Influence des perturbations anthropiques, des conditions environnementales et des traits individuels sur l'utilisation de l'espace d'un ongulé alpin

Mémoire

Julien Hénault Richard

Maîtrise en biologie
Maître ès sciences (M.Sc.)

Québec, Canada

Résumé

L’étude de l’utilisation de l’espace permet de comprendre comment les individus se répartissent spatialement et comment ils interagissent entre eux et avec l’environnement. Mon projet portait sur l’utilisation de l’espace des chèvres de montagne en fonction de trois grands types de facteurs : les perturbations anthropiques, les conditions environnementales et la période de reproduction. Dans le cadre de travaux portant sur les impacts potentiels du développement d’un centre de ski alpin, nous avons démontré que les chèvres de montagne évitaient spatialement les perturbations anthropiques. Concernant l’influence des conditions environnementales, nos résultats indiquent que la quantité de neige fraichement tombée limite l’utilisation de l’espace des chèvres de montagne de manière plus importante que l’épaisseur totale de neige au sol. Enfin, durant la période de reproduction, les mâles augmentent leurs déplacements mais l’utilisation de l’espace semble peu influencée par leur masse ou leur âge. Nos résultats illustrent comment l’étude de l’utilisation de l’espace peut contribuer à la conservation de la faune.

Abstract

Space use studies allow a better understanding of the spatial distribution of individuals and how they interact among themselves and with their environment. We studied space use of mountain goats in relation to three main factors: anthropogenic disturbances, environmental conditions, and the reproductive period. During a project on the potential impacts of the development of a ski station, we showed that mountain goats spatially avoided anthropogenic disturbances linked to recreational activities. Regarding the influence of environmental conditions, our results revealed that recently fallen snow limits mountain goat space use substantially more than cumulative snow depth. Finally, during the reproductive period, males increased movements but age and mass did not affect space use. Our results underline how space use studies can inform wildlife conservation.

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Remerciements

Je tiens tout d'abord à remercier mon directeur Steeve Côté qui m'a donné l'opportunité de réaliser ce projet. J'ai toujours senti que Steeve me faisait confiance, ce qui m'a permis de m'accaparer le projet et d'en faire le mien. Ce processus m'a permis d'apprendre beaucoup de mes erreurs et de ses conseils quand j'en avais besoin. Je dois également une fière chandelle à mon codirecteur John Wilmshurst qui m'a été d'une aide indispensable sur le terrain. Je me suis très souvent rendu à son bureau avec des questions de toutes sortes et il a toujours su m'aider. J'ai aussi beaucoup appris de son expérience avec les parcs nationaux afin de naviguer les eaux tumultueuses de la bureaucratie fédérale et de la gestion d'un bien public. Son grand dévouement a été visible à plusieurs reprises, e.g. lorsque je l'appelais au beau milieu de la nuit pour aller faire une capture sous toutes sortes de conditions, malgré plusieurs obligations il trouvait moyen de venir nous aider. Bref, je n'aurais jamais été en mesure de compléter ce projet sans l'aide de ces deux scientifiques aguerris. Malgré qu'ils soient plutôt différents, les deux se soumettent à une grande rigueur et sont menés par une véritable passion pour l'écologie, deux traits qui me semblent indispensables pour réussir dans le milieu.

Merci aussi à Kevin White avec qui j'ai collaboré pour le 3ème chapitre, Kevin m'a donné accès à une importante base de données et m'a aidé tout au long du processus d'analyse et de rédaction. Il est également passé me voir à Jasper pour une rencontre de quelques jours dont je garde de très bons souvenirs.

Entreprendre une nouvelle étude sur les chèvres de montagne, comme je l'ai fait pour ce projet, requiert de la patience, de la détermination, de l'aide de plusieurs personnes et de l'argent. J'ai eu la chance d'être épaulé par deux organismes : Marmot Basin ski area et Parcs Canada qui ont financé l'ensemble de mon projet. De plus, ces deux organismes se sont impliqués en m'offrant de l'aide indispensable sur le terrain. Pour Marmot Basin, je tiens à remercier particulièrement Jason Paterson, Rob Ford et Rob Ellen qui m'ont apporté un soutien logistique important et se sont assurés que j'ai tout à ma disposition pour réaliser le projet. Je remercie également l'ensemble du « Snow safety team » qui m'a accueilli pendant quelques jours et m'a fourni des données de neige de qualité. Plusieurs employés de Parcs Canada m'ont grandement aidé à réaliser ce projet, particulièrement lors des captures. Merci à Steve Malcolm, Goeff Skinner, Terry Winkler et Grant Peregoodoff qui ont passé de longues heures enfermées avec nous dans une petite cache humide à raconter des histoires et espérer capturer des chèvres de montagne.

J’ai également eu la chance d’avoir trois assistants de terrains exceptionnels. Mon terrain était particulièrement exigeant d’un point de vue physique en raison des longues heures de marche et des conditions difficiles et d’un point de vue psychologique en raison de la difficulté à travailler avec des chèvres peu enclines à la recherche. Je sais que j’ai souvent poussé leurs limites et les miennes, mais tout le monde gardait le sourire. Merci à Chrystel, qui a du subir un des étés les plus froids et humides à Jasper de mémoire d’homme et toutes les difficultés d’une première saison de terrain. Elle s’en est tirée avec beaucoup de détermination et m'a maintenant dépassé alors qu’elle amorce son doctorat. Merci à Jonathan, qui était aussi motivé et enthousiaste qu’on peut l’être à marcher tous les jours tout au long de l’été. Merci à Élisabeth qui a su repousser ses limites à plusieurs reprises tout en restant toujours positive.

Je me dois aussi de remercier les membres du labo desquels j’ai également beaucoup appris et avec qui j’ai partagé plusieurs bons moments. Tout d’abord, les deux piliers Sonia et Caro qui s’assurent qu’on ne manque de rien et qui ont réponse à à peu près tout. Ensuite, il y a ceux qui m’ont donné ma première chance dans le labo : Marie-Andrée et Alex avec qui j’ai travaillé à Anticosti. Il y a les guerriers, qui étaient là à mon arrivée et qui sont toujours là : Glenn, Maël et Emilie. Ils m’ont tous grandement aidé à leur manière, Glenn a lu et commenté à peu près tout ce que j’ai écrit au cours de ma maitrise et m’a instruit en génétique, Maël m’a souvent secouru dans R et ARCgis et Emilie qui m’a généreusement accueilli à mon arrivée à Québec et qui a aussi lu plusieurs de mes écrits. Il y a les vieux : Joëlle, Marianne, Karine, Will, Yolande, Bert, Gaëlle, Janick qui ont quitté depuis, mais qui m’ont montré comment ça marchait les vraies affaires. Il y a aussi les partenaires de montagne : Rachel, Patrick et Karina qui me comprennent mieux que les autres lorsqu’on parle de chèvres. Il y a les migrateurs qui sont ceux qui ironiquement vont moins sur le terrain : Alex, Alice-Anne, Brett. Il y a les brouteurs de J-P : Sébastien, Valérie et j’ajouterais Julien qui changent notre point de vue en regardant la ressource végétale avant l’animal. Il y a les anticostiens : Michaël, Nicolas et Amélie que j’apprécie beaucoup même si je ne sais pas trop quoi dire à leur sujet. Je tiens également à remercier Jerod et Orphé du labo de Daniel Fortin avec qui j’ai partagé la gestion du chapitre de la Wildlife et plusieurs problèmes statistiques.

Je voudrais remercier ma famille qui m’a toujours supporté dans ce que je fais. Finalement, je voudrais remercier pour son aide et son support Sab avec qui je partage à peu près tout : mon labo, ma vie et mon amour.

Avant-propos

Ce mémoire comprend 3 chapitres en anglais sous forme d'articles scientifiques, ainsi qu'une introduction et une conclusion générales écrites en français. Ce mémoire s'inscrit principalement dans le contexte d'un projet appliqué portant sur les impacts potentiels du développement du centre de ski de Marmot Basin dans le Parc national Jasper en Alberta, sur la population régionale de chèvres de montagne. Le chapitre 1 traite des effets du centre de ski et des activités récréatives sur l'utilisation de l'espace des chèvres de montagne. Dans le chapitre 2 je me suis penché sur les effets de la neige récemment tombée et de l'épaisseur totale de neige sur l'utilisation de l'espace des chèvres de montagne. Les chapitres 1 et 2 ont été écrits avec Steeve Côté et John Wilmshurst. Le deuxième chapitre a été soumis à la Revue canadienne de zoologie. Pour le troisième chapitre, j'ai analysé des données récoltées par Kevin White et ses collègues du « Alaska Department of Fish and Game » dans le but d'explorer les liens entre l'effort reproducteur, les traits individuels et l'utilisation de l'espace des mâles chèvres de montagne. Steeve Côté et Kevin White ont révisé plusieurs versions de ce chapitre. Le troisième chapitre est paru dans le journal « Behavioral ecology and sociobiology ».

Introduction

Une connaissance approfondie de l'écologie des espèces est primordiale afin de gérer et de conserver adéquatement les populations sauvages (Primack 2002; Festa-Bianchet et Côté 2008). Une partie intégrante de l'écologie d'une espèce est définie par les déplacements et l'utilisation de l'habitat de celle-ci. Ces éléments représentent les composantes fondamentales des patrons d'utilisation de l'espace (Muller et Fangan 2008). L'étude de l'utilisation de l'espace permet de mieux comprendre comment les individus se répartissent spatialement et comment ils interagissent entre eux et avec l'environnement qui les entoure. L'utilisation de l'espace nous informe sur plusieurs aspects de la vie faunique qui ont d'importantes implications pour la conservation, la gestion et la compréhension de la dynamique des populations. Par exemple, la présence de corridors de déplacement ou de migration, les possibilités d'échange génétique intra ou interpopulations, les facteurs limitant la distribution, les habitats sélectionnés ainsi que les réactions face aux perturbations anthropiques peuvent tous être définis par l'utilisation de l'espace (Boyce et al. 2002; Burgman et Fox 2003). La compréhension de l'utilisation de l'espace d'une espèce cible permet aux gestionnaires de définir des secteurs clés afin de les gérer et les protéger adéquatement selon leurs rôles respectifs (Hodgson et al. 2009). Ce mémoire vise à étudier l'utilisation de l'espace d'un ongulé alpin en fonction de trois grands types de facteurs : les perturbations anthropiques, les conditions environnementales et la période de reproduction.

Variation dans l'utilisation de l'espace

En informant sur les caractéristiques du paysage les plus recherchées par un animal dans son domaine vital, la sélection d'habitat permet d'extrapoler ou de prédire l'utilisation de l'espace (Boyce et al. 2002). Les patrons d'utilisation de l'espace observés sont déterminés par un grand nombre de déplacements résultant d'une interaction entre le comportement animal et l'environnement (Murrell et Law 2000; Morales et al. 2005). Ainsi, les facteurs biotiques (ressources, compétition, prédation) et abiotiques (environnement) influencent l'utilisation de l'espace par la faune (Johnson et al. 2002, Gaillard et al. 2010, McLoughlin et al. 2010) et leur effet varie en fonction des caractéristiques et de l'état des individus (Borger et al. 2008). Par exemple, un individu en mauvaise condition physique sera davantage affecté par des conditions environnementales difficiles qu'un individu en bonne condition physique, ce qui limitera son utilisation de l'espace.

L’utilisation de l’espace étant le résultat de plusieurs étapes de déplacements distinctes, celle-ci peut varier en fonction de l’échelle spatiale (Johnson 1980) et temporelle (Borger et al. 2008) à laquelle on l’observe. Ainsi, un individu montrera vraisemblablement des patrons d’utilisation de l’espace distincts à différents stades de sa vie, puisque ses besoins liés à l’approvisionnement et à la reproduction changent avec l’âge (Alerstam et al. 2003; Borger et al. 2008). L’utilisation de l’espace d’un individu varie aussi selon les saisons et les conditions changeantes auxquelles il fait face, et ce afin d’assurer sa survie (Mysterud et al. 2008; Zeng et al. 2008; Aublet et al. 2009). Enfin, à plus fine échelle, l’utilisation de l’espace d’un individu varie au cours d’une journée. Il partage son temps entre des secteurs permettant un approvisionnement en ressources suffisant, et d’autres où le risque de prédation est moindre et où il peut se reposer (Ager et al. 2003). Le cycle jour-nuit détermine en grande partie le patron d’activité quotidien et souvent, le niveau d’activité augmente à l’aube et au crépuscule (Festa-Bianchet et Côté 2008, Pépin et al. 2009, Massé et Côté 2013).

La faune des régions tempérées ou alpines font face à de grands contrastes saisonniers. Les étés courts et les hivers longs qui limitent la disponibilité de fourrage sont caractéristiques des conditions retrouvées à des latitudes élevées. Les taux d’activité et de déplacements des herbivores sont donc fortement influencés par les conditions climatiques et la saisonnalité (Mysterud et al. 2008, Zeng et al. 2008, Aublet et al. 2009). Au cours de l’hiver, la neige peut grandement influencer l’utilisation de l’espace. La neige diminue les déplacements (von Hardenberg 2000; Fortin et Andruskiw 2003; Ratikainen et al. 2007), les niveaux d’activité (Beir et McCullough 1990), la taille des aires utilisées (Lovari et al 2006; Rivrud et al. 2010; van Beest et al. 2011) et l’accessibilité au ressources (Mysterud et al. 1997; Robinson and Merrill 2012). Ces modifications résultent principalement de l’augmentation des coûts énergétiques liés aux déplacements dans la neige (Parker et al. 1984). De plus, la neige augmente les risques de prédation (Peterson et Allen 1974; Hebblewhite 2005; Robinson and Merrill 2012) et le niveau de stress des individus (Moen 1976). Afin de limiter les conséquences néfastes entrainées par des conditions hivernales difficiles, plusieurs espèces d’ongulés modifient leur distribution spatiale en migrant dans des secteurs moins enneigés à plus faible altitude ou latitude (Mysterud 1999). Malgré tout, la neige vient souvent diminuer la survie des espèces herbivores (Turner et al. 1994; Loison et al. 1999; Coulson et al. 2001). Ainsi, l’hiver qui entraine une combinaison de stress alimentaire et de coûts énergétiques élevés, résulte en une période critique pour plusieurs animaux, dont les ongulés (Coulson et al. 2001; Garrot et al. 2003; Lovari et al. 2006).

Certains facteurs biotiques en lien avec la saisonnalité ont également une influence sur les patrons et les taux de déplacement des ongulés. La période du rut, par exemple, impose des contraintes particulières aux mâles qui tentent de trouver, de défendre et de se reproduire avec un nombre maximal de partenaires (Willish et Ingold 2007, Brivio et al. 2010). Durant cette période, l'effort reproducteur ou la quantité d'énergie investie dans la reproduction peut varier grandement entre les individus (Pelletier 2005). Délaissant souvent l'acquisition de ressources (Willisch and Ingold 2007; Brivio et al. 2010), les mâles vont allouer une grande partie de leurs réserves énergétiques dans la recherche et l'accaparement de femelles (Mainguy et Côté 2008). Ce comportement engendre une augmentation des déplacements des mâles durant le rut (Pépin et al. 2009; White et al. 2012). Le niveau accru de compétition intra-sexuelle pendant la période reproductive va mener certains individus à se déplacer jusqu'à des populations voisines (Hogg 2000; Jarnemo 2011). Ainsi, ces changements dans l'utilisation de l'espace vont refléter une partie de l'effort reproducteur des individus. Les femelles tendent pour leur part à réduire leurs déplacements en période de parturition (Festa-Bianchet et Côté 2008), tandis que les jeunes mammifères vont souvent suivre leur mère au cours de la première année de leur vie.

Les perturbations anthropiques et leurs conséquences

Les perturbations anthropiques ont le potentiel de modifier l'utilisation de l'espace et d'affecter plusieurs aspects de la vie de la faune sauvage (Knight et Gutzwiller 1995; Liddle 1997). Il est donc important de bien en connaitre les conséquences, spécialement dans un contexte de conservation. Les perturbations anthropiques peuvent se traduire pour l'animal en un contact direct avec les humains, une diminution de sa tranquillité ou une modification de son habitat.

Les deux premiers types de perturbations ont un effet direct sur la faune, mais présentent une grande étendue d'intensités, allant d'une personne rencontrant un animal à une mise à mort intentionnelle. Le troisième type de perturbations a un effet indirect sur l'habitat faunique et résulte de n'importe quelle modification d'origine anthropique pouvant aller de l'établissement d'un sentier de randonnée à celui d'une ville entière. Différents types de perturbations engendrent des réponses variées de la part des animaux et des conséquences différentes sur ceux-ci. Souvent, les animaux réagissent aux stimuli parce qu'ils les perçoivent comme étant différents de leur environnement naturel (Geist 1978) et parce qu'ils associent les perturbations anthropiques à un risque de prédation (Frid et Dill 2002).

Les perturbations anthropiques peuvent engendrer un large éventail de conséquences pour les ongulés. Des perturbations répétées pourraient pousser ceux-ci à éviter les secteurs perturbés. L'évitement est spatio-temporel, c'est-à-dire que les individus se déplacent vers un secteur différent à la suite de la perturbation ou évitent un secteur lorsque la perturbation a lieu et reviennent une fois celle-ci terminée (Hamr 1988; Yarmoloy et al. 1988; Wakefield et Attum 2006). Des perturbations chroniques pourraient mener à l'abandon d'un secteur alors que les niveaux élevés d'activité et de bruit d'origine anthropique sont les principales causes de l'évitement d'habitats de qualité (Sawyer et al. 2006). La taille de la zone sous l'influence d'une perturbation augmente avec la distance à laquelle un animal peut percevoir la perturbation, soit en raison de la visibilité ou de la propagation du bruit dans l'habitat (Miller et al. 2001). Puisque la plupart des ongulés peuvent percevoir ces stimuli sur des distances de plusieurs dizaines à quelques centaines de mètres, les impacts indirects d'activités récréatives peuvent affecter une zone plus grande que les impacts directs (Sawyer et al. 2006). Dans la plupart des cas, les ongulés vont quitter des habitats préférés pour des habitats moins appropriés, modifiant la capacité de l'individu à répondre à tous ses besoins et engendrant une augmentation du risque de prédation (Bender et al. 1998). Les perturbations anthropiques peuvent également mener à des réactions de stress et à des modifications comportementales qui entraînent généralement une diminution des gains et une augmentation des dépenses énergétiques (Geist 1978; Duchesne et al. 2000; Frid et Dill 2002). Ultimement, ces conséquences réduisent la valeur adaptative des individus et la taille des populations (Geist 1978; Knight et Gutzwiller 1995; Frid et Dill 2002).

La modification et la destruction de l'habitat constituent les principales menaces pour les espèces sauvages aux États-Unis et probablement dans le monde (Czech et al. 2000). La taille de la zone affectée et l'intensité de la modification de l'habitat influencent la réaction des animaux (Liddle 1997). Les pertes ou les modifications de l'habitat, qu'elles soient directes ou indirectes, forcent les ongulés à trouver de nouveaux habitats propices ou à occuper un habitat sous-optimal (Bender et al. 1998). Par exemple, les caribous forestiers (*Rangifer tarandus*) évitent les secteurs où la forêt a été coupée ce qui limite la quantité d'habitats disponible (Courtois et al. 2008).

Certaines perturbations anthropiques peuvent tout de même avoir des conséquences bénéfiques pour les ongulés. Puisque les prédateurs évitent souvent les zones habitées davantage que les proies, l'utilisation de ces zones peut servir de tactique d'évitement de la prédation par les proies (Robinson et al. 2010). C'est notamment le cas des wapitis (*Cervus canadensis*) du Parc national

Jasper qui utilisent les zones perturbées et à proximité des infrastructures humaines pour éviter la prédation par les loups (*Canis lupus*) (Beschta and Ripple 2007).

Jusqu'à récemment, les effets des centres de ski sur la faune et l'environnement avaient rarement été documentés (Morrison et al. 1995; mais voir Rixen et Rolando 2013). Les perturbations généralement associées au développement de centres de ski affectent premièrement l'habitat et consistent en routes d'accès, coupe d'arbre (piste ou sous-bois), installation de remontées mécaniques, développement d'infrastructures, compaction du sol, modification de la période de couvert de neige et changements dans la végétation (Morrison et al. 1995; Rixen 2013). Les activités récréatives reliées aux centres de ski peuvent également engendrer des impacts directs sur la faune entrainant des modifications d'utilisation de l'habitat en plus d'augmenter le niveau de stress des individus (Hamr 1988; Ferguson and Keith 1982; Arlettaz et al. 2013). Les perturbations directes au cour de l'hiver peuvent entrainer des dépenses énergétiques supplémentaires alors que les réserves et les ressources sont limités (Hammit and Cole 1987).

Habituation

Lorsqu'une perturbation persiste, les ongulés comme les autres espèces d'animaux peuvent s'habituer et tolérer une activité prévisible et non menaçante (Geist 1978). Les situations où la faune tolère la présence humaine sans signes clairs de réactions physiologiques ou comportementales ont été décrites comme de l'habituation (Shackley 1996). Dans la plupart des cas où les stimuli ne semblent pas avoir de conséquences néfastes pour les animaux, l'habituation est souvent partielle ou négligeable (Geist 1978; Frid et Dill 2002). Ainsi, l'habituation apparente ou l'absence de réponse comportementale claire n'indique pas nécessairement une absence de réaction face aux stimuli (MacArthur et al. 1982; Ellenberg et al. 2006). Par exemple, MacArthur et al. (1982) ont noté que des mouflons (*Ovis canadensis*) qui ne montraient pas de réactions visibles en présence d'humains voyaient tout de même leur rythme cardiaque augmenter. Chaque habituation est spécifique à son contexte et présente des limites spatio-temporelles (Higham et Shelton 2011). Ainsi, des individus habitués peuvent réagir fortement à une perturbation semblable dans un contexte différent.

Modèle d'étude : Utilisation de l'espace et budget d'activité des chèvres de montagne

La chèvre de montagne *(Oreamnos americanus)* est un ongulé alpin vivant exclusivement dans les montagnes de l'ouest de l'Amérique du Nord (Festa-Bianchet et Côté 2008). Elles sont ségrégées selon leur sexe et forment des groupes de femelles avec jeunes et des groupes de mâles adultes, sauf durant la période du rut qui a lieu en novembre (Festa-Bianchet et Côté 2008, Mainguy et al. 2008).

Les domaines vitaux varient entre 3 et 90 km^2 et tendent à être plus grands pour les mâles que pour les femelles, surtout pendant le rut (White 2006; Poole et al. 2009; Mountain Goat Management Team 2010). Les différences de taille des domaines vitaux entre les populations des divers sites sont probablement liées à la structure du paysage et à la distribution des ressources, tandis que les différences entre les sexes sont probablement liées aux comportements sociaux et reproducteurs (Singer et Doherty 1985, Côté et Festa-Bianchet 2003). À l'intérieur du domaine vital, les patrons de déplacement quotidiens varient en fonction des saisons et du sexe des individus. En général, les déplacements quotidiens sont plus importants pour les groupes de femelles (2-5 km/jour) que pour les groupes de mâles (moins de 1 km/jour) (Singer et Doherty 1985, Côté et Festa-Bianchet 2003). Côté et Festa-Bianchet (2003) suggèrent que les groupes de femelles se déplacent davantage afin de rendre leur position moins prévisible pour les prédateurs.

Les chèvres de montagne passent la majorité de leur temps à proximité de terrains de fuite, généralement caractérisés par des pentes abruptes et accidentées dont l'inclinaison varie entre 30 et 65° (Smith 1977, Haynes 1992, Gross et al. 2002), difficilement accessibles aux grands prédateurs (Chadwick 1983; Gross et al. 2002; Poole et al. 2009). La majorité des études ont trouvé que la distance au terrain de fuite est le principal facteur affectant l'utilisation de l'espace des chèvres de montagne (Von Elsner-Schack 1986, Poole et Heard 2003, Hamel et Côté 2007), ce qui appuie l'hypothèse selon laquelle la prédation est le principal facteur limitant des populations naturelles de chèvres de montagne (Festa-Bianchet et Côté 2008). De plus, il a été montré que les femelles accompagnées de jeunes, plus vulnérables à la prédation, demeurent plus près de terrains de fuite que les individus moins vulnérables (Hamel et Côté 2007). Les terrains de fuite peuvent également servir d'abri contre les conditions météorologiques inhospitalières des montagnes (Chadwick 1977, Von Elsner-Schack 1986). Même si des migrations saisonnières ont lieu dans certaines populations, l'association avec les terrains de fuite est observée annuellement (Hjeljord 1973). Les rares occasions où il est possible d'observer des chèvres de montagne à une certaine distance des terrains de fuite sont lors de déplacements effectués pour la migration, la dispersion ou pour accéder à des salines.

L'été, les chèvres de montagne sélectionnent surtout les zones alpines, au-dessus de la ligne des arbres, où elles profitent de la qualité nutritive de la végétation alpine durant cette période. Il semble qu'elles évitent les zones forestières en raison du risque plus élevé de prédation (Côté et Festa-Bianchet 2003).

L'hiver est une période critique pour les chèvres de montagne en raison de l'accès limité aux ressources et des conditions météorologiques difficiles. Durant cette saison, les déplacements sont limités en raison de la neige au sol (Hjeljord 1973, Chadwick 1983) et les domaines vitaux hivernaux sont réduits entre 2 et 50 % de la taille des domaines vitaux estivaux (Taylor et al 2006, Poole et al. 2009). Les chèvres de montagne utilisent des zones où le couvert de neige est minimal durant l'hiver (Smith 1977). Ces zones se trouvent soit sous couvert forestier ou en terrain abrupt et accidenté balayé par de forts vents (Hebert et Turnbull 1977, Côté et Festa-Bianchet 2003, Poole et al. 2009). Les caractéristiques de la topographie et du couvert forestier jouent probablement un plus grand rôle que l'accessibilité aux ressources dans la sélection d'habitat durant l'hiver (Taylor et Brunt 2007). Afin de survivre à la longue période hivernale, les chèvres de montagne utilisent une tactique d'économie d'énergie en limitant leurs déplacements (Poole et al. 2009), elles perdent néanmoins environ 30 % de leur masse au cours de l'hiver (Festa-Bianchet et Côté 2008). Une perturbation forçant les chèvres de montagne à changer de site d'hivernage pourrait entraîner des conséquences néfastes en raison de la disponibilité d'habitats convenables limitée par la neige au sol, des dépenses énergétiques élevées causées par des déplacements dans la neige et de faibles réserves d'énergie à la fin de l'hiver (Poole et al. 2009).

Enfin, comme l'ensemble des ongulés nord-américains, les chèvres de montagne utilisent des salines pour compléter leur nutrition. Ce comportement faciliterait la digestion et permettrait de pallier à un manque de minéraux (Ayotte et al. 2008). L'utilisation de salines est répandue chez les chèvres de montagne, la grande majorité des visites s'effectuant entre la fin mai et la mi-août. L'utilisation de salines par chaque individu est variable, et ce, même à l'intérieur d'une population (Ayotte et al. 2008, Poole et al. 2010). Certains individus peuvent se déplacer sur de longues distances (jusqu'à 17 km), souvent dans des zones forestières, afin de rejoindre une saline (Poole et al. 2010). Les salines et leurs sentiers d'accès sont considérés comme des composantes importantes de l'habitat et de l'écologie des chèvres de montagne (Hebert et Cowan 1971; Hengeveld et al. 2003). Il semble que celles-ci soient très fidèles aux salines qu'elles visitent, et ce, sur plusieurs générations (Hengeveld et Caldwell 2004). L'incapacité ou la réticence à accéder à une saline pourrait créer une carence en ressources essentielles qui mènerait à une diminution de la valeur adaptative des individus et éventuellement à une diminution de la viabilité de la population (Goslin 2003).

Les chèvres de montagne et les perturbations anthropiques

Comparativement à la plupart des autres ongulés de l'Amérique du Nord, les chèvres de montagne sont plus sensibles aux perturbations anthropiques (Smith 1976; Penner 1988; Côté 1996) et semblent s'y habituer difficilement (Côté 1996; Gordon et Reynolds 2000; Côté et al. 2013). Toutefois, certaines populations exposées à des stimuli prévisibles et continus ont montré un certain niveau d'habituation face aux perturbations (Singer 1978; Penner 1988). Dans la plupart des cas, par contre, les conséquences des perturbations sont considérées comme additives et entraînent des modifications dans le comportement, l'utilisation de l'espace et la dynamique de population (Foster et Rahs 1983, Joslin 1986). Les chèvres de montagne réagissent fortement à plusieurs activités humaines : survol d'aéronefs (Côté 1996; Gordon et Reynolds 2000; Côté et al. 2013), exploration sismique (Joslin 1986), développement industriel (Foster et Rahs 1983), circulation routière (Singer 1978), passage de véhicules tout-terrain (St-Louis et al. 2013) et rencontre avec des humains (Foster et Rahs 1983). Généralement, les chèvres de montagne vont s'éloigner rapidement de ces sources de perturbations, demeurer alertes pendant de longues périodes ou éviter les secteurs perturbés. Ainsi, une zone tampon de 1,5 à 2 km a été suggérée et utilisée afin de limiter les impacts d'activités industrielles et de vols d'hélicoptère sur les chèvres de montagne (Foster et Rahs 1983; Côté 1996; Mountain Goat Management Team 2010; Cadsand 2012). Par contre, les impacts d'activités récréatives non motorisées sur les ongulés, et spécifiquement sur les chèvres de montagne, sont méconnus (Mountain Goat Management Team 2010). Généralement, les humains se déplaçant à pied engendrent des réactions plus fortes chez les animaux comparativement à des véhicules motorisés ou des vélos, possiblement parce que les déplacements des gens à pied sont moins prévisibles (Papouchis et al. 2001; Stankowich 2008) et pourraient être davantage perçus comme un risque de prédation.

Objectifs et hypothèses

Ce mémoire s'inscrit principalement dans le contexte d'un projet appliqué portant sur les impacts potentiels du développement du centre de ski de Marmot Basin dans le Parc national Jasper en Alberta, sur la population régionale de chèvres de montagne. Bien que certaines parties du mémoire soient en lien direct avec ce projet appliqué, d'autres parties étudient des aspects plus fondamentaux de l'utilisation de l'espace des chèvres de montagne.

Le premier chapitre est en lien direct avec le projet appliqué et résume les principaux résultats concernant l'utilisation de l'espace des chèvres de montagne en fonction des perturbations anthropiques. À l'aide de données provenant de colliers GPS et d'observations directes, nous avons déterminé l'influence du centre de ski de Marmot Basin et d'activités récréatives de faible impact (randonnée pédestre) sur l'utilisation de l'espace par les chèvres de montagne.

Le deuxième chapitre étudie l'influence des conditions de neige sur l'utilisation de l'espace des chèvres de montagne. En raison du vent presque constant que l'on retrouve en milieu alpin, le couvert de neige durcit et se déplace constamment. Ainsi, nous émettons comme hypothèse que la quantité de neige fraîche est plus représentative des conditions rencontrées par la faune en milieu alpin et qu'elle devrait être plus limitante que l'épaisseur totale de neige pour l'utilisation de l'espace par les chèvres de montagne. Nous testons cette hypothèse en étudiant les relations entre différentes mesures de neige et l'utilisation de l'espace à court terme des chèvres de montagne durant deux hivers. Pour ce faire, nous avons utilisé des colliers GPS installés sur des chèvres à proximité de la montagne de Marmot où le centre de ski de Marmot Basin enregistre les conditions de neige 2 fois par jour tout au long de l'hiver.

Le troisième chapitre étudie l'utilisation de l'espace des chèvres de montagne mâles au cours du rut. Les déplacements des mâles pendant le rut peuvent influencer leurs opportunités de reproduction et engendrer des coûts. Ainsi, l'utilisation de l'espace des mâles en période de reproduction pourrait être utilisée comme mesure de l'effort reproducteur. Par l'analyse d'une base de données géospatiales de 47 individus provenant de la région de Lynn Canal en Alaska et munis de collier GPS sur une période de 5 ans (2005-2009), nous visons à : 1) étudier les relations entre des caractéristiques des mâles (âge et masse) et leur utilisation de l'espace et à 2) déterminer la fréquence des migrations reproductrices. Les hypothèses générales sont : 1) les mâles possédant une masse élevée pour leur classe d'âge sont en meilleure condition et peuvent donc investir davantage dans les déplacements pendant le rut, 2) les mâles plus âgés et plus dominants ont un accès privilégié aux femelles et ont donc moins besoin de se déplacer et 3) les jeunes mâles sont plus portés à participer à une migration reproductive afin d'éviter la compétition avec les mâles dominants.

Chapitre 1 : Space use analyses suggest avoidance of a ski area by an alpine ungulate - L'utilisation de l'espace d'un ongulé alpin suggère l'évitement d'un centre de ski

Julien Hénault Richard[1], Steeve D. Côté[1] et John Wilmshurst[2]

[1] Département de biologie et Centre d'études nordiques, Université Laval, 1045 av. de la médecine, Québec, QC, Canada, G1V 0A6

[2] Parcs Canada, Parc national Jasper, Jasper, Alberta, Canada

Résumé

Le développement des activités récréatives engendre une pression anthropique grandissante sur les espaces sauvages de la planète. Ainsi, afin de gérer les aires protégées de manière appropriée, il est important de comprendre les effets des activités récréatives sur l'environnement. Puisque les perturbations anthropiques peuvent entrainer des changements dans l'utilisation de l'habitat par la faune, les études d'utilisation de l'espace permettent de déterminer la réaction de la faune face à ces perturbations. Les chèvres de montagne (*Oreamnos americanus)* sont sensibles aux perturbations anthropiques et doivent être gérées conséquemment. De 2011 à 2013, nous avons étudié l'utilisation de l'espace des chèvres de montagne dans le Parc national Jasper en Alberta, un des parcs les plus visités en Amérique du Nord, afin de déterminer l'influence d'un centre de ski alpin sur celles-ci. La comparaison de l'utilisation prédite par des modèles de sélection d'habitat et de l'utilisation observée à l'aide de colliers satellites nous a permis de démontrer l'évitement du centre de ski. Les chèvres de montagne mâles semblent moins sensibles aux perturbations anthropiques que les femelles. La présence d'une saline, qui est une composante importante de l'habitat et de l'écologie des chèvres de montagne, à moins de 1 km du centre de ski pourrait en partie expliquer pourquoi la montagne de Marmot est toujours grandement utilisée malgré l'évitement du centre de ski. Le développement et les activités liés à des centres de ski ont le potentiel d'exclure les chèvres de montagne d'habitat de qualité et devrait être gérer dans cette perspective. Notre approche est utile pour identifier des zones où des divergences entre l'utilisation de l'espace prédite et observée surviennent et où plus d'attention est nécessaire afin de comprendre l'utilisation de l'espace de la faune dans un contexte de perturbation anthropique.

Abstract

The development of recreational activities imposes growing anthropogenic pressure on wilderness areas worldwide. Because anthropogenic disturbances may result in modifications of wildlife habitat use, space use studies may be useful to identify wildlife response towards recreational activities. Mountain goats (*Oreamnos americanus*) are highly sensitive to anthropogenic disturbances. From 2011 to 2013, we studied mountain goat space use in Jasper National Park, Canada - one of the most popular wilderness areas in North America – and assessed how it was influenced by an alpine ski area. Comparison of predicted use from habitat selection models and observed use defined by GPS collars data revealed avoidance of the ski area. Female mountain goats appeared to be more sensitive to human disturbance than males. The presence of a natural salt lick less than 1 km from the ski area could partly explain why the area is still highly used by mountain goats despite the avoidance of the ski area. Development and activities related to ski areas have the potential to exclude mountain goat from high quality habitat and should be considered. Our approach is useful in identifying areas where discrepancies between predicted and observed space use occur and where more attention is needed to understand animal space use in the context of disturbance.

Introduction

Accessibility and use of wild areas by recreationists have increased dramatically in the last 3 decades (Knight and Gutzwiller 1995; Buckley 2004). One factor contributing to this trend is the growing popularity of recreational activities that inevitably increases the demand for supporting infrastructure. This in turn imposes anthropogenic pressure on wilderness areas worldwide (Knight and Gutzwiller 1995). Protected areas that offer such recreational opportunities are thus facing increased pressure on their principal roles of protecting wilderness and educating users (Hammit and Cole 1987; Liddle 1997) due to potential conflicts with emerging recreational activities (Cole and Knight 1991). Thus, it is essential to understand the effects of recreational activities on wilderness to successfully manage protected areas.

Human disturbance has been shown to have many consequences for animals. First, repeated disturbance may cause animals to avoid affected areas. The avoidance may be spatial; animals move to a different area following disturbance, or temporal; animals avoid an area when the disturbance is occurring and return when the disturbance has ended (Harm 1988; Yarmoloy et al. 1988; Lusseau 2004; Wakefield and Attum 2006). The extent of area avoided increases with the distance that an animal perceives the disturbance (Miller et al. 2001). Habitat alteration or destruction represent a large part of animal disturbance and is the main cause of species endangerment in the United States (Czech et al. 2000), and possibly worldwide. Direct or indirect habitat loss force animals to find new suitable habitat or occupy marginal habitat and can result in overall population declines (Bender et al. 1998). Although wildlife generally avoids humans, they may habituate to and tolerate a predictable non-threatening activity (Geist 1978; Knight 2009). Wildlife habituation is most related to resource availability, where animals tolerate human presence because it is associated with access to resources (Hammit and Cole 1987).

Space use analyses are useful to detect and understand wildlife reaction to anthropogenic disturbances. Animal movements and habitat use are fundamental parts of animal ecology and can contribute to the analysis of interactions between animal behaviour and the environment (Morales et al. 2005; Mueller and Fangan 2008; Fieberg and Börger 2012). While space use defines the extent of area used by animals, habitat selection reflects resource needs within that space. Measuring space use relative to its availability is a surrogate measure of habitat value and potential constraints on its use (Manly et al. 2002). Predation risk is a defining constraint on habitat selection (Dussault et al. 2005; Hebblewhite 2005) and because human activity may be perceived as predation risk by prey species, it may also be a significant constraint on habitat selection (Frid and Dill 2002).

Until recently, the effects of ski areas on the environment and wildlife had rarely been documented (Morrison et al. 1995; but see Rixen and Rolando 2013). Typical disturbances related to ski areas are mostly indirect through habitat alteration: service roads, tree removal (ski runs and gladeing), chair lift installation, infrastructure development, soil compaction, variation in the duration of the period of snow cover and changes in vegetation (Morrison et al. 1995; Rixen 2013). Direct impacts on wildlife may also result from recreational activities occurring within or close to the ski areas. For example, in Europe, chamois (*Rupricapra rupricapra*) react strongly to approaching downhill skiers (Hamr 1988). Disturbance occurring during winter may induce costly displacement to wildlife at a time when energy reserves and resources are limited and most species attempt to conserve energy by limiting their movements and range (Hammit and Cole 1987). Ski area maintenance activities occurring at any time of the year and avalanche control activity during winter may also represent sources of animal disturbance.

In comparison to other North American ungulates, mountain goats *(Oreamnos americanus)* are particularly sensitive to anthropogenic disturbances (Geist 1978; Gordon and Reynolds 2000; Festa-Bianchet and Côté 2008). Cases of mountain goat habituation are known but limited (Singer 1978; Penner 1988; Gordon and Reynolds 2000; Côté et al. 2013). In most cases, impacts of disturbances to mountain goats are thought to be additive and result in important changes in behaviour, space use and population dynamics (Foster and Rahs 1983; Joslin 1986). Mountain goats appear to react adversely to many activities: aircraft flight (Côté 1996; Gordon and Reynolds 2000; Côté et al. 2013), seismic exploration (Joslin 1986), industrial development (Foster and Rahs 1983), road traffic (Singer 1978), all-terrain vehicles (St-Louis et al. 2013) and human confrontation (Foster and Rahs 1983). Buffer areas of 1.5 km to 2 km have been suggested and used to limit the impact of helicopter and industrial activities on mountain goats (Foster and Rahs 1983; Côté 1996; Mountain Goat Management Team 2010; Cadsand 2012). The impacts of non-motorized recreational activities on mountain goats are, however, poorly understood (Mountain Goat Management Team 2010). Humans on foot generally induce stronger reactions from animals than motorized vehicles, possibly because foot traffic is less predictable (Papouchis et al. 2001; Stankowich 2008). It is thought that any recreational activity occurring in areas inaccessible to motorized traffic may result in disturbance or displacement of mountain goats (Mountain Goat Management Team 2010). It seems that where recreation and mountain goat habitat overlap, special attention needs to be paid to coexistence (Foster and Rahs 1983; St-Louis et al. 2013; Côté et al. 2013).

Mountain goats are generalist herbivores (Laundré 1994). They spend the vast majority of their time in close proximity to escape terrain (Haynes 1992; Gross et al. 2002) and are associated with mid to high elevations especially in summer, where they take advantage of the high forage availability above the treeline and the relative protection from predators. Natural licks used to supplement nutrition (Ayotte et al. 2008), and their access trails are considered important components of mountain goat habitat and ecology (Hebert and Cowan 1971; Hengeveld et al. 2003). It appears that mountain goats show strong fidelity to specific licks and access trails, and demonstrate traditional use over successive generations (Hengeveld and Caldwell 2004). Inability or unwillingness to access a lick could result in a deficiency of essential resources possibly leading to decreased fitness and eventually decreased population viability (Goslin 2003). Based on habitat selection models, GPS collar data and behavioral observations, we studied the effects of an existing alpine ski area on the space use of mountain goats. We also evaluated the potential effects on mountain goats behaviour by assessing the reactions of mountain goats toward hikers and human activity in proximity of a crucial habitat feature, a mineral lick. We could not evaluate the reaction of mountain goats toward skiers but reaction toward hikers should be a conservative indication of how they would react to skiers, as skiers will move with greater speed which usually induces stronger reactions (Frid and Dill 2002). We hypothesized that mountain goats would react adversely to any human activity and avoid the ski area at all times, but particularly during winter when activity level associated with the ski area is higher. As such, we predicted that high quality habitat within the ski area would be used less than high quality habitat outside the ski area, and that human presence and activity would limit the use of a natural lick. Finally, we predicted that mountain goats should move away from hikers.

Materials and Methods

Study site

Marmot Basin is the only downhill ski area in Jasper National Park and is located on Marmot Mountain (53.80°N, 118.08°W), approximately 10 km south of the town of Jasper in west central Alberta, Canada. Marmot Mountain is part of the Trident Range, which delimited the 125 km^2 study area. The region is at the front of the subarctic and humid continental climates and is divided in three ecosystems: montane, subalpine and alpine. The ski area has been in operation since 1964 and is usually open from mid-November to early-May.

Licks

The Whistlers Creek mineral lick is located in a narrow valley less than 1km to the north of the ski area (Figure 1.1). The lick is just below tree line at an elevation of 1915 m. The ground is covered with grasses and forbs and the lick is surrounded by subalpine forest containing mostly white spruce

(*Picea glauca)*, Engelmann spruce (*Picea engelmannii)* and subalpine fir (*Abies lasiocarpa)*. To evaluate the use of the Whistlers Creek lick by non-collared individuals, two camera traps were set from late May to early September from 2010 to 2013. We collected a total of 45,980 pictures that provided information on timing and duration of visits as well as visiting group composition. To determine whether some individuals used other licks, we also used cameras to monitor the Muhigan lick located about 7 km from the Whistlers creek lick from June 2012 to August 2013. We recorded 26,388 photos from that lick.

Captures

We captured and marked 8 individuals with GPS collars (GPS PLUS Iridium collars, VECTRONIC Aerospace GmbH, Berlin, Germany) and ear tags from 2011 to 2013. Of those 8 individuals, 5 were females aged 3 years old and older and 3 were males aged 4 years old and older. The Whistlers Creek lick site was used for captures with self-triggered Stevenson style wooden box traps. Before handling, mountain goats were immobilized with an intramuscular injection of xylazine hydrochloride (Rompun, Bayvet Division, Etobicoke, Ontario, Canada) at a dosage of 5mg/kg. Following handling procedures, the effect of xylazine was reversed by intramuscular injection of 0.9-1.2 mg of idazoxan (RX 811059, Reckitt and Colman, Kingston-upon-Hull, United Kingdom; Haviernick et al. 1998). All captured animals were hobbled and a mask was placed over their eyes to minimize outside stimuli. Animals received supplemental oxygen during handling. All capture and handling procedures were approved by the animal care committee of Université Laval, Québec and Parks Canada.

GPS data

The GPS collar recording schedule was: from May 1st to October 14th (summer), every 3 hours and; from December 16th to April 30th (winter), every 6 hours. GPS data used in this study were recorded between June 2011 and August 2014. Seasons were defined using expert knowledge and a literature review of mountain goat movements and activity. Out of the approximately 25,000 location points obtained by GPS collars, we removed all data with improbable elevations or with a Dilution of Position (DOP) over 10 (~ 3% of the locations), that occurs as a result of poor satellite coverage (D'Eon and Delparte 2005). After screening we based our analyses on 23,434 valid location points from 8 individuals.

Field observations

To estimate the use of Marmot Mountain by uncollared individuals and behavioural response of mountain goats towards hikers, field observations of mountain goats were conducted frequently using binoculars and spotting scopes. Over 3 field seasons (2011-2013), we spent 152 observation-days within the Trident Range area and recorded 277 mountain goat groups for a total of 839 individual observations. Mountain goat herds are sexually segregated and form distinct nursery (females with young) and bachelor groups (adult males) for most of the year except during the rut (Festa-Bianchet and Côté 2008). Group size, location, composition and activity were recorded for each observation. To limit disturbance we generally tried to avoid approaching mountain goats. When encounters occurred within 1km, we recorded the distance between us and mountain goats, and their reactions to our presence according to 4 classes (Table 1.1). Distances were measured using a laser range finder (Bushnell Elite 1500, Bushnell Performance Optics, Overland Park, KS, USA) with a 1km detection range. Hiking group size varied from 1 to 3 persons, but 2 persons were present for the great majority of encounters.

Table 1.1 Description of mountain goat reaction classes to humans on foot, Jasper National Park, Alberta, Canada, 2011 to 2013.

Classes	Description
1	Notice our presence but do not modify its previous behavior.
2	Look at us regularly. If feeding, continue to feed while moving away slowly. If bedded, stay bedded.
3	Alert, look at us continuously and intensively. If away from escape terrain, move away, if in escape terrain, stand and stay alert.
4	Run away.

Space use

GPS data were used to estimate individual and population habitat use and home ranges. Home range sizes were determined with 95% kernel density estimates (KDE; Silverman 1986) in R, version 2.13.0 (R Development Core Team 2011).. The value of the smoothing parameter (h) was determined using the reference method which assumes that the utilisation distribution (UD) is bivariate normal (Worton 1995). Home range locations were identified through an Adaptive Local Convex Hull (a-LCH) as this method can identify range boundaries more precisely (Getz et al. 2004; 2007). A-LCH are Kernels constructed from all points within a radius "*a*" such that the distances of all points within the radius to the reference point sum to a value less than or equal to *a* (Getz et al. 2007). The value of *a* was set as the maximum distance between any two points in the analysed data set (Getz et al. 2007). A-LCH represent the smallest areas containing a given utilisation distribution percentage. We analysed summer and winter space use separately. Because of collar malfunction and animal death, 5 individuals (3 females and 2 males) were followed over and entire year. As such, only these individuals were used in the annual home range analyses. All home range and UD analyses were performed with the "adehabitatHR" package in R (Calenge 2006).

Because no trapping occurred at the Muhigan lick or at the Whistlers Creek lick in 2010, we could compare temporal patterns of lick use with and without trapping activity. We compared proportions of daytime visits between sites or years with and without trapping. We used the arcsines of the square root of proportion of daytime visits to overcome the non-normal distribution of proportions tested with a linear model (Sokal and Rohlf 1995).

Using direct field observation and camera data, we evaluated the importance of the Whistlers Creek lick to lactating females. With a binomial model, we compared the probability of seeing a female with kid at the mineral lick and elsewhere on the mountain.

Habitat selection

To characterise mountain goat habitat selection we calculated a Resource Selection Function (RSF) with a presence/availability design (Boyce et al. 2002; Fortin et al. 2008). To predict the relative probability of use within the study area we used logistic regression comparing characteristics of used versus random points within the study area. Because of the limited number of individuals we combined female and male locations for the analyses. We performed RSF analyses separately for summer and winter seasons to account for changes in environmental conditions. For summer we had a total of 17,397 locations from 8 individuals (5 females and 3 males), while we had 6,037 locations from 6 individuals (4 females and 2 males) for winter. An equal number of available locations selected randomly within the population home range were used in the analyses. The seasons were defined in the same manner as for the GPS data (see above).

We selected a set of 7 predictive variables and biologically meaningful interactions among these variables that could influence mountain goat habitat selection (calculated at a resolution of 24 X 24 m). Topographical (physical) characteristics of the landscape are most useful for characterising mountain goat habitat (Gross et al. 2002; Poole et al. 2009). Moreover, collared mountain goats spent the vast majority of their time in the alpine, so the use of vegetation cover types was not relevant to our analyses. Therefore, we included only abiotic and topographical variables in the RSF analyses. The abiotic characteristics of the landscape were all derived from a Digital Elevation Model (DEM) (ASTER global digital elevation model) data with 24m cells (Table 1.2). For each grid cells we calculated the distance to the nearest escape terrain which was defined by slopes of ≥40° or 84% (Poole et al. 2009; Shafer et al. 2012). Solar radiation is known to influence mountain goats space use (Taylor et al. 2006; Poole et al. 2009; White et al. 2012) as it is an index of snow depth and density (Pomeroy et al. 1998). Solar radiation was calculated using the *area solar radiation* function in ArcGIS which gives the total amount of solar radiation in watts that reached each cell during each analysed period. Slope, curvature and aspect grids were produced using the DEM surface tool (Jenness 2004) in ArcGIS. In the models, aspect effects were estimated using flat areas as reference. We used either the solar radiation or aspect variable in a model because they were closely related. We did the same for curvature and ruggedness because the latter was calculated using the curvature values. We centered elevation values to the average elevation in the study area (2104m) to improve interpretability and limit correlation with the squared elevation variable (Schielzeth 2010). Squared elevation was used to allow a non-linear relation with elevation, which was expected as mountain goats in the area use elevations between 2000m and 2500m.

We developed an *a priori* set of candidate models based on literature and field observations (Appendix 1). Individual's identity and year of observation were included as random effects in all models to account for individual and annual variability in habitat selection. We then assessed the strength of competing models based on Akaike's information criterion and parsimony (AIC; Anderson and Burnham 2002). We performed a *k*-fold cross validation on the best model for each period to evaluate predictive strength (Boyce et al. 2002). The *k*-fold cross validation represents a Spearman-rank correlation, thus correlation values closer to 1 represent a higher prediction success. For each period, we repeated the cross validation 10 times and we calculated an average correlation score with standard deviation. Because mountain goats showed high site fidelity, GPS data suffered from autocorrelation. Generalized estimating equations (GEE) are often used to obtain robust standard errors in presence of autocorrelation (Fortin et al. 2005). In our case, the autocorrelation is such that we could not identify time lags when autocorrelation stopped, which is necessary to perform GEE. Nevertheless, effect sizes are robust to this and therefore valid, while standard error and p-values are underestimated (Nielson et al. 2002). Spatial analyses were conducted in ArcGIS (version 10, 2010, ESRI, Redlands, CA, USA) and R (version 2.12.2, 2011, The R Foundation for Statistical Computing), which was also used for statistical analyses.

Table 1.2 Description of variables used in modelling habitat selection by mountain goats in Jasper National Park, Alberta, Canada, 2011 to 2013.

Variable	Description
curvature	A numerical value indicating the shape of a slope. Positive values represent a convex slope while negative values represent a concave slope
ruggedness	An index representing the standard deviation of curvature in a 100m radius around each grid cell (Poole et al. 2009)
east	Aspects were calculated using a value between 0 and 360°, which was then classified in four different aspects
north	
south	
west	
solar radiation	A value in watts (W) representing the cumulative amount of solar energy reaching a cell
centered elevation	Elevation value minus average elevation (average = 2104m)
elevation^2	Square of the centered elevation value
distance escape	Distance to nearest slope ≥40°

Predicted and observed use

To quantify the use of the ski area by mountain goats, we measured the number of points recorded in areas of high use probability within and outside the ski area on Marmot Mountain. Because all collared individuals used the west, north-west and south-west faces of Marmot Mountain which are surrounding the ski area, we assumed that high quality habitat located within and outside the ski area was available to all individuals. We assigned high probability of use to cells having a year round RSF prediction ≥ 0.7. We then summed the number of observations within these areas of high use probability for both parts of Marmot Mountain (ski area vs others). We report the number of observations per square kilometer of high use probability terrain.

Results

Collared mountain goats inhabiting the Trident Range area remained almost exclusively above tree line, but avoided the very highest elevations. With a few exceptions (long distance movements by males), this general pattern was observed year round for both sexes. Mountain goats of both sexes remained close to escape terrain year round, as females and males spent 91% and 88% of their time, respectively, within 100 m of escape terrain, and >70% of their time within 50 m of escape terrain.

Home ranges

Home range size varied among seasons (Appendix 2). For individuals of both sexes, the largest seasonal home ranges occurred during summer, while the smallest seasonal home ranges occurred during winter. Male home ranges overlapped with female home ranges, but were much larger

(Table 1.3). The ski area was not part of the females' and seldom part of the males' home ranges, but other areas of Marmot Mountain were used intensively by both sexes (Figures 1.1 and 1.2). Males represent the majority of mountain goat use on Marmot Mountain during winter (67.7% of observations over 2 winters).

Table 1.3 Individual annual home range sizes measured with Kernel density estimates for mountain goats, Jasper National Park, Alberta, Canada, 2011 to 2013. (UD: Utilisation distribution; percentage of time spent in each area)

	area (km^2)				
	Females			Males	
% of UD	#444	#557	#565	#475	#562
50	7.9	11.3	2.5	18.8	12.4
75	15.8	21.0	6.7	37.5	28.7
90	23.4	33.3	12.5	68.8	52.6
95	28.1	40.5	16.6	106.3	69.9

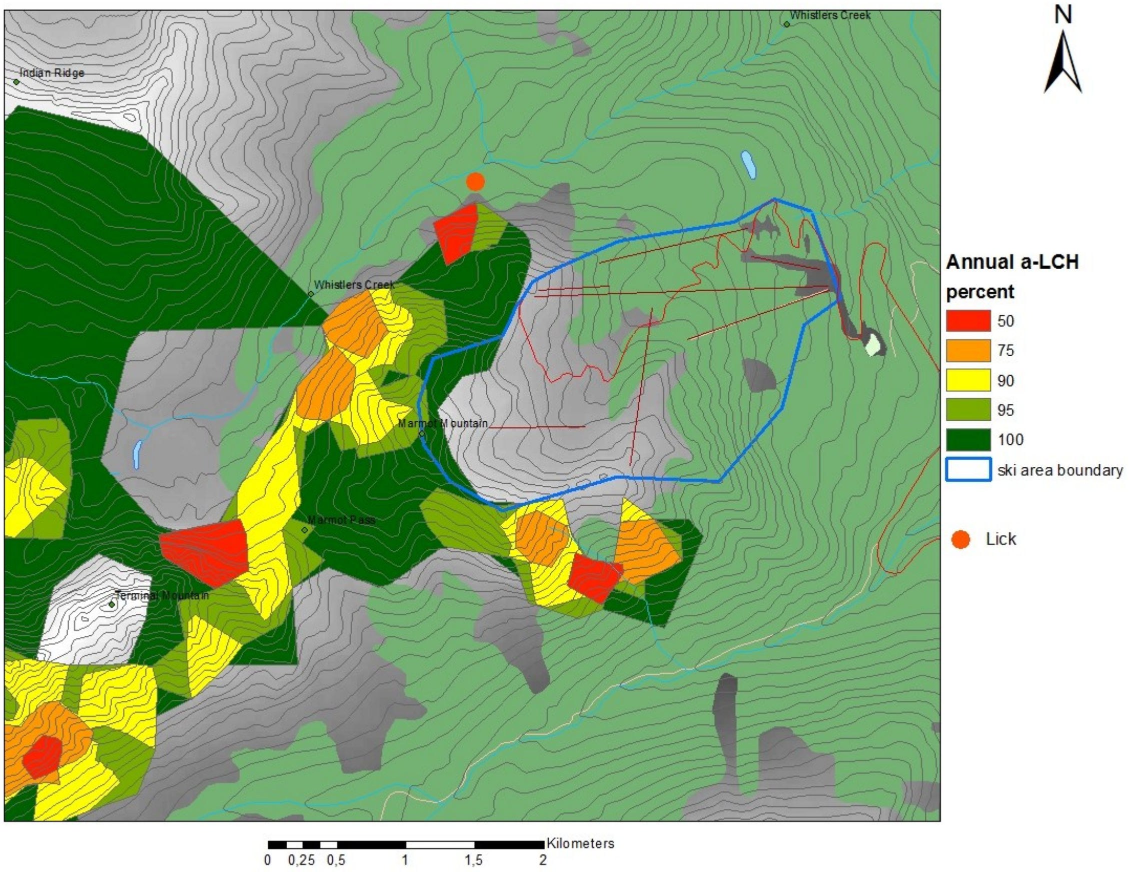


Figure 1**Erreur ! Utilisez l'onglet Accueil pour appliquer 0 au texte que vous souhaitez faire apparaître ici.**.1 Annual home range for a group of 3 adult female mountain goats around Marmot Mountain, Jasper National Park, Alberta, Canada in 2012. Adaptive Local convex hull (a-LCH)

shows the smallest combination of areas containing a certain utilisation distribution percentage represented by colors.

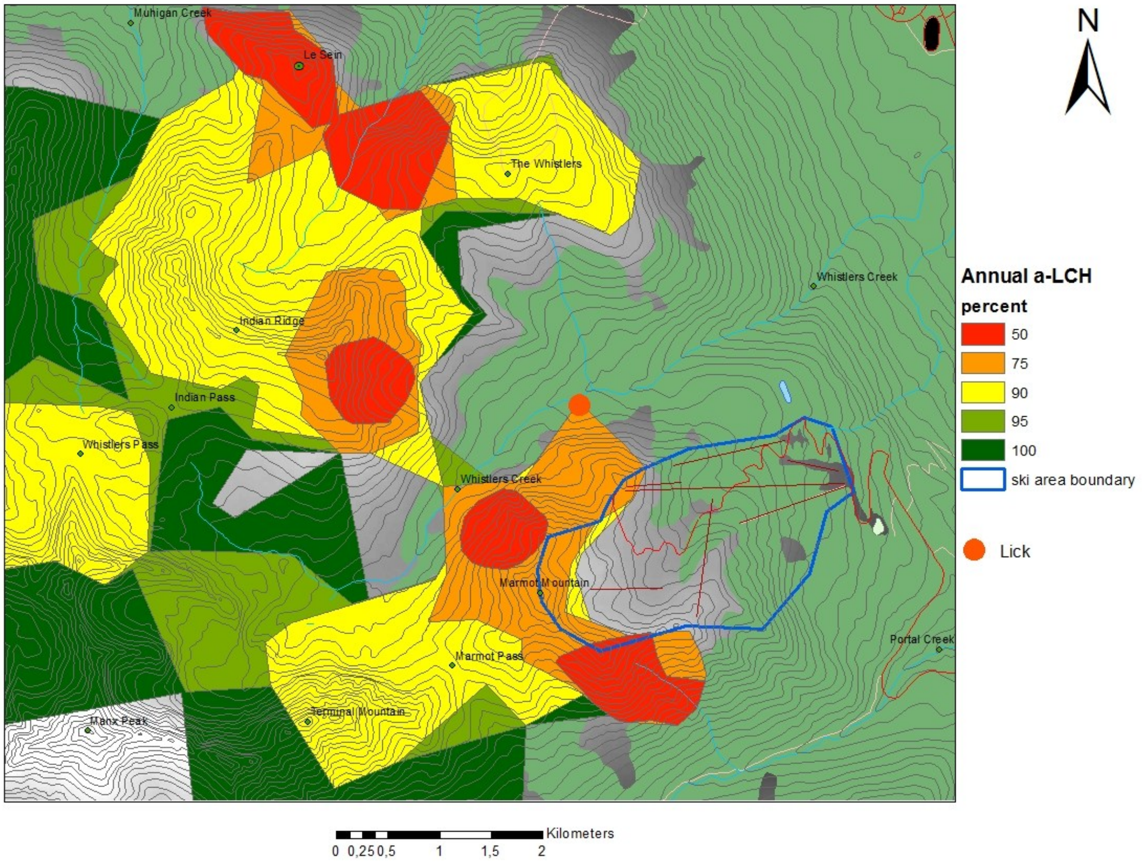


Figure 1.2 Annual home range for a group of 2 adult male mountain goats around Marmot Mountain, Jasper National Park, Alberta, Canada in 2012. Adaptive Local convex hull (a-LCH) shows the smallest combination of areas containing a given utilisation distribution percentage (represented by colors).

Resource Selection Function

The best RSF model was the same for both seasons and contained: the ruggedness index, total solar radiation for the season, elevation and elevation squared, and distance to escape terrain. The best model also included 3 interactions involving elevation, which was interacting with distance to escape terrain, solar radiation and ruggedness (Appendix 1). Mountain goats consistently used rugged terrain and stayed close to escape terrain throughout the year, but more so during winter. Mountain goats tended to use higher elevations in summer than in winter. Mountain goats used areas with more solar radiation, especially in winter (Appendix 3).

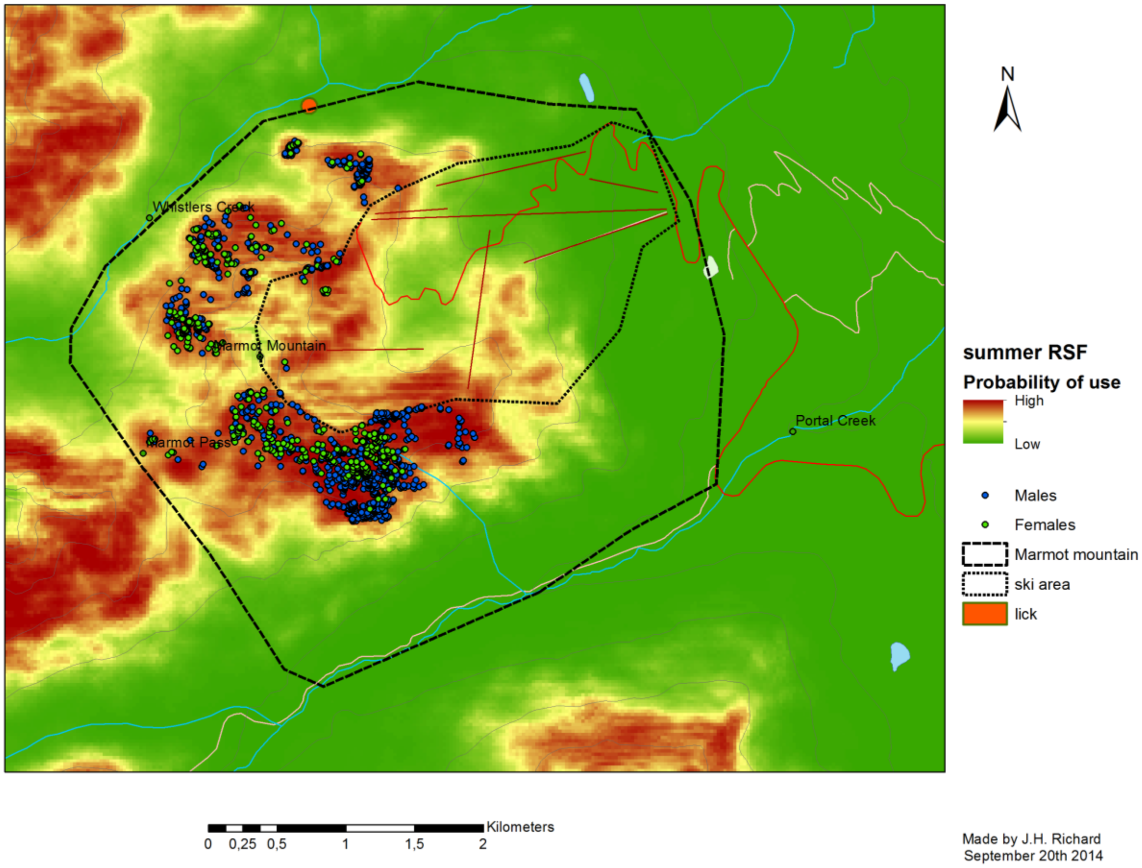
Use of ski area

Comparison of RSF predictions and actual space use suggested ski area avoidance (Figure 1.3). During summer, GPS collars recorded more than twice as many male and 9 times more female mountain goat locations/km^2 of high use probability areas outside the ski area compared to within the ski area (Table 1.4). During winter, the ski area was never used by mountain goats while areas of Marmot mountain located outside the ski area were used regularly (Table 1.4). In addition, during 2012 and 2013, none of the collared individuals used the north face of Marmot Mountain when it was open for off-piste users (ca. March 22nd to April 15th 2012, ca. March 7th to March 30th 2013), however, it was used when the area was closed.

Table 1.4 Distribution of GPS mountain goat locations recorded between 2011 and 2014 on Marmot Mountain, Jasper National Park, AB

Season	Site	high use probability areas (km^2)	number of **male** GPS locations	number of **female** GPS locations	**total** number of GPS locations	**male** locations/km2 of high use probability areas	**female** locations/km2 of high use probability areas	**total** locations/km2 of high use probability areas
Winter	Ski area	0.28	0	0	0	0	0	0
	Rest of Marmot mountain	2.02	1163	273	1436	575.7	135.1	710.8
Summer	Ski area	0.40	118	11	129	296.5	27.6	324.1
	Rest of Marmot mountain	1.92	1222	472	1694	635.7	245.5	881.3

A)



Made by J.H. Richard
September 20th 2014

B)

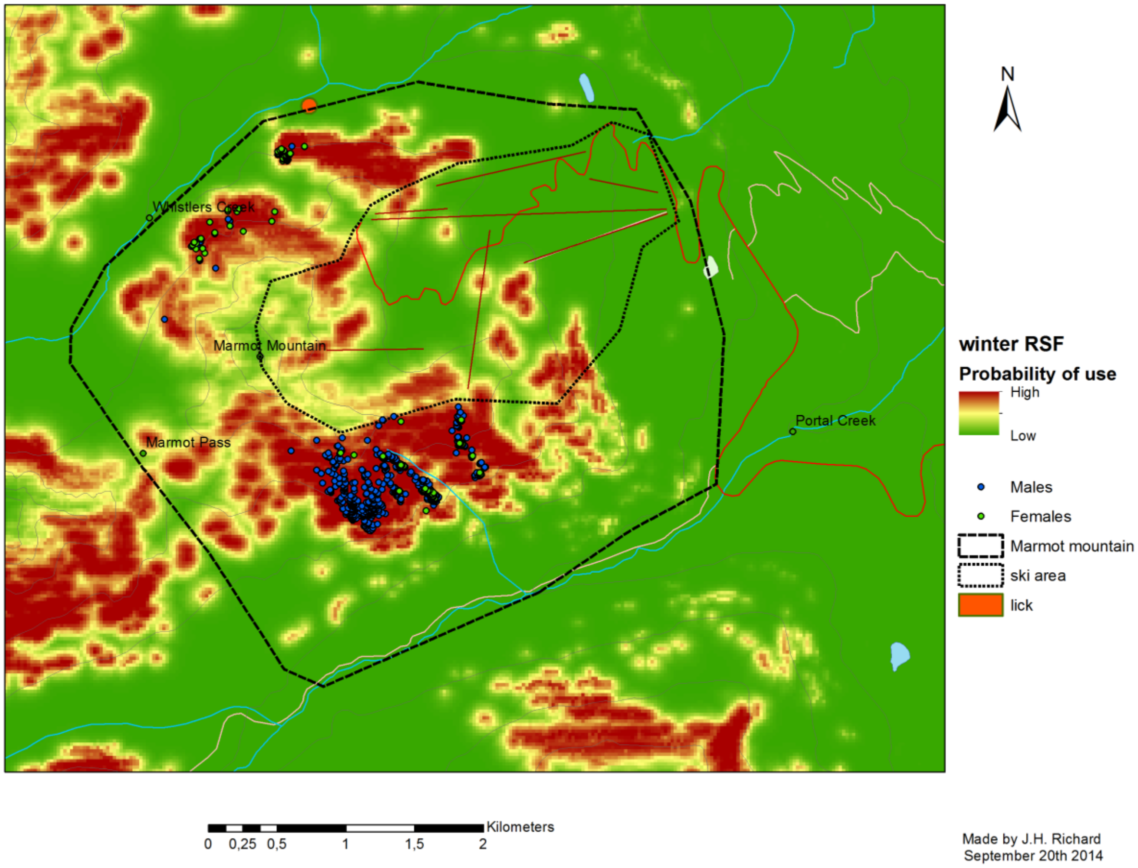


Figure 1.3 Mountain goat A) summer (3 males and 5 females) and B) winter (2males and 5 females) locations and RSF predicted relative probability of use around Marmot Basin, Jasper National Park, Alberta, Canada, 2011 to 2013.

Reactions to human encounters

Mountain goats reacted to our presence on each occasion we were within 1 km of them and moving. We recorded 26 encounters within 1 km: 16 male groups and 10 female groups which were used in this analysis. The distance between observers and mountain goats varied from 15 m to 830 m. A linear model showed that the average reaction class for nursery groups or lone females was 3.5 (standard error= .27), significantly higher than for males which averaged 2.1 (standard error= 0.35, t= -3.91, p= 0.0007).

Mineral lick use

From direct observations and collar data, it appears that Marmot Mountain is the only access route used by mountain goats to reach the Whistlers Creek lick. Camera data showed repeated observations of marked individuals at the lick, indicating that individual mountain goats visit the lick on multiple occasions each year.

Using a total of 276 visits recorded by cameras at both licks, a linear model revealed that when no trapping occurred (Whistlers Creek 2010, Muhigan 2012 and 2013) proportion of day-time use was significantly higher than when trapping activity occurred (Whistlers Creek 2011 to 2013) (0.69 vs 0.30, t= -3.98, p-value = 0.01). This result suggests that trapping activities induced a change in mountain goat behaviour. Trapping activities included: frequent visits to the trap site, time spent in a blind installed near the traps and animal captures.

Similarly, we observed mountain goats approaching the Whistlers Creek lick on 11 occasions (Appendix 4). These observations also suggest that female and nursery groups are more sensitive to human presence and activity than males. Nevertheless, lactating females appeared more likely to use the lick than non-lactating females (Odds ratio= 1.67, standard error = 0.27, z = 1.90, p-value=.06, number of observations = 234).

Discussion

Space use

Mountain goats appeared sensitive to human presence and avoided the ski area at all times but more markedly during winter when human activity level was higher. Nevertheless, goats used the vicinity of the ski area regularly. The use of high elevations throughout the year and close association with escape terrain by mountain goats is similar to what has been observed in other Rocky Mountain populations (Festa-Bianchet and Côté 2008; Poole et al. 2009) suggesting that elevation use and association with escape terrain by goats are not impaired by the ski area. Home ranges of both sexes tended to be larger (Table 1.3) than at Caw Ridge, Alberta (females=28 km^2, males= 40 km^2) or especially Lynn Canal Alaska (females=10 km^2, males= 13 km^2), but similar to southeast British Columbia (females =33 km^2, males= 83.5 km^2), which is likely the most similar landscape to the Trident range (Festa-Bianchet and Côté 2008; Poole et al. 2009; White unpublished data). Differences in home range sizes among sites seem to be linked to landscape structure, resource availability and home range estimation methods (Singer and Doherty 1985; Côté and Festa-Bianchet 2003). These results suggest that although home range size is probably not significantly modified by the presence of the ski area, home range location is limited by its presence, indicating that while the current ski area footprint may not be affecting the local goat population, cumulative expansion of this or other recreational uses could begin to limit goat access to habitat.

Overall, mountain goats habitat selection remains largely constant in both seasons, highlighting their high fidelity to rugged alpine habitat. The use of higher elevations in summer could be explained by mountain goats following the vegetation green-up to benefit from higher nutritional value of plants and decreased predation risk (Albon and Langvatn 1992). Moreover, temperatures are warmest during that period and mountain goats could use higher elevations in an attempt to limit thermal stress, similar to what has been found for Alpine Ibex (*Capra Ibex,* Grignolio et al. 2004). Closer association with escape terrain and rugged area in winter has been reported as snow is shed from steep, rugged terrain while also serving as shelter from harsh weather (Von Elsner-Schack 1986). Mountain goats also appear to use areas with greater solar radiation, which could limit snow depth and increase snow density (Pomeroy et al. 1998). Habitat selection observed around Marmot Mountain appears similar to other Rocky Mountain goat populations (Gross et al. 2002; Poole et al. 2009). These similarities suggest that there is sufficient habitat available to compensate for apparent habitat avoidance within the ski area. Some high quality habitat is, however, avoided, suggesting that the ski area or the activities on it altered habitat sufficiently to make it unsuitable for mountain goats. Because there is no information on population size prior to the ski area implementation, it is impossible to determine whether population size was affected by it. The loss of high quality habitat appears limited in size compared to undisturbed surrounding habitat, which suggests that if population size was affected by the ski area, the influence was probably limited. Nevertheless, smaller habitat patches are bound to sustain smaller population sizes (Mantyka-Pringles et al. 2012). Our sample size may appear limited, but it represents approximately half of the individuals using Marmot Mountain (Richard et al. 2014). Also, because mountain goats are highly gregarious, each recorded locations may represent a small group of animals.

Observed versus predicted space use

Home range maps and location points indicate a very limited use of the ski area by mountain goats while habitats in close proximity to the ski area are more heavily used. The topography of Marmot Mountain likely plays a role in separating the ski area from areas used by mountain goats. The ski area boundary is located on a ridge, which shields other faces of Marmot from the activities occurring within it and limits the amount of skiing on the out-of-bound faces of Marmot (Figure 1.3). Even when mountain goats did cross the ski area boundary they did not venture far within it. While avoidance of the ski area could be due to poor habitat, RSFs identified high relative probabilities of use of the highest and steepest parts of the ski area outside the winter season based on physical traits of the landscape. This is an indication that some parts of the ski area would be suitable for mountain goats in the absence of human use. On Marmot Mountain, areas of high probability of use were between 2 and 9 times more likely to be used outside the ski area than within the ski area during summer. In winter, when human activity level is much higher mountain goats avoided completely high use probability areas within the ski area, while still using the rest of Marmot mountain regularly. Consequently, comparison of seasonal habitat selection predictions and seasonal habitat use revealed clear avoidance of high quality habitat within the ski area. Although the absence of systematic information on mountain goats habitat use prior to the establishment of the Marmot Basin ski area prevents us from assessing space use changes, it is clear that mountain goats avoid the ski area and its related activities. It is not possible to know exactly why mountain goats are not using the ski area as much as other parts of the mountain, but the level of activity occurring almost year round is likely a major contributing factor. This situation is particularly apparent in winter when human activity level is at its highest. Examples of disturbance resulting in animal space use alteration are common and mountain goats have shown decreased use of previously occupied habitat following disturbance (Gordon and Reynolds 2000). Similarly to what we found, Hamr (1988) showed that disturbance occurring in an alpine tourist area displaced chamois (*Rupicapra rupicapra*) from quality foraging habitat for prolonged periods and altered home range use patterns. In Vail, Colorado, elk's (*Cervus elaphus*) use of the most developed part of the ski area was only 4% of pre-development levels (Morrison et al. 1995). In Elk island National Park (Canada), elk and moose (*Alces alces*) avoided areas with high levels of cross-country skiing during winter (Ferguson and Keith 1982). In central Europe, western capercaillie (*Tetrao urogallus)* also avoided areas with high recreation intensity during the ski season (Thiel et al. 2008). Overall, it has been shown that species sensitive to human presence may be displaced permanently by it (Knight and Gutzwiller 1995), and activities and development related to ski areas clearly have this potential. Displacement to less desirable and often poorer habitat may be more detrimental to wildlife than harassment or habitat changes (Hammitt and Cole 1987) because it may result in reduced foraging efficiency (Knight and Gutzwiller 1995) and increased predation risk (Geist 1978; Lusseau 2004). As such, human activities may displace wildlife from prime habitat and reduce fitness (Miller et al. 2001). Proximity of anthropogenic disturbance may lower predation risk of habituated wildlife if predators remain more sensitive to human disturbance (Sutherland 2007).

Summer RSF predictions suggest that the ski area contains some areas of suitable habitat. Mountain goats, however, rarely used the ski area in summer. During summer human activity within the ski area is restricted to maintenance and while activity level is low, it is nonetheless relatively constant. This suggests that summer activity is sufficient to limit mountain goat use of the ski area or that mountain goats avoid the area year round due to previous disturbance experiences. The presence of cleared ski runs provides resources for grizzly bears (*Ursus arctos*) which are regularly seen in the ski area in early summer (J.H.Richard, pers. obs). Grizzly bears are an important predator of mountain goats (Festa-Bianchet et Côté 2008) and their presence in the ski area could explain part of the early summer avoidance. Mountain goat habitat use appears more influenced by predator avoidance than forage availability (Hengeveld et al. 2003). This suggests that disturbance causing an increase in predation risk by reducing available escape terrain or increasing the presence of predators in proximity of mountain goat habitat could have a significant impact on mountain goat space use.

Habitat selection predictions suggest that there is about 25% less high quality winter habitat than high quality summer habitat within the ski area. It appears that this high quality habitat is unavailable to mountain goats because of high human activity level during winter. Other observations could also partly explain the absence of mountain goats within the ski area during winter. Most windswept ridges used by mountain goats, however, are found outside the ski area. Mountain goat movements and ranges are limited in winter (Taylor et al 2006; Poole et al. 2009). Females tend to stay in another valley about 7 km to the west and are rarely seen on Marmot Mountain during winter, even if there is good habitat outside the ski area. Females do not use the Whistlers Creek lick in winter, while many female visits on Marmot Mountain during summer are to access the lick. Nevertheless, females could be limiting their use of Marmot Mountain in winter to avoid human disturbances (Parker 1984; Hammit and Cole 1987). Ski areas are usually located on the leeward side of mountains where snow accumulates, while animals generally avoid these areas of deep snow during winter (Poole and Mowat 2005; Bruggerman et al. 2008). When animals are located close to ski areas in winter, disturbance is expected to be particularly detrimental because most wildlife species then face high energetic cost and low energetic gain (Liddle 1997; Canfield et al. 1999; Braunisch et al. 2011).

Reactions to human encounters

Stronger reactions to human encounters by female mountain goats suggest that they are more sensitive to disturbance than males. Also, males are seen more often than females on Marmot Mountain, particularly during winter. As such, males appear to be more tolerant to human presence than females and are thus capable of better coping with the high human activity on Marmot Mountain during winter. Hamr (1988) found that male chamois were also more tolerant to human activities than females with kids. In general, female groups with young are more sensitive to disturbance than male groups or groups without young which could be related to vulnerability to predation (Knight and Gutzwiller 1995; Liddle 1997; Stankowich 2008). Male mountain goats also tend to use riskier areas than females (Festa-Bianchet and Côté 2008), supporting the assumption that prey species perceive disturbance as predation risk (Frid and Dill 2002). We were not able to assess mountain goat reactions beyond 1 km, however up to and including this distance, mountain goats detected and responded to human activity. This indicates that mountain goats may react to human presence from longer distances. Even in the absence of hunting in the area for over 100 years, mountain goats perceive human presence as threat and appear to relate human presence to predation risk. Minor disturbance may cause a stress response from animals (Canfield et al. 1999) and, as Macarthur et al. (1982) have shown, bighorn sheep (*Ovis canadensis*) heart rate increased in presence of humans even in the absence of a behavioral response. Elevated stress or excitement levels may have a number of ill effects on animals, especially when stress is chronic (Geist 1978; Arlettaz et al. 2007; Thiel 2008). These effects may ultimately lead to a reduction in fitness (Miller et al. 2001) and survival of affected animals (Geist 1978; Cole et al. 1997; Sapolsky et al. 2000).

Mineral Lick use

The ski area does not appear to limit access to the Whistlers Creek lick, but mountain goats, especially females, approaching the lick are sensitive to human presence and activity. Moreover, trapping activity modified the temporal pattern of lick visits, even if humans were rarely present at the lick. A similar situation has been observed at a lick located next to a highway in Glacier National Park, Montana (Singer 1978; Pedevillano and Wright 1987). In that case, mountain goats shifted to crepuscular and nocturnal use when visitor activity was high (Singer 1978; Pedevillano and Wright 1987). Such shifts in activity patterns may be caused by predators (Kronfeld-Schor and Dayan 2003) or hunters (Kilgo et al. 1998, Crosmary et al. 2012), as prey species will attempt to reduce temporal overlap with them. Thus, suggesting again that human disturbances may be perceived as predation risk by prey species.

Lactating females appeared to use the lick more often than non-lactating females. We have also observed at least 2 cases of male travelling long distance movements (~20km) to reach the lick. These observations suggest that the lick is an important regional resource for mountain goats. Mineral licks are considered essential component of the landscape (Dormaar and Walker 1996) and their distribution influences movement and space use of ungulate populations (Ayotte et al. 2006). The presence of numerous, clearly visible, worn down trails leading to the Whistlers Creek lick suggest that this lick has been used for a number of years. If access to the lick is altered by human disturbance, this could have negative implications for mountain goats by decreasing the availability of a high value resource. Mineral deficiencies may lower animal condition and fertility, and increase mortality (Underwood 1977). We suggest that mountain goats habituated to the ski area boundary at least partly because of the proximity of the lick. As such, mountain goats may be more tolerant to the activities of the ski area in summer than in winter because they need to access the lick.

Conclusion

By contrasting actual space use with the probability of use resulting from a Resource Selection Function we showed that the Trident range's mountain goats clearly avoided the Marmot Basin ski area. These results suggest that the development and recreational activities occurring in alpine ski areas have the potential to alter the space use of large mammals with cumulative, detrimental consequences.

Acknowledgments

We are grateful to Jasper National Park's human-wildlife conflict specialists: G. Skinner, S. Malcolm, G. Peregoodoff and T. Winkler for help with captures. We thank D. Emond for help with statistical analysis. We also wish to thank C. Losier, J. Frenette, E. Martin who provided great assistance during field work. Moreover, R. Ellen, R. Ford and J. Paterson provided help with logistic on and around the ski hill. C. Dussault, G. Gauthier, S. Plante and G. Yannic provided helpful comments on an earlier version of this manuscript. J.H. Richard was supported by a scholarship from Ski Marmot Basin and Parks Canada.

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Appendix 1. AIC scores of Resource Selection Function models for mountain goats in the Trident Range, Jasper National Park, AB, 2011-2013

Table 1.5 List of tested models for RSF analyses.

Model	Model Structure
1.0	curvature+aspect+elevation+elevation^2+distance escape
1.1	curvature+aspect+elevation+elevation^2+distance escape+distance escape*elevation
1.2	curvature+aspect+elevation+elevation^2+distance escape+elevation*aspect
1.3	curvature+aspect+elevation+elevation^2+distance escape+elevation*curvature
1.4	curvature+aspect+elevation+elevation^2+distance escape+elevation*distance escape+elevation*aspect
1.5	curvature+aspect+elevation+elevation^2+distance escape+elevation*distance escape+elevation*aspect+elevation*curvature
2.0	ruggedness+aspect+elevation+elevation^2+distance escape
2.1	ruggedness+aspect+elevation+elevation^2+distance escape+distance escape*elevation
2.2	ruggedness+aspect+elevation+elevation^2+distance escape+elevation*aspect
2.3	ruggedness+aspect+elevation+elevation^2+distance escape+elevation*ruggedness
2.4	ruggedness+aspect+elevation+elevation^2+distance escape+elevation*distance escape+elevation*aspect
2.5	ruggedness+aspect+elevation+elevation^2+distance escape+elevation*distance escape+elevation*aspect+elevation*ruggedness
3.0	ruggedness+solar radiation+elevation+elevation^2+distance escape
3.1	ruggedness+solar radiation+elevation+elevation^2+distance escape+distance escape*elevation
3.2	ruggedness+solar radiation+elevation+elevation^2+distance escape+elevation*solar radiation
3.3	ruggedness+solar radiation+elevation+elevation^2+distance escape+elevation*ruggedness
3.4	ruggedness+solar radiation+elevation+elevation^2+distance escape+elevation*distance escape+elevation*solar radiation
3.5	ruggedness+solar radiation+elevation+elevation^2+distance escape+elevation*distance escape+elevation*solar radiation+elevation*ruggedness

Models in bold were selected to represent the probability of use by mountain goats

Table 1.6 AIC scores for winter RSF models for mountain goats in the Trident Range, Jasper National Park, AB, 2011-2013, based on 6,037 locations. Individuals' identity and year were used as random variables.

Model #	Model Structure	Number of parameters	Δ AICc	AIC weight
3.5	ruggedness+solarradiation+altitude+altitude2+distance_escape+altitude*distance_escape+altitude*solar radiation+altitude*ruggedness	17	0	1
2.5	ruggedness+aspect+altitude+altitude2+distance_escape+altitude*distance_escape+altitude*aspect+altitude*ruggedness	17	45.0	<.001
3.4	ruggedness+solar radiation+altitude+altitude2+distance_escape+altitude*distance_escape+altitude*solar radiation	16	50.9	<.001
2.4	ruggedness+aspect+altitude+altitude2+distance_escape+altitude*distance_escape+altitude*aspect	16	84.1	<.001
3.3	ruggedness+solar radiation+altitude+altitude2+distance_escape+altitude*ruggedness	15	95.7	<.001
3.1	ruggedness+solar radiation+altitude+altitude2+distance_escape+distance_escape*altitude	15	119.5	<.001
2.3	ruggedness+aspect+altitude+altitude2+distance_escape+altitude*ruggedness	15	147.7	<.001
1.5	curvature+aspect+altitude+altitude2+distance_escape+altitude*distance_escape+altitude*aspect+altitude*curvature	17	163.8	<.001
1.4	curvature+aspect+altitude+altitude2+distance_escape+altitude*distance_escape+altitude*aspect	16	169.8	<.001
2.1	ruggedness+aspect+altitude+altitude2+distance_escape+distance_escape*altitude	15	197.0	<.001
3.2	ruggedness+solar radiation+altitude+altitude2+distance_escape+altitude*solar radiation	15	202.1	<.001
2.2	ruggedness+aspect+altitude+altitude2+distance_escape+altitude*aspect	15	251.8	<.001
1.1	curvature+aspect+altitude+altitude2+distance_escape+distance_escape*altitude	15	257.8	<.001
1.2	curvature+aspect+altitude+altitude2+distance_escape+altitude*aspect	15	327.7	<.001
3	ruggedness+solar radiation+altitude+altitude2+distance_escape	14	328.1	<.001
2	ruggedness+aspect+altitude+altitude2+distance_escape	14	384.6	<.001
1.3	curvature+aspect+altitude+altitude2+distance_escape+altitude*curvature	15	423.7	<.001
1	curvature+aspect+altitude+altitude2+distance_escape	14	431.7	<.001

Table 1.7 AIC scores for summer RSF models for mountain goats in the Trident Range, Jasper National Park, AB, 2011-2013, based on 17,397 locations. Individuals' identity and year were used as random variables.

Model #	Model Structure	Nunber of parameters	Δ AIC	AIC weight
3.5	ruggedness+solar radiation+altitude+altitude2+distance_escape+altitude*distance_escape+altitude*solar radiation+altitude*ruggedness	20	0	0.99
2.5	ruggedness+aspect+altitude+altitude2+distance_escape+altitude*distance_escape+altitude*aspect+altitude*ruggedness	20	36.7	<.001
3.4	ruggedness+solar radiation+altitude+altitude2+distance_escape+altitude*distance_escape+altitude*solar radiation	19	96.9	<.001
3.2	ruggedness+solar radiation+altitude+altitude2+distance_escape+altitude*solar radiation	18	101.4	<.001
2.3	ruggedness+aspect+altitude+altitude2+distance_escape+altitude*ruggedness	18	145.5	<.001
3.3	ruggedness+solar radiation+altitude+altitude2+distance_escape+altitude*ruggedness	18	151.6	<.001
2.4	ruggedness+aspect+altitude+altitude2+distance_escape+altitude*distance_escape+altitude*aspect	19	208.6	<.001
2.2	ruggedness+aspect+altitude+altitude2+distance_escape+altitude*aspect	18	209.2	<.001
3.1	ruggedness+solar radiation+altitude+altitude2+distance_escape+distance_escape*altitude	18	308.5	<.001
3	ruggedness+solar radiation+altitude+altitude2+distance_escape	17	311.0	<.001
2.1	ruggedness+aspect+altitude+altitude2+distance_escape+distance_escape*altitude	18	325.8	<.001
2	ruggedness+aspect+altitude+altitude2+distance_escape	17	330.6	<.001
1.5	curvature+aspect+altitude+altitude2+distance_escape+altitude*distance_escape+altitude*aspect+altitude*curvature	20	533.8	<.001
1.2	curvature+aspect+altitude+altitude2+distance_escape+altitude*aspect	18	575.1	<.001
1.4	curvature+aspect+altitude+altitude2+distance_escape+altitude*distance_escape+altitude*aspect	19	577.1	<.001
1.3	curvature+aspect+altitude+altitude2+distance_escape+altitude*curvature	18	623.5	<.001
1	curvature+aspect+altitude+altitude2+distance_escape	17	660.4	<.001
1.1	curvature+aspect+altitude+altitude2+distance_escape+distance_escape*altitude	18	661.8	<.001

Appendix 2- Home range sizes

Table 1.8 Seasonal range size measured with Kernel density estimates for a group of 3 female mountain goats, Jasper National Park from 2011 to 2013. (UD: Utilisation distribution: areas with different probabilities or rate of usage by individuals)

	area (km2)					
	#444		#557		#565	
% of UD	summer	winter	summer	winter	summer	winter
50	5.9	5.9	6.7	3.9	3.5	1.6
75	13.1	13.0	14.9	7.9	9.1	3.2
90	21.6	21.5	24.6	13.8	16.1	5.3
95	26.3	27.1	31.8	19.4	21.3	6.7

Table 1.9 Seasonal range size measured with Kernel density estimates for 2 male mountain goats, Jasper National Park from 2011 to 2013. (UD: Utilisation distribution, percentage of time spent in each area)

	area (km^2)			
	#475		#562	
% of UD	summer	winter	summer	winter
50	12.5	5.8	14.3	6.4
75	31.3	12.8	31.4	16.2
90	87.7	23.4	56.2	28.3
95	131.5	31.6	74.3	36.7

Appendix 3 – Resource Selection Function results

Table 1.10 Seasonal RSF results for 3 female mountain goats in Trident Range area, Jasper National Park from 2011 to 2013 (r_s: average Spearman-rank correlation between predicted and observed data, SD: standard deviation, SE: standard error).

	winter (rs=0.99, SD= .01)			**summer** (rs=0.99, SD= .003)		
Variables	effect	SE	pvalue	effect	SE	pvalue
Intercept	-1.012	0.222	5.13E-06	-1.920	0.150	< 2e-16
Ruggedness	0.434	0.030	< 2e-16	0.393	0.016	< 2e-16
solar radiation	4.28E-06	3.53E-07	< 2e-16	1.56E-06	1.24E-07	< 2e-16
centered_altitude	0.001	0.001	0.102	0.004	0.001	1.03E-13
altitude^2	-1.86E-05	6.77E-07	< 2e-16	-1.96E-05	3.95E-07	< 2e-16
distance_escape	-0.020	0.001	< 2e-16	-0.005	1.89E-04	< 2e-16
altitude*distance_escape	2.59E-05	4.49E-06	8.57E-09	-8.72E-06	1.15E-06	2.93E-14
altitude*solar_radiation	1.38E-08	1.87E-09	1.50E-13	5.89E-09	5.63E-10	< 2e-16
altitude*rugged	-0.001	1.38E-04	7.50E-13	-0.001	7.02E-05	< 2e-16

Appendix 4. Description of observations of mountain goats approaching the Whistlers Creek lick, Jasper National Park, Alberta, Canada, 2011 to 2013.

Table 1.11 Description of observations of mountain goats approaching the Whistlers Creek lick, Jasper National Park, Alberta, Canada, 2011 to 2013.

Observed	**Observer locations**	**Approaching behaviour**	**Later behaviour**
6 males	4 observed from a blind installed near the traps	3 reached the lick without hesitation	NA
		1 turned around	
	2 observed from the mountain	2 reached the lick without hesitation	
5 females	2 observed from a blind installed near the traps	2 turned around	1 did not reach the lick for at least 2 days
			1 reached the lick the following night
	2 observed from the mountain	2 did not notice our presence and reached the lick after observing from the cliff	NA
	1 observed from the mountain	1 noticed our presence and turned around	1 did not reach the lick for at least 2 days

Chapitre 2 : The effect of snow on space use of an alpine ungulate : recently fallen snow tells more than cumulative snow depth

- L’effet de la neige sur l’utilisation de l’espace d’un ongulé alpin : la neige fraiche serait plus pertinente que l’épaisseur de la neige

Julien Hénault Richard[1], John Wilmshurst[2] et Steeve D. Côté[1]

[1] Département de biologie et Centre d’études nordiques, Université Laval, 1045 av. de la médecine, Québec, QC, Canada, G1V 0A6

[2] Parcs Canada, Parc national Jasper, Jasper, Alberta, Canada

Résumé

Durant l’hiver, la neige est l’un des facteurs environnementaux les plus limitants pour la grande faune des régions tempérées ou arctiques. L’épaisseur de neige peut limiter l’utilisation de l’espace, augmenter les dépenses énergétiques liées aux déplacements, limiter la disponibilité des ressources et ultimement affecter la survie. La plupart des études concernant les effets de la neige sur l’utilisation de l’espace de la faune ont utilisé des mesures d’épaisseur de neige. Par contre, la quantité de neige fraiche pourrait être plus représentative des conditions rencontrées par la faune, particulièrement en région alpine ou arctique où le vent déplace et compacte constamment le couvert nival. De 2011 à 2013, nous avons étudié l’utilisation de l’espace des chèvres de montagne (*Oreamnos americanus,* De Blainville, 1816) dans le Parc national Jasper en Alberta. Durant l’hiver, les déplacements quotidiens et hebdomadaires, diminuaient en fonction de la quantité de neige fraiche, mais pas en fonction de l’épaisseur de neige au sol. Ces résultats indiquent que la neige fraiche devrait être incluse dans les études d’utilisation de l’espace de la faune durant l’hiver. Les déplacements limités et la petite taille des aires utilisées par les chèvres de montagne soulignent la tactique d’économie d’énergie utilisée par cette espèce durant l’hiver.

Abstract

Snow is one of the most limiting environmental factors for large wildlife of temperate and Arctic zones during winter. Snow depth may limit space use, increase energy expenditure related to movement, limit resource availability and ultimately affect individual survival. Most of the studies on the effect of snow on animal space use have used cumulative snow depth. The amount of recently fallen snow, however, could be more relevant for wildlife, especially in alpine and northern environments, where wind shifts and hardens the snow cover constantly. From 2011 to 2013, we studied space use of mountain goats (*Oreamnos americanus,* De Blainville, 1816) within Jasper National Park in Alberta, Canada. During winter, daily and weekly movements decreased with the amount of recently fallen snow, but not with cumulative snow depth. These results indicate that recently fallen snow should be included in wildlife space use studies during winter. Limited movement and range size of mountain goats also highlight the energy saving tactic used in winter by this species.

Introduction

For wildlife of temperate latitudes or higher, adapting to the winter season is key for their survival and snow may influence the environmental constraints they have to cope with as well as their behaviour. For example it is known to decrease movements (Von Hardenberg et al. 2000; Fortin and Andruskiw 2003; Ratikainen et al. 2007), activity levels (Beir and McCullough 1990), range size (Lovari et al 2006; Rivrud et al. 2010; Van beest et al. 2011) and resource accessibility (Mysterud et al. 1997; Massé and Côté 2012; Robinson and Merrill 2012). In addition to the increasing energy costs of locomotion (Parker et al. 1984; Dailey and Hobbs 1989), snow increases predation risk (Peterson 1974; Hebblewhite 2005; Robinson and Merrill 2012) and stress levels (Moen 1976) while modifying habitat use or selection (Poole and Mowat 2005; Bruggerman et al. 2008). Ultimately, this may lower survival (Turner et al. 1994; Loison et al. 1999; Coulson et al. 2001). Thus, it is relevant to know how animals cope with snow to better understand their vulnerability to harsh winter conditions.

Most studies on the effect of snow on animal space use have estimated the effect of cumulative snow depth or snow cover (Hebblewhite 2005; Ratikanen et al. 2007; Poole et al. 2009; Witt et al. 2012). In alpine habitats, winds can shift and harden the snow pack rapidly. Because cumulative snow depth is low in windblown areas and is quickly hardened in others, the amount of recently fallen snow could be more relevant than cumulative snow depth for wildlife. Alpine ungulates face long winters with frequent snowfall. Although space use (Lovari et al 2006; Poole et al. 2009) and movements (White 2006) are generally limited in winter, finer temporal scale movements and local space use are both poorly known due largely to the difficulties of working in alpine environments during winter. This is especially true for mountain goats (*Oreamnos americanus,* De Blainville, 1816) that often use rugged windswept ridges during winter (Poole et al. 2009).

Predation appears to be the main cause of mortality for mountain goats (Festa-Bianchet and Côté 2008). As such, predation risk appears to be the main factor influencing mountain goat space use as they are gregarious and strongly associated with escape terrain (steep slopes, usually ≥40°) (Hamel and Côté 2007; Gross et al. 2002; Festa-Bianchet and Côté 2008). Escape terrain is not only used to avoid predation (Chadwick 1983; Gross et al. 2002; Poole et al. 2009) but also as shelter from harsh weather (Chadwick 1977; Von Elsner-Schack 1986). The mountain goat antipredator strategy largely relies on detecting predators by sight from distance and then moving into escape terrain where large predators are unable to follow (Festa-Bianchet and Côté 2008). This strategy requires good visibility and rapid movement (Festa-Bianchet and Côté 2008). In winter, predator detection, already limited by long nights may be exacerbated by falling snow.

Mountain goats tend to walk through snow instead of bounding over it like most other ungulates. This trait interestingly affords efficient movement through deep snow compared to other similar size ungulates (Dailey and Hobbs 1989), but less efficient movement than wolves (*Canis lupus*, L., 1758) or cougars (*Puma concolor*, L., 1771), their main winter predators that have lower foot loading (Telfer and Kelsall 1984; Alexander et al. 2006; Festa-Bianchet and Côté 2008). Mountain goat movements are shorter in winter than during other times of the year (Hjeljord 1973; Chadwick 1983; White 2006), and winter ranges are much smaller; 2% to 50% of the size of summer ranges, even if they are used for a longer period of time (Taylor et al 2006; Poole et al. 2009). This suggests that snow limits mountain goat space use as they tend to save their energy by limiting movements in snow. During winter, mountain goats also tend to use areas with low cumulative snow depths often characterised by rocky wind-swept outcrops and ledges found in steep rugged terrain (Hebert and Turnbull 1977; Côté and Festa-Bianchet 2003; Poole et al. 2009). Association with escape terrain is stronger during winter (Poole and Heard 2003; White 2006), but little is known about the effect of snow on this association. During winter, darkness may last for 15 hours a day. Night-time movements of mountain goats, however, have never been reported in the literature. It thus appears important to better understand space use of mountain goats during night-time and the possible relation with snow conditions. We hypothesised that 1) recently fallen snow would have a greater influence on mountain goat movement rate than cumulative snow depth that may be compacted, 2) night-time movements would be limited compared to day-time movements because of predation risk, especially in presence of recently fallen snow, and 3) because of increased predation risk, association with escape terrain would increase at night and in presence of recently fallen snow.

Materials and Methods

The study area was located near Marmot Mountain (53.80°N, 118.08°W) in the Trident Range (125km^2), Jasper National Park, west central Alberta, Canada (Figure 2.1). This region of the Canadian Rockies is at the front of the subarctic and the humid continental climates and is divided in three ecosystem types: montane, subalpine and alpine. Most of the study area (~75%) is located above tree line between 1900m and 3000m of elevation. It is covered by krummholtz, rocks and sparse alpine vegetation, below 1900m we find subalpine forest containing mostly: white spruce (*Picea glauca,* (Moench) Voss*)*, Engelmann spruce (*Picea engelmannii,* Parry ex. Engelm.) and subalpine fur (*Abies lasiocarpa,* (Hooker) Nuttall). The predator community in the area is largely intact and included wolves, brown bears (*Ursus arctos*, L., 1758), black bears (*Ursus Americanus*, Pallas, 1780), cougar, wolverine (*Gulo gulo*, L., 1758), coyotes (*Canis latrans,* Say, 1823) and golden eagle (*Aquila chrysaetos*, L., 1758). The data collection occurred over 2 winter seasons (2011-2012 and 2012-2013) from December 16th to April 30th. This period excludes the rut of mountain goats and all movements and activities related to reproduction that occurs in late November-early December (Festa-Bianchet and Côté 2008). We defined two winter periods; early winter from mid-December to February and late winter from March to April, which we used to compare home range size. Mountain goats from the area appear to remain exclusively above treeline throughout winter and use rocky wind-swept outcrops or ledges found in steep rugged or exposed terrain.

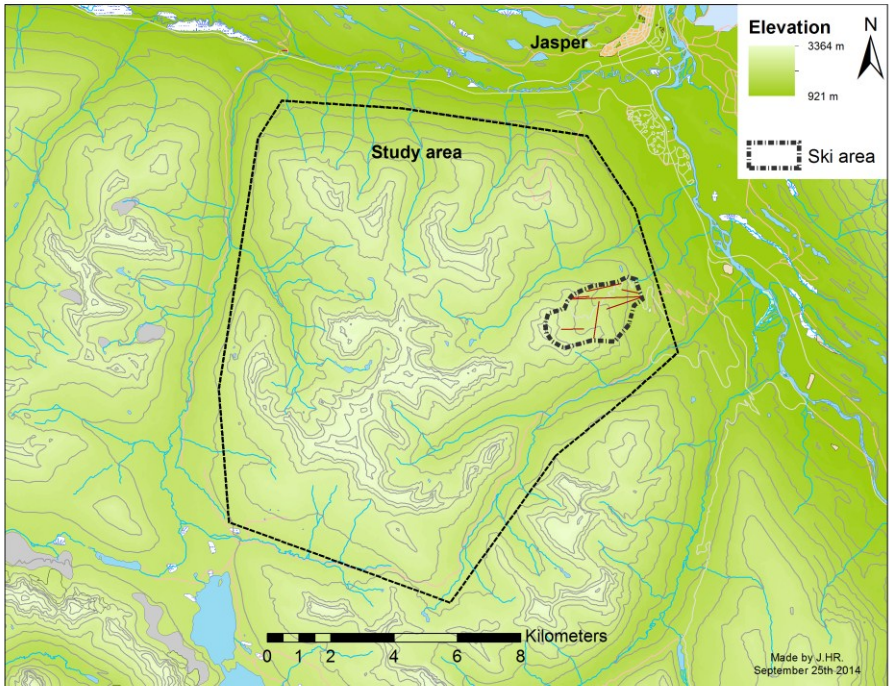

Figure 2.1 Map of the study area where we followed mountain goat space use (*Oreamnos americanus,* De Blainville, 1816) during winter 2011-2012 and 2012-2013 in relation to snow conditions, Jasper National Park, AB.. Topography and elevation are represented by 100 m contour lines and lighter color at higher elevation.

Captures

We captured and marked six individuals with GPS collars (GPS PLUS Iridium collars, VECTRONIC Aerospace GmbH, Berlin, Germany). Individuals were captured with self-triggered

Stevenson style wooden box traps. Before handling, mountain goats were immobilized with an intramuscular injection of xylazine hydrochloride (Rompun, Bayvet Division, Etobicoke, Ontario, Canada) at a dosage of 5mg/kg. Following handling procedures, the effects of xylazine was reversed by intramuscular injection of 0.9 to 1.2 mg of idazoxan (RX 811059, Reckitt and Colman, Kingston-upon-Hull, United Kingdom; Haviernick et al. 1998) according to the dosage of xylazine given to the animal. All captured animals were hobbled and a mask was placed over their eyes to minimize outside stimuli. Animals received supplemental oxygen during handling. All capture and handling procedures were approved by the animal care committees of Université Laval, Québec and Parks Canada.

Two males and two females were collared and followed over two winters (2011-2012, 2012-2013), two additional females were followed during the second winter for a total of 6 individuals, representing 10 individuals /winter. The collar of one of the females stopped working in February, so we did not analyse its winter home range. Winter home range sizes of individuals followed over 2 seasons were averaged. Two females followed during winter 2012-2013 had kids which could have influenced their space use. GPS collars recorded the location of each individual every 6 hours. We removed all data that showed unrealistic altitude and had a dilution of position (DOP) over 10 (~3% of the locations), which occurs as a result of poor satellite coverage.

Snow data

Snow data were recorded by the snow safety team at the Marmot Basin ski area. Measurements of total snow depth and snow fallen since the last measurement were made twice daily (at 7:00 am and 3:45 pm) throughout the winter at an elevation of 1975m. The snow measurement station was located on flat ground just below tree line. Even if snow measurements did not necessarily reflect actual snow conditions encountered by mountain goats in the surrounding mountains, the measurements represent a relative measure of the snowfall and cumulative snow depth in the area. Except for 1 individual that was approximately 25 km south of the weather station, all individuals were within 7 km of the weather station at all times. Recently fallen snow was defined as the amount of snow fallen in the previous 24 hours, while cumulative snow depth was the total snow depth. We used the mean value of each snow variable calculated at two different time scales (daily and weekly). Total snowfalls during both winter seasons were greater than the previous 20 years average (347 ± 100 cm, standard deviation). The 2011-2012 season was particularly severe with a total snowfall of 555 cm while 363 cm were received in 2012-2013. Cumulative snow depth on April 30th was 142cm in 2012 and 133cm in 2013, and maximum snow depth reached 180cm in

2011-2012 and 147cm in 2012-2013. Abundant snow depth at the end of April indicates that snow did not melt before the end of the winter period.

Statistical analyses

We used mixed-linear models to analyse movement and distance to escape terrain in relation to snow conditions (cumulative snow depth and recently fallen snow) and day length. Range sizes were determined with 95% kernel density estimates (KDE) (Silverman 1986) in R, version 2.13.0 (R Development Core Team 2011). The value of the smoothing parameter (h) was determined using the reference method which assumes that the utilization distribution (UD) is bivariate normal (Worton 1995). All measured distances included the variation in elevation estimated with a 24 m X 24 m digital elevation model (DEM) raster. We first estimated distances in two dimensions, drawing a straight line between successive locations (i.e. planimetric distance). Afterwards, we adjusted the distances for the elevation difference between the two locations using Pythagoras' theorem (i.e. surface area distance),

$$D=\sqrt{(d^2+h^2)} \qquad \text{(Eq. 1)}$$

where D represents the corrected distance, d is the distance between 2 successive locations and h is the altitude difference between both locations. Every 6 hour movement steps were summed for each day and each week of the winter. We obtained 4175 single step movements, 1156 daily movements and 161 weekly movements. Day and night were determined using the sunrise and sunset times. GPS locations were recorded 4 times a day at 1:00, 7:00, 13:00 and 19:00. In Jasper the sunrise occurs around 9:00 in December and 7:00 in April while the sunset occurs around 16:30 in December and 21:00 in April. Thus, we determined that movements recorded between 19:00 and 7:00 occurred at night, while movements recorded between 7:00 and 19:00 occurred during the day.

Because mountain goats are often found in escape terrain, we considered two variables associated with escape terrain. First, we analysed the probability of being in escape terrain with a binomial dependent variable that indicated whether mountain goats were in or away from escape terrain. Second, we analysed the effect of distance from escape terrain using locations where mountain goats were not in escape terrain as the dependent variable. Both models were used to analyse the effects of snow conditions and time of day on 1) the probability of being in escape terrain and 2) the distance to escape terrain.

We built a set of models where the base model contained individual identity and year as random variables and day length as a fixed variable to analyse the differences in space use metrics. We added recently fallen snow and cumulative snow depth to evaluate the relationship between mountain goat space use and snow conditions. We also added a night-time variable to analyse 6h movement categories. We log transformed all distance metrics used as dependent variables to meet the assumption of normality of the residuals. We chose best models using lowest AIC scores (Burnham and Anderson 2004) and reported 95% confidence intervals. We chose the most parsimonious competing model because additional variables contained in more complex models did not explain enough variation to justify their inclusion (Arnold 2010). To verify that small sample size yielded robust results we performed parametric bootstrap tests on all models and report the 95% confidence intervals obtained for each explanatory variable (Efron and Tibshirani 1993). The influence of sex was assessed in all models, but never improved the model's fit, thus we removed it from all analyses. We performed all analyses with the package *lme4* (Bates et al. 2011) in the software R, version 2.13.0 (R Development Core Team 2011).

Results

Space use

Late winter range sizes were approximately half the size of early winter range sizes for females and about 5% of early winter range sizes for males (Table 2.1). Average daily movement in winter was 446 m (Standard Error [SE] =15.58 m, range 2 – 4263 m). The best model explaining daily movements contained only a negative effect of the recently fallen snow amount and a positive effect of day length (Table 2.2, Figure 2.2).

Table 2.1. Early (mid-December to February) and late winter (March-April) range sizes measured with Kernel density estimates for A) 3 female and B) 2 male mountain goats (*Oreamnos americanus,* De Blainville, 1816), Jasper National Park from 2011 to 2013. (UD (utilisation distribution): areas with different probabilities or rate of usage by individuals).

A) Females	area (km2)					
	early winter			late winter		
% of UD	#444	#557	#565	#444	#557	#565
50	7.8	4.2	2.3	3.1	2.6	0.8
75	16.3	8.8	4.5	6.8	4.7	2.0
90	26.0	15.7	7.1	12.0	7.2	3.6
95	32.7	21.0	8.6	16.1	8.9	4.7
B) Males		#475	#562	#475	#562	
50		8.4	8.7	0.4	0.4	
75		18.7	19.4	1.0	1.0	

90	31.4	32.3	2.1	2.2
95	40.1	41.4	2.9	3.1

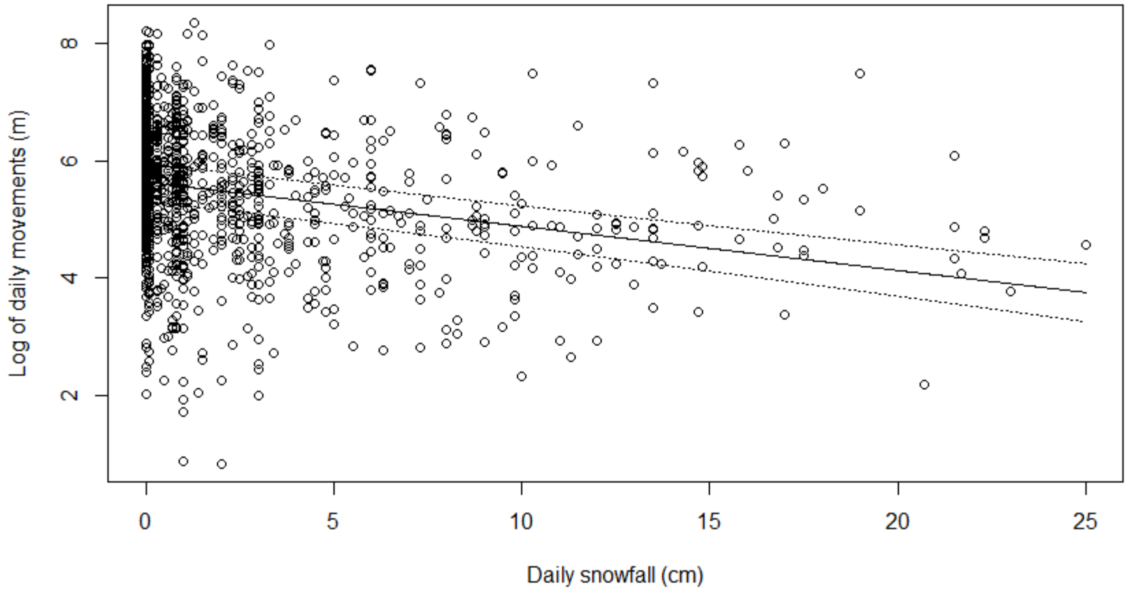

Figure 2.2 Log of daily movements in relation to snow fallen in the previous 24 hours for mountain goats (*Oreamnos americanus,* De Blainville, 1816) during winter, Jasper National Park.

Table 2.2. A) AIC scores for linear mixed-models with individuals' identity and year as random variables and B) estimates of the best model explaining the log of daily movements in relation to snow conditions and day length for mountain goats (*Oreamnos americanus,* De Blainville, 1816) during winter, Jasper National Park. Bold characters indicate significant effects (CI: confidence interval, boot: parametric bootstrap).

A) Model number	Model structure	Number of parameters	Δ AICc	AICc weight
1	Recently fallen snow + Day length	9	0	0.98
3	Recently fallen snow+ Cumulative snow depth + Day length	10	8	0.02
2	Cumulative snow depth +Day length	9	55	0.00
0	Day length	8	69	0.00

B)	β(x)	Standard error	2.5% CI	97.5% CI	Boot 2.5% CI	Boot 97.5% CI
Intercept	5.12	0.22	4.68	5.56		
Recently fallen snow	**-0.08**	**0.01**	**-0.09**	**-0.06**	**-0.09**	**-0.06**
Day length	**0.05**	**0.01**	**0.02**	**0.08**	**0.02**	**0.08**

Movements recorded at 6h intervals were shorter at night than during the day (Table 2.3 B) (β (Night) = -1.671, SE = 0.051, 95%CI = -1.770 to -1.572). Night-time movements averaged 48.9 m/6h (Standard Error [SE] =2.6 m, range 0 – 2050 m), while day-time movements averaged 192.3 m/6h (Standard Error [SE] = 7.0 m, range 0 – 3989 m).

Table 2.3 A) AIC scores for linear mixed-models with individuals' identity and year as random variables and B) estimates of the best model explaining the log of 6h movements in relation to snow conditions and day length for mountain goats (*Oreamnos americanus,* De Blainville, 1816) during winter, Jasper National Park. Bold characters indicate significant effects (CI: confidence interval, boot: parametric bootstrap).

A) Model number	Model structure	Number of parameters	ΔAIC	AICc weight
1	Recently fallen snow + Day length + Night-time	11	0	0.50
3	Recently fallen snow + Cumulative snow depth + Day length + Night-time	12	0	0.50
2	Cumulative snow depth + Day length + Night-time	11	38	0.00
0	Day length + Night-time	10	67	0.00

B)	β(x)	Standard error	2.5% CI	97.5% CI	Boot 2.5% CI	Boot 97.5% CI
Intercept	3.70	0.15	3.40	3.99		
Recently fallen snow	**-0.05**	**0.01**	**-0.06**	**-0.04**	**-0.06**	**-0.04**
Night-time	**-1.67**	**0.05**	**-1.77**	**-1.57**	**-1.77**	**-1.57**
Day length	**0.05**	**0.01**	**0.03**	**0.08**	**0.03**	**0.08**

The best models explaining weekly movements (Table 2.4) contained only the amount of recently fallen snow, and thus the effect of day length was not significant. Very similar results (not shown) were obtained for weekly home range (Kernel 95%) and core range sizes (Kernel 50%).

Table 2.4 A) AIC scores for linear mixed-models with individuals' identity and year as random variables and B) estimates of the best model explaining the log of weekly movements in relation to snow conditions and day length for mountain goats (*Oreamnos americanus,* De Blainville, 1816) during winter, Jasper National Park. Bold characters indicate significant effects (CI: confidence interval, boot: parametric bootstrap).

A) Model number	Model structure	Number of parameters	Δ AICc	AICc weight
1	Recently fallen snow + Day length	9	0	0.99
3	Recently fallen snow+ Cumulative snow depth + Day length	10	9.7	0.01
0	Day length	8	25.4	0.00
2	Cumulative snow depth + Day length	9	26.7	0.00

B)	β(x)	Standard error	2.5% CI	97.5% CI	Boot 2.5% CI	Boot 97.5% CI
Intercept	7.86	0.32	7.24	8.48		

Recently fallen snow	**-0.13**	**0.02**	**-0.17**	**-0.09**	**-0.17**	**-0.09**
Day length	0.02	0.02	-0.02	0.06	-0.02	0.06

Escape terrain

The base model containing day length and night-time effects was the best to explain the probability of being in escape terrain (Table 2.5-A). The only significant effect found in the model was an increased probability of being in escape terrain at night (Table 2.5-B). When considering only distances from escape terrain greater than zero, the best model included only a positive effect of cumulative snow depth, while mountain goats remained closer to escape terrain at night than during the day and as day length increased (Table 2.6).

Table 2.5 A) AIC scores for linear mixed-models with individuals' identity and year as random variables and B) estimates of the best model explaining the probability of being in escape terrain in relation to snow conditions, time of day and day length for mountain goats (*Oreamnos americanus,* De Blainville, 1816) during winter, Jasper National Park. Bold characters indicate significant effects (CI: confidence interval, boot: parametric bootstrap).

A) Model number	Model structure	Number of parameters	Δ AICc	AICc weight
0	Night-time + Day length	9	0	0.62
1	Night-time + Day length + Recently fallen snow	10	1.2	0.34
2	Night-time + Day length + Cumulative snow depth	10	2	0.23
3	Night-time + Day length + Recently fallen snow+ Cumulative snow depth	11	3	0.139

B)	β(x)	Standard error	2.5% CI	97.5% CI	p_value	Boot 2.5% CI	Boot 97.5% CI
Intercept	-0.67	0.27	-1.20	-0.14	0.01		
Night-time	**0.14**	**0.07**	**0.01**	**0.27**	**0.04**	**0.00**	**0.26**
Day length	0.01	0.02	-0.02	0.03	0.73	-0.03	0.03

Table 2.6 A) AIC scores for linear mixed-models with individuals' identity and year as random variables and B) estimates of the best model explaining the log of distance to escape terrain in relation to snow conditions, time of the day and day length for mountain goats (*Oreamnos americanus,* De Blainville, 1816), Jasper National Park. Bold characters indicate significant effects (CI: confidence interval, boot: parametric bootstrap).

A) Model number	Model structure	Number of parameters	Δ AICc	AICc weight
0	Night-time + Day length	9	0	0.99
1	Night-time + Day length + Recently fallen snow	10	11.61	0.00
2	Night-time + Day length + Cumulative snow depth	10	12.1	0.00
3	Night-time + Day length + Recently fallen snow+ Cumulative snow depth	11	21.83	0.00

B)	β(x)	Standard error	2.5% CI	97.5% CI	Boot 2.5% CI	Boot 97.5% CI
Intercept	3.51	0.11	3.30	3.72		
Night-time	**-0.09**	**0.02**	**-0.12**	**-0.05**	**-0.12**	**-0.06**
Day_length	0.01	0.00	-0.00	0.01	-0.00	0.01

Discussion

Snow depth is known to impede animal movements (Von Hardenberg et al. 2000; Fortin and Andruskiw 2003; Ratikainen et al. 2007). As predicted, we found that space use of mountain goats was primarily affected by the amount of recently fallen snow rather than cumulative snow depth *per se*. Daily and weekly movements decreased with the amount of recently fallen snow but not with cumulative snow depth. These results demonstrate that at short temporal scales recently fallen snow appears more limiting for mountain goat space use than cumulative snow depth. This situation may occur for ungulates living in alpine and Arctic environments where regular winds shift and harden snowpack (Stewart and al. 1995; Déry and Yau 2001). Even if mountain goats can move more easily through deep snow relative to similar size ungulates (Dailey and Hobbs 1989), they may remain in very small areas for extended periods of time during winter, and probably reuse existing trails. Movements in these trails would be hindered by recently fallen snow filling the trails, but less so as the snow becomes packed. Because movement in snow causes high energy expenditure for large mammals (Parker et al. 1984), reduction of movements in presence of recently fallen snow would limit energy expenditure (Rivrud et al. 2010). Over the entire winter season, variation in cumulative snow depth is, however, much greater than variation in recently fallen snow which could explain the reported negative effects of cumulative snow depth or snow cover on movements and winter range size of multiple ungulate species (Von Hardenberg et al. 2000; D'Eon and Serrouya 2005; Poole and Mowat 2005; Ratikanen et al. 2007; Poole et al. 2009; Rivrud et al. 2010; Van Beest et al. 2011). Cumulative snow depth likely plays a more significant role in the overall winter distribution of mountain goats as they seek areas with shallow snow accumulation. This has been found for a number of ungulates (Smith 1976; Schaefer and Messier 1995; Poole and Mowat 2005; Bruggerman et al. 2008; Poole et al. 2009). In mountain goats two wintering strategies occur:

1) populations from interior regions (e.g. the Rockies), such as ours, spend winter above treeline on windswept ridges while 2) coastal populations living in areas of greater snowfall, migrate downhill to spend winters in low elevation forested areas (Hebert and Turnbull 1977). While both these space use patterns appear to reflect a selection for shallower snowpack, these different tactics suggest cumulative snow depth largely influences space use of mountain goats. Nevertheless, we suspect that even in the coastal regions, mountain goat movements would be largely influenced by recently fallen snow and that cumulative snow depth would have a greater influence on the distribution of mountain goats in the landscape. The reported effects of recently fallen snow support findings indicating that snow is the main environmental factor explaining differences in movement behavior for ungulates (Singh et al. 2012). This is one of the first indications, however, that recently fallen snow could be more important than cumulative snow depth at short temporal scales. Reduced movements during snowfalls, possibly related to low visibility, could also partly explain these results. However, we related space use with snow conditions recorded within the previous 24 hours, thus we believe that our results primarily reflect the effect of snow on the ground. Contrary to range sizes that were minimal in late winter, daily movements increased with day length as winter advanced. Previous work (Richard et al. 2014) showed that mountain goat activity appears limited to periods of daylight, this suggests that increased day length enables mountain goats to be active for longer periods and thus, travel longer distances. Late winter is also a favourable period for crusting events occurring when solar radiation and warm daytime temperature combined with cold night temperature create a crust on the snow. Crusting conditions, however, may occur at any time during the winter due to anomalous winter rain events and wind effects creating hardened snow slabs. These crusts could support mountain goats and enable them to move over longer distances or be non-supportive, making movements more difficult than unconsolidated snow. We, however, do not have the data to test these hypotheses.

Late winter ranges were much smaller than early winter ranges. Greater snow depth in late winter could possibly have a limiting influence on range sizes. Yet, as our results showed limited effect of cumulative snow depth on movements, it appears that the main factor causing this change is possibly the depletion of energy reserves, which forces mountain goats to conserve energy. This could appear contradictory to the results on daily movements that showed increased movements with day length or as winter advanced. It, however, appears that as winter advances, mountain goats, males in particular, modify their space use patterns by remaining in smaller areas while being active and moving for longer periods each day likely because of increased day length. By using smaller areas in late winter, mountain goats may restrict their space use to steep and rugged areas with good snow shedding, and save energy by using packed trails that make movements easier than unpacked snow. In relation to energy depletion, White et al. (2011) found that winter climate, especially total snowfall, exerted the strongest effect on mountain goat survival. Due to their thick winter pelage mountain goats are very tolerant of cold temperatures (Côté and Festa-Bianchet 2003). Thus, cold winter temperature is unlikely to play a major role in mountain goat space use. Temperature close to or above 0°C during winter could, however, significantly affect mountain goat space use by considerably changing the snowpack characteristics and the type of precipitations (rain vs snow).

Night-time movements were much shorter than day-time movements, which was expected (Rideout 1978; Singer and Doherty 1985; Pelletier et a. 2009), but has been rarely tested. Like most other ungulates (Beier and McCullough 1990; Ager et al. 2003; Massé and Côté 2013), mountain goats appear to concentrate movements in daylight hours. Movements may also differ between day and night because of differences in predation risk (Mysterud and Østbye 1999).

Escape terrain is used by mountain goats for the safety it provides against predation (Chadwick 1983; Gross et al. 2002; Poole et al. 2009) and shelter from harsh weather (Chadwick 1977; Von Elsner-Schack 1986). Mountain goats often rest in escape terrain (McFetridge 1977). Consequently, it was expected that as mountain goats spend more time resting during winter, they should also spend more time in, or close to escape terrain, especially at night. We suggest that this should occur due to the energy saving tactic used by mountain goats (Poole et al. 2009), which have limited access to food resources in winter (Houston and Stevens 1988). Contrary to our hypothesis, we found that snow conditions did not affect the probability of being in escape terrain or the distance to escape terrain. We predicted that mountain goats would stay closer to escape terrain in presence of freshly fallen snow because this would make them more vulnerable to predation. Greater snow depth could limit mountain goat capacity to escape predator and rapidly reach escape terrain. This, however, does not appear to be the case. As such, perhaps predation risk is relaxed during winter because one of the main predators of mountain goats, the grizzly bear, is in hibernation. Moreover, shallower snowpack in the surrounding valleys attract other species of wintering ungulates such as elk and deer which could incite other large predators like wolves and cougars to remain at lower elevation to benefit from larger prey density. In any case, time of day and day length had larger effects on distance to escape terrain than snow conditions. Mountain goats remained closer to escape terrain at night when they were mostly inactive. In accordance with late winter small range sizes, mountain goats also remained closer to escape terrain as day length increased and spring approached apparently because of limited energy reserves at this time of year. Ungulates are more vigilant and more sensitive to disturbance when away from escape terrain (Hochman and Kotler 2006; Tadesse and Kotler 2012). Likewise, more vulnerable animals are known to remain closer to escape terrain (Hamel and Côté 2007; Rachlow and Bowyer 1998). As such, closer association with escape terrain at night and as winter advances and energy reserves are depleted could indicate that these variables influence their vulnerability to predation. For example, more difficult predator detection at night and limited available energy to flee from predators in late winter could explain the relation between these variables and the use of, or distance from, escape terrain. Limited movements and range sizes of mountain goats highlight the energy saving tactic they use in winter. While providing information on the relative influence of different snow metrics on mountain goat space use, our study also provides information on night-time movements and use of escape terrain, which is scarce in the literature. Our results demonstrate the importance of considering freshly fallen snow in wildlife space use studies, and thus have potential implications for other alpine and Arctic ungulates.

Acknowledgments

We are grateful to D. Emond for help with statistical analysis, to the entire Marmot Basin snow safety team who collected the snow data and to G. Gauthier and C. Dussault for helpful comments on a previous version of the manuscript. We thank Jasper National Park's human-wildlife conflict specialists: G. Skinner, S. Malcolm, G. Peregoodoff and T. Winkler for help with captures. We also wish to thank C. Losier, J. Frenette and E. Martin who provided great assistance during field work. Moreover, R. Ellen, R. Ford and J. Paterson provided help with logistics on and around the ski hill. J.H. Richard was supported by a scholarship from Ski Marmot Basin and Parks Canada.

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Appendix 5 Movement and day length

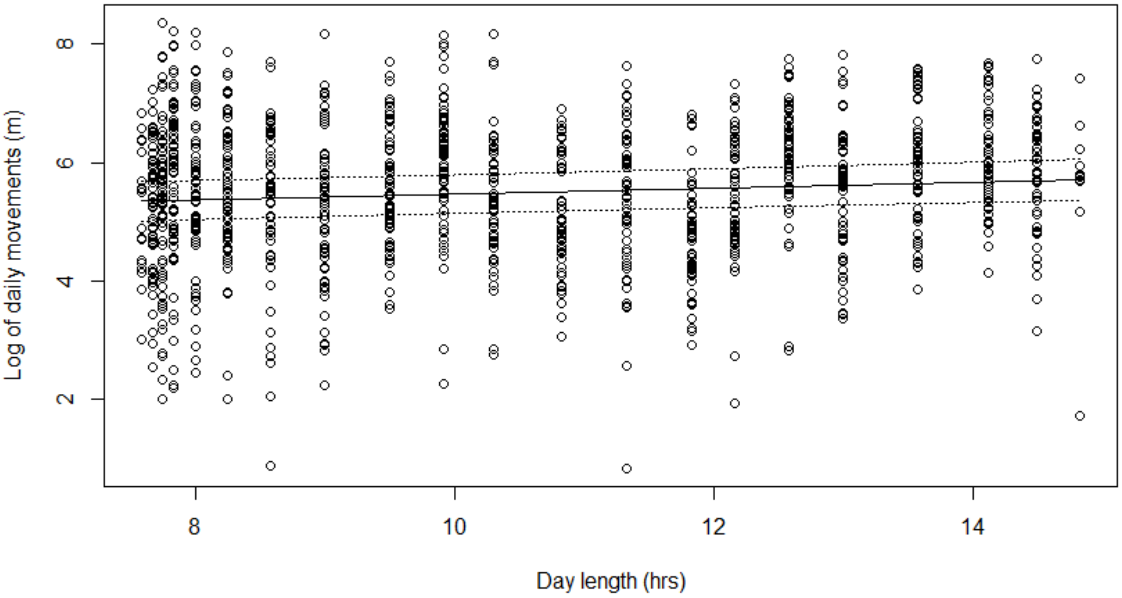

Figure 2.3 Log of daily movements in relation to day length for mountain goats (*Oreamnos americanus,* De Blainville, 1816) during winter, Jasper National Park.

Chapitre 3 : Mating effort and space use of an alpine ungulate during the rut

- Effort reproducteur et utilisation de l’espace d’un ongulé alpin durant le rut

Julien Hénault Richard[1], Kevin S. White[2] et Steeve D. Côté[1]

[1] Département de biologie et Centre d’études nordiques, Université Laval, 1045 av. de la médecine,
Québec, QC, Canada, G1V 0A6

[2]Alaska Department of Fish and Game, Division of Wildlife Conservation, 802 Third Street,
Douglas, PO Box 110024, Alaska, USA

Résumé

Chez les mâles ongulés, le rut mène généralement à une augmentation des déplacements. Puisque les déplacements engendrent des coûts énergétiques et des opportunités d'approvisionnement manquées, ils pourraient être un indicateur de l'effort reproducteur des mâles. De 2005 à 2008, nous avons étudié l'utilisation de l'espace durant le rut de 44 chèvres de montagne (*Oreamnos americanus*) mâles provenant de trois sous-populations voisines du sud-est de l'Alaska. À l'aide de modèles mixtes et une sélection de modèles par AIC, nous avons analysé les relations entre les traits individuels des mâles et leur utilisation de l'espace. Nous n'avons trouvé aucune migration reproductive entre les sous-populations. Les distances entre les domaines vitaux saisonniers n'étaient liées à aucun trait individuel. Les déplacements quotidiens, la taille des domaines vitaux et la distance totale parcourue pendant le rut ne variaient pas avec l'âge ou la masse des individus. Ainsi, les traits individuels semblent peu influencer l'utilisation de l'espace des mâles pendant le rut et les parons d'utilisation de l'espace observés ne supportent aucune des hypothèses les plus courantes concernant l'effort reproducteur.

Abstract

In ungulates, the rut generally leads to increased intra and inter-population movements for males. Because movements induce energetic costs and missed feeding opportunities, they could be an indication of male mating effort. We studied space use of 44 male mountain goats (*Oreamnos americanus*) from three neighboring subpopulations in southeast Alaska, during the rut from 2005 to 2008. Using mixed models and an information theoretic approach with AIC, we analysed the relationships between individual traits of males and their space use. We found no indication of breeding migration between subpopulations. Distances between individual seasonal ranges were not related to any individual trait. Daily movements, home range sizes and total distance travelled during the rut did not vary with mass or age of individuals. As such, effects of individual traits on male space use during the rut appear weak and observed space use patterns do not support any of the main mating effort hypotheses.

Introduction

In polygynous ungulates, males typically undergo large physiological and behavioral changes during the reproductive period as they compete for access to females (Pelletier et al. 2009; Brivio et al. 2010). The proportion of time allocated to reproduction may vary greatly among adult males (14-84%; see Pelletier 2005). Males often decrease time spent feeding (Willisch and Ingold 2007; Brivio et al. 2010) and allocate most of their resources to find and tend estrous females (Mainguy and Côté 2008), resulting in increased movement rates (Pépin et al. 2009; White et al. 2012). Some males may also travel between spatially discrete rutting areas (Hogg 2000; Jarnemo 2011). Different behavioural tactics result in variation in energy allocated to reproductive behaviour by males.

The effort males allocate to reproductive behaviour is a function of age (Mysterud et al. 2003) and body condition (Yoccoz et al. 2002; McElligott et al. 2003; Mainguy and Côté 2008). Multiple hypotheses have been developed to explain variation in mating effort (i.e., the relative amount of energy devoted to reproduction) among males. The mating strategy effort hypothesis predicts that courtship behavior should peak in prime-aged males irrespective of body condition or mass (Yoccoz et al. 2002). The terminal investment hypothesis predicts that reproductive effort increases with age, because the value of each offspring increases as the number of future potential offspring decreases (Pianka and Paker 1975; Clutton-Brock 1984). The individual quality hypothesis predicts that males with more resources (i.e., greater age-specific body mass) at the start of the rut should allocate more energy to reproductive behaviour than smaller individuals irrespective of age (Pelletier et al. 2006). Because increased movements during the rut represent a cost to males (Dailey and Hobbs 1989, Alerstam et al. 2003) and are expected to increase the opportunity of finding and tending a higher number of receptive females (Pépin et al. 2009), distance traveled by rutting males can be considered an indirect measure of mating effort (Pelletier et al. 2006). Thus, the mating strategy effort, the terminal investment and the individual quality hypotheses predict that movements during the rut should peak in prime aged males, older males and males with greater age-specific body mass, respectively.

Mate competition is an important driver explaining the spatial repartition of males during the breeding season (Hogg 2000; Parga and Lessnau 2008; Jarnemo 2011). As a result of intra-sexual competition, males may adopt migration tactics during the breeding season (Hogg 2000), by moving among populations and returning to their original population after the rut (Berger 2004). Breeding migration has been reported for bighorn sheep, *Ovis canadensis* (20 to 50% of male bighorn sheep of all ages; Festa-Bianchet 1991; Hogg 2000) and red deer, *Cervus elaphus*

(Pemberton et al. 1992; Jarnemo 2011). Breeding migration is thought to provide males with increased breeding opportunities because of decreased mate competition in cases where low numbers of males, particularly large males, are present in neighboring subpopulations (Dobson 1982; Hogg 2000). Breeding migration could also be an inbreeding avoidance mechanism, although most studies suggested that it is mainly driven by intra-sexual competition (Hogg 2000; Jack and Fedigan 2004; Parga and Lessnau 2008; Jarnemo 2011).

We tested the reproductive effort hypotheses in an alpine ungulate, the mountain goat (*Oreamnos americanus*). As such we examined whether individual characteristics influence space use and movement patterns during the breeding season. Similar to other North-American mountain ungulates (i.e., bighorn sheep), mountain goats are polygynous, exhibit sexual segregation, do not form harems, demonstrate high fidelity to their native population (particularly among females) and dispersal is mostly performed by males (Geist 1964; Festa-Bianchet 1986; Festa-Bianchet et Côté 2008). Compared to females, male mountain goats show high movement rate during the rut (White et al. 2012). This increase in movement induces cost to individual that could be related to the reproductive effort deployed by males. Reproductive effort of male mountain goats appears to be more related to pre-rut body mass than age (Mainguy and Côté 2008). Male mountain goats use two main reproductive tactics according to their age and social rank (Mainguy et al. 2008). The same tactics are used by bighorn sheep as described by Hogg (1984). Tending, which is most successful, normally involves the defense of a single female by a dominant male (Hogg 1984). Coursing is mostly used by young and subordinate males and consists of acquiring access to females by pursuing them and isolating them from dominant males (Hogg 1984). Because females appear to be distributed throughout the populations' range (unpubl. Data) it seems reasonable to assume that regardless of the reproductive tactic used by a male, more movement will result in more reproductive opportunities.

Although breeding migrations have been reported in mountain goats (Mainguy et al. 2008), previous studies have not examined the frequency and the characteristics of breeding migrations in this species. Because social rank of male mountain goats is positively related to age (Côté 2000; Mainguy et Côté 2008), we hypothesised that: movements, range size and frequency of breeding migration will decrease with age as individuals gaining social rank have priority access to females. However, movements, range size and frequency of breeding migration should increase with mass as individuals have more resources to devote to reproduction.

Materials and methods

Study area

We studied mountain goats in a ca. 1100 km^2 area within the Pacific Coastal Mountains biogeographic region (Gallant et al. 1995). The site is located in a mainland coastal mountain range east of Lynn Canal, a maritime fjord located south of Haines in southeastern Alaska, USA (58°N, 134°W). Elevations range from sea level to 1920 m. The area is mountainous and includes perennial snowfields and glaciers (typically above 1200m), and broken terrain that descends to the coastline at lower elevation. Anthropogenic development and activity (regulated hunting, tourism, and mining) occur in the site but are highly localized and encompass only a small proportion of the area (White et al. 2011).

Mountain goats in the area are split in three subpopulations (Shafer et al. 2011, 2012) and typically perform seasonal migrations of 5 to 10 km between high elevation alpine summer habitat and low elevation wintering areas (White et al. 2012). Fall downslope migrations are roughly synchronized with the first major alpine snowfall (i.e., mid-October), whereas spring upslope migrations correspond with the onset of snow melt and the pre-parturition period (i.e., early-May; White et al. 2012).

Male rutting strategies

We assessed how individual characteristics (age and mass) influenced movements of males during the rut from 2005 to 2009. We determined male rutting movements by 1) the size of rutting ranges, 2) the daily distance travelled by males and 3) the total distance travelled during the rut. Based on direct observations from Caw Ridge, Alberta (54°N, 119°W) (Mainguy et al. 2008) and to make sure we included all rut related movements, we defined the rutting period as October 15th to December 15th of each year. We defined winter as December 16th to May 14th and summer as May 15th to October 14th based on snow cover on the ground and timing of altitudinal migrations (White et al. 2011).

We captured mountain goats using standard helicopter darting techniques (Taylor 2001, White et al. 2012); animals were immobilized by carfentanil citrate injection, which was reversed with naltrexone hydrochloride once the handling procedures were completed. All animals were equipped with Telonics TGW-3590 GPS radio-collars (Telonics Inc., Mesa, AZ) weighing 1.14kg. For more details on capture procedures and collar characteristics see White et al. (2006, 2012). Radio-collars collected locations every 6 h (fix success: 80 to 85%) with an average collar deployment period of about 515 days per male (min= 125 days, max= 915 days, standard deviation (sd)= 221 days). GPS location accuracy varied between 30m and 60m for open and closed-forested areas, respectively (White et al. 2012). We discarded GPS locations with Positional Dilution of Precision (PDOP) greater than 10 (Taylor et al. 2004; D'Eon and Delparte 2005). We also performed a visual screening to remove highly improbable points (D'Eon and Delparte 2005). We obtained data on 44 males from three subpopulations (Shafer et al. 2012, White et al. 2012). Because mass was only determined at capture, which occurred in late summer, we retained only the first rutting season for each male. Subpopulations are separated by glacial river valleys and marine waters and are genetically distinct (Shafer et al. 2012, White et al. 2012). All capture procedures were approved by the State of Alaska Animal Care and Use Committee.

We determined age for each individual at capture. We determined age by counting horn annuli and in some cases, cross-validated by examination of tooth eruption (Smith 1988). Cementum annuli analyses were performed for animals that died during monitoring (30% of collared individuals). We calculated the daily distances travelled from the sum of all movements within a single day. We considered daily distance travelled only when we had at least 3 successful fixes per 24 hours. Seasonal (rut, winter and summer) range sizes were calculated using 95% Minimum Convex Polygons (MCP). Centers of seasonal ranges were estimated by calculating the arithmetic mean of all locations collected during a given period (Von Hardenberg et al. 2000). Total distance travelled during the rut was the sum of all single step movements recorded for the period. To assess the relative location of males during the rut compared to the rest of the year, we measured distances between the center of a given rutting range and the center of the previous summer range and the center of the following winter range, for each individual in each year. All distances measured included the variation in elevation estimated with a 30m x 30m digital elevation model (DEM) raster. We first estimated distances in two dimensions, drawing a straight line between each successive location (i.e. planimetric distance). Afterwards, we adjusted the distances for the elevation difference between the two locations using Pythagoras' theorem (i.e., surface area distance),

$$D=\surd(d^2+\Delta h^2)$$

where D represents the corrected distance, d is the distance between 2 successive locations and Δh is the altitude difference between both locations.

Statistical analyses

Because individuals were captured on different dates and age-specific relative mass is more relevant to test mass-related hypotheses (e.g. individual quality) than absolute mass, we used a mass index representing seasonally-adjusted age-specific relative mass. Following Mainguy and Côté (2008), we first obtained seasonally-adjusted mass by estimating the average growth rate of all adult males (≥3 years old) during the 4 years of capture (2005-2008) between July 28th and October 15th with a linear regression of mass as the dependent variable and date of capture as a fixed factor. We obtained a linear growth of 0.26kg per day that we used to adjust mass at September 15th. We then used seasonally-adjusted mass in a GLMM, with age and age^2 as fixed factors and year fitted as a random term. We used the residual value obtained for each individual as the seasonally-adjusted age-specific relative mass in all space use analyses.

Using linear mixed models, we analysed the relationship between individual traits of males and their space use. To evaluate the effect of age and mass on males' space use, we built a set of 10 candidate models containing different combinations of age, age^2 and mass variables directly related to each tested hypothesis (Appendix 6). We included age^2 and mass^2 to enable non-linear relations of space use metric with age and mass. We used the same set of models to explain each space use metric. We centered age measurements by subtracting the mean value of each to avoid collinearity with squared terms and improve statistical interpretation (Schielzeth 2010). For daily distance travelled, we included individual and subpopulation identity, as well as year as random variables to control for repeated measures on the same individual, subpopulations' range and genetic characteristics, and annual environmental conditions, respectively. For rutting range size and total distance travelled during the rut only subpopulation and year were included as random effects because we had only one observation per individual. Daily distance travelled and rutting range size were log transform to respect the assumption of the models. Best models were chosen by lowest Akaike information criterion (AIC) score for daily distance travelled and lowest AICc score for rutting range size and total distance move during the rut, which had small sample size (n=44) (Burnham and Anderson 2004). We also compared different combinations of random variables to assess their influence on male space use during the rut. Because these variables should be accounted for from a biological stand point, we kept all previously mentioned random variables regardless of their effect on AIC scores. We performed all analyses with the package "lme4" (Bates et al. 2011) in the software R, version 2.13.0 (R Development Core Team 2011) and we used 95% confidence intervals to test the effects of parameters included in the best models.

Results

Size of rutting ranges

The 44 rutting ranges averaged 12.7 km^2 (Standard Error (SE) = 1.69, range: 1.28 – 47.27 km^2. The best model (Δ AICc = 0, k=7, AICc wi = 0.11) explaining rutting range size included only the random variables (subpopulation and year) (Table 3.1-A). We found no support for any of the models containing age or mass effects. Comparison of null models indicates that year and subpopulation did not explain variation in rutting range size (Table 3.2-A).

Daily distance travelled

The daily distance travelled by males averaged 909 m (SE=21.8, range: 2 – 11924 m, N=2459 daily movements). The best model (Δ AICc = 0, k=51, AICc wi = 0.11) explaining total daily distance travelled included only random variables (animal identity, subpopulation and year) (Table 3.1-C). Again we found no support for any of the models containing age or mass effects. Comparison of null models indicates that year, subpopulation and individual identity all accounted for some of the variation in daily distance travelled during the rut (Table 3.2-C).

Total distance travelled during the rut

The total distance travelled by males during the rut averaged 50.78 km (SE=2.79, range: 11.30 – 873.29 km). The best model (Δ AICc = 0, k=7, AICc wi =0.11) explaining total distance travelled during the rut included only the random variables (subpopulation and year) (Table 3.1-B). Once again we found no support for any of the models containing age or mass effects and the comparison of null models suggests that year and subpopulation accounted for some of the variation in total distance travelled during the rut (Table 3.2-B).

Table 3.1 A) AICc values for linear models explaining rutting range size and B) total distance travelled during the rut of male mountain goats, C) AIC values for linear models explaining daily distance travelled during the rut from 2005 to 2008, east of Lynn Canal AK, USA.

A) Model number	Model structure	number of parameters	AICc	Δ AICc	AICc weight
0	Null (1|pop)+ (1|year)	7	997.10	0.00	0.11
3	Mass	8	997.37	0.27	0.11
1	Age	8	999.56	2.46	0.10
5	age+mass	8	999.96	2.86	0.10
4	mass+mass^2	9	1000.04	2.94	0.10
6	age+mass+age*mass	10	1000.28	3.18	0.09

2	age+age^2	9	1002.10	5.00	0.09
7	age+age^2+mass	10	1002.60	5.50	0.08
9	age+age^2+mass+age*mass	11	1003.13	6.03	0.08
8	age+age^2+mass+mass^2	11	1005.58	8.48	0.07
10	age+age^2+mass+mass^2+age*mass	12	1006.28	9.18	0.07
B)					
0	Null (1|pop)+ (1|year)	7	121.92	0.00	0.11
3	Mass	8	123.61	1.69	0.10
1	Age	8	124.47	2.55	0.10
4	mass+mass^2	9	125.17	3.25	0.09
6	age+mass+age*mass	10	125.80	3.88	0.09
5	age+mass	8	126.30	4.38	0.09
9	age+age^2+mass+age*mass	11	126.34	4.42	0.09
2	age+age^2	9	127.02	5.10	0.09
7	age+age^2+mass	10	129.04	7.12	0.08
10	age+age^2+mass+mass^2+age*mass	12	129.34	7.42	0.08
8	age+age^2+mass+mass^2	11	130.81	8.89	0.07
C)			AIC	Δ AIC	AIC weight
0	Null (1|pop/name)+ (1|year)	51	7487.30	0.00	0.11
3	Mass	52	7489.10	1.80	0.10
1	Age	52	7489.20	1.90	0.10
2	age+age^2	53	7490.70	3.40	0.09
4	mass+mass^2	53	7490.90	3.60	0.09
5	age+mass	53	7491.00	3.70	0.09
6	age+mass+age*mass	54	7491.30	4.00	0.09
7	age+age^2+mass	54	7492.60	5.30	0.09
9	age+age^2+mass+age*mass	55	7493.30	6.00	0.08
8	age+age^2+mass+mass^2	55	7494.30	7.00	0.08
10	age+age^2+mass+mass^2+age*mass	56	7494.80	7.50	0.08

Table 3.2 A) AICc values for null models containing different intercepts explaining rutting range size and B) total distance travelled during the rut of male mountain goats, C) AIC values for null models explaining daily distance travelled during the rut from 2005 to 2008, east of Lynn Canal AK, USA.

A) Model number	Model structure	number of parameters	AICc	Δ AICc
2	~(1|year)	4	976.41	0.00
1	~(1|pop)	3	976.79	0.38
3	~(1|pop)+ (1|year)	7	978.41	2.00
0	~1	NA	992.87	16.46
B)				

0	~1	NA	118.21	0.00
2	~(1|year)	4	121.53	3.32
1	~(1|pop)	3	121.60	3.39
3	~(1|pop)+ (1|year)	7	122.87	4.65
C)			AIC	Δ AIC
3	~(1|name)	44	7487.29	0.00
4	~(1pop/name)+(1|year)	51	7490.70	3.41
2	~(1|year)	4	7607.34	120.05
1	~(1|pop)	3	7612.40	125.11
0	~1	NA	7614.37	127.08

Distance between seasonal ranges and breeding migration

Males did not move between subpopulations during the breeding season. We found maximum net displacement distances ranging from 2.4 km to 14.2 km (average: 6.1 km) with two displacements exceeding 10km. The best models for examining the relationships between individual male traits (mass, age) and distance between the center of individual rutting ranges and centre of winter ranges or centre of summer ranges were null models containing only random effects (subpopulation and year)(Table 3.3). Distances between centers of individual rutting ranges and summer ranges averaged 2139 m (SE= 234, range: 315 - 6302m, N=44), while distances between centres of rutting ranges and winter ranges averaged 1767 m (SE=210, range: 189 – 8062 m, N=44) (Figure. 3.1). Comparison of null models suggests that year and subpopulation did not explain variation in distances between seasonal ranges (Table 3.4).

Table 3.3 A) AICc values for linear models explaining distance between rutting range and winter range and B) distance between rutting range and summer range of male mountain goats from 2005 to 2008, east of Lynn Canal AK, USA.

A) Model number	Model structure	number of parameters	AICc	Δ AICc	AICc weight
0	null (1|pop)+ (1|year)	7	121.92	0.00	0.11
3	Mass	8	123.61	1.69	0.10
1	Age	8	124.47	2.55	0.10
4	mass+mass^2	9	125.17	3.25	0.10
6	age+mass+age*mass	10	125.80	3.88	0.09
5	age+mass	8	126.30	4.38	0.09
9	age+age^2+mass+age*mass	11	126.34	4.42	0.09
2	age+age^2	9	127.02	5.10	0.09
7	age+age^2+mass	10	129.04	7.12	0.08

10	age+age^2+mass+mass^2+age*mass	12	129.34	7.42	0.08
8	age+age^2+mass+mass^2	11	130.81	8.89	0.07
B)					
0	null (1|pop)+ (1|year)	7	109.13	0.00	0.10
4	mass+mass^2	9	109.31	0.18	0.10
3	Mass	8	111.15	2.02	0.09
2	age+age^2	9	111.30	2.17	0.09
1	Age	8	111.54	2.41	0.09
8	age+age^2+mass+mass^2	11	112.17	3.04	0.09
6	age+mass+age*mass	10	112.27	3.14	0.09
7	age+age^2+mass	10	113.43	4.30	0.08
5	age+mass	8	113.72	4.58	0.08
10	age+age^2+mass+mass^2+age*mass	12	114.36	5.23	0.08
9	age+age^2+mass+age*mass	11	114.54	5.41	0.08

Table 3.4 A) AICc values for null models containing different intercepts explaining distance between rutting range and winter range and B) distance between rutting range and summer range of male mountain goats from 2005 to 2008, east of Lynn Canal AK, USA.

A) Model number	Model structure	number of parameters	AICc	Δ AICc
0	~1	NA	102.50	0.00
2	~(1|year)	4	106.92	4.43
1	~(1|pop)	3	107.25	4.75
3	~(1|pop)+ (1|year)	7	109.24	6.74
B)				
0	~1	NA	104.40	0.00
1	~(1|pop)	3	109.20	4.80
2	~(1|year)	4	109.20	4.80
3	~(1|pop)+ (1|year)	7	111.63	7.23

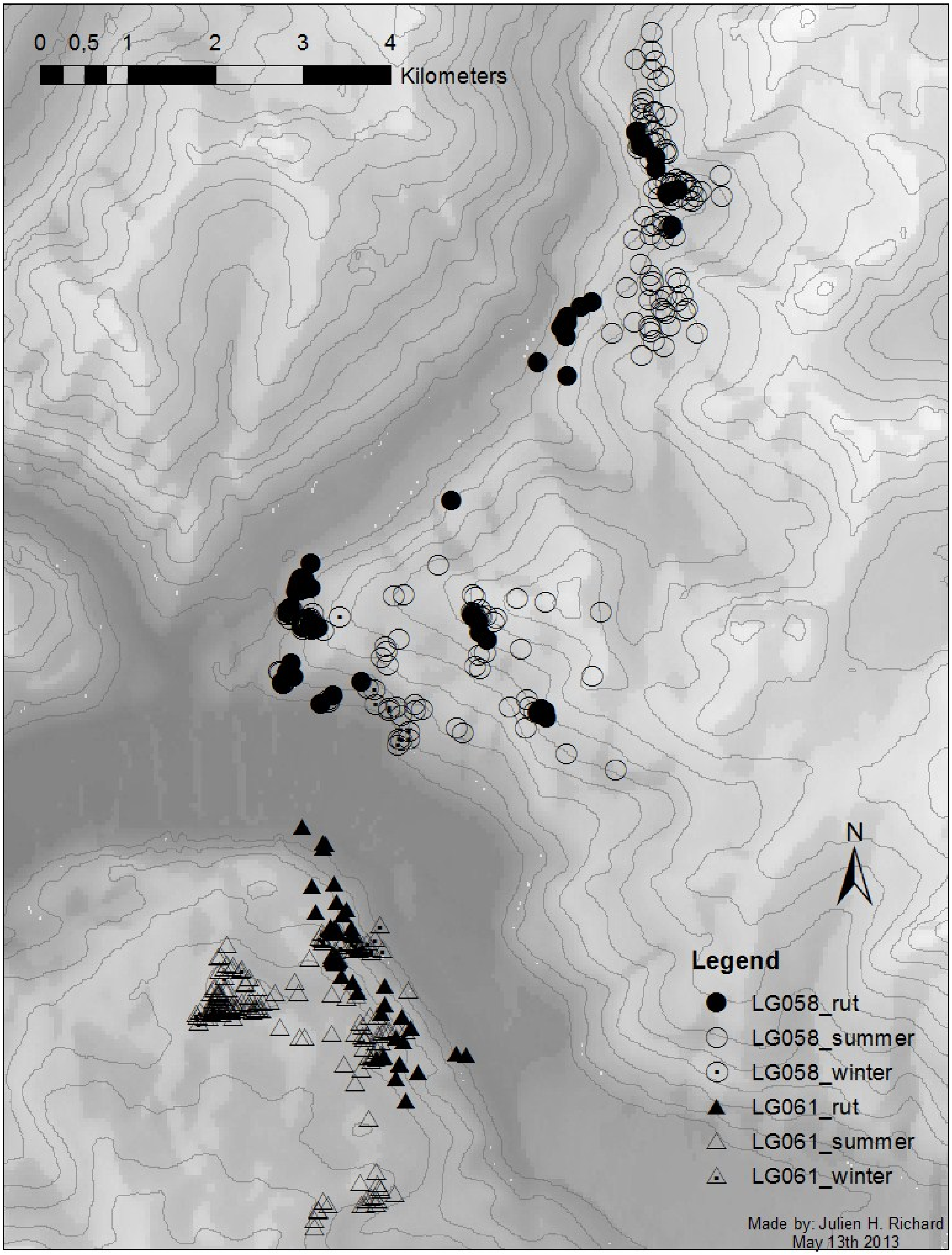

Figure 3.1 Example of movements during summer, rut and winter 2007-2008 for "LG061, a 10 year old male mountain goat of 150kg and LG058, a 5 year old male of 110kg, east of Lynn Canal, Alaska, USA.

Discussion

We aimed to: 1) test reproductive effort hypotheses in male mountain goats; and 2) identify individual characteristics influencing male space use, movement patterns and frequency of breeding migration during the rut. Our results revealed no support for any of the main mating effort hypotheses. Moreover, displacements between rutting ranges and summer or winter ranges mostly reflected the seasonal altitudinal migration performed by mountain goats in this region. No breeding migration has been observed.

Age does not appear to play a key role in the determination of space use patterns during the rut as none of the space use metrics appeared linked to male age. Because social rank is positively associated with age in mountain goats (Côté 2000; Mainguy et al. 2008), this suggests that intra-sexual competition plays a limited role in the space use of male mountain goats during the rut. This contradicts predictions from the mating strategy effort and the terminal investment hypotheses. As such, the change in rutting tactics from coursing when young and subordinate to tending when older and dominant (Mainguy et al. 2008) does not appear to influence space use of male mountain goats. This was unexpected, because the coursing tactic implies more movements than the tending tactic as individuals roam over large areas to find untended females or run at tended females and attempt to disrupt the association with the tending male (Hogg 1984). It has, however, been shown that consorting male baboons (*Papio cynocephalus*), similar to tending ungulate males, travelled shorter distances than non-consorting males (Alberts et al. 1996).

We documented no effect of seasonally-adjusted age-specific relative mass on space use during the rut. This suggests that the effort allocated to reproduction in terms of movements is not related to mass, even if lighter individuals have less stored reserves and may be less inclined to allocate energy in search for females. Results are different than previous studies which suggested that reproductive effort in ungulates is mostly related to pre-rut body mass (McElligot et al. 2003; Pelletier 2005; Mainguy et Côté 2008). The absence of relation could indicate that allocation of energy reserves in reproductive effort does not involve changes in male space use during the rut or that space use is not limited by the amount of stored reserves (Mainguy and Côté 2008).

The absence of relation between mass and space use, and thus mating effort, does not support the individual quality hypothesis (Pelletier et al. 2006). Even if rutting males are known to lose weight during the reproductive period (Yoccoz et al. 2002) and heavier individuals have more stored resources to allocate to reproduction, they do not seem to invest more in reproduction-related movements. This is inconsistent with the idea that males should adjust their reproductive effort according to their phenotypic condition (Festa-Bianchet et al. 1998).

The absence of relationships of individual traits, subpopulation traits and annual conditions on movements among seasonal ranges suggests that these movements are probably more linked to fine scale landscape characteristics or unmeasured individual traits or behaviour. The comparison of null models suggests that the influence of environmental conditions, reflected by the effect of the year random factor, on distance travelled by rutting males is greater than the influence of individual traits. The rut occurs in late autumn when snowfalls are common. Snow limits movements (Von Hardenberg et al. 2000; Fortin and Andruskiw 2003; Ratikainen et al. 2007) and may trigger altitudinal migration (White 2006). Therefore, snow could limit mountain goat movements and influence space use during the rut. Variations of distance traveled among subpopulations also suggest that the influence of subpopulations traits on movements of rutting males is greater than the influence of measured individual traits. Several subpopulations traits may explain this, but we suggest that subpopulation size, composition and distribution as well as characteristics of the used landscape are amongst the most likely determinant factors. The size and the composition of the subpopulation could influence the level of competition between males and the number of available females which could both influence space use during the rut. The distribution of the subpopulation in the landscape influences the mean distance between individuals and therefore the movements of males as they search for females. The characteristics of the landscape likely have a similar effect as it has been suggested that differences in mountain goats home range sizes are probably linked to differences in landscape structure (Côté and Festa-Bianchet 2003). The large influence of individual identity on daily movements suggests high individual variations in movements. Individual movement patterns appear constant throughout the year (J.H. Richard pers. obs.), which suggests that perhaps different personalities occur in males with some more sedentary, and others more mobile (Boone et al. 2008; van Overveld and Matthysen 2010).

Although our assumption linking space use during the rut and mating effort appeared reasonable, the absence of influence of individual age or mass on space use suggests that space use during the rut may not be a good predictor of mating effort, at least when confounding factors as outlined above are present. Even if increased movements induce increased energy expenditure, it does not necessarily indicate increases in mating effort. Because female mountain goats form groups, males do not necessarily need to travel long distances to participate in reproduction. Therefore, direct observations of mating attempts appear essential to determine mating effort.

The absence of breeding migration suggests high fidelity of males to their population, even during the rutting season. Although this would be expected by definition of genetic subpopulations, especially given high genetic differentiation among subpopulations (Shafer et al.2012), this contrasts with previous observations on mountain goats at Caw Ridge, Alberta, where breeding migration cases were noticed (Mainguy et al. 2008). However, in the Caw Ridge area, mountain goats occur in relatively small, isolated populations compared to more continuous range in the Alaskan Coastal Mountains. Using observational data from Caw Ridge, we found a total of 8 cases of breeding migrations by adult males during 3 successive rut seasons (2004-2006; S.D. Côté, unpublished data). Of those 8 males, 7 were young (≤ 5 years) and one was prime aged (7 years old), suggesting that breeding migration is mostly performed by young subordinate individuals. Males performing breeding migrations represented 7 to 11% of all adult males present at Caw Ridge during each year. It is possible that we missed some breeding migrations in Alaska because not all males were marked. However, the size and duration of the sampling should have been sufficient to detect at least some cases of breeding migrations. Compared to Caw Ridge, the larger occupied area and the lower density of mountain goats in Lynn Canal probably limit the benefits of performing breeding migration. In Alberta, about 15 to 20km separate the closest mountain goat population (Mount Hamell) from Caw Ridge. Although breeding migration may be performed to other populations more distant from Caw Ridge, a similar 15km movement occurring in Lynn Canal would result in an intrapopulation movement for most mountain goats in the area. Moreover, because of the lower density of mountain goats found in Lynn Canal the social pressure to engage in a breeding migration should be less important than in Caw Ridge. We thus concur with Hogg (2000) that the likelihood of breeding migration is likely context dependent. In any case, we can conclude that breeding migration is less common in mountain goats than for example in bighorn sheep, where breeding migration concerns 33% of adult males on average (Festa-Bianchet 1986; Festa-Bianchet 1991). This could be related to mountain goat's preference for steeper slopes (Laundre 1994; Shafer et al. 2012) that could limit willingness to migrate far from these escape areas as migration often involved movements through more risky forested areas (Festa-Bianchet and Côté 2008).

Intra-sexual competition is thought to be the main driver explaining male ungulate breeding migration or dispersal (Hogg 2000; Jarnemo 2011), because males tend to migrate to areas with fewer or lower quality competitors (Rogers 1987; Festa-Bianchet 1991; Hogg 2000). The absence of breeding migration could indicate that levels of intra-sexual competition were similar in the 3 subpopulations studied. Moreover, environmental conditions and anthropogenic pressures (such as hunting) were similar in the three studied subpopulations (White et al. 2012), suggesting similar adult male survival. This could limit the benefit of breeding migrations because the probability of males acquiring enhanced breeding opportunities via movement to another population appears low.

Although the 3 subpopulations were separated by important geographical features (i.e., marine fjords, glaciers and rivers), we have evidence that some individuals are capable of crossing glaciers and small river valleys (K.S. White unpublished data). Moreover, male mountain goats have been reported to travel long distances in inhospitable terrain (Festa-Bianchet and Côté 2008; Mathew and Heath 2008; Shafer et al. 2011). However, the additional risks associated with crossing treacherous geographical features combine with the higher predation risk in forested areas could limit movements between the Alaskan subpopulations.

Mountain goats are spatially structured (Shafer et al. 2011), indicating that dispersal and breeding migration events can have important effects on the genetic structure of populations. Moreover, mountain goat sex ratios are typically highly biased towards females (Gonzalez-Voyer et al. 2003) which highlights the importance of properly understanding male space use patterns. Yet, previous research relative to space use during the rut has been limited for this species. In a conservation perspective, understanding movements during the reproductive period will inform on the level of interactions in meta-population sub-units. To our knowledge, this is the first study to explicitly assess the relation between individual traits and space use of male mountain goats during the rut. Our results do not support any of the main hypothesis on mating effort and suggest that individual characteristics, such as mass and age, do not determine the spatial reproductive tactic used by males. Our results suggest that movements and space use are thus poor predictors of reproductive effort.

Acknowledgments

We are grateful to A.-S. Julien and D. Emond for help with statistical analysis and to J. Wilmshurst, M. Apollonio and an anonymous reviewer for valuable comments on an earlier version of the manuscript. Funding was provided by the Alaska Department of Fish and Game, Alaska Department of Transportation and Public Facilities and Coeur Alaska. We thank J. Jemison, N. Barten, D. Larsen, R. Scott, A. Crupi, C. Rice, K. McCoy and L. Butler for their help with capture, handling and monitoring of mountain goats. Aerial capture support was provided by R. Madrid and M. Horton (Temsco Helicopters). Fixed-wing aerial support was provided by L. Bennett, C. Schroth, J. Norvell, M. Morris, D. Larsen and P. Valkenburg. We thank J. Mainguy, M. Houle, E. Cardinal and J. Taillon for their help studying the rut of goats at Caw Ridge. JHR was supported by a scholarship from Ski Marmot Basin and Parks Canada.

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Appendix 6

List of tested model and biological explanations for the relevance of each tested models

Table 3.5 List of tested models for the relation between individual traits and space use of rutting male mountain goats

Model number	Model structure	Number of parameters
0	Null	7
1	Age	8
2	age+age^2	9
3	Mass	8
4	mass+mass^2	9
5	age+mass	8
6	age+mass+age*mass	10
7	age+age^2+mass	10
8	age+age^2+mass+mass^2	11
9	age+age^2+mass+age*mass	11
10	age+age^2+mass+mass^2+age*mass	12

Model #1 Age: movements increase linearly with age, which supports the terminal investment hypothesis

Model #2 Age+age^2: movements increase non-linearly with age, a convex shape curve would indicate that prime aged individuals move more, which would support the mating strategy effort. An exponential curve would suggest movements increase with age and do so more quickly as individuals age; this would support the terminal investment hypothesis.

Model #3 Mass: movements increase linearly with mass, which support the individual quality hypothesis.

Model #4 Mass+mass2: movements increase non-linearly with mass, this could represent a threshold in the mass above or below which movements are limited; this would support the individual quality hypothesis.

Model #5 Age+mass: movements increase with age and mass, this would indicate that a combination of the terminal investment hypothesis and the individual quality hypothesis best explain rutting movements

Model #6 Age+mass+ mass*age: movements increase with age and mass, this would indicate that a combination of the terminal investment hypothesis and the individual quality hypothesis best explain rutting movements. The interaction term would enable the detection of variation in the effect of mass as animals age: for example young individuals might only participate in the rut if they are in good condition.

Model #7 Age+age^2+mass: movements increase non-linearly with age, a convex shape age effect would indicate that prime aged individuals move more, which would support the mating strategy effort. An exponential shape age effect would suggest movements increase with age and do so more quickly as individuals age; this would support the terminal investment hypothesis. Increased movements with age would suggest that the individual quality hypothesis also help explain rutting movements. Movements could also increase linearly with mass which would support the individual quality hypothesis.

Model #8 Age+age^2+mass+mass^2: movements increase non-linearly with age, a convex shape age effect would indicate that prime aged individuals move more, which would support the mating strategy effort. An exponential shape age effect would suggest movements increase with age and do so more quickly as individuals age; this would support the terminal investment hypothesis. Increased movements with age would suggest that the individual quality hypothesis also help explain rutting movements. Movements could also increase non-linearly with mass, this could represent a threshold in the mass above or below which movements are limited; this would support the individual quality hypothesis.

Model #9 Age+age^2+mass+age*mass: movements increase non-linearly with age, a convex shape age effect would indicate that prime aged individuals move more, which would support the mating strategy effort. An exponential shape age effect would suggest movements increase with age and do so more quickly as individuals age; this would support the terminal investment hypothesis. Increased movements with age would suggest that individual quality hypothesis also help explain rutting movements. Movements could also increase linearly with mass which would support the individual quality hypothesis. The interaction term would enable the detection of variation in the effect of mass as animals age: for example young individuals might only participate in the rut if they are in good condition.

Model #10 Age+age^2+mass+mass^2: movements increase non-linearly with age, a convex shape age effect would indicate that prime aged individuals move more, which would support the mating strategy effort. An exponential shape age effect would suggest movements increase with age and do so more quickly as individuals age; this would support the terminal investment hypothesis. Increased movements with age would suggest that the individual quality hypothesis also help explain rutting movements. Movements could also increase non-linearly with mass, this could represent a threshold in the mass above or below which movements are limited; this would support the individual quality hypothesis. The interaction term would enable the detection of variation in the effect of mass as animals age: for example young individuals might only participate in the rut if they are in good condition.

Conclusion

Cette étude sur l'utilisation de l'espace des chèvres de montagne a permis de répondre à une problématique réelle de conservation tout en approfondissant nos connaissances sur cette espèce encore peu étudiée. Grâce à l'étude de l'utilisation de l'espace nous avons pu approfondir notre compréhension de : 1) l'influence de perturbations anthropiques causées par des activités récréatives sur les chèvres de montagne, 2) l'influence des conditions de neige sur l'utilisation de l'espace des chèvres de montagne et 3) les relations entre les traits individuels des mâles et leur effort reproducteur.

Perturbations anthropiques et utilisation de l'espace

Le premier chapitre décrit les réactions des chèvres de montagne face aux perturbations anthropiques émanant d'un centre de ski alpin et d'activités récréatives qui y sont reliées. Nous avons démontré que les chèvres de montagne évitent le centre de ski de Marmot Basin. Les chèvres de montagne, particulièrement les femelles, réagissent fortement à la présence humaine et à des activités récréatives de faible impact comme la randonnée pédestre. De plus, les patrons temporels de l'utilisation d'une saline sont modifiés par l'activité humaine et la présence humaine limite l'utilisation des salines.

Nous avons quantifié l'évitement du centre de ski en utilisant les probabilités relatives d'utilisation prédites par des modèles de sélection d'habitat (Manly et al. 2002). Cette méthode a permis d'identifier les secteurs où les probabilités relatives d'utilisation étaient élevées et de comparer leur utilisation réelle selon leur emplacement à l'intérieur ou à l'extérieur des limites du centre de ski. Nous avons déterminé qu'il y a peu d'endroits ayant une forte probabilité d'utilisation à l'intérieur des limites du centre de ski en hiver. Il était donc logique d'observer très peu de chèvres de montagne dans ce secteur à cette période. Durant l'hiver, l'exposition des différentes pentes du centre de ski fait en sorte que la neige s'y accumule de manière importante ce qui est favorable pour le ski, mais défavorable pour les chèvres de montagne. Tout au cours de l'année, par contre, des parties des secteurs les plus élevés et abrupts du centre de ski présentent des caractéristiques intéressantes pour les chèvres de montagne soit la présence de terrains de fuite associés à des secteurs dégagés supportant de la végétation alpine. Malgré la présence de cet habitat propice et du plus faible niveau d'activité anthropique durant l'été, les chèvres utilisaient rarement le centre de ski et demeuraient en périphérie de celui-ci. Les perturbations directes résultant de rencontres entre des humains travaillant ou prenant part à des activités récréatives sur la montagne et les chèvres de montagne pourraient avoir contribué à cette situation. De plus, les effets indirects liés à la modification de l'habitat à l'intérieur des limites du centre de ski jouent probablement un rôle. La coupe et l'éclaircissement de la forêt qui ont eu lieu lors de la mise en place des pistes de ski, ainsi que le débroussaillage des pistes, qui est réalisé régulièrement, ont entrainé des modifications significatives de l'habitat sur la montagne de Marmot. Ces modifications de l'habitat ont ensuite entrainé des modifications dans la communauté d'espèces végétales et animales qui s'y retrouve. L'ouverture de la forêt a créé des milieux plus productifs en début d'été, ce qui attire les ours noirs (*Ursus americanus*) et les grizzlys (*Ursus arctos*). Les grizzlys sont parmi les principaux prédateurs des chèvres de montagnes (Festa-Bianchet et Côté 2008). Leur présence régulière sur la montagne de Marmot en début d'été pourrait être un facteur qui mène à l'évitement du centre de ski à cette période. Il semble donc que plusieurs activités liées au centre de ski ont le potentiel d'affecter l'utilisation de l'espace des chèvres de montagne et la somme de ces effets a fort probablement entraîné la situation d'évitement que l'on observe actuellement. Néanmoins, il aurait été profitable d'avoir des données concernant l'utilisation de l'habitat par les chèvres de montagne préalablement à l'implantation du centre de ski (dans les années 1960) afin de déterminer plus précisément les impacts de ses activités.

Des observations comportementales nous indiquent que les chèvres de montagne de la région demeurent craintives lorsqu'elles rencontrent des humains. Ainsi, la présence humaine liée au centre de ski et au tramway situé sur la montagne voisine de Whistlers ne permet pas aux chèvres de montagne de s'habituer à la présence humaine dans d'autres contextes. Certains individus peuvent s'approcher des humains près du tramway de Whistlers, mais réagiront fortement lorsqu'on les rencontre dans d'autres secteurs. Les chèvres de montagne qui utilisent la montagne de Marmot sont craintives lorsqu'on les rencontre lors de randonnées pédestres. Le caractère imprévisible de la randonnée hors-piste limite les possibilités d'habituation des animaux à ce genre d'activité (Cassirer et al. 1992; Stankowich 2008; Neumann et al. 2010). De plus, en hiver, les randonneurs en ski se déplacent plus rapidement que lors de randonnées pédestres ce qui pourrait accentuer la réaction des chèvres de montagne à leur égard (Frid and Dill 2002).

La saline de Whistlers Creek, situé à moins de 1 km du centre de ski de Marmot Basin, semble cruciale pour les chèvres de montagne de la région. Celles-ci déploient beaucoup d'efforts pour s'y rendre même si son utilisation augmente le risque de prédation puisqu'elle se situe en forêt. Puisque la montagne de Marmot est le seul accès utilisé par les chèvres de montagne pour atteindre la saline, il est important de maintenir ce corridor de déplacement afin d'assurer l'accessibilité à cette ressource. Les résultats mentionnés plus haut et les connaissances sur la vulnérabilité des chèvres de montagne face aux perturbations anthropiques (Foster et Rahs 1983; Joslin 1986; Côté et al. 2013), suggèrent qu'un éventuel développement ou une hausse du niveau d'activité sur les versants nord et nord-ouest limiterait l'accès à la saline. La présence de la saline et du corridor de déplacement pour s'y rendre a pu contribuer au patron d'utilisation de l'espace que l'on observe présentement. Les chèvres de montagne ont pu s'habituer aux limites du centre de ski et maintenir leur utilisation des autres versants de la montagne afin de continuer à accéder à la saline.

Les impacts de l'évitement actuel du centre de ski sur la population de chèvres de montagne sont probablement limités puisqu'ils affectent une petite portion du paysage environnant. Par contre, l'expansion du centre de ski sur les autres versants de la montagne de Marmot pourrait entraîner des conséquences plus graves. Les versants sud et nord-ouest sont des aires d'hivernage principales pour certains individus. Un niveau d'activité plus important mènerait probablement à un évitement ou un abandon de ces secteurs. Toutes perturbations entraineraient également une augmentation des dépenses énergétiques des chèvres de montagne pendant une saison critique au cours de laquelle elles tentent de limiter les dépenses d'énergie au maximum.

L'ensemble de ces résultats a mené à l'élaboration de recommandations concernant le développement potentiel du centre de ski de Marmot Basin. Bien que certaines parties des analyses concernent assez peu d'individus, ceux-ci représentent environ la moitié des individus qui utilisent la montagne de Marmot, ce qui donne une bonne représentation de l'utilisation de l'espace de la population. Afin d'assurer la persistance à long terme de la population, nous recommandons qu'aucun développement n'ait lieu à l'intérieur d'un rayon de 1 km autour de la saline de Whistlers Creek (figure 4.1). En raison de la topographie des environs, ceci devrait être suffisant pour maintenir l'utilisation de la saline et une partie de son accès. Nous recommandons également de ne pas développer et de limiter l'activité dans les aires d'hivernage principales des chèvres de montagne pour assurer l'accès à des aires d'hivernage de qualité qui sont essentielles pour les chèvres de montagne. De plus, le maintien de ces limitations à l'intérieur des zones d'hivernage principales tout au long de l'année assurerait de maintenir l'accessibilité à la saline. En effet, les sentiers utilisés par les chèvres de montage pour accéder à la saline se retrouvent presque entièrement dans un rayon de 1 km autour de la saline et dans l'aire d'hivernage située sur le versant nord-ouest.

Bien que cette étude concerne seulement 1 centre de ski, plusieurs de ces conclusions semblent applicables dans un contexte plus général concernant la cohabitation de chèvres de montagne et de centre de ski alpin. Durant l'hiver, les chèvres de montagne vont généralement chercher à utiliser des secteurs où la neige s'accumule moins afin de faciliter leur déplacement et l'accès aux ressources alimentaires (Hebert et Turnbull 1977; Côté et Festa-Bianchet 2003; Poole et al. 2009).

Pour leur part, les centres de ski alpin sont situés dans des endroits où la profondeur de neige est grande afin d'offrir de bonnes conditions de glisse. Ainsi, les chèvres de montagne se retrouveront rarement à l'intérieur de limites d'un centre de ski durant l'hiver. Par contre, les centres de ski alpin occupent habituellement un ou deux versants d'une montagne qui sont les plus propices à leur activité. Il est donc possible que des chèvres de montagne se trouvent à proximité du centre de ski durant l'hiver sans que leur présence soit détectée à l'intérieur des limites du centre de ski. Dans ces cas, les activités hors-piste ont le potentiel de perturber des chèvres de montagne qui serait présente. Même dans les cas où ces perturbations seraient rares, les perturbations engendrées pourraient être problématiques puisque : 1) le caractère imprévisible des activités hors-piste limite la possibilité d'habituation de la faune face à ces activités (Cassirer et al. 1992; Stankowich 2008; Neumann et al. 2010), 2) les ongulés alpins tentent de limiter au maximum leur dépense énergétique durant l'hiver et les perturbations viendraient augmenter ces dépenses en raison d'une hausse de leurs niveaux de stress et de vigilance (Hjeljord 1973; Chadwick 1983; Poole et al. 2009) et 3) dans les cas où les individus voudraient s'éloigner des perturbations, leurs dépenses énergétiques seraient encore plus grandes en raison du couvert de neige (Parker et al. 1984; Canfield 1999). Il semble donc important de limiter le niveau d'activité anthropique près des habitats utilisé par des chèvres de montagne durant l'hiver.

Durant l'été, plusieurs centres de ski sont utilisés pour des activités récréatives comme la randonnée pédestre ou le vélo de montagne. Bien que ce ne fût pas le cas sur la montagne de Marmot alors que l'activité anthropique estivale se résumait à l'entretien des infrastructures, les chèvres de montagne évitaient tout de même le centre de ski. Ceci suggère que, même si le niveau d'activité anthropique est plus faible en hiver qu'en été, les chèvres de montagnes se retrouveront à l'intérieur des limites du centre de ski que très rarement, et ce, même en présence d'habitat favorable. Ainsi, les activités hivernales d'un centre de ski couplé avec les activités d'entretien estivales sont suffisantes pour limiter l'utilisation de cet espace par les chèvres de montagne. De plus, les modifications de l'habitat qui sont engendrées par la présence de centre de ski contribuent à changer les communautés végétales et fauniques présentes dans ces endroits. Ces modifications ont le potentiel de diminuer la qualité de l'habitat pour les chèvres de montagne.

Malgré la présence d'un centre de ski et d'un accès par téléphérique au milieu alpin situé sur la montagne voisine, les chèvres de montagne réagissent toujours fortement à la présence humaine. Ceci indique que, comme il a été mentionné auparavant (Côté 1996; Gordon et Reynolds 2000; Côté et al. 2013), les chèvres de montagne s'habituent difficilement aux activités anthropiques. En accord avec le principe mentionné plus haut, les chèvres de montagne semblent davantage tolérer la présence humaine là où elle est plus prévisible. Par contre dans les endroits où la présence humaine est plus rare les chèvres de montagne réagiront fortement à la présence humaine. Nous avons également noté que les chèvres sont sensibles à la présence humaine à proximité de saline naturelle. Puisque ces salines semblent très prisées par les chèvres de montagne il apparait nécessaire d'assurer leur accessibilité et le maintien de leur intégrité.

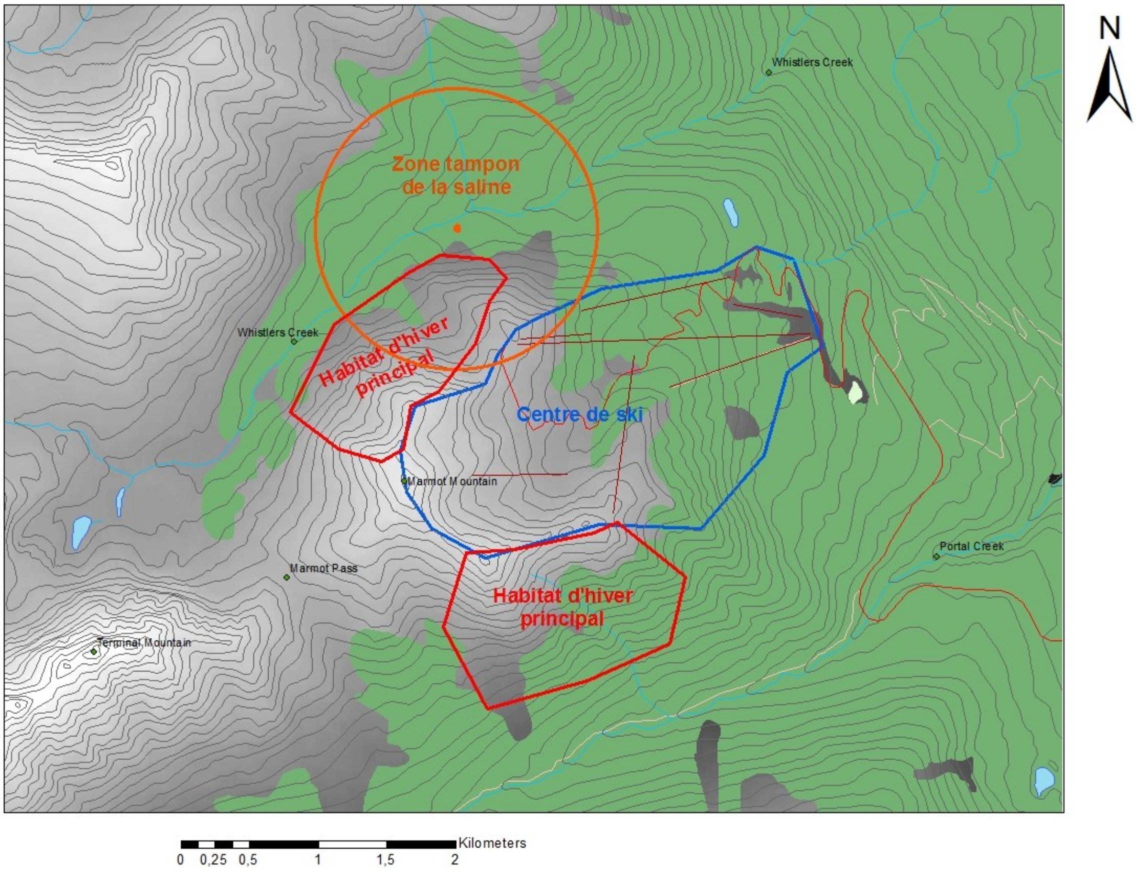

Figure 4.1 Localisation des habitats d'hiver principaux et recommandation de zone tampon autour de la saline de Whistlers Creek lick, Marmot Mountain, Parc National Jasper 2013.

Neige et utilisation de l'espace

L'ensemble des résultats concernant l'influence de la neige sur l'utilisation de l'espace des chèvres de montagne supporte notre hypothèse de départ qui voulait que le vent et les radiations solaires que l'on retrouve dans les environnements alpins durcissent et déplacent constamment le couvert nival, conférant ainsi un plus grand impact aux précipitations de neige récentes qu'à la neige accumulée. En effet, la quantité de neige fraîche est plus limitante que l'épaisseur de neige pour l'utilisation de l'espace des chèvres de montagne. Les résultats sont les mêmes en ce qui concerne les déplacements à l’échelle de la journée ou à l’échelle de la semaine, ainsi que pour la taille des aires utilisées au cours d’une semaine. Il serait intéressant d’approfondir sur les conséquences indirectes du vent, qui modifie les conditions de neige en milieu alpin, sur l’utilisation de l’espace de la faune. Bien que nos résultats supportent notre hypothèse initiale, nous n’avons pas étudié l’effet réel du vent sur les conditions de neige et sur l’utilisation de l’espace de chèvres de montagne et il serait intéressant de confirmer le mécanisme que nous suggérons. De plus, les conditions de vent pourraient venir modifier la période pendant laquelle la neige peut être considérée comme fraîche et durant laquelle elle limite les déplacements de manière significative.

Nous croyons également que l’utilisation de petites aires hivernales entraîne l’utilisation fréquente de sentiers communs ce qui facilite les déplacements durant l’hiver. Ce phénomène pourrait être similaire chez plusieurs autres espèces d’ongulés de régions tempérées ou arctiques qui utilisent des petites aires hivernales (Lovari et al 2006; Rivrud et al. 2010; van Beest et al. 2011). Dans ces conditions, les précipitations de neige recouvrent les sentiers et limitent temporairement l’utilisation de l’espace des animaux en raison des coûts de déplacement élevés dans la neige. Après quelque temps, les sentiers reprennent forme, ce qui facilite les déplacements des animaux, peu importe l’épaisseur de neige au sol. Il serait donc intéressant d'en savoir plus sur le processus de formation de sentier dans la neige et sur l’influence que ces sentiers peuvent avoir sur l’utilisation de la faune durant l’hiver.

Bien que l’épaisseur de neige influence peu les déplacements et la taille des aires utilisées par les chèvres de montagne, cette variable a certainement un impact important sur la répartition des chèvres dans le paysage. En effet, les chèvres recherchent généralement les secteurs où la neige s’accumule moins pour passer l’hiver (Smith 1977; Poole et al. 2009). Une fois dans ces secteurs, la quantité de neige fraîche a un impact plus important sur leur utilisation de l’espace que l’épaisseur de celle-ci.

Le risque de prédation jouerait un rôle dans la plus forte probabilité de retrouver les chèvres de montagne en terrains de fuite la nuit. Les chèvres de montagne utilisent souvent les terrains de fuite pour se reposer à l’abri des prédateurs (McFetridge 1977). C’est d’autant plus vrai la nuit lorsque la détection des prédateurs par la vue est plus difficile. Nous avions prédit que les chèvres de montagne devraient demeurer plus près des terrains de fuite lorsqu’il y a plus de neige en raison de leur plus grande vulnérabilité dans ces conditions. En présence de grandes quantités de neige, il serait difficile pour les chèvres de montagne d’échapper à un prédateur si elles se trouvaient loin de terrains de fuite et que leurs déplacements étaient ralentis par la neige. Contrairement à nos hypothèses, les conditions de neige influencent peu l'association avec les terrains de fuite. Seule l'épaisseur de neige influençait la distance au terrain de fuite, et ce, positivement. Ce résultat contradictoire suggère que, lorsque l'épaisseur de la neige augmente et que la disponibilité des ressources végétales diminue, les chèvres de montagne doivent s'éloigner des terrains de fuite afin d'avoir accès à de la végétation non ensevelie.

À notre connaissance, il s'agit de la première étude soulignant l'importance de considérer la quantité de neige fraîche dans la détermination de l'utilisation de l'espace de la grande faune. Il serait souhaitable d'approfondir ce sujet en étudiant : 1) cette relation chez d'autres espèces d'ongulés, 2) la manière dont les différentes mesures de neige affectent les dépenses énergétiques des individus, et 3) la durée de la période pendant laquelle la neige fraîche doit être considérée avant que son effet sur l'utilisation de l'espace diminue.

Traits individuels et utilisation de l'espace pendant le rut

Les résultats du troisième chapitre suggèrent que : 1) les migrations reproductrices sont peu fréquentes chez les chèvres de montagne, et que 2) l'utilisation de l'espace des mâles durant le rut est peu influencée par leurs traits individuels (âge, masse).

L'absence de migration reproductive indique que les mâles demeurent fidèles à leur population même en période de rut. Les chèvres de montagne adultes sont connues pour être fidèles aux sites qu'elles utilisent (Côté et Festa-Bianchet 2003), mais certaines mentions de migration reproductive sont présentes dans la littérature (Mainguy et al. 2008). Ces cas de migrations reproductives semblent toutefois limités aux jeunes mâles et concernent entre 7 et 11 % des mâles adultes chaque année (S.D. Côté, données non publiées). Nos résultats proposent également que les migrations reproductives sont moins courantes chez la chèvre de montagne que chez le mouflon d'Amérique (Festa-Bianchet 1986; Festa-Bianchet 1991).

Les migrations reproductives ont été décrites par des observations sur les mouflons d'Amérique. Bien que les mouflons et les chèvres de montagne partagent plusieurs caractéristiques écologiques, les chèvres semblent être plus étroitement liées aux habitats alpins et abrupts que les mouflons (Laundre 1994). Ce trait pourrait limiter les déplacements sur de longues distances qui les forceraient à s'éloigner de ces types d'habitat afin de rejoindre une autre population. Nous proposons que des différences de structure du paysage, de répartition et de densité des populations pourraient influencer la participation aux migrations reproductives dans différents sites. En effet, plus les autres populations sont accessibles et nombreuses, plus les possibilités de participer à une migration reproductive seront grandes. La distance séparant les populations pourrait également jouer un rôle, car une très grande distance serait trop coûteuse à parcourir à plusieurs reprises. Dans ces cas, les mâles pourraient se contenter de parcourir la distance une fois et de rester dans la nouvelle population par la suite. Plusieurs jeunes mâles montrent en effet des comportements de dispersion au cours desquels ils se déplacent sur de longues distances pour aller s'établir dans une autre population (Festa-Bianchet et Côté 2008). En diminuant le niveau de compétition dans la population d'origine, ce comportement limiterait les cas de migration reproductive par la suite. De plus, la composition et l'organisation sociale de la population influencent probablement les probabilités de migrations reproductives. Les populations dans lesquelles les mâles forment de grands groupes seraient plus propices aux migrations reproductives, puisque le niveau de compétition apparaîtrait plus élevé pour les mâles. Puisque les mâles mouflons forment généralement de plus grands groupes (Risenhoover and Bailey 1982; Festa-Bianchet 1986), ceci expliquerait en partie la plus grande prévalence des migrations reproductives chez cette espèce. Nous proposons, comme Hogg (2000), que les migrations reproductives sont dépendantes du contexte de chaque population. Peu importe la cause des migrations reproductives, il est important d'approfondir nos connaissances sur l'utilisation de l'espace des mâles en période reproductive afin de mieux comprendre les interactions entre les populations. À ce titre, l'identification de frontières claires et distinctes faciliterait notre détection de ce comportement. En effet, puisque les mâles peuvent se déplacer sur d'assez longues distances, il est important de bien connaître les limites de l'aire utilisée par une population afin de détecter un déplacement en dehors de ces limites. De plus, les études de génétique du paysage constitueraient une avenue intéressante pour étudier les interactions entre les populations (ex. Shafer et al. 2012).

Surprenamment, l'âge des mâles, qui explique en grande partie le rang social des individus (Côté 2000; Mainguy et Côté 2008), n'a pas eu d'effet sur l'utilisation de l'espace durant le rut. Ce résultat implique que malgré le changement de tactique reproductive avec l'âge passant du « coursing » au « tending » (Mainguy et al. 2008), les individus de tous âges ont une utilisation de l'espace qui est semblable. Ce résultat laisse aussi croire que la compétition intrasexuelle a peu d'effet sur l'utilisation de l'espace des mâles durant le rut. Puisque les mâles devraient ajuster leur effort reproducteur en fonction de leur condition phénotypique (Festa-Bianchet 1998), nous croyions que la masse relative des mâles pourrait influencer leurs déplacements en période de rut. Par contre, nous n'avons pas trouvé de support pour cette hypothèse. Ainsi, il semble que d'autres facteurs qui n'ont pas été mesurés dans cette étude comme la distribution des femelles, la structure du paysage et la densité des populations pourraient mieux prédire l'utilisation de l'espace durant le rut. Il est également possible que les effets de l'âge et de la masse soient dépendants du contexte de chaque sous-population. Il est également possible que la fréquence à laquelle les déplacements étaient compilés par les colliers GPS n'était pas suffisante pour déceler des modifications plus fines dans les patrons d'utilisation de l'espace des mâles.

Les faibles corrélations entre l'utilisation de l'espace des mâles pendant le rut et leurs traits individuels sont un résultat inattendu. À notre connaissance, il s'agit de la première étude qui utilisait des mesures d'utilisation de l'espace comme mesure de l'effort reproducteur. Bien que les résultats semblent peu concluants, nous croyons qu'il s'agit d'un résonnement logique, et qui mérite qu'on s'y attarde davantage. Les déplacements au cours du rut engendrent des coûts énergétiques, mais aussi des occasions de se reproduire. Les déplacements sont donc cohérents avec l'effort reproducteur qui est la quantité relative d'énergie consacrée à la reproduction. Les observations directes de tentatives de reproduction représentent néanmoins une méthode permettant une quantification de l'effort reproducteur qui est plus facilement interprétable. Par contre, de telles observations ne sont pas toujours possibles en raison de nombreuses contraintes logistiques.

Nous avons noté une grande variabilité dans les patrons individuels d'utilisation de l'espace des mâles. Cette variabilité associée à une taille d'échantillon limité pour chaque classe d'âge et sous-population a pu rendre plus difficile l'identification de patrons généraux. Des différences individuelles dans les patrons de déplacement semblent également observables tout au long de l'année alors que certains individus vont se déplacer de manière importante comparativement à d'autres, plutôt sédentaires. L'étude et la prise en compte de ces personnalités différentes seraient intéressantes et faciliteraient l'identification de relations entre les traits individuels et l'utilisation de l'espace en terme d'effort reproducteur. Il serait également souhaitable de combiner les résultats d'une étude semblable sur l'effort reproducteur avec des données de succès reproducteur pour avoir une meilleure compréhension de la situation. Encore une fois, la génétique serait un outil fort utile.

Conclusion générale

Ce mémoire illustre le large éventail de sujets pouvant être traités à l'aide de l'étude de l'utilisation de l'espace. L'utilisation de l'espace nous a permis de déterminer comment les chèvres de montagne réagissaient aux perturbations anthropiques afin d'élaborer des mesures d'atténuation dans un contexte de conservation. Nous avons également amélioré le niveau de connaissances concernant les modifications d'utilisation de l'espace par les ongulés alpins en fonction des conditions environnementales. Ainsi, nous comprenons mieux comment les chèvres de montagne s'ajustent aux conditions difficiles qu'elles rencontrent en hiver, une période critique pour l'espèce.

Enfin, nous avons approfondi nos connaissances fondamentales en testant des hypothèses sur les liens entre l’utilisation de l’espace, les traits individuels et l’effort reproducteur des mâles. Ainsi, l’utilisation de l’espace nous permet plusieurs types d’études allant de sujets très fondamentaux, à des problématiques appliquées en gestion et en conservation.

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