats, drying samples at 60 °C, and weighting plants after 48 hours of drying.

Habitat characteristics within the bison range

During the summer of 2005, we conducted extensive surveys in open and forest areas located throughout the bison range. This information was used to obtain a general assessment of food availability within the major habitat cover types found across the bison range (i.e., deciduous forest, conifer forest, meadow). In each meadow (n = 83), vegetation was characterised in 15 to 40 randomly located quadrats (0.25 m^2), depended on meadow size. The vegetation in forest sites (deciduous stands, n = 30; conifer stands,

$n = 17$) was evaluated in 5 randomly located quadrats of 0.25 m^2. Vegetation was characterised as previously outlined (see *Habitat sampling*).

Statistical models of habitat selection

Habitat selection by plains bison was studied using resource selection functions (RSF). An RSF is defined as any statistical function that gives a measure proportional to the probability of resource use by an animal (Manly et al., 2002). RSFs were estimated by comparing habitat characteristics at animal locations with characteristics at random locations drawn within our three specific spatial extents. Resource units at animal locations were scored 1, whereas units at random locations were scored 0 (Manly et al., 2002). To create RSF models, we assume a particular function between the relative probability of use (w), and a vector of *n* predictor variables, **x** (Boyce et al., 2002):

$$w_{(\mathbf{x})} = \exp(\beta_1 x_1 + \beta_2 x_2 + \ldots + \beta_k x_k)$$

where $x_{1\ldots k}$ are independent habitat variables, and $\beta_{1\ldots k}$ are selection coefficients estimated using logistic regression (Arthur, 1996; Boyce et al., 2002; Manly et al., 2002). $\beta_i > 0$ reflects selection for habitat attribute *i* (i.e., a larger proportion of locations are associated with attribute *i* compared to random expectations), whereas $\beta_i < 0$ reflects relative avoidance.

At the park and 700-m buffer scales, we used the GIS to characterise habitat at used and available locations, whereas at the meadow scale those locations were characterised from ground surveys. We built candidate RSFs at each of our three spatial scales for the summer and winter seasons. Variables considered in RSFs were chosen from previous research. Candidate RSF models were created based on variables that could influence the trade-off between costs and benefits of selection, at each scale, and in regard to group size effect. Prior to calculating RSFs, we screened predictor variables for colinearity, and independent variables included in RSFs were not strongly correlated (i.e., $r < 0.5$).

Independent covariates used in broad scale analyses (park and 700-m buffer scales) were: a set of dummy variables representing 7 land cover types (i.e., meadow, riparian, deciduous forest, conifer forest, agricultural land, water, and road) with deciduous forest being used as the reference category, the proportion of the different cover types found within a 700 m radius centered on each location, density of hard edges (km/km^2) within a 700 m radius, distance to the nearest water point (m), slope (^{o}), and SWE (cm). At the meadow scale, independent variables considered in RSFs were: proportion of total dry biomass comprised of each plant groups (i.e., *Carex atherodes*, *Agropyron* spp., *Calamagrostis inexpansa, Scolochloa festucacea,* and all *Forbs*), slope (^{o}), water depth (cm), a dummy variable representing the presence or absence of water, SWE (cm), and distance to forest edge (m). Plant groups used in RSFs are the most common plants in the park. Variables included in candidate RSF models at each of our three spatial scales are summarized in Table 1.

Table 1. Description of the variables used in candidate RSF models.

Variable	**Description (units)**
g	Group size
SWE	Snow water equivalence (cm)
snow	$SWE + SWE^2$
hwater	Water depth (cm)
distwat	Distance to water (m)
slope	Slope (°)
distforest	Distance to forest edge (m)

dedge	Density of hard edges in a radius of 700 m (km/km^2)
water	Water
road	Road
meadow	Meadow
deciduous	Deciduous forest
conifer	Conifer forest
pmead	Proportion of meadows in a radius of 700 m
pagri	Proportion of agricultural lands in a radius of 700 m
caat	Percentage of total dry biomass of *Carex atherodes* in a quadrat of 0.25 m^2
cain	Percentage of total dry biomass of *Calamagrostis inexpensa* in a quadrat of 0.25 m^2
agro	Percentage of total dry biomass of *Agropyron* spp. in a quadrat of 0.25 m^2
scfe	Percentage of total dry biomass of *Scolochloa festucacea* in a quadrat of 0.25 m^2
forbs	Percentage of total dry biomass of all *forbs* in a quadrat of 0.25 m^2

Park scale

At the park scale, we built RSFs using mixed model of logistic regressions (Gillies et al., 2006). We took into account the non-independence among the observations of a given bison by considering "individual" as a random effect. During winter, because maps of SWE varied for each of the four snow surveys of open sites (i.e., the winter was characterised using four snow maps, each associated with a specific winter period), random effects became nested (i.e., animal within winter period), which allowed for the use of a single analysis for the entire winter.

To assess whether habitat selection varied with group size, RSF were built for small (≤ 15 individuals) and large (> 15 individuals) herds. We considered a threshold of 15 individuals to discriminate between small and large bison groups because it insured that analyses were based on at least 100 observations for each group size category and each season. Composition of bison groups showed temporal variation. As a consequence, each time that group size was determined for each radio-collared bison, we assumed that group cohesion would remain for 24 hours; hence we associated all the GPS locations (i.e., 8 locations, given our 3-hour schedule) of that individual with that particular group size for that day. Field observations conducted within the park over the years indicate that this approach should be conservative (Fortin, M.-E. and Fortin, D., *unpublished data*). Because of our interest in group size effects, the analysis only considered GPS locations during the 24-hour periods where group size was determined, and other locations were dropped from the analyses. To build RSF models we used 515 bison GPS locations for small groups and 109 for large groups in summer, whereas we used 242 GPS locations for small groups and 125 for large groups in winter. To evaluate resource availability, we identified habitat characteristics at 4527 random locations (i.e., approximately a ratio of 5 random locations per bison GPS location, as Johnson et al., 2002a) throughout the park.

Given that RSFs are based on a comparison between used and available resources, and that, at the park scale, a single set of random locations was drawn (i.e., 4527 points) to characterise resource availability for both large and small groups, the comparison of used locations should inform on habitat covariates discriminating habitat selection by large and small bison herds. Therefore, to gain further insights into group size effects on habitat selection, we used a mixed model (random effect: animal in summer or animal nested within winter period in winter) of logistic regression to compare habitat characteristics at locations occupied by individuals when in a large versus a small group. Because RSFs at the landscape scale were based on mixed models of logistic regressions with nested random effects, we estimated models using "glmmPQL" available for R (R Development Core Team, 2006). With this approach, robust *P*-values can be calculated, but AIC estimates are biased. Therefore, model selection at the landscape scale was based on *P*-values, and final RSFs included only variables with $P \leq 0.05$.

700-m buffer scale

RSFs at the 700-m buffer scale were estimated using conditional logistic regression. Conditional logistic regression can account for temporal changes in the resource available to an animal by matching each used resource unit to a potentially different set of random resource units (Arthur et al., 1996). In our analysis, each GPS location was paired to 10 random locations drawn within a 700 m buffer radius. Because of the paired design used here, group size could be included directly in the RSF as an independent variable. Indeed, each observed location was associated with a given group size, which was then matched to a set of random locations that was accessible to that specific group. In contrast, we could not directly consider group size as an independent variable in our analysis at the landscape scale because each observed group was not assigned to the specific set of random points. Instead, all observed locations were compared to all random ones (as, e.g., Boyce et al., 2003).

We selected the most parsimonious RSF model based on the quasi-likelihood under independence criterion (QIC) value, as proposed by Pan (2001), which accounts for the autocorrelation in our observations. We also determined whether the parameter estimates (β) of the final RSF were different from 0. Because individuals were relocated every 3 hours, successive locations were not independent from one another. Such autocorrelation does not influence β values, but it biases their standard errors (Nielsen et al., 2002). Robust standard errors of RSF parameters can still be obtained using a robust sandwich estimate of the covariance matrix (Lin and Wei, 1989). The approach requires dividing observations into independent clusters. A cluster may consist of GPS locations that are autocorrelated, as long as GPS locations are independent between clusters (Wei et al., 1989). As indicated previously, our analyses were based on strings of locations gathered during 24 hour periods centered on the time that group size was determined for a particular individual. Because group size was determined approximately every 7 days in both seasons, and that we considered only data during those days, we were able to create independent clusters. Each cluster consists in a sequence of successive GPS locations for a given animal, during a period of 24 hours. We dropped all GPS data collected between two 24 hour periods where group size was estimated, creating statistically independent clusters. The females were generally independent, but a few pairs of radio-collared bison spent more than 10 % of their time together. When these females were together (i.e., < 100 m apart), we assumed that decisions were non-independent, and we thus assigned their GPS data to the same cluster. In the end, analyses were based on 4037 bison locations (9 females) grouped in 53 clusters in summer, and 6864 (9 females) animal locations in 40 clusters in winter. Effects of group size were included in our a priori models from interaction with other independent variables (see Table 1).

Meadow scale

We used conditional logistic regressions to build RSFs at the meadow scale. Conditional logistic regression at this scale ensured that behavioural observation events, plant phenology and snow cover characteristics, were taken into account when comparing used to available resources. Moreover, selection within a given meadow became contingent on local availability of resources. We assigned a set of random resource units to each observed bison based on the location and time of meadow used. When two focal bison used the same meadow at the same period of time, they were grouped in the same stratum and were assigned to the same set of random resource units. One stratum thus consisted in a set of observed locations that were matched with a single survey of random locations. Observations of foraging bison were grouped into 33 strata in summer and into 31 strata in winter, whereas observations on resting individuals formed 35 strata in summer and 30 strata in winter. Selection among a priori RSF models was based on Akaike's Information Criterion (AIC). Distinct RSF models were produced for foraging and resting individuals.

Results

Food availability among habitat cover types

Vegetation sampling conducted within the bison range in summer 2005 revealed that total dry biomass of vegetation (excluding shrubs and trees) was at least 3 times higher in meadows than in forest areas (Table 2). In forest sites, forbs were the most abundant group of plants. In open areas, *Grasses* and *Carex* spp. were the most abundant. Furthermore, *C. atherodes*, a plant species strongly selected by bison in summer and winter (Fortin et al., 2003), was more abundant in meadows than in forest areas. In fact, *C. atherodes* was never recorded in conifer forests. The average percent of total dry biomass of *C. atherodes* was 15.1 ± 1.8 % within meadows and 0.9 ± 0.4 % in deciduous forest.

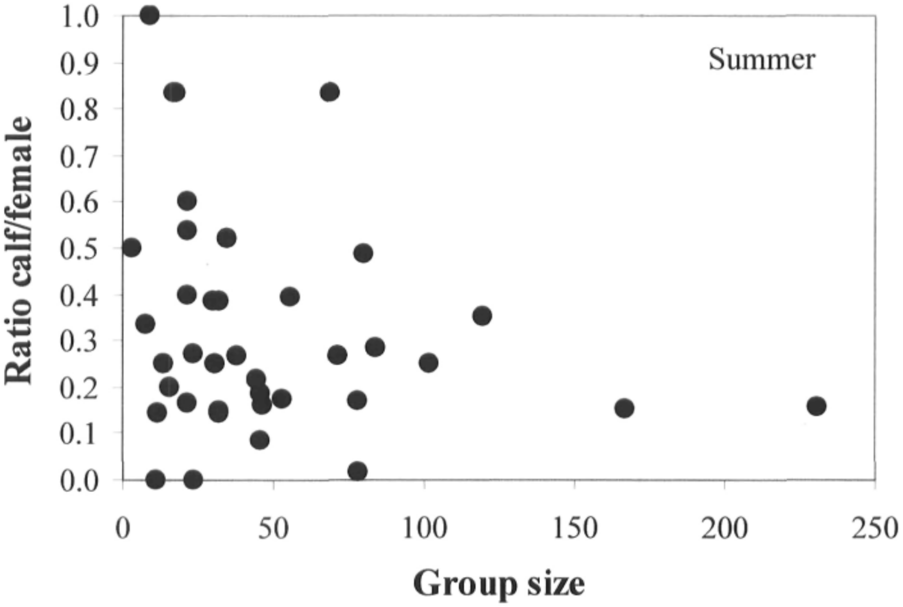
Table 2. Average total of dry biomass (g/m^2) and percent of total dry biomass of four plant groups found in quadrats (*n*) located in meadows and forest areas (i.e., deciduous and conifer) throughout the bison range in Prince Albert National Park in August 2005.

Type	***n***	**Total biomass**		***Carex* spp.**		***Grasses***		***Forbs***		**Others**	
		mean (g/m^2)	se	mean (%)	se	mean (%)	se	mean (%)	se	mean (%)	se
meadow	1470	308.7	8.0	31.6	2.7	33.6	2.1	27.6	2.3	7.8	1.2
deciduous	150	103.2	5.2	4.7	0.9	21.7	1.3	70.2	1.7	3.4	0.7
conifer	85	47.2	5.6	11.8	2.1	10.2	1.5	40.7	3.5	37.3	4.4

Characteristics of groups associated with radio-collared bison

Overall, 96.7 % of the scheduled GPS locations were successfully recorded among the nine radio-collared bison. Based on these locations, we calculated that the average time pairs of radio-collared females spent in the same group (i.e., inter-individual distance < 100 m) was 7.8 ± 0.9 % (mean ± se, n = 36 possible pairs among all 9 females) in summer and 2.5 ± 1.3 % in winter (n = 36). The distance between pairs of radio-collared bison averaged 3.3 ± 0.13 km (n = 36) in summer and 12.9 ± 1.0 km (n = 36) in winter.

Group size was determined for each collared female on average 10 times (range: 6-12 times/individual) in summer and 7 times in winter (range: 2-15 times/individual). Group size calculation considered a single observation when two of the 9 females were in the same herd. Overall, we found that group size of radio-collared bison averaged 44 ± 5 individuals (range: 3-231, n = 51) in summer and 14 ± 1 (range: 3-40, n = 49) in winter. The average proportion calf/female within the groups associated with the collared females was 0.36 ± 0.04 (range: 0-1, n = 37) in summer and 0.32 ± 0.02 (range: 0-0.5, n = 22) in winter. The proportion calf/female was independent from group size in winter (β = 0.0071, $P = 0.18$), but it tended to decrease with herd size in summer (β = -0.0008, P = 0.08). This latter trend was largely caused by two observations associated with the largest herds in summer (Figure 1). Indeed, the trend largely weakened if the two largest herds recorded were excluded from the summer analysis ($P = 0.77$).



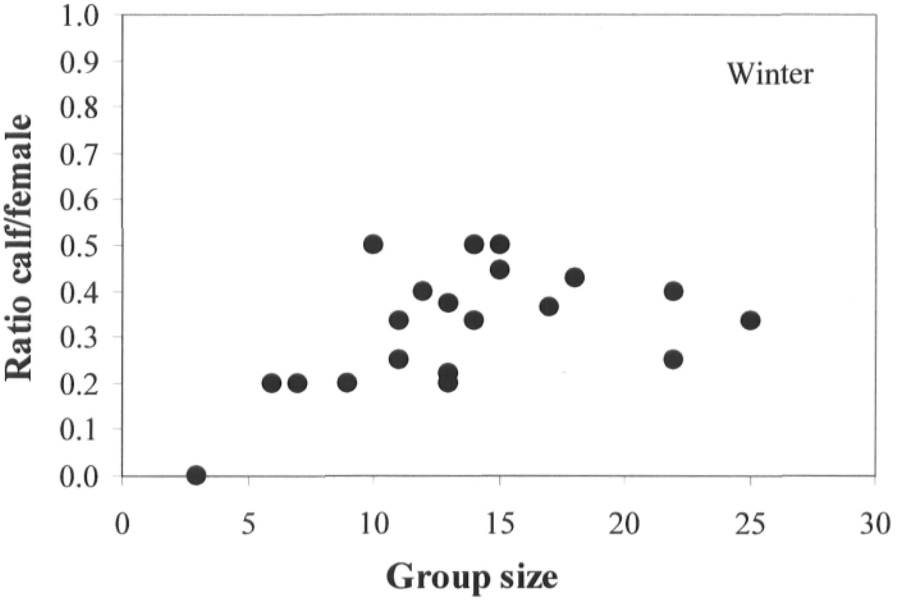


Figure 1. Calf/female ratio with respect to group size of the herds associated with the nine radio-collared female bison followed in Prince Albert National Park during summer 2005 and winter 2006.

Habitat selection

Park scale

At the park scale, we calculated distinct RSFs when radio-collared bison were in small ($\leq$ 15 individuals) and large ($>$ 15 individuals) groups. We found that, independently of group size, bison selected areas surrounded by a large proportion of meadows and a high density of edges during both winter and summer (Table 3). In summer, bison also selected areas near water, and they avoided conifer forests. Also in summer, individuals selected roads only when part of small groups, and meadows when part of large groups. In winter, groups of all sizes selected meadows. Finally, winter distribution of bison was related to spatial patterns of snow water equivalent (SWE) across the landscape. When SWE was > 12.0 cm for large groups and > 15.1 cm for small groups, respectively, the probability of bison occurrence decreased with increasing SWE (Figure 2).

Table 3. Resource selection functions at the park scale for small ($\leq$ 15 individuals) and large ($>$ 15 individuals) groups of plains bison in Prince Albert National Park, during summer 2005 and winter 2006. Analyses were based on 515 bison locations for small groups and 109 for large groups in summer, and on 242 locations for small groups and 125 for large groups in winter. Resource availability was quantified from 4527 random locations. Independent variables are described in Table 1.

Season	**Group size**	**Variable**	**β**	**se**	***t***	***P***
Summer	Small	(intercept)	-5.67	0.43	-13.24	< 0.0001
		pmead	5.20	0.68	7.63	0.0000
		dedge	115.69	51.42	2.25	0.025
		conifer	-3.38	0.72	-4.69	< 0.0001
		distwat	-1.70	0.47	-3.63	0.0003
		road	1.64	0.43	3.86	0.0001
	Large	(intercept)	-4.43	0.18	-25.06	< 0.0001
		pmead	5.57	0.28	20.17	< 0.0001
		dedge	98.69	17.44	5.66	< 0.0001
		conifer	-3.63	0.29	-12.58	< 0.0001
		meadow	0.60	0.09	6.49	< 0.0001
		distwat	-1.42	0.14	-9.89	< 0.0001
Winter	Small	(intercept)	-10.41	0.55	-19.10	< 0.0001
		pmead	2.59	0.34	7.63	< 0.0001
		dedge	215.32	19.47	11.06	< 0.0001
		meadow	1.95	0.11	17.70	< 0.0001
		SWE	1.05	0.15	6.98	< 0.0001
		SWE^2	-0.10	0.02	-5.63	< 0.0001
	Large	(intercept)	-12.59	0.81	-15.56	< 0.0001
		pmead	4.35	0.41	10.54	< 0.0001
		dedge	269.40	25.10	10.77	< 0.0001
		meadow	2.20	0.15	14.79	< 0.0001
		SWE	1.26	0.24	5.30	< 0.0001
		SWE^2	-0.15	0.03	-5.34	< 0.0001

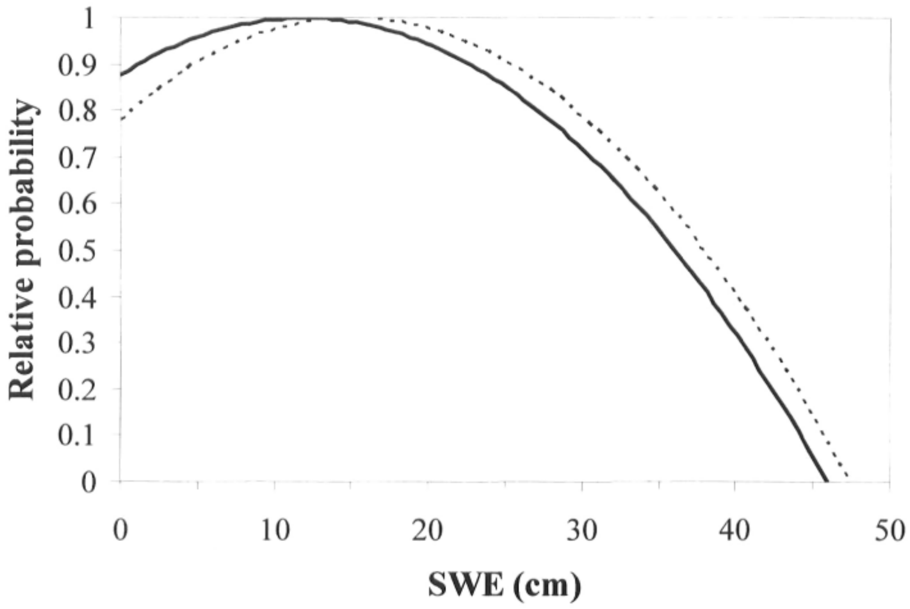


Figure 2. Relative probability of occurrence by small (≤ 15 individuals: dashed line) and large (> 15 individuals: solid line) groups of plains bison in Prince Albert National Park, as a function of snow water equivalent (SWE). Relative probability was calculated based on the resource selection functions displayed in Table 3.

To identify factors that may discriminate between the spatial distribution of small and large groups of bison, we contrasted habitat characteristics at locations where those groups were observed. In summer, large groups used areas that offered a larger proportion of meadows than did small groups (Table 4). Also, roads and areas surrounded by a high density of hard edges (i.e., transition zone between open and forest areas) were used less intensively by large than by small herds in summer. In winter, the use of areas with high edge density was more important for large groups, whereas small groups made stronger use of areas largely surrounded by meadows. Finally, compared to small groups, large bison herds made stronger use of meadows and weaker use of areas with high SWE.

Table 4. Comparison of landscape attributes at the locations of small (≤ 15 individuals) and large (> 15 individuals) groups of plains bison in Prince Albert National Park during summer 2005 and winter 2006. Small group was the reference category (i.e., dependent variable took a value of 0 for groups ≤ 15 individuals and a value of 1 for larger groups) in the mixed model of logistic regression. Independent variables are described in Table 1.

Season	**Variable**	**β**	**se**	***t***	***P***
Summer	(intercept)	1.95	0.49	3.98	0.0001
	pmead	4.33	1.26	3.43	0.0007
	dedge	-172.67	70.43	-2.45	0.015
	road	-1.55	0.54	2.89	0.004
Winter	(intercept)	-2.75	1.74	-1.58	0.11
	pmead	-4.14	2.08	-1.99	0.047
	dedge	603.53	96.49	6.26	< 0.0001
	meadow	0.91	0.24	-3.93	0.0001
	SWE	-0.95	0.36	2.50	0.01

700-m buffer scale

At the 700-m buffer scale, a priori RSF models were built from independent variables susceptible to influence the distribution of plains bison, and group size effects was tested in interaction with these variables. Selection among a priori candidate RSF was based on QIC (Table 5). In summer, two RSF models (S1 and S2) explained bison spatial distribution with rather similar parsimony (i.e., ΔAIC ≤ 2, cf. Burnham and Anderson, 2002). Comparison between the two best RSF models and the other candidate models revealed the importance of the spatial distribution of meadows, roads, water, the density of hard edges, the local proportion of meadows and agricultural lands on bison distribution (Table 5). Also, the influence of edge density and the proportion of agricultural lands in a 700-m buffer depended on group size. However, group size effect on meadow selection was weak at best. Indeed, model S2 performed just as well as model

S1 without accounting for the interaction “meadow×g” (Table 5), which had P = 0.14 for model S1.

The potential effect of agricultural lands on the winter distribution of bison could not be assessed at this scale because radio-collared females were never located within 700-m of agricultural lands in winter (hence models including the variable “pagri” models did not converge because agricultural lands were neither used nor available, at this scale). Among candidate models (Table 5), RSF W1, W2 and W3 described the data with comparable parsimony (i.e., ΔAIC ≤ 2, Burnham and Anderson 2002). Comparison of these three RSF with other candidate models revealed that meadows, the proportion of meadows within a 700-m buffer and snow water equivalent were all important to explain the winter probability of bison occurrence across the landscape (Table 5). On the other hand, comparison among models W1-W3 showed some ambiguity in the potential role of edge density and the interaction between group size and the local proportion of meadows on bison distribution (Table 5). Model W1 had the lowest QIC, and the extra parameter “dedge” in model W2 had P = 0.66, whereas “pmead×g” in model W3 had P = 0.56.

Overall, we considered RSFs S2 and W1 as final models; hence further inference at the 700-m buffer scale focused on these two RSFs. These final models revealed a selection for meadows in both summer and winter (Table 6). In winter, the strength of this selection increased with the group size. In addition to the selection for meadows, bison probability of occurrence across the landscape was positively related to the proportion of meadows during both seasons (Table 6). In winter, bison selected areas largely surrounded by meadows regardless of group size, but in summer, the selection for areas with high proportion of meadows became stronger as the group size increased (Table 6). The RSF S2 (Table 6) indicated that the relative probability of occurrence of bison in small herds (< 43 individuals) decreased with the proportion of meadows within a 700-m buffer, whereas this probability increased for large groups (≥ 43 individuals) (Figure 3). Also in summer, the spatial distribution of bison was influenced by the density of hard edges (Table 6). When bison were in groups smaller than 77 individuals, they preferentially used areas bordered by high density of edges, whereas the probability of occurrence of larger groups (≥ 77 individuals) decreased with increasing edge density. Moreover, bison avoided areas largely surrounded by agricultural lands in summer, an avoidance that increased with group size (Table 6). Additionally, roads were selected in summer, whereas open water (e.g., lake, river) was avoided (Table 6). Group size effect was not detected for these two habitat components, i.e., QIC value of RSF model increased when we included group size interaction with these variables (Table 5). Finally, snow water equivalent (SWE) had a quadratic effect on the winter probability of bison occurrence, which revealed that the probability of bison occurrence decreased with SWE only when SWE got > 6.5 cm (Table 6).

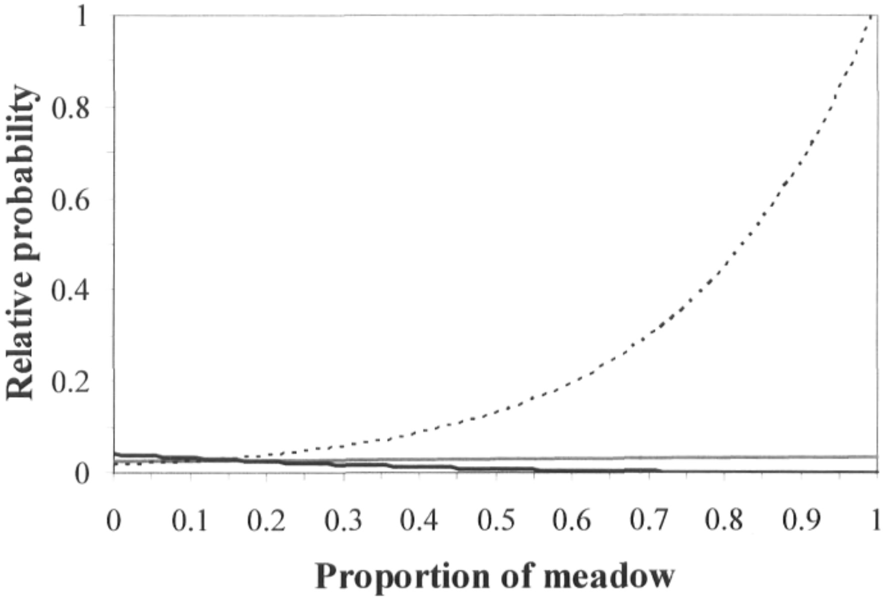
Table 5. Candidate models of habitat selection by plains bison in Prince Albert National Park at the 700-m buffer scale during summer 2005 and winter 2006. The number of estimated parameters (K), quasi-likelihood under independence criterion (QIC) and difference in QIC with the lowest scoring model (ΔQIC) are given for each model. Analyses were based on 4037 bison locations in summer, and 6864 in winter. Each bison location was matched to 10 random locations used to quantify local resource availability. Independent variables are described in Table 1.

Model	**Model structure**	**K**	**QIC**	**ΔQIC**
	Summer:			
S1	meadow + meadow×g + water + road + dedge + dedge×g + pmead + pagri + pagri×g	9	2699.10	0.00
S2	meadow + water + road + dedge + dedge×g + pmead + pagri + pagri×g	8	2699.41	0.31
S3	meadow + meadow×g + water + road + dedge + pmead + pagri + pagri×g	8	2709.32	10.22
S4	meadow + water + water×g + road + dedge + dedge×g + pmead + pagri + pagri×g	9	2714.30	15.2
S5	meadow + water + road + road×g + dedge + dedge×g + pmead + pagri + pagri×g	9	2717.87	18.77

S6	meadow + water + road + dedge + dedge×g + pmead	6	2719.55	20.45
S7	meadow	1	2736.24	37.14
S8	water + road + dedge + dedge×g + pmead + pagri + pagri×g	7	2915.79	216.69
S9	dedge	1	2984.05	284.95
S10	road	1	2994.03	294.93
	Winter:			
W1	meadow + meadow×g + pmead + snow	5	1393.43	0.00
W2	meadow + meadow×g + pmead + dedge + snow	6	1394.86	1.43
W3	meadow + meadow×g + pmead + pmead×g + snow	6	1394.87	1.44
W4	meadow + meadow×g + pmead + dedge + dedge×g + snow	7	1395.45	2.02
W5	meadow + pmead + snow	4	1396.2	2.77
W6	meadow + meadow×g + pmead	3	1426.11	32.68
W7	meadow + meadow×g	2	1447.64	54.21
W8	meadow	1	1449.66	56.23
W9	pmead + snow	3	1510.56	117.13
W10	snow	1	1561.18	167.75

Table 6. Resource selection functions at the 700-m buffer scale for plains bison in Prince Albert National Park during summer 2005 and winter 2006. Independent variables are described in Table 1.

Variable	**Model S2**			**Model W1**		
	β	se	P	β	se	P
meadow×g				0.056	0.028	0.048
meadow	1.39	0.14	<0.0001	0.81	0.49	0.10
water	-1.09	0.48	0.02			
road	0.87	0.32	0.006			
pagri×g	-0.31	0.18	0.10			
pagri	-2.16	1.11	0.05			
dedge×g	-1.57	0.80	0.05			
dedge	120.16	60.67	0.048			
pmead×g	0.069	0.015	<0.0001			
pmead	-2.98	1.05	0.05	6.97	1.64	<0.0001
SWE				0.053	0.23	0.02
SWE^2				-0.12	0.027	<0.0001



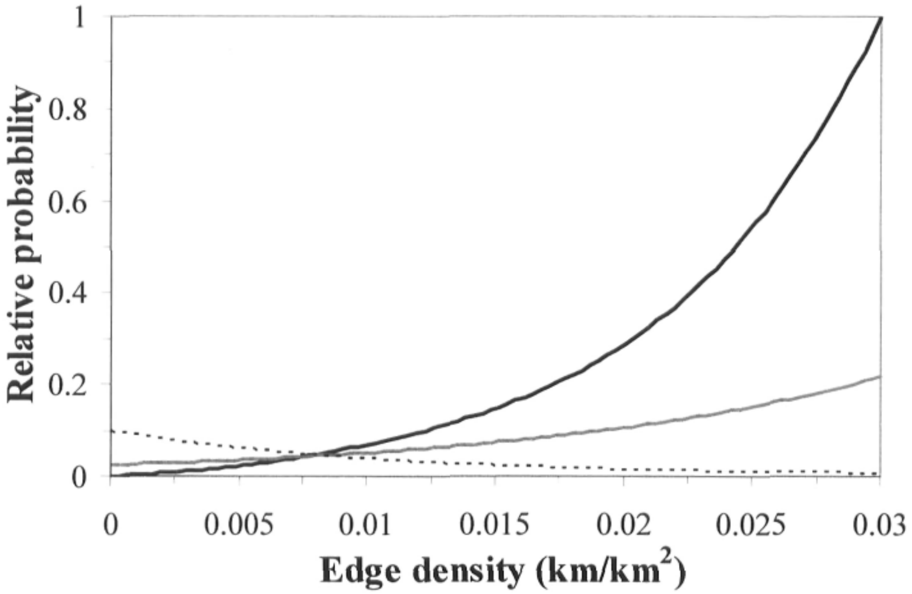


Figure 3. Relative probability of bison occurrence at the 700 m buffer scale for three group sizes of plains bison in Prince Albert National Park, as a function of the proportion of meadow within a 700-m radius and edge density. Bison group sizes displayed are 2 (solid black line), 44 (grey line) and 100 individuals (dashed line). Relative probabilities were calculated from model S2 displayed in Table 6.

Meadow scale

Over the summer, a total of 134 and 157 randomly selected bison were located while foraging and resting within meadows, respectively. Group size associated with these focal individuals averaged 43 ± 7 individuals (range: 2-231, n = 45). In winter, we observed 85 foraging and 47 resting individuals, with group size of the focal bison averaging 13 ± 1 individuals (range: 2-40, n = 36). Group size calculation was based a single observation when > 1 individual was observed in the same herd.

RSFs were estimated for both resting and foraging sites. Comparison of candidate models revealed that foraging sites were selected on the basis of both biotic and abiotic factors (Table 7). In summer, two RSF models (FS1 and FS2) explained bison spatial distribution with similar parsimony (i.e., $\Delta AIC \leq 2$, cf. Burnham and Anderson 2002). Comparison of these two RSF models to other candidate models indicated the influence of four plant groups (i.e., *Carex atherodes*, *Agropyron* spp., *Calamagrostis inexpansa,* and *Forbs*) and snow water depth on the distribution of foraging bison (Table 7). In model FS1 we also noted a group size effect on *C. atherodes* selection, and this interaction had a $P = 0.06$. In winter field data provided similar support to models FW1, FW2 and FW3. These three RSF models suggested that *Carex atherodes*, *Agropyron* spp., *Calamagrostis inexpansa* and snow water equivalent influenced distribution of plains bison during foraging activity (Table 7). In model FW1 and FW2, SWE had a quadratic effect on bison relative probability of occurrence, but influence of snow cover was not significant (FW1: SWE had $P = 0.29$ and SWE^2 had $P = 0.10$, FW2: SWE had $P = 0.41$ and SWE^2 had $P = 0.15$). In the model FW3, effect of SWE is linear and significant with $P = 0.02$. Moreover, in model FW1, we noted a group size effect on *C. atherodes* selection, but this interaction "caat×g" appeared rather weak ($P = 0.10$). Indeed, model FW3 performed just as well as model FW1 without accounting for SWE^2 and the interaction "caat×g" (Table 7). Overall, we considered FS1 and FW3 as the final RSF model.

Final RSF models indicated a selection for foraging sites offering high percentage of total dry biomass of *C. atherodes*, a trend that remained consistent between seasons (Table 8). In summer, the strength of selection for *C. atherodes* decreased with group size. Additionally, the odds of selecting a given foraging site in summer decreased with the percent of total dry biomass made out of forbs, *Agropyron* spp., and *Calamagrostis inexpansa*, as well as with water depth. This avoidance was independent from group size, as models that included such interaction related to our field observations with less parsimony (Table 7). In winter, bison selected foraging areas not only based on the percent of total dry biomass made out of *C. atherodes*, but also of *C. inexpansa* and

Agropyron spp. Finally, bison avoided sites with more snow cover, as there was a gradual decrease in the probability bison occurrence with SWE.

Table 7. Candidate models of foraging site selection at the meadow scale for plains bison in Prince Albert National Park during summer 2005 and winter 2006. For each model, number of parameters estimated (K), Akaike's Information Criterion (AIC), and the difference in AIC with lowest scoring model (ΔAIC) are given. A total of 134 bison were observed foraging in summer, and 85 in winter. Resource availability was quantified at 1074 random locations in summer and 401 in winter. Independent variables are described in Table 1.

Model	**Model structure**	**K**	**AIC**	**ΔAIC**
	Summer:			
FS1	caat + caat×g + cain + agro + forbs + hwater	6	440.0	0.0
FS2	caat + cain + agro + forbs + hwater	5	440.7	0.7
FS3	caat + cain + agro + forbs	4	497.4	57.4
FS4	caat + hwater	2	508.8	68.8
FS5	cain + agro + forbs + hwater	4	531.6	91.6
FS6	caat + cain	2	532.1	92.1
FS7	caat + cain + agro	3	533.5	93.5
FS8	caat + caat×g	2	534.9	94.9
FS9	caat	1	544.0	104
FS10	caat + scfe	2	546.0	106
	Winter:			
FW1	caat + caat×g + cain + agro + snow	6	165.8	0.0
FW2	caat + cain + agro + snow	5	166.3	0.5
FW3	caat + cain + agro + SWE	4	166.7	0.9
FW4	caat + cain + agro	3	208.1	42.3
FW5	caat + agro	2	247.2	81.4
FW6	caat + snow	3	257.9	92.1
FW7	cain + agro + snow	4	273.5	107.7
FW8	caat + cain	2	280.8	115
FW9	caat	1	305.2	139.4
FW10	snow	1	308.7	142.9

Table 8. Resource selection functions for bison foraging within meadows in Prince Albert National Park during summer 2005 and winter 2006. Values are shown for models FS1 and FW3 of Table 7. Independent variables are described in Table 1.

Variables		**Model FS1**			**Model FW3**	
	β	se	P	β	se	P
caat	0.049	0.001	<0.0001	0.077	0.011	<0.0001
caat×g	-0.00016	0.00008	0.06			
cain	-0.11	0.04	0.003	0.08	0.01	<0.0001
agro	-0.02	0.01	0.02	0.062	0.016	<0.0001
forbs	-0.06	0.01	<0.0001			
hwater	-0.15	0.02	<0.0001			
SWE				-0.77	0.33	0.02

Comparison of candidate models showed that the selection of resting sites by bison was only related to abiotic factors (Table 9). The most parsimonious RSF (i.e., RS1 and RW1) imply that slope influenced the selection of resting site, a response that was dependent on group size during both seasons (Table 10). Individuals were more likely to select resting sites with a steeper slope when they were part of large than small groups (Figure 4). If we consider the median size of bison herds observed in each season, the probability of occurrence generally increased with slope in summer, whereas it most commonly decreased in winter. In summer, bison also preferred to rest at sites where water was absent. In fact, bison simply never rested at sites where the ground was covered by water (0 out of 157 observed resting sites). Finally, the winter probability of bison occurrence during resting activity decreased with the distance to forest edge (Table 10).

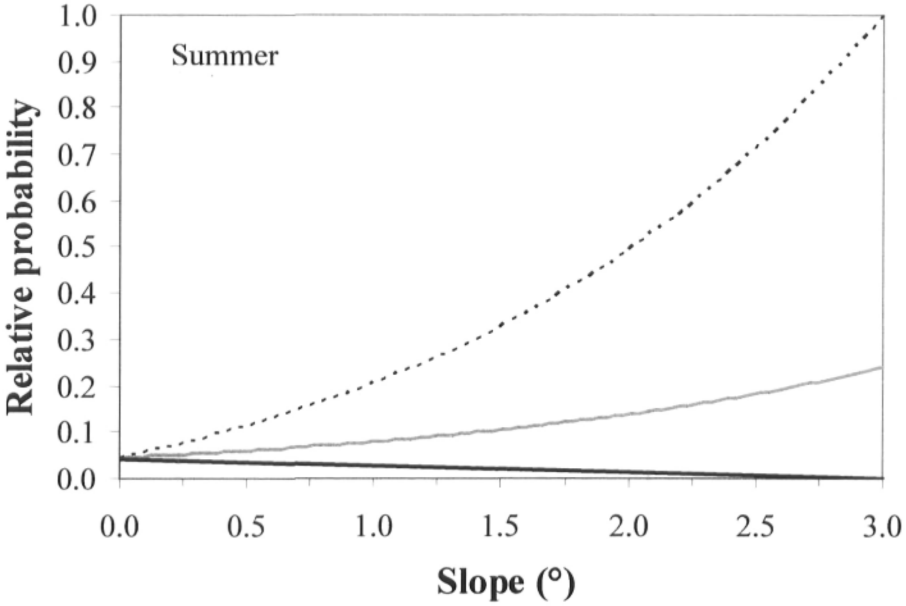
Table 9. Candidate models of resting site selection at the meadow scale for plains bison in Prince Albert National Park during summer 2005 and winter 2006. For each model, number of parameters estimated (K), Akaike's Information Criterion (AIC), and the difference in AIC with the lowest scoring model (ΔAIC). A total of 157 bison were observed resting in summer, and 47 in winter. Resource availability was quantified at 1177 random locations in summer and 434 in winter. Independent variables are described in Table 1.

Model	**Model structure**	**K**	**AIC**	**ΔAIC**
	Summer:			
RS1	slope + slope×g + water	3	675.7	0.0
RS2	water	1	713.3	37.6
RS3	slope + slope×g	2	748.6	72.9
RS4	distforest	1	755.8	80.1
RS5	slope	1	762.4	86.7
RS6	caat	1	765.9	90.2
RS7	forbs	1	786.1	110.4
RS8	agro	1	793.6	117.9
RS9	cain	1	795.5	119.8
	Winter:			
RW1	distforest + slope + slope×g	3	113.4	0.0
RW2	distforest + distforest×g + slope + slope×g	4	114.1	0.7
RW3	distforest + slope + slope×g + snow	5	115.6	2.2
RW4	distforest	1	117.8	4.4
RW5	distforest + slope	2	118.7	5.3
RW6	distforest + snow	3	120.0	6.6
RW7	slope + slope×g	2	221.8	108.4
RW8	caat	1	236.9	123.5
RW9	snow	1	239.5	126.1
RW10	slope	1	240.3	126.9

Table 10. Resource selection functions for bison resting within meadows in Prince Albert National Park during summer 2005 and winter 2006. Values are shown for models RS1 and RW1 of Table 9. Independent variables are described in Table 1.

Variable	**Model RS1**			**Model RW1**		
	β	se	P	β	se	P
slope	-0.084	0.143	0.56	-1.34	0.54	0.022
slope×g	0.0065	0.001	0.0004	0.095	0.04	0.013
distforest				-0.16	0.03	< 0.0001
water	-16.72	*	*			

* Standard error and associated P-value could be properly calculated because sites with water were never used for resting even though such sites were generally available in the meadow



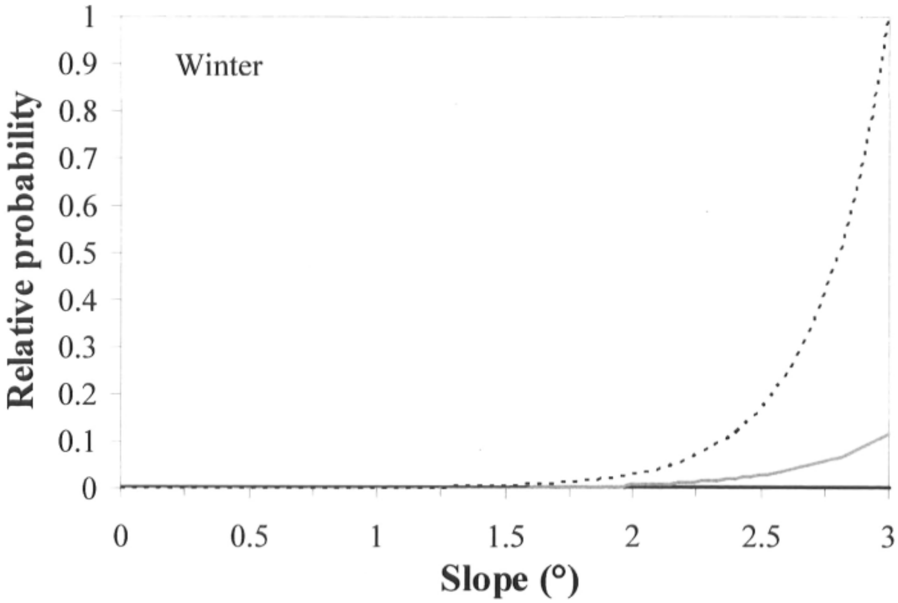


Figure 4. Relative probability of occurrence for bison resting within meadows in Prince Albert National Park, as a function of slope for groups comprised of 2 (solid black line), 43 (grey line) and 100 bison (dashed line). Relative probability was calculated from the resource selection functions displayed in Table 10.

Discussion

Our study shows that patterns of habitat selection by female plains bison varied depending on whether individuals were in small or large groups, a group size effect detected at each of our three spatial scales (i.e., park, 700-m buffer, and meadow scales). Group size effects on habitat selection were studied using resource selection functions (RSF). RSFs can be powerful tools to illuminate the link between animal distribution and the spatial complexity of landscapes, with the consequence that the use of RSF models in ecological studies has greatly increased over the past few years. RSFs have helped us understand habitat selection of diverse animal species, but although RSF have been applied to gregarious animals, group size effects on the resource selection process remained generally overlooked. There is an intensive body of research on density dependent habitat selection (e.g., ecological research based on Ideal Free Distribution and Isodar theories: Sutherland, 1997; Ramp and Coulson, 2002; Morris, 2003), but this field seems to have developed in parallel to RSF studies. Understanding the spatial dynamics of animal species may often require consideration of the complexity of the habitat selection process. A fruitful approach thus should account for the potential influence of multiple landscape attributes on animal distribution together with the fact that variation in group size may modulate the selection for those features. McLoughlin et al. (2006) are among the few authors that have used RSF to study the influence of the presence of conspecifics on a multi-variable resource selection pattern, but they did not consider that habitat selection is a process that can be scale dependent (Manly et al., 2002; Boyce and McDonald, 1999; Boyce, 2006). Our approach is novel because it involves multi-scale habitat selection based on RSF (which allow for the simultaneous consideration of a wide range of landscape attributes) while considering that resource selection decisions may change with group size.

Habitat selection

We found that the spatial distribution of free-ranging plains bison was best explained when considering multiple attributes of landscape complexity, as well as when accounting for the fact that habitat selection is scale-dependent process that involves decisions that vary with group size. Habitat selection by bison in Prince Albert National Park can be largely explained based on trade-offs between individual goals, such as acquiring nutrients while maintaining low energetic costs and avoiding predation.

Influence of costs of locomotion on resource selection

Snow negatively affects movements and feeding of ungulates (Parker et al., 1984; Telfer and Kelsall, 1984; Boertje, 1985; Fancy and White, 1985; Fortin et al., 2005b), and by doing so, it may restrict landscape use by individuals (Reynolds et Peden, 1987; Schaefer and Messier, 1995; Fortin et al., 2003; Dussault et al., 2005; Mao et al., 2005). At each of our three spatial scales, we observed that snow water equivalent (SWE) had non linear effects on bison probability of occurrence: snow had little effect until a threshold of SWE was reached, at which point, snow had an adverse affect on probability of bison occurrence. The presence of a threshold in the effect of snow on landscape use by large herbivores has been previously reported (Turner et al., 1994; VanCamp, 1975). At the meadow scale, response to snow cover was observed only during foraging activity. Snow condition is known to influence fine-scale foraging decisions of bison (VanCamp, 1975; Fortin, 2003). Foraging in deeper snow may involve higher energy costs, because bison consume vegetation that generally lies underneath the snow. Foraging pattern of bison at the meadow scale thus reflect a trade-off between a search for certain food items and an avoidance for deep SWE that may hamper foraging (Fortin, 2003). The preference of bison for areas with low snow water equivalent for each of the three spatial extents investigated indicates that snow influences bison distribution at multiple scales.

Bison require daily access to water (McHugh, 1958). Therefore, water can represent an important limiting factor in summer, and individuals may need to trade-off the need to obtain high quality forage, to access water frequently and to minimize energy costs of travel to reach water holes. As a result, bison tend to stay and graze near water (McHugh, 1958; Fischer and Gates, 2005), a trend that we observed at the park scale. At the 700-m buffer scale, however, bison used lakes and other water holes less often than expected from a random pattern. This distinction between scales may reflect two levels of decisions. First bison tend to select part of the landscape where they may have access to water. Once in such areas, the avoidance for open water at a finer hierarchical level may reflect the fact that water was used sporadically and rapidly (i.e., relative to our 3-hour relocation interval) for drinking, but was avoided during other activities (e.g., walking, foraging, resting). Indeed, our observations at the meadow scale showed that bison preferred to forage where the water level was low and to rest at dry sites.

The role of energy costs of locomotion on habitat selection at broad scales might also be reflected by the effect of roads on probability of bison occurrence. In summer, bison spatial distribution is positively influenced by roads, but, as previously reported by Bruggeman et al. (2006), bison did not preferentially use the park's roads in winter. The less important road effects in winter may be explained by broad scale pattern of bison distribution in Prince Albert National Park. Bison are opportunistic in their use of road, and they seem to only use them when they are conveniently located to move between meadows. There is a rather intensive road (including man-made trails) network linking meadows in the summer range, but not in the winter range. Thus, there might be fewer opportunities to travel along roads in winter, and individuals would simply extend their own trail network. Also, movements of bison groups create a system of well-packed trails through deep snow (McHugh, 1958; Morgan, 1980; Telfer and Kelsall, 1984). Most roads in the bison range are not plowed during winter, with the consequence that their use might not be more energy efficient than the use of bison trails. Furthermore, because the presence of snow increases cost of locomotion (Parker et al., 1984), bison tend to reduce their movements during winter (Morgan, 1980; Fortin et al., 2003; Bruggeman et al., 2006), which may also explain the absence of road effects on the winter distribution of bison.

Trade-off between food availability and predation risk

In addition to abiotic factors (i.e., SWE, water and road), the trade-off between food availability and predation risk could also explained broad-scale patterns of habitat selection by bison. Plains bison are known to forage in open areas regardless of predation risk (Hermàndez and Laundré, 2005; Ripple and Beschta, 2006). However, landscape features can influence sensitivity of ungulates to predators (Hebblewhite et al., 2005), and bison in Prince Albert National Park are known to flee into the forest as a response to perceived risk (Fortin and Andruskiw, 2003). Edges have been considered in many studies as a landscape feature that may alter predation risk (Dussault et al., 2005; Hernàndez et al., 2005; Bergman et al., 2006), and we suggested that hard edges are likely viewed by plains bison as an entry into safer areas. Therefore, to minimize predation risk and maximize food accessibility, bison select areas offering several escape possibilities (i.e., hard edges) and providing the highest biomass food for bison (i.e., meadows). As expected, habitat selection by plain bison demonstrated the importance of this trade-off. At broad scales, bison selected meadows during both seasons, and during summer they avoided conifer forests, which offered the lowest biomass of forage. Bison were also influenced by areas providing high food availability in a 700 m radius, as they selected sites surrounded by a large proportion of meadows. In response to predation risk, bison tended to select landscape areas surrounded with a high density of hard edges.

Predation risk and competition for food are both influenced by group size, and if the nature of the trade-offs between these two factors can vary, so can habitat selection. Dilution effects and collective scanning generally lead to lower predation risks for larger groups than smaller groups of prey (Dehn, 1990; Lima, 1995; Roberts, 1996), assuming that the composition of a group does not vary with its size. We observed little variation in the composition (i.e., ratio calf/female) of bison groups as a function of their size, for the radio-collared female bison. We may thus expect that, in our study, large groups were less at risk than small groups. This link between group size and risk may influence habitat selection. For example, assuming that the search for areas with a large proportion of edges may constrain the spatial distribution of bison, we could predict that the selection for hard edge would be less important for large than small groups. Consistently, selection for hard edges decreased with increasing group size at the two broadest scales in summer. This trend was not observed in winter. Instead, we detected group size effects on the selection for meadows in winter, which may also be linked to density dependent changes in trade-offs. For example, resource depletion in meadows should be faster for large than small groups. Under the hypothesis that inter-meadow movements are driven by resource depletion, we would expect that the frequency of movement between meadows would increase with group size, and larger groups should spend relatively more time in the forest (because they would make more frequent inter-meadow movements). This behavioural response to resource depletion should translate into a decrease in the selection of meadows by large compared to small bison groups. On the other hand, 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 in the wolf-bison system. In this case, predation risk should increase the frequency of inter-meadow movements, which should lead to a decrease in the strength of meadow selection. This risk-sensitive hypothesis thus should lead to a less important selection for meadows by bison in smaller than in larger groups. Our observations were most consistent with the risk-sensitive than the competition hypothesis, as we observed stronger selection for meadows by large than small bison groups at the two broadest scales. Also, if small groups decrease predation risk by increasing inter-meadow movements, they are more likely to use roads to minimize energy expenses. Thus, our results again support the risk-sensitive hypothesis, because we found that at the park scale, road selection during summer was stronger for smaller than larger bison groups.

In addition to the selection for meadows at broad scales, bison selected areas within meadows to either rest or forage. We observed that spatial distribution of foraging bison was influenced by the distribution of various plant species. Bison generally make foraging choices that maximise their short-term energy intake rate (Bergman et al., 2001; Fortin et al., 2002). The contingency model of optimal diet specifies that a decrease in the encounter rate with the most profitable (i.e., ratio between digestible energy content and handling time) food items should lead to diet expansion (Stephens and Krebs, 1986). In Prince Albert National Park the food item most profitable for bison is *Carex atherodes* during both summer and winter (Fortin et al., 2002). Assuming that competition by either exploitation or interference leads to a decrease in the encounter rate of individuals with *C. atherodes*, and that competition increases with group size, one could predict a broader diet for large than small bison groups. An increase in diet breadth may then be associated with a decrease in the strength of selection for *C. atherodes*. Consistently with these principles of optimality, we found that foraging sites were selected on the basis of the abundance of *C. atherodes* during both summer and winter. Moreover, the selection for *C. atherodes* in summer decreased with group size. On the other hand, the observed selection for sites offering high abundance of *Calamagrostis inexpansa* in winter does not seem linked to the maximize short-term energy intake rate, as the profitability of this plant species is relatively low (Fortin et al., 2002).

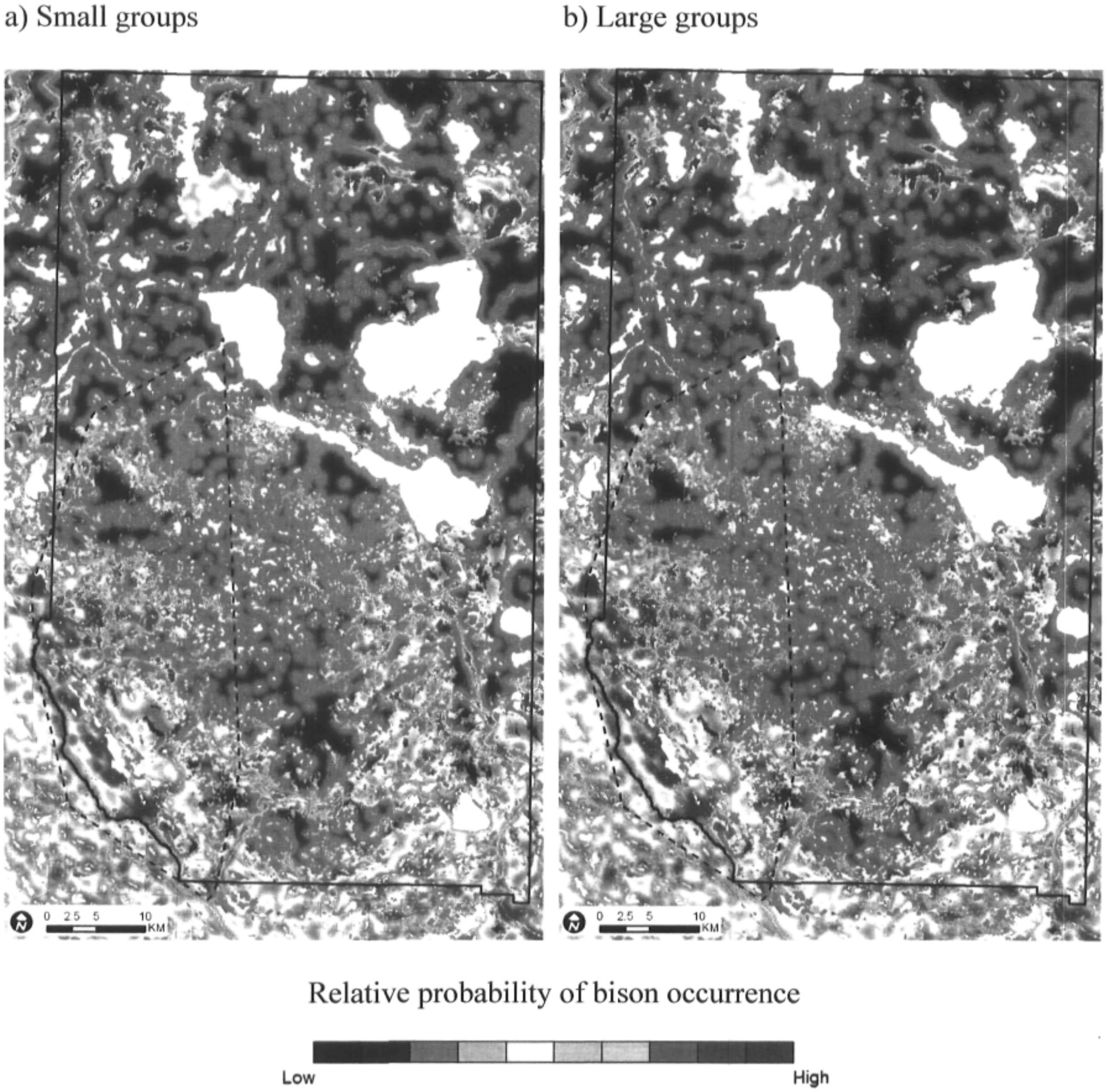
Selection of resting sites

Selection of resting sites within meadows by plains bison was only influenced by abiotics factors during both seasons. Bison preferred to rest at dry sites in summer and near forest edges in winter. Choice of bison to rest closer to forest cover may be in an anti-predator strategy during the season when average group size is the lowest. Indeed, increasing distance to edge is often associated with an increase in risk of predation (Blumstein and Daniel, 2003; While and McArthur, 2005). On the other hand, Fortin (2000) also reported a selection of meadow edges by bison. He did not link this pattern to predation risk, but instead he attributed this selection to thermoregulatory benefits. Therefore, importance of hard edges on the spatial distribution of bison was observed at various scales, and depended on spatial scale. This habitat feature thus may represent more than just an escape structure for bison. Finally, we also observed that the influence of slope on the selection of resting site was influenced by group size. Overall, our results suggest that even at fine scales, group size influences habitat selection and spatial distribution of plains bison.

Conclusion and management implications

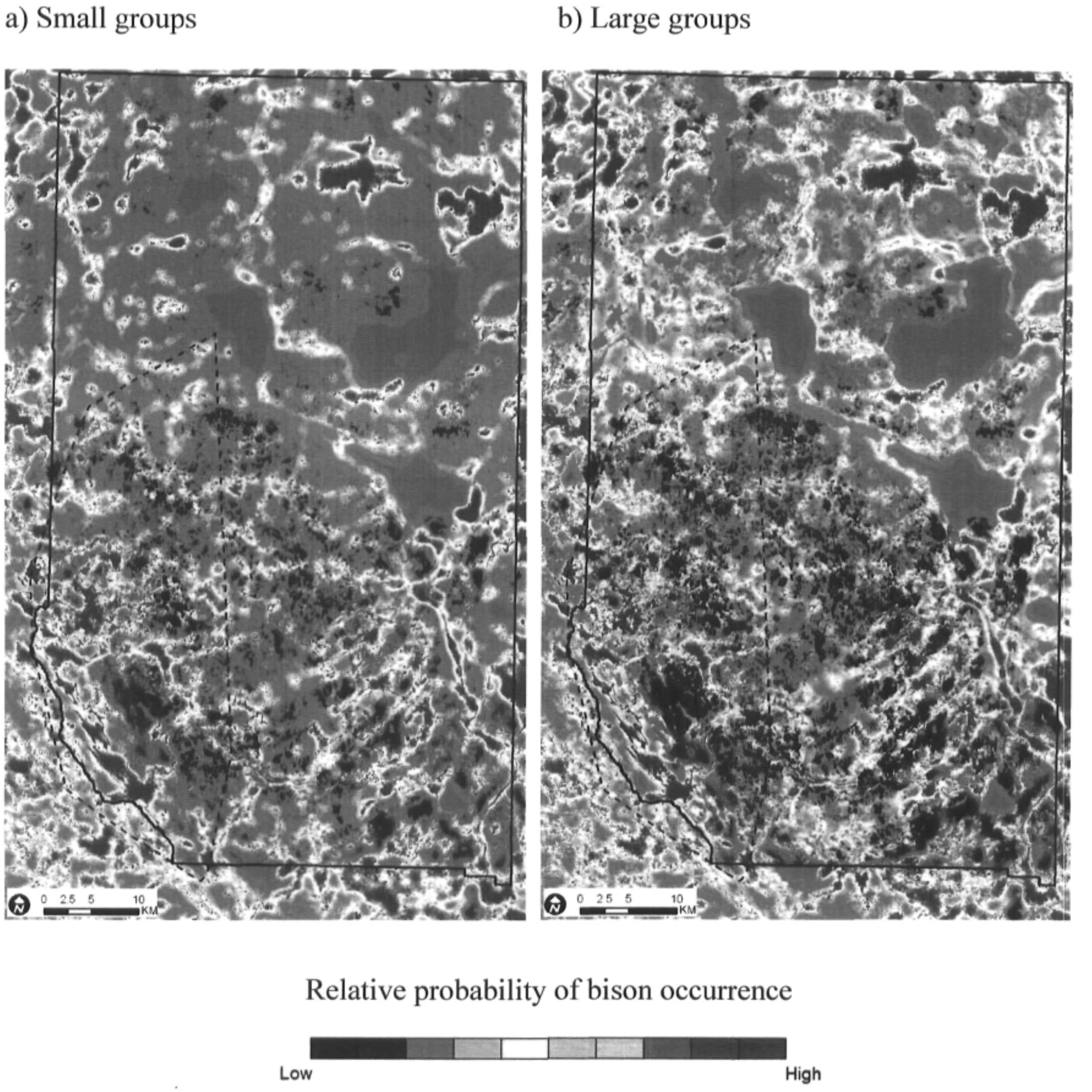
We found that factors influencing the spatial distribution of bison were scale-dependent, which exposed the hierarchy in bison habitat selection. At broad scales, bison choose to live in areas where landscape features provide high food availability, shallow snow cover and low predation risk. In addition to explicitly select specific habitat features, small bison groups can also respond to predation risk by increasing the frequency of their movements. At a finer scale, the trade-off between costs of moving in the snow and the benefit associated with the consumption of specific food items seems to be driving bison distribution during foraging activity. Overall, our approach outlines the hierarchy between factors that influence bison distribution at different spatial scales, and it demonstrates that habitat selection changed with the group size at all of our three spatial scales. Using RSFs, we showed that patterns of habitat selection are a multi-variable phenomenon affected by trade-offs operating at different spatial scales, as well as by group size, which may change the nature of these trade-offs.

Resource selection functions can be used to map the relative probability of occurrence of individuals over the scale that selection occurs (Boyce and McDonald, 1999; Boyce et al., 2003, Hebblewhite et al., 2005). At the park scale, we used RSFs to map occurrence probability of small and large bison groups during both seasons (Figure 5 and Figure 6). Differences between summer and winter patterns of habitat selection by plains bison were evident. Spatial representation of summer RSF models showed that bison are more likely to occur in the southwest corner of Prince Albert National Park, whereas during winter, the bison distribution was more patchy and the probability of bison occurrence was higher in the northern and eastern portion of the Park's greater area. Patterns of bison distribution across the park also varied between small and large bison groups, and we can see that large bison groups were more likely to occur north of the park than small groups during winter (Figure 6). However, the trends of habitat selection were usually the same for each season. We also observed that bison largely occur near and out of the park boundaries during summer. This selection is problematic because bison do venture on to private lands and occasionally cause damage as has been observed. Even though small bison groups were more often observed outside Park boundaries than large herds, RSF models did not indicate important differences in occurrence probability of small and large bison groups on private lands. Thus, with the increase of the bison population in the park (i.e., the population has tripled in 10 years), we anticipate an increase in the frequency of bison excursions on to private lands, because our analyses indicated high potential for range expansion outside the park boundaries (Figure 5). Our habitat selection study revealed factors that influence spatial distribution of plains bison in Prince Albert National Park, and it provides a spatially explicit description of bison probability of occurrence that may offer a basis for the development of management strategies that could encourage bison to remain within the park. Thus, habitat selection studies are important for the management of animal populations. These studies identify limiting factors and provide information that can be useful for the conservation of free-ranging plains bison in Canada.


a) Small groups

b) Large groups

Figure 5: Relative probability of occurrence of plains bison in the Prince Albert National Park's greater ecosystem in summer, as evaluated based on RSF models at the park scale for small (≤ 15 individuals) and large (> 15 individuals) bison groups. The solid line represents the Parks' boundaries and dashed line delimits the range covered by radio-collared bison.



a) Small groups

b) Large groups

Figure 6: Relative probability of occurrence of plains bison in the Prince Albert National Park's greater ecosystem in winter, as evaluated based on RSF models at the park scale for small (≤ 15 individuals) and large (> 15 individuals) bison groups. The solid line represents the Parks' boundaries and dashed line delimits the range covered by radio-collared bison.

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Conclusion générale

L'étude a montré que le patron de sélection d'habitat par le bison des plaines (*Bison bison bison*) du parc national de Prince Albert varie en fonction de l'abondance des individus à différentes échelles spatiales. L'effet de la taille du groupe sur la sélection des ressources par le bison a été analysé à l'aide des fonctions de sélection des ressources (RSF). Les RSF sont un outil puissant pour comprendre la répartition spatiale des individus car elles permettent de tenir compte de la complexité des environnements hétérogènes sur l'organisation spatiale des animaux. Étant donné sa grande utilité dans le domaine de l'écologie, l'utilisation des RSF a largement augmenté au cours des dernières années. Par contre, malgré que les RSF aient été appliquées à des animaux grégaires (e.g., Mladenoff et al., 1999; Boyce et al., 2003), l'effet de la taille du groupe sur le processus de sélection de l'habitat a toutefois été peu exploré à l'aide de cette méthode. Pourtant, plusieurs études ont montré que la sélection de l'habitat pouvait varier en fonction de la densité et de l'abondance des individus (e.g., Pimm et al., 1985; Mitchell et al., 1990; Ramp et Coulson, 2002; Morris, 2003; Shepherd et Litvak, 2004). L'étude de McLoughlin et al. (2006) est l'une des rares à avoir utilisé des RSF pour comprendre les effets de la densité des individus sur la sélection de l'habitat par les grands herbivores. Cette étude ne tient toutefois pas compte que la sélection des ressources peut s'effectuer à plusieurs échelles spatiales. L'importance de l'échelle spatiales dans la compréhension de la sélection de l'habitat a été largement discutée (Senft et al., 1987; Manly et al., 2002; Boyce et McDonald, 1999; Boyce, 2006) et démontrée (Schaefer et Messier, 1995; Rettie et Messier, 2000; Johnson et al., 2002; Boyce et al., 2003; McLoughlin et al., 2004; Dussault et al., 2005). Notre approche est donc nouvelle car en plus d'utiliser les RSF afin de tenir compte de la complexité du processus de sélection de l'habitat à plusieurs échelles spatiales, elle considère que ce processus peut être influencé par la taille du groupe.

Sélection de l'habitat

La sélection de l'habitat par le bison des plaines du parc national de Prince Albert au cours de l'été 2005 et l'hiver 2006 peut être largement expliquée par le compromis entre l'acquisition de nourriture, les dépenses énergétiques reliées à l'exploitation de la ressource et le risque de prédation, ainsi que par l'effet de la taille du groupe sur ce compromis. Par exemple, à vastes échelles spatiales les bisons favorisaient l'utilisation des endroits où la disponibilité de la nourriture était la plus élevée en sélectionnant les sites formés d'une grande proportion de prés et, à l'échelle du parc, en évitant les forêts de conifères. À fine échelle spatiale, les bisons maximisaient leurs gains énergétiques à cours terme en sélectionnant les zones à l'intérieur du pré où l'abondance de *Carex atherodes* était la plus élevée. Par contre, l'acquisition des ressources par les bisons était dépendante de l'abondance des individus. Ainsi, à l'échelle du cercle de 700-m la sélection des zones entourées d'une grande proportion de prés augmentait avec la taille du groupe, alors qu'à l'intérieur du pré, l'intensité de la sélection pour *Carex atherodes* diminuait.

L'importance des coûts d'exploitation des ressources sur le patron de répartition spatiale des bisons a été révélée par la sélection ou l'évitement de certaines composantes de l'environnement, telles que les routes et le couvert de neige. La présence de route dans le paysage était positivement associée à la répartition estivale du bison à vastes échelles spatiales. À chacune des trois échelles spatiales les bisons évitaient les endroits où le couvert de neige (tel que caractérisé par son équivalent en eau) était important. À l'échelle du pré, les caractéristiques du couvert de neige n'ont toutefois eu aucun effet sur la sélection des sites de repos. Au contraire, la répartition du bison lors du comportement d'alimentation semblait refléter un compromis entre les gains d'énergie et la recherche de conditions de neige favorables, car en plus de sélectionner *Carex atherodes*, les bisons sélectionnaient aussi des plantes à faible profitabilité, telles qu'*Agropyron* spp. et *Calamagrostis inexpansa*. L'effet négatif de la neige sur les déplacements et le comportement d'alimentation des ongulés s'ajoute à une quantité croissante d'évidence empirique à cet égard (Houston, 1982; Parker et al., 1984; Telfer et Kelsall, 1984; Boertje, 1985; Fancy et White, 1985; Boyce et al., 2003; Dussault et al., 2005; Mao et al., 2005). Finalement, puisque les bisons ont quotidiennement besoin d'eau (McHugh, 1958), l'acquisition de cette ressource influençait les compromis à la base de la sélection de l'habitat. En effet, à l'échelle du parc les bisons favorisaient l'utilisation des endroits situés à proximité des points d'eau. Par contre, puisque l'utilisation de cette ressource est sporadique et de courte durée, l'utilisation des points d'eau était inférieure à ce qu'on pouvait s'attendre de façon aléatoire. En effet, les bisons évitaient les sites inondés à échelle étendue ainsi qu'à l'intérieur des prés lors des activités d'alimentation et de repos.

La sélection de l'habitat par le bison des plaines du parc national de Prince Albert semble également indiquer que les individus faisaient un compromis entre la disponibilité de la nourriture et le risque de prédation. En général, les bisons favorisaient l'utilisation des sites où la disponibilité de la nourriture était élevée (i.e., prés, zones où la proportion de prés est élevée) et où le risque de prédation était faible (i.e., zones à fortes densités de bordures offrant donc de bonnes possibilités de fuite). Ce compromis était toutefois dépendant de l'abondance des individus. En effet, le risque de prédation peut diminuer avec l'augmentation de la taille du groupe (Dehn, 1990; Lima, 1995; Roberts, 1996) et la fréquence des déplacements (Mittchell et Lima, 2002). Afin de diminuer la prédictibilité de leur localisation et par conséquent leur risque de prédation (Mittchell et Lima, 2002), il est possible que les petits groupes de bisons aient augmenté la fréquence de leurs déplacements entre les prés. Une telle réaction face au risque de prédation pourrait effectivement expliquer que les petits groupes de bison sélectionnaient les prés moins fortement que les grands groupes au cours de la saison hivernale. Une tendance observée aux deux plus vastes échelles spatiales. De plus, comparativement aux grands groupes, les petits groupes sélectionnaient davantage les zones à forte densité de bordures au cours de l'été. Aucun effet de la densité des bordures n'a été observé à l'échelle du cercle de 700-m durant la période hivernale. Au cours de l'hiver, les bisons choisissaient premièrement de s'établir dans les zones du parc qui procurent à la fois une forte disponibilité de nourriture, un faible couvert de neige et un risque de prédation faible, alors qu'à plus fine échelle, le compromis entre les coûts de déplacement dans la neige et l'acquisition de nourriture devenaient l'enjeu majeur de la sélection.

La répartition spatiale du bison à une échelle fine dépend toutefois de l'activité des individus. Durant l'approvisionnement, la répartition des bisons était associées aux caractéristiques abiotiques du pré ainsi qu'à la disponibilité de certains types de plantes, alors que durant les périodes de repos, la répartition spatiale des bisons était uniquement influencée par des facteurs abiotiques, tel que la présence d'eau, la pente et la distance par rapport à la forêt. En effet, ces derniers facteurs diminuaient la probabilité d'occurrence des bisons et l'effet de la pente était également dépendant de la taille du groupe.

Au cours de ce mémoire, nous avons discuté d'un ensemble de possibilités pouvant expliquer la réponse des bisons à l'hétérogénéité et la complexité de leur environnement en relation avec l'abondance des individus. Par contre, il est probable qu'il existe des explications alternatives à celles proposées dans ce document. Toutefois, il demeure indéniable que notre approche a montré que la répartition du bison des plaines était influencée à la fois par des facteurs abiotiques et biotiques à une variété d'échelles spatiales, et que l'effet de ces facteurs sur la sélection de l'habitat change en fonction de la taille du groupe.

La population de bisons du parc national de Prince Albert

Caractériser la sélection de l'habitat par les animaux en utilisant les fonctions de sélection des ressources (RSF) a permis de cartographier la probabilité d'occurrence du bison des plaines dans le parc national de Prince Albert et ses environs. En utilisant ainsi les RSF, nous avons mis en lumière les facteurs qui influençaient la répartition spatiale des individus et identifié les zones importantes pour la population où des mesures d'aménagement pourraient être posées afin d'éviter un éventuel conflit entre les hommes et le bison. Ces informations sont d'autant plus importantes puisque depuis mai 2004, les populations sauvages de bisons des plaines sont considérées comme menacées au Canada selon le Comité sur la Situation des Espèces en Péril du Canada (COSEPAC). L'étude fournit donc une base utile au développement de mesures d'aménagement qui permettront de préserver ce trésor national qu'est la population de bisons des plaines du parc national de Prince Albert.

Perspectives d'avenir

En terminant, bien que cette étude offre une contribution scientifique originale concernant les effets de la taille du groupe et de l'échelle spatiale sur le processus de sélection d'habitat, certaines perspectives de recherche restent encore à explorer. Par exemple, il serait intéressant de comparer l'effet de l'échelle spatiale sur la répartition des individus en utilisant une méthode permettant d'inclure directement une variable « échelle » dans les modèles. Plusieurs échelles pourraient alors être considérées dans un modèle unique. De plus, puisque la population de bison des plaines du parc national de Prince Albert est en constante augmentation depuis plusieurs années, il serait important d'étudier l'effet de la taille de la population sur la sélection de l'habitat par les bisons. Une telle étude permettrait de prévoir la répartition spatiale des individus en fonction de la croissance de la population et fournirait des outils utiles à l'élaboration de stratégies de gestion afin de mieux conserver la population de bisons des plaines du parc national de Prince Albert.

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