UNIVERSITÉ DU QUÉBEC À MONTRÉAL

SPRING DISPERSAL AND HABITAT SELECTION OF BOREAL CARIBOU (*RANGIFER TARANDUS CARIBOU*) IN NORTHERN QUEBEC

THESIS
PRESENTED
AS A PARTIAL REQUIREMENT FOR
THE MASTERS IN BIOLOGY

BY
TYLER RUDOLPH

MAY 2011

UNIVERSITÉ DU QUÉBEC À MONTRÉAL

MOUVEMENTS ET SÉLECTION D'HABITAT LORS DES DÉPLACEMENTS PRINTANIERS DU CARIBOU FORESTIER (*RANGIFER TARANDUS CARIBOU*) DANS LE NORD-DU-QUÉBEC

MÉMOIRE PRÉSENTÉ COMME EXIGENCE PARTIELLE

DE LA MAITRISE EN BIOLOGIE

PAR

TYLER RUDOLPH

MAI 2011

REMERCIEMENTS

Je tiens à remercier du fond de mon cœur les généreuses contributions de maintes personnes à la réalisation de ce projet. À Pierre Drapeau, mon directeur, à la fois pour son optimisme et pour son esprit de guerrier, celui qui m'a offert cette opportunité de poursuivre un sujet fort intéressant et qui m'a fourni des moyens pour y réussir. À mon bras droit du laboratoire, Maxime Allard, pour son enthousiasme envers des problèmes complexes et pour sa capacité à trouver des solutions quand j'étais arrivé au bout. Aux autres confrères et consœurs du labo pour leur support technique, moral et amical tout au long de cette aventure : Nicolas Bergeron, Philipe Cadieux, Ugo Ouellet-Lapointe, Antoine Nappi, Virginie Arielle-Angers, Marianne Cheveau, Michel Saint-Germain, Annie Hibbert, Simon Bédard, et Raphael Dubé. Aux professionnels de recherche du Centre d'étude de la forêt : Marc Mazerolle, Stéphane Daigle, Daniel Lesieur, Robert Schneider (post-doc), et surtout Mélanie Desrochers pour avoir réalisé une quantité inoubliable de mise à jour numérique des cartes spatiales!... À Jenna Jacobs et Dave Gervais, merci de votre générosité et camaraderie. Au grand philosophe Alain Leduc pour son appréciation de la subtilité (« le diable est dans les détails » comme on dit) et pour son sens d'humour apaisant et toujours aiguisé. À tous mes amis géniaux du CEF; vous faites de ce travail un véritable plaisir. À Maryse Marchand particulièrement d'être venue généreusement à ma rescousse un certain dimanche soir : je t'en dois une!

Aux endroits plus lointains, j'offre un gros merci à Vincent Brodeur, notre partenaire principal du MRNF à Chibougamau, pour son intégrité et pour sa bonne volonté à faire pousser le dossier du caribou forestier. Merci également à ses excellents techniciens Stéphane Rivard et Lyna Lambert (on a eu du fun chez vous!), ainsi que Denis Vandal et Jacynthe Barrette du MRNF de La Sarre. Un grand merci aux chercheurs qui m'ont éclairé des pistes le long de mon développement, dont Steve Ferguson, Chris Johnson, John Fieberg, Jon Horne, Hall Sawyer, John Marzluff,

Brian Kertson, Daniel Fortin, Nicolas Courbin, et James Forester. Je tiens également à remercier la communauté R de m'avoir permis de régler bien des problèmes de programmation au fil des ans, notamment Milton Ruser, Roger Bivand, Adrian Baddeley, Gene Leynes, Vito Muggeo, et Clément Calenge. Merci également à Jeffrey McDonald et Vladimir Timochevsk de l'Université McGill d'avoir facilité mon utilisation de Krylov.

Merci à Jim Schaefer et à Louis Imbeau d'avoir consenti à réviser ce mémoire. Votre contribution a grandement amélioré la qualité du document.

Last but certainly not least, j'aimerais remercier les deux femmes les plus importantes dans ma vie. To my mother Carol, for encouraging me to get an education and for always standing behind me: I did it! À Jacynthe, mon rayon de soleil, qui a tant enduré et qui a tant donné d'elle-même pour la réalisation de cette œuvre: je n'y serais point arrivé sans toi.

AVANT-PROPOS

Le présent mémoire de maîtrise a été rédigé sous la forme de deux articles ainsi qu'une introduction et une conclusion générale. Le texte est écrit en anglais pour faciliter son accessibilité dans le milieu des sciences, mais un résumé est également fourni en français. Conformément aux exigences de la maîtrise en sciences biologiques à l'UQÀM, j'ai procédé au traitement des données, à l'analyse des résultats et à la rédaction des articles à titre de premier auteur. Le premier article, intitulé « **Variation in seasonal onset behaviour and potential consequences for studies of seasonal habitat selection** », a été soumis à la revue *Rangifer* en janvier 2011; mon directeur Pierre Drapeau en sera le seul co-auteur. La soumission du deuxième article, intitulé « **Spring dispersal and habitat selection of boreal caribou in northern Quebec** », est prévue cet été. Encore une fois, Pierre Drapeau en sera le seul co-auteur.

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ANOVA :	Analysis of Variance
BBMM :	Brownian bridge movement model
RSF :	Resource selection function
RSPF :	Resource selection probability function
RUF:	Resource utilization function
SI :	Straightness Index (*D/L*)
UD :	Utilization Distribution

RÉSUMÉ

La conservation du caribou forestier est un enjeu clé de la gestion écosystémique. Le plan de rétablissement du caribou forestier, publié par le Québec en 2009, propose une approche de gestion forestière qui comprend le maintien de la connectivité entre des massifs de protection afin de faciliter les déplacements du caribou. Cependant, la majorité des études sur le caribou forestier se concentrent sur des périodes sédentaires soient l'hiver et la mise bas. Dans cette étude nous avons étudié le comportement du caribou boréal du Nord-du-Québec durant une période de déplacement, la dispersion printanière, afin de mieux caractériser les attributs d'habitats qui semblent faciliter la connectivité.

Dans le premier chapitre de ce mémoire, nous privilégions une méthode d'analyse (partition récursive) à base individuelle qui permet d'obtenir des dates correspondant à trois saisons critiques dans le cycle de vie annuel du caribou forestier soient l'hiver, la dispersion printanière, et la mise bas. Ensuite nous comparons les dates obtenues par cette approche avec a) des dates obtenues par une méthode effectuée sur des données communes à la population (régression polynomiale mixte), et b) celles ayant été établies par consensus des experts pour notre région d'étude. Les résultats démontrent que même à l'intérieur d'une saison relativement stable il y a une variabilité individuelle et annuelle importantes quant à la période temporelle qui y correspond. Le modèle estimé sur les données communes de la population n'a pas obtenu les mêmes dates que celui estimé à l'échelle individuelle. Par ailleurs, les dates obtenues par consensus des experts différaient de façon importante des dates obtenues au moyen de l'étude du comportement des individus, particulièrement l'hiver et à la mise bas. Les dates correspondant à la mise bas étaient les moins différentes dans les trois cas. Nous concluons qu'afin de réduire le biais dans les études de sélection d'habitat, lors de la délimitation de la saison d'intérêt il est préférable d'utiliser des méthodes quantitatives qui sont basées sur le signal biologique de mouvements des individus d'une population plutôt que d'adopter des dates fixes et/ou établies *a priori* pour une région.

Dans le deuxième chapitre nous abordons en premier lieu le patron de déplacement printanier du caribou forestier. En général, le caribou n'a pas utilisé les mêmes parcours de déplacement d'une année à l'autre, quoiqu'il semble avoir montré une certaine fidélité à sa destination finale (site de mise bas). Les mouvements des individus étaient orientés mais il n'y avait pas de direction prédominante à l'échelle de la population. Les caribous en déplacement à proximité d'un réseau routier important (> 5km/km^2) tendaient à tourner en rond sans se rendre très loin (i.e. tortuosité élevée), alors que les caribous en déplacement au-delà de 30 km d'un réseau routier important faisaient des déplacements plus directionnels (quasi-linéaire) et se rendaient nettement plus loin. Ceci pourrait indiquer que les chemins forestiers imposent un effet de barrière à la dispersion du caribou, ce qui pourrait avoir des conséquences néfastes pour la survie des populations sous forme de trappes écologiques.

Le deuxième élément abordé dans chapitre deux est la sélection d'habitat du caribou forestier durant ses déplacements printaniers. Nous avons d'abord quantifié sa distribution printanière par le biais d'un modèle de mouvement Brownian bridge (MMBB), qui génère une surface de probabilité continue que nous avons ensuite utilisé comme variable réponse dans un modèle de sélection d'habitat. En général le caribou n'a pas démontré de sélection ou d'évitement fort vis-à-vis les attributs de son environnement durant ses déplacements saisonniers. Il a toutefois manifesté des tendances qui reflètent des compromis entre chercher une nourriture de qualité et minimiser le risque de prédation et les coûts énergétiques des déplacements. Par exemple, le caribou tendait à sélectionner des landes à lichen et des milieux humides tout en évitant des secteurs ayant une forte densité en coupes et/ou en chemins forestiers. Il tendait également à se tenir plus proche des basses terres et des cours d'eau lorsqu'accessible (à l'intérieur de 500 m). Par ailleurs, les chemins forestiers semblaient provoquer un comportement d'évitement chez le caribou boréal jusqu'à 15 kilomètres de distance, et les coupes forestières jusqu'à 10 kilomètres. Nous concluons que, étant donné le faible degré de fidélité aux parcours de déplacement printanier, planifier des corridors de déplacement fixes ne semble pas une approche très prometteuse pour maintenir la connectivité des paysages. Cela étant dit, la fidélité du caribou à ses parcours de déplacement risque d'être plus importante sur des territoires fortement aménagés puisque la connectivité de ses paysages serait moindre. Néanmoins, puisque le caribou en déplacement semble éviter les perturbations récentes, une densité accrue d'interventions forestières sur le paysage ne pourrait que nuire à la connectivité du territoire pour cet animal. Afin de mieux viser la conservation de cette espèce menacée, nous suggérons de minimiser la coupe ainsi que les chemins forestiers dans les secteurs encore occupés par le caribou forestier. Lorsque les interventions y sont envisagées, nous recommandons de ne passer qu'une fois par voie d'hiver en faisant des coupes localisées de petite envergure (coupe partielle, coupe sélective), tout en assurant la réhabilitation des chemins forestiers par la suite.

Mots clés : caribou forestier, écotype boréal, comportement de déplacement, dispersion printanière, méthodes quantitatives, variabilité temporelle, consensus des experts, connectivité du paysage, Brownian bridge movement model (BBMM), sélection d'habitat, resource selection probability function (RSPF), réponse fonctionnelle.

ABSTRACT

The forest-dwelling woodland caribou is a threatened species in Canada considered to be particularly vulnerable to the direct and indirect effects of habitat alteration and fragmentation, a significant part of which has been attributed to industrial forest management. Recommendations for the conservation of caribou on managed landscapes include the maintenance of functional connectivity between seasonal ranges. While much is presently known about caribou space use behaviour during the winter and calving periods, relatively little is known about migratory phases of its annual life cycle. We investigate movement behaviour and habitat selection of boreal woodland caribou during spring dispersal in northern Quebec. We argue that spring dispersal is a critical yet often overlooked period in the annual life cycle of woodland caribou.

In Chapter 1, we develop an individual-based quantitative method for identifying seasonal shifts in caribou movement behaviour and we demonstrate its use in determining the onset of the winter, spring dispersal, and calving seasons. Using pooled data for the population we demonstrate an alternate approach using polynomial regression with mixed effects. We then compare the onset dates obtained using the individual-based method with a) those estimated using the population-based model and finally b) those adopted by expert consensus for our study area. Distributions of individual-based onset dates were normally distributed with prominent modes. However results revealed considerable variation in individual onset times even for calving, which varied the least. Population-based estimates were closer to the peaks of individual estimates than were expert-based estimates, which fell outside the one-tailed 90 % and 95% sample confidence intervals of individual-based estimates for spring and winter, respectively. Both expert- and population-based estimates were late for winter and early for both spring and calving. We discuss the potential consequences of neglecting to corroborate conventionally used dates with observed seasonal trends in the movement behaviour of sample animals. We conclude by recommending that researchers adopt an individual-based quantitative approach and a variable temporal window for data set extraction.

In Chapter 2 we investigate spring movement parameters and habitat selection of boreal caribou.

First, we examine individual dispersal paths for evidence of directionality, orientation, and interannual fidelity. Individual movements were oriented overall but there was no predominant direction at the population level. While caribou did exhibit fidelity to traditional calving site locations, there was little interannual overlap in travel routes used; this raises questions about the perceived utility of fixed travel corridors. Inspection of path tortuosity revealed that caribou traveling within 30 km on average of highly roaded areas (> 0.5 km/km^2) were more likely to circle about extensively with little net displacement (i.e. random movements), whereas caribou beyond the 30 km threshold were more likely to exhibit quasi-linear (i.e. oriented) movements. This indicates that roads may represent semi-permeable barriers to caribou dispersal, which has profound implications for population survival if they are unable to space away from predators at calving.

Second, we use a Brownian bridge movement model to estimate the probability of occurrence of boreal caribou during spring dispersal and we conduct linear regression with mixed effects to estimate a Resource Selection Probability Function. Overall caribou space-use patterns revealed trade-offs between optimal foraging, predator avoidance and energy conservation. In general caribou stayed close to waterways when they were within 500m and were slightly less likely to be found at higher elevations. Caribou selected lichen woodlands and all forms of wetlands, particularly herb-dominated, and they were less likely to be found in zones of higher road and cutblock densities. This being said, caribou were less selective during spring dispersal that they are known to be at other times of the year. Our primary recommendation for forest management is to reduce harvesting and road network development in areas still occupied by caribou. Where harvesting is permitted in zones occupied by woodland caribou we suggest localized small-scale interventions (e.g. partial or selective cutting) with permanent retention using temporary winter roads. Road deactivation and rehabilitation is of critical importance in conserving caribou on managed landscapes.

Key words: woodland caribou, boreal ecotype, spring dispersal, seasonal behaviour, temporal variation, movement rates, quantitative methods, individual-based method, expert consensus, landscape connectivity, semi-permeable barriers, Brownian bridge movement model (BBMM), habitat selection, resource selection probability function (RSPF), functional response.

INTRODUCTION

Context

All North American caribou and Eurasian reindeer belong to the same species - *Rangifer tarandus* - and are widespread across the Northern Hemisphere. These can be further divided into five subspecies according to their morphological (Banfield 1961) and genetic differences (Roed 1992). Canada has three subspecies: the Peary caribou of the Arctic Islands (*Rangifer tarandus pearyi*), the barren-ground caribou (*Rangifer tarandus groenlandicus*) and the woodland caribou (*Rangifer tarandus caribou*).

For functional purposes, woodland caribou are often subdivided into ecotypes based on demographic and behavioural adaptations (Kelsall 1984). Forest-dwelling ecotypes of the subspecies caribou include the Northern and Southern Mountain populations of British Columbia, Washington and Idaho, the Newfoundland and Atlantic (Gaspésie 2004) populations, and the Boreal population (Thomas & Gray 2002). The Boreal population, which includes the southern taiga populations of Ontario, Québec and Labrador, has been classified as Threatened by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC 2002) since 2000 (Thomas & Gray 2002).

Caribou populations are particularly sensitive to mortality loss for a number of reasons. In contrast with most ungulates, female caribou may take 28-40 months to reach sexual maturity (Bergerud 1971b; Valkenburg et al. 2003). Reproductive rate is low and generally inelastic at one fawn per year (Bergerud 2000, *but see* Shoesmith 1976), yet mortality rate among calves is exceedingly high, in some cases surpassing 50% in the first two weeks (Bergerud & Elliott 1986). Caribou are also more vulnerable to predation than other ungulates (Seip 1991b). They are smaller, weaker and less likely to defend their young (Bergerud et al. 1990), leaving them particularly susceptible to acute mortality (Miller et al. 1985). Woodland caribou are strongly associated with mature coniferous forest (Cumming 1992), feeding primarily on terrestrial lichens in the winter (Antoniak & Cumming 1998; Wilson 2000), which are high in digestible carbohydrates but low in protein (Bergerud 1972). Consequently, caribou commonly lose up to 20% of their body mass each winter (Jacobsen & Skjenneger 1975), which in principle leaves them particularly susceptible to predation.

Importance of Predation

Predation is widely considered to be the major factor limiting caribou population growth in forested mainland environments (Bergerud 1988; Seip 1991b; Cumming 1992; Bergerud 1996; Ouellet et al. 1996; Rettie & Messier 1998; Wittmer et al. 2005b; Bergerud 2006), as density-dependent limitation of winter forage has yet to be described for large, lichen-dominated, continental ranges of wild, forest-dwelling woodland caribou (Arsenault et al. 1997; Bergerud & Luttich 2003). Wolf predation in particular is the proximate cause of adult mortality (Bergerud & Elliott 1998), though secondary predators such as wolverine (Chowns & Gates 2004), black bear (Bergerud & Elliott 1998; Rettie & Messier 1998), lynx (Bergerud 1983), coyote (Mosnier et al. 2003), and golden eagle (Crête & Desrosiers 1995) can play a major role in some areas, especially in calf mortality. This being the case, caribou populations are approximately three times more sensitive to adult female mortality than to changes in rate of recruitment (Fancy et al. 1994; Wittmer et al. 2005b; Haskell & Ballard 2007), which can vary highly from year to year (Bergerud 1971b, 1980; Fancy et al. 1994).

In response to the threat of predation, woodland caribou have evolved numerous antipredator strategies. Being morphologically adapted to swimming via hollow hairs and webbed hooves (Klein 1992), caribou frequently inhabit island, shoreline and bog areas to facilitate water escape (Bergerud 1985; Cumming & Beange 1987; Ferguson et al. 1988; Bergerud et al. 1990). In fact, proximity to islands as escape habitat is a common trait in remnant Ontario populations (Ferguson et al. 1988). A second antipredator strategy consists of "spacing out" or dispersing, especially during calving, in order to increase the search effort required by predators (Bergerud & Page 1987; Bergerud 1990; Seip 1991b; Bergerud 1996; Brown et al. 2003), this being the most important determinant of kill rate (Mech 1992). At characteristic low densities of 1-4 animals/100 km^2 (Thomas & Gray 2002), caribou alone could not sustain wolves in the absence of alternate prey like moose and deer (Messier 1985; Bergerud & Elliott 1986; Bergerud 1988; Thomas & Gray 2002). Finally, caribou reduce the risk of predation by avoiding habitats preferred by predators and their alternate prey (Bergerud et al. 1984; Seip 1991b; Ouellet et al. 1996; Rettie & Messier 2000). In his study of predator-prey dynamics in northeastern Alberta, James (1999a) tested this spatial separation hypothesis and found that caribou and moose selected different habitat types, while moose and wolves selected the same habitat type (*see also* Bowman et al. 2010). Wolf predation on caribou was higher near upland habitats selected by moose, yet lower than expected relative to their abundance on the landscape. Seip (1992) found wolf predation on caribou was greater in areas where caribou lived in close proximity to moose. Wolf predation on caribou is therefore opportunistic and secondary to that of moose, which are larger, less dispersed and thus more profitable prey (Kunkel & Pletscher 2000).

Role of forest management in range recession

Once occurring throughout Canada and most of the northern United States (Kelsall 1984; Zager et al. 1996), woodland caribou range has receded over time in a way that roughly mirrors the northward expansion of human settlement and development (Schaefer 2003; Racey 2005). Forest management in particular is believed to have had a deleterious effect on range occupancy due to a combination of factors likely driven by increased access to hunters and predators as well as changes in forest composition that indirectly alter predator-prey relationships (Bergerud 1974a; McLoughlin et al. 2003; Wittmer et al. 2007). Forest age is considered a main quality of habitat suitability for woodland caribou, which are strongly associated with mature forest (Palidwor & Schindler 1995; Apps & Kinley 1998; Higgelke & MacLeod 2000; Szkorupa 2002). Industrial forestry has effectively increased the proportion of early seral habitats on the landscape (Harper et al. 2002; Bergeron et al. 2007), thus promoting the northward expansion of moose and deer which are associated with these habitats (Peterson 1955; Simkin 1965; Bergerud 1974a; Schwartz & Franzmann 1991; Forbes & Theberge 1993; Rempel et al. 1997). Wittmer *et al.* (2007) found a direct link between the proportion of early seral stands within home ranges and caribou population declines in British Columbia. Though caribou have coexisted with wolves for millennia in North America (Bergerud & Page 1987; Seip 1991b; Bergerud & Luttich 2003), their antipredator "spacing out" strategy may be compromised by increased competition for predator-free space, or apparent competition (Holt 1977), with species like moose and deer in the managed boreal forest (Racey et al. 1991; Cumming 1992; Bergerud 1996). Introduction and proliferation of alternate prey supports increases in wolf populations (Seip 1991a), ultimately leading to increased rates of predation on caribou (Seip 1991b). Because wolf populations are sustained by alternate prey, they continue to grow as caribou populations decline (Seip 1991b). Under such conditions, caribou populations are prone to extinction where they fail to separate themselves spatially or temporally from alternate prey species and their predators (Seip 1992; Holt & Lawton 1994; Messier 1995; Rettie & Messier 2000; Wittmer et al. 2005b).

Habitat fragmentation

Representing discrete metapopulations with limited interactions between groups (Ouellet et al. 1996; Stuart-Smith et al. 1997; Rettie & Messier 1998; Courtois et al. 2003d; McLoughlin et al. 2004), woodland caribou are relatively sedentary, traveling in small groups (~8-15 individuals) (Brodeur 2007, pers. comm.) at low densities and annually returning to the same range (Ferguson & Elkie 2004a). A species with very large individual home range requirements (on the order of 200-800 km^2, Racey et al. 1999; Courtois et al. 2002a), it is highly susceptible to habitat fragmentation and local extinction (Smith & Peacock 1990; Andrén 1994; Courtois 2003; Apps & McLellan 2006). Compounding the effect of industrial forestry on predator-prey dynamics in the boreal forest is the impact of roads, which may act as conduits for hunters and predators and serve as semi-permeable barriers to dispersal for woodland caribou (Curatolo & Murphy 1986; Rettie & Messier 1998; Dyer 1999; James & Stuart-Smith 2000; Chetkiewicz et al. 2006). Where there is limited human activity, linear features such as roads provide efficient access into caribou range for wolves (Bergerud et al. 1984; Edmonds & Bloomfield 1984; Thurber et al. 1994; Seip & Cichowski 1996; Stuart-Smith et al. 1997; Dyer et al. 2001; Houle et al. 2007). Higher road densities increase the likelihood of encounter between the two species and caribou mortality is generally higher in proximity to roads (James 1999a; James & Stuart-Smith 2000), an effect exacerbated by both traffic- and hunting-related mortality (Johnson 1985; Benoit 1996). Kinley & Apps (2001) found that landscapes of higher road density and old forest fragmentation were spatially related to an unsustainable rate of caribou mortality.

Predation risk and response to disturbance

It has been widely posited that broad-scale habitat selection by woodland caribou is driven by predator avoidance, while foraging and energetic constraints take priority at finer scales (Johnson 1980; Ferguson et al. 1988; Seip 1992; Rettie & Messier 2000; Courtois et al. 2002a; Johnson et al. 2002b; Bergerud & Luttich 2003; Mosnier et al. 2003; Brown 2005; Gustine et al. 2006b). Predation risk has been defined as the probability of being encountered and subsequently captured by a predator during some time period (Lima & Dill 1990). Caribou may use knowledge of predation risk associated with vegetation types and landscape features and avoid such types in accordance with perceived risk (Bouskila & Blumstein 1992; Barten et al. 2001). For example, caribou density generally declines as road density increases (Cameron et al. 1992; Nellemann & Cameron 1998). They also tend to abandon, avoid or underutilize harvested areas (Freddy 1979; Darby & Duquette 1986; Chubbs et al. 1993; Cumming & Beange 1993; Stepaniuk 1997; Hillis et al. 1998; Rettie & Messier 2000; Smith et al. 2000; Courtois et al. 2004; Vors 2006). In Alberta, Dyer *et al.* (2002) found that caribou crossed roads six times less frequently than randomly modeled roads during late winter. Caribou in Newfoundland avoided clear-cuts and related disturbance during summer by up to 15km (Chubbs et al. 1993). Avoidance of roads and harvested areas may represent the most important form of functional habitat loss for caribou (Nellemann & Cameron 1998; Smith et al. 2000; Dyer et al. 2001; Weclaw & Hudson 2004).

Reactions of caribou to changes in perceived risk may vary. Smith *et al.* (2000) found that range size and movement rate decreased with increased timber harvesting, whereas Courtois (2003) found that caribou increased home range size and movement rates and reduced fidelity to seasonal home ranges when subjected to habitat fragmentation. Remnant populations may be displaced into poor habitat or into closer proximity to moose and wolves (Cumming & Hyer 1998). Alternately, those continuing to occupy the same range may decline in the face of heightened predation (Rettie 1998; Rettie & Messier 2000). Exhibiting strong fidelity to geographical calving areas (Schaefer et al. 2000a; Ferguson & Elkie 2004a), forest-dwelling caribou populations thus far do not seem to have successfully adapted to industrial forestry regimes of the 20th Century in the absence of appropriate refuge habitat (Ferguson et al. 1988; Cumming & Beange 1993; Bergerud 2006).

Seasonal migration and landscape connectivity

Species persistence in fragmented landscapes depends on the ability of organisms to move among resource patches (Fahrig & Merriam 1985; Lefkovitch & Fahrig 1985; Henein & Merriam 1990; Henein et al. 1998). White & Garrott (1990) defined migration as a regular, round-trip movement of individuals between two or more areas or seasonal ranges. While the celebrated barren-ground caribou of northern Canada and Alaska are well-known for their seasonal mass migrations (Kelsall 1968), forest-dwelling caribou are relatively sedentary in comparison (Bergerud 1988, 1996). In fact, some populations or individual animals exhibit little or no differentiation between winter and summer areas (Paré & Huot 1985; Ouellet et al. 1996; Stuart-Smith et al. 1997; Schaefer et al. 2000a). However modest, coinciding periods of increased activity related to semi-annual migrations of woodland caribou have been observed across populations of woodland caribou (Brown et al. 1986; Bergerud et al. 1990; Ferguson et al. 1998; Brown et al. 2000), which may travel up to several hundred kilometres in a given year (Cumming & Beange 1987; Edmonds 1988; Seip 1992). Spring dispersal is a form of one-way migration among woodland caribou that leads to a spacing out, or dispersion, of individuals, thereby reducing the risk of encountering a predator when calves are most vulnerable (Bergerud & Page 1987; Turchin 1998).

Habitat selection by woodland caribou is considered hierarchical and scale-dependent (Rettie & Messier 2000; Johnson et al. 2002b; Mosnier et al. 2003; Brown 2005; Gustine et al. 2006b). Courtois (2003) determined that at the landscape scale (i.e. annual home range) caribou selected habitats that minimize the risk of predation, while at the scale of the seasonal home range resource selection was driven by a combination of factors including predator avoidance and forage and mating opportunities. Johnson *et al.* (2002b) found that short-term occupancy of risk-prone cover types led to highest risk of predation during interpatch movements of mountain caribou. Interseasonal movements have been interpreted as random by some researchers (Darby & Pruitt 1984; Cumming & Beange 1987; Stuart-Smith et al. 1997). In contrast, seasonal movements of collared females in central Manitoba appeared to be well-defined, predictable, and directional (Brown et al. 2000). In general, individual animals have more tortuous pathways in good quality habitat and move further and faster over unfavorable terrain (Crist et al. 1992; Johnson et al. 1992; With 1994b). It has been assumed that caribou follow natural relief features corresponding with direction of travel such as waterways or ridge lines, preferentially selecting conifer habitats (Racey et al. 1999). Johnson *et al.* (2002b) found that caribou chose level topography and waterways as movement corridors in north-central British Columbia. Saher (2005) found two phases of habitat selection among migratory woodland caribou in west-central Alberta : punctuated movement (travel) and periodic resting/foraging bouts. Individuals selected travel routes through less rugged areas that were closer to water, while resting/foraging in older forests with a greater component of pine at greater distances from water (Saher & Schmiegelow 2005). Ferguson and Elkie (2004b) found that woodland caribou in northwest Ontario were more likely to avoid water, open areas, and disturbed areas during the travel seasons, favouring coniferous over deciduous forest. In general, predation risk is higher outside areas of core habitat use (Sebbane et al. 2002; Johnson et al. 2002b; Biro et al. 2003; Kojola et al. 2004; Frair et al. 2007). Avoidance of waterways may be a predator avoidance tactic as riparian habitats are likely important for alternate prey species (moose, deer) (Barten et al. 2001); likewise, open habitats facilitate prey detection (Kunkel & Pletscher 2000; Creel et al. 2005). Yet in contrast with expectations (Stuart-Smith et al. 1997; Rettie & Messier 2000), Ferguson & Elkie (2004b) did not find that caribou noticeably avoided disturbed areas (recent burns and cutovers). Overall, however, woodland caribou in northwest Ontario were considered to be less selective during migration than they are known to be at other times of the year.

If one is managing for connectivity in the landscape, one is trying to understand how altering other elements of landscape structure will affect it, and then assess what the importance of those changes will be to critical ecological outcomes, such as population persistence (Taylor et al. 2004). The degree to which a landscape facilitates or impedes movement of organisms among resource patches is referred to as landscape connectivity (Taylor et al. 1993). Structural connectivity is related to landscape spatial structure (e.g. habitat patch size and configuration) independent of attributes of the species under study, whereas functional connectivity incorporates the notion of species movements and behavior across heterogeneous landscape matrices (Tischendorf & Fahrig 2000). While there are numerous metrics for quantifying landscape spatial structure (McGarigal & Marks 1995), these measures are often inaccurately equated with landscape connectivity (Goodwin & Fahrig 2002; Bender & Fahrig 2005). Remarking on the limitation of spatial models in the absence of behavioral information, Lima & Zollner (1996) stressed the need for a « behavioral ecology of ecological landscapes », one which accounts for risk and behavioral uncertainty variables across a range of scales.

Conserving woodland caribou on the managed landscape

Arsenault (2003) defined critical habitat for the woodland caribou as « a perpetual supply of large, contiguous areas of suitable calving, summer and winter habitat allowing viable populations to disperse at low densities (0.03-0.05/km^2) to avoid predators, and having no or very limited human access or disturbance ». While numerous caribou management and recovery strategies have been developed at the Provincial and Federal levels (Racey et al. 1999; The Mountain Caribou Technical Advisory 2002; Arsenault 2003; Alberta Woodland Caribou Recovery 2004; Courtois et al. 2004; Schmeltzer et al. 2004; Network 2005; Manitoba 2006; Yukon Fish and 2007), the amount of woodland caribou range presently under legal protection is considered insufficient given its role as a focal species for boreal forest conservation (Lambeck 1997; Bunn et al. 2000; CPAWS 2006). Appropriate management of the land base adjacent to parks and protected areas is thus paramount given the scale at which caribou populations inhabit the landscape (median range = 9,000 km^2) (Vors 2006). Recognizing that stand succession is inevitable and that caribou have evolved in environments subject to variable natural disturbance regimes, harvesting portions of caribou winter range may be seen as a way of exploiting unused timber resources while simultaneously accelerating succession as a means of recruiting future caribou habitat (Seip 1998; Racey et al. 1999; Courtois et al. 2004; Forest 2005). This being the case, Cumming *et al.* (1996) noted that disturbance patterns produced by fire are not necessarily favourable to woodland caribou. Furthermore, while they may use only a portion of the suitable winter habitat available to them in a given year (Berger et al. 2000), caribou are also known to vary wintering locations from year to year (Shoesmith & Storey 1977; Darby & Pruitt 1984; Edmonds 1988; Stuart-Smith et al. 1997; Brown et al. 2000; Bergerud 2006), perhaps as a means of exploiting forage-induced temporal changes in lichen abundance (Wittmer et al. 2006). Clearly, caribou exhibit greatest philopatry in the snow-free season (Brown & Theberge 1985; Schaefer et al. 2000a); identification and protection of traditional calving areas is therefore critical and has been widely recommended (Racey et al. 1999; Lantin 2003). However, maintaining habitat connectivity between seasonal home ranges and across heterogeneous landscapes is challenging because it requires coordinated planning at large temporal and spatial scales, often across multiple management units and jurisdictions (Boyce 2006). Furthermore, resource selection and movement behavior can vary both regionally and among individuals within a population (Johnson et al. 2001; Gustine 2005), and inferences about ecological mechanisms may be scale- and structure-dependent (Gardner et al. 1989; Bowers & Matter 1997; Johnson 2000; Bender & Fahrig 2005; McLoughlin et al. 2005b; Boyce 2006; Gustine et al. 2006b). With a view to ecosystem management and a sustainable timber supply, attempts to provide a « mosaic » of large blocks (Courtois et al. 2004) in alternating rotation as either harvest units or caribou winter range must be complemented by a suite of well-devised, smaller-scale management interventions. Yet in order to minimize habitat fragmentation and facilitate the antipredator spacing-out strategy of woodland caribou (Bergerud 1990), spatially explicit matters pertaining to patch size and configuration, retention, silviculture treatments and road management require careful consideration (James et al. 2005). Though it is commonly presumed that populations will adapt to large harvest-induced shifts in core winter range, the functional connectivity of seasonal home ranges is far from guaranteed without an understanding of factors influencing woodland caribou migration behaviour.

Project Rationale

Over the past century, forest-dwelling woodland caribou (*Rangifer tarandus caribou*) have experienced dramatic population declines across North America (Cringan 1957; Bergerud 1974a; Heard & Vagt 1998; Mallory & Hillis 1998; Courtois et al. 2003b). Anthropogenic landscape disturbance is an important cause of range recession due to a combination of factors likely driven by increased access to hunters and predators as well as changes in forest composition that indirectly alter predator-prey relationships (Bergerud 1974a; McLoughlin et al. 2003; Wittmer et al. 2007). Classified as threatened in 2002 by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC 2002), woodland caribou have become a species of major management concern in Canada's boreal forest, prompting numerous Provincial and Federal strategies addressing this species-at-risk (Racey et al. 1999; The Mountain Caribou Technical Advisory 2002; Arsenault 2003; Alberta Woodland Caribou Recovery 2004; Courtois et al. 2004; Schmeltzer et al. 2004; Network 2005; Manitoba 2006; Yukon Fish and 2007). While ecosystem-based management is alleged to minimize the negative effects of human interventions, more detailed information may be required to effectively address the needs of woodland caribou (Seip 1998), a species highly vulnerable to predation with a strong aversion to forestry and related activities (Bergerud 1988; Cumming & Hyer 1998; James & Stuart-Smith 2000; Smith et al. 2000; Dyer et al. 2002; Vors et al. 2007; Wittmer et al. 2007). Managed landscapes must be modeled after the range of natural variability in forest ecosystems (Drever et al. 2006) and designed in such a way as to simultaneously maintain core habitat requirements, landscape connectivity and facilitate spatial separation between woodland caribou, conspecifics, and alternate prey species such as moose and their predators (Seip 1991b; Rettie & Messier 1998; James 1999b; Courtois et al. 2004; Team 2005; Manitoba 2006). However, while core habitat requirements are generally well-understood (Cumming 1992), finer-scale resource selection and movement behavior can be variable and difficult to predict (Gustafson & Gardner 1996; Johnson et al. 2001; Gustine 2005).

Objectives

In this study, we argue that a better understanding of caribou dispersal behaviour will inform more effective conservation measures toward the functional connectivity of disturbed landscapes. Until fairly recently, few researchers have specifically investigated the biological phenomenon of spring dispersal in woodland caribou (Ferguson & Elkie 2004b; Saher 2005; Saher & Schmiegelow 2005), yet it is perhaps one of the most critical periods in their annual life cycle. The general objective of this study is therefore to characterize spring dispersal behaviour in a population of boreal forest-dwelling woodland caribou of northern Quebec. The first objective (Chapter 1) is to delineate the seasonal onset of spring dispersal as a function of individual movement rates using quantitative methods, for failing to account for temporal variation in seasonal onset behaviour may introduce bias and potentially lead to erroneous conclusions. We therefore elaborate an individual-based method (recursive partitioning) for identifying seasonal shifts in movement behaviour and demonstrate its use in delineating three critical periods: winter, spring dispersal, and calving. The second objective (Chapter 2) is to characterize movement behaviour and habitat selection during spring dispersal. 1) We begin by examining movement trajectories for evidence of directionality and common orientation using vector statistics. Since habitat fragmentation due to forest harvesting and road network development may inhibit dispersal of woodland caribou (Dyer et al. 2002), we likewise examine the efficiency of directed movements using a bias-corrected Straightness Index (*SI*) (Batschelet 1981), and we proceed to model the relationship between path tortuosity (1-*SI*) and mean proximity to zones of high road density. 2) We estimate the spatial distribution and extent of spring dispersal using a Brownian Bridge movement model (BBMM) (Bullard 1991), which models uncertainty relating to animal movements and GPS location accuracy and generates a continuous probability surface or Utilization Distribution (UD) (Van Winkle 1975). In order to evaluate the effectiveness of fixed travel corridors in the maintenance of connectivity between seasonal ranges (Courtois et al. 2004), we assess the degree to which caribou exhibit interannual fidelity to seasonal travel routes by measuring interannual overlap in BBMM UDs. Finally, 3) we estimate a Resource Selection Probability Function (RSPF) describing habitat selection during spring dispersal. Specifically, we model the probability of utilization during spring dispersal (based on UD values) as a function of numerous environmental covariates using Akaike's Information Criterion (AIC) to select the most parsimonious model. These approaches permit us to effectively evaluate the biological phenomenon of spring dispersal in northern Quebec, including the role of environmental factors as they relate to caribou dispersal behaviour, and the potential influence of anthropogenic disturbance on dispersal success.

ARTICLE 1

VARIATION IN SEASONAL ONSET BEHAVIOUR AND POTENTIAL CONSEQUENCES FOR STUDIES OF SEASONAL HABITAT SELECTION

Tyler Rudolph[1,2] and Pierre Drapeau[1,2]

[1]Université du Québec à Montréal, Département des Sciences Biologiques
[2]Chaire industrielle CRSNG UQAT-UQÀM en aménagement forestier durable,
Université du Québec en Abitibi-Témiscamingue

Abstract: The biology of terrestrial mammals is strongly influenced by seasonal changes in environmental conditions. Studies of animal space use behaviour are therefore inherently seasonal in nature. We develop an individual-based quantitative method for identifying seasonal shifts in caribou movement behaviour and we demonstrate its use in determining the onset of the winter, spring dispersal, and calving seasons. Using pooled data for the population we demonstrate an alternate approach using polynomial regression with mixed effects. We then compare the onset dates obtained using the individual-based method with a) those estimated using the population-based model and finally b) those adopted by expert consensus for our study area. Distributions of individual-based onset dates were normally distributed with prominent modes. However results revealed considerable variation in individual onset times even for calving which varied the least. Population-based estimates were closer to the peaks of individual estimates than were expert-based estimates, which fell outside the 90 % and 95% sample confidence intervals of individual-based estimates for spring and winter, respectively. Both expert- and population-based estimates were late for winter and early for both spring and calving. We discuss the potential consequences of neglecting to corroborate conventionally used dates with observed seasonal trends in the movement behaviour of sample animals. We conclude by recommending researchers adopt an individual-based quantitative approach and a variable temporal window for data set extraction.

Keywords: seasonal behaviour, temporal variation, movement rates, quantitative methods, individual-based method, expert consensus, woodland caribou.

INTRODUCTION

The life history traits of mammals are in no small part a function of the bioclimatic environments in which they live (Klein 1982). In the northern boreal forest of Canada, the biological activity of terrestrial mammals is regulated by seasonal shifts in temperature and precipitation which, in turn, directly or indirectly influence the quality and availability of food and protection habitat (Pruitt 1957; Telfer & Kelsall 1984; Post & Stenseth 1999). Members of the *Cervidae* family, for example, exhibit growth dormancy in winter when the metabolic demands of thermoregulation are high and plant nutrients essential for body tissue development are in short supply (Irving et al. 1955; Wood et al. 1962; McEwan 1970). They also reduce foraging and restrict movements at this time in order to minimize heat loss and the depletion of body reserves (McEwan & Whitehead 1970; Ozoga & Gysel 1972; Gates 1979; Ferguson & Elkie 2004a). Spring, in contrast, is a time of increased energetic expenditure when the demands of pregnancy reach their peak and female cervids prepare to give birth (Moen 1976). Though considered sedentary in comparison to their migratory cousins, forest-dwelling woodland caribou (*Rangifer tarandus caribou*) are known to make concerted movements away from wintering areas in the spring as a means of attaining low densities and thereby reducing detection by predators (Bergerud & Page 1987; Cumming & Beange 1987), Chapter 2). This phenomenon is known as spring dispersal and is characterized by punctuated increases in movement activity (Ferguson & Elkie 2004a). In contrast, at calving time female caribou are virtually immobile, functionally limited in their movements for up to several weeks until calves are vigorous enough to travel (Lent 1966; Espmark 1971; Clutton-Brock & Guiness 1975). This period coincides with the emergence of high-quality plant vegetation required for lactation and consequentially, calf development (Klein 1990; Lantin et al. 2003; Post et al. 2003).

A brief overview of a portion of their annual life cycle demonstrates the central role of seasonality in understanding the biology of woodland caribou. Like many species, caribou exhibit shifts in biological activity that parallel changes in their natural environment. It is for this reason that investigations of animal space use behaviour tend to outline and differentiate between seasonal periods of study (Lesage et al. 2000; Rettie & Messier 2000; Rominger et al. 2000; Brown et al. 2003). For example, one wishing to understand winter foraging ecology would probably not include observations made at a time when there was no snow on ground, for if one were to do this, the results obtained would not be representative of the biological activity being investigated. For this reason the majority of researchers identify seasonal periods using first-hand knowledge of regional populations, climatic conditions, and plant phenology (Apps et al. 2001; Jones et al. 2007; Hins et al. 2009).

It may be argued, however, that nothing is static in ecological systems; climate change, for example, may alter the patterns we have come to expect, not only with respect to weather but also to animal behaviour (Weladji et al. 2002; Sharma et al. 2009). As a case in point, between 1969 and 1998 the peak calving time of reindeer in Norway was delayed by 6-8 days in one region yet advanced by 2-6 days in another (Flydal & Reimers 2002). This may have important consequences for biological inference if we fail to account for such variation in our study of seasonal processes. For example, were we to overlook this subtle yet important shift in the timing of a relatively predictable biological event, we could erringly include an entire week of observations consisting of migratory behaviour in a characterization of caribou calving site selection (Reimers et al. 2007). Fortunately this would not normally occur since the calving period is generally well identified regionally using field observations (Rettie & Messier 2001). This being said, even peak onset of calving can vary on an annual basis by as much as 15 days (Eloranta & Nieminen 1986; Cameron et al. 1993; Post & Klein 1999). Furthermore, calving times for individuals within a population may vary by as much as a month or more (Bergerud 1975; Eloranta & Nieminen 1986; Rettie & Messier 1998; Post & Klein 1999; Ferguson & Elkie 2004a). However accurate our assessment of peak calving time, this suggests that using a fixed temporal window to study calving site selection may generate biased results, even for a period as biologically predetermined as calving.

Given the variable and often unpredictable behaviour of free-ranging animals (Gustafson & Gardner 1996; Johnson et al. 2001; Gustine 2005), we propose an approach to analyzing seasonal space use that accounts for individual variation in seasonal onset times. We argue that by varying the temporal window of analysis to more effectively capture the biological phenomenon under investigation, we can improve population-level estimates by reducing misclassification, thereby improving biological inferences.

A number of quantitative approaches have been used to identify seasonal shifts in the behaviour of woodland caribou. These require *a priori* biological knowledge and can be rule-based (Mahoney & Schaefer 2002b; Saher & Schmiegelow 2005; Courbin et al. 2009) or model-based (Ferguson & Elkie 2004a; Dyke 2008). We propose an intuitive and simple model-based approach called individual-based recursive partitioning, which by contrasting seasonal fluctuations in movement rates provides statistical evidence for candidates based on the analysis of variance (ANOVA) and biologically-informed decision rules. We demonstrate how this approach can be used to delineate three contrasting seasonal periods in the annual life cycle of woodland caribou: winter, spring dispersal, and calving. Finally, we compare the results of this approach with a) dates obtained using polynomial regression with pooled data (population estimates), and b) dates established by expert consensus (conventional estimates) for our study area in northern Quebec.

1.1. Study Area

The study area comprises a 109,116 km^2 tract of boreal forest in northern Quebec situated between 49°52' and 51°46' N and 71°17' and 79°31' W (**Figure 1.1**). Part of the black spruce-feathermoss bioclimatic domain, it is dominated by black spruce (*Picea mariana*) in association with feathermoss (*Pleurozium schreberi*) and/or various lichen species. Jack pine (*Pinus banksiana*) and balsam fir (*Abies balsamea*) occur to a lesser extent, in addition to trembling aspen (*Populus tremuloides*), paper birch (*Betula papyrifera*), tamarack (*Larix laricina*), and (rarely) balsam poplar (*Populus balsamifera*). Forest understory is dominated by mosses and ericaceous shrubs with few herbaceous species. The western flank of the region forms part of the Clay Belt and is dominated by large sphagnum bog and fen complexes. Terrain is broad and mildly sloping with occasional topographic relief (45-825m AMSL) and there are numerous rivers and waterways interconnecting the region. Treed wetlands and upland forest intersperse with bog/fen complexes and lichen or shrub-dominated uplands with occasional rock barrens. The region receives approximately 960 mm of precipitation annually with monthly average temperatures ranging from -19° (January) to + 16° (July) Celsius.

Constituting Québec's second-largest timber supply region, the study area encompasses both the northern limit of commercial forestry activity and the southern limit of continuous woodland caribou distribution (Courtois 2003). Primary disturbances include forest fire (100-500 year fire cycle; Bergeron et al. 2001) and forest harvesting, which is presently concentrated in the southern portion of the study area. Large mammal species include forest-dwelling woodland caribou, moose (*Alces alces*), wolf (*Canis lupus*) and black bear (*Ursus americanus*). Reliable population estimates are unavailable, but caribou densities are estimated to be between 1.5 and 2.1/100 km^2, with individuals occupying average annual home ranges of ~4386 km^2 (St-Pierre et al. 2006). In the northern sector, infrequent range overlap takes place with populations of the tundra-forest ecotype of woodland caribou (*Rangifer tarandus caribou*) (Courtois et al. 2003d).

METHODS

2.1 Caribou Capture and GPS Telemetry

Animal relocation data were obtained via GPS (Global Positioning System) collar transmitters (Telonics model TGW 3680) fitted on 26 female caribou by members of the Québec Ministry of Natural Resources and Wildlife in March 2004 and January 2005. Captures were conducted using ASTAR 350BA or EC120 helicopters and a net gun (Potvin & Breton 1988). Individuals sampled were evenly distributed among three regional populations: the Nottaway (west), Assinica (central), and Témiscamie (**Figure 1.1**). Satellite transmissions were uploaded three times daily (7-hr fix interval) between January 2005 and March 2007. Relocations were filtered for positional accuracy in order to remove large location errors: those based on 4 or more satellites (3-D) were eliminated if they had corresponding horizontal dilution of precision (HDOP) values greater than or equal to 25, whereas those based on 3 satellites (2-D) were eliminated if they had HDOP values greater than or equal to 8 (Dussault et al. 2001; D'eon & Delparte 2005; Lewis et al. 2007). The Horizontal Dilution of Precision reflects the horizontal accuracy (latitude/longitude) of GPS position fixes by adjusting the error estimates according to the geometry of the satellites used. This resulted in a roughly 4% data reduction per individual.

Although movement rates have been known to vary among female caribou according to reproductive status (Paré & Huot 1985; Fancy & Whitten 1991; Ferguson et al. 1998), high pregnancy rates are pervasive in woodland caribou populations so we assumed no error due to variation in reproductive condition (Parker 1981; Rettie & Messier 1998).

Spatial relocations were projected from the World Geodesic coordinate system (WGS 84) into Quebec Lambert Conformal Conic (1983) prior to further manipulation. In order to render our data temporally uniform, we rarified data sets to one relocation per individual per day, retaining that relocation obtained closest to 12:00 noon. Because estimates of movement rates may be biased when fix interval varies (Johnson et al. 2002b), distance calculations based on more than one consecutive day between successive relocations were not retained for analyses. Furthermore, individual-year combinations comprising less than 100 observations were eliminated from analyses. Resulting sample sizes ranged from 231 to 365 ($\bar{x} = 319$).

2.2 Temporal Focus of Study

We chose the winter, spring and calving seasons because they represent critical periods in the annual life cycle of woodland caribou (Darby & Pruitt 1984; Environment Canada 2008). We were also particular interested in characterizing spring dispersal behaviour of boreal caribou and this represented the first stage of our analysis (Chapter 2). Our goal was to identify peak onset dates for the winter, spring dispersal, and calving periods on an individual basis through quantitative analysis of movement patterns. Our first step was to plot the pooled average of distance travelled per day (Julian Day, origin = January 1^{st}) for all individuals in order to visually identify seasonal “neighbourhoods” of change in movement behaviour. A similar graphic showing the pooled average net displacement for all individuals was consulted to corroborate these general time periods (“temporal neighbourhoods”) and evaluate distances traveled during spring dispersal. Net displacement was defined as the Euclidean distance between an animal’s location on any given day and its location on January 10 of the same year. This date was chosen as the "anchor" point because almost all individuals were found to have settled into their wintering areas by this time. By then consulting these diagnostic plots we were able to focus on specific time periods corresponding with seasonal changes in the movement behaviour of our study population.

2.3 Individual-based modeling

2.3.1 Step 1: Smoothing

In order to minimize noise attributed to periodic variation in individual movement behaviour (e.g. circadian rhythms), we began by fitting a polynomial regression model for each unique individual-year combination (using the number of terms determined to be optimal for the population-based model elaborated below), then used the residuals from these models to construct a correlogram of residual distance values (y) over time (x) using Moran's *I*. This detrending process ensured that overall seasonal trends in movement rates were conserved while enabling us to test for periodic serial correlation at a higher temporal resolution (Legendre & Legendre 1998). Using a maximum lag time of 15 days, the majority of individual-year distributions revealed a significant recurring pattern every 4 days. Thus, prior to proceeding, we passed a 4-term (1 observation/day) smoothing window (moving average) over the raw distance values observed for each individual-year time-series.

2.3.2 Step 2: Modeling seasonal shifts in individual movement behaviour

Smoothed distance values were progressively subdivided into temporally homogenous groups using recursive partitioning (De'ath & Fabricius 2000). We conducted this exercise using the rpart package of the R software (Team 2010;

Therneau et al. 2010). A function of distance over time based on the analysis of variance, the result is a univariate regression tree in which temporally discrete blocks are optimally separated so as to maximize the between-groups sums of squares. A complexity parameter is incorporated to permit only those partitions which improve the explained variance by an established threshold (i.e. $\Delta R^2 >= 0.01$). Cross-validation is employed to obtain the predicted error, and the optimal tree is determined based on the lowest estimate plus or minus one standard error.

In order to determine individual onset dates for winter, spring dispersal and calving, we conducted a separate recursive partitioning exercise for each individual-year distribution by modeling log-transformed daily movement rates (km/day) as a function of Julian Day. In order to provide enough data to effectively capture the onset of winter and thus include potentially early onset times, we included the previous year in recursive partitioning exercises when selecting for these dates. Individuals displaying erratic behaviour (i.e. considerable deviation from expected observed pattern) and those missing data during critical periods of interest were excluded from subsequent analyses for the year(s) in question.

In particular with respect to the beginning and end of spring dispersal, as a parallel point of reference we examined an alternate model where net displacement (km) was the response variable. Net displacement was defined as the Euclidean distance between an animal's location on any given day and its location on January 10 of the same year. While the results we report were primarily obtained from changes in movement rates, this alternate model provided evidence of important changes in net displacement (Courbin et al. 2009), thereby supporting our final choice of onset dates for these periods.

Both simple and robust, the individual-based method delineates significant distinctions between periods of higher versus lower biological activity. However, due to inherent variation in movement behaviour, *a priori* knowledge of caribou biology is necessary to select the most probable dates or breaks among numerous statistically plausible choices for the onset of a given season. For the onset of winter, we chose the candidate "break" that most aptly corresponded with the lull in movement activity that characterizes this seasonal shift, though the closer the candidate was to the pooled mean onset time the more likely it was to be considered. Because we were interested in eventually examining habitat selection during spring dispersal (Chapter 2), when there were numerous options potentially demarcating the beginning of this season (and likewise the end of the preceding winter), we chose among the earliest conceivable options in order to capture the full biological signal of the period we intended to study. As females generally become stationary for several days during calving, the onset of this period was generally easy to identify; however in the event of fluctuations we opted for the later of available options in order to fully capture the biological phenomenon of spring dispersal. Once the onset dates of winter, spring dispersal, and calving had been determined for every qualifying individual-year data sequence, population means (μ) and their associated standard errors (SE) were estimated for each season using a non-parametric bootstrap procedure. A coverage test was first conducted in order to determine the most appropriate method for estimating standard error.

2.4 Population-based modeling

As a point of comparison, we developed a population-based polynomial regression model with mixed effects in order to estimate the onset dates of winter, spring dispersal, and calving periods based on season-specific shifts in movement rate (log-transformed to improve normality) as a function of Julian day (origin = Jan. 01). This is similar to the approach published by Ferguson & Elkie (2004a); however because we were working with a sample of a much larger population and wished to take into account individual and annual variability in seasonal onset behaviour, a random intercept was specified for each individual and each nested individual-year combination. Specifying the grouped structure of the data reduces the effective sample size to the number of unique individuals and not the total number of observations (Gillies et al. 2006). Models were estimated using Maximum Likelihood, and polynomials were independently re-centered about their respective means (orthogonal polynomials) to facilitate convergence and eliminate correlation between terms. The model takes the following form:

$y_i = X_i\beta + Z_i b_i + \varepsilon_i$, where:

$X_i\beta = \beta_0 + \beta x + \beta x^2 + \beta x^3 + \ldots + \beta x^k$ is the standard linear model structure for the fixed effects component, and:

$Z_i bi = b_1 x + b_2 x^2 {}_{+} b_3 x^3 \ldots + b_k x^k$, where b_k is the variance-covariance matrix of the random effects and ε_i is an estimation of the residual error.

We compared a series of candidate models in which polynomial terms were sequentially added and Akaike's Information Criterion for small sample sizes (AIC_c) was calculated iteratively in order to identify the best candidate model based on the principle of parsimony. In order to define at least three seasons, we began with five terms and sequentially added up to 25 polynomial terms, stopping at the first model in the sequence where ΔAIC_c ceased to be negative, the best candidate model being the one immediately prior (**Figure 1.8**). Inflection points in the fitted curve indicated season-specific changes in movement rate, and these were obtained by solving for x=0 in the second derivative of the fixed effects component of the regression equation (Ferguson & Elkie 2004a).

RESULTS

3.1 General Findings

Pooled averages of distance travelled per day are shown in **Figure 1.2**. Corresponding with the onset of late winter, a significant drop in movement rate was noted to take place in early January. A sudden increase in movement rate in early April corresponded with the onset of spring dispersal, followed by a substantial drop in movement rate which indicated the start of calving in late May. Between January 10 and June 30, the minimum daily average distance was 530 m on March 16 while the maximum daily average distance was 5.93 km on April 21. The maximum distance recorded in one day was 54.6 km by caribou 2003014 on May 9.

Pooled averages of net displacement per day are shown in **Figure 1.3**, which reveals a distinct migratory pattern from early April until late May. On average there was little departure from wintering areas until the onset of spring dispersal, at which time animals proceeded to travel consistently further away from their wintering areas, reaching a maximum daily average displacement of 49.3 km from their wintering grounds on June 6. The maximum net displacement recorded for one animal between January 10 and June 15 was 208.76 km by caribou 2003008 on June 09, 2005.

3.2 Individual-based models

Examining caribou movement behaviour on a yearly basis at the scale of the individual revealed a fairly distinct pattern altogether similar to that reflected by the pooled mean values. Generally speaking (**Figure 1.4**), movement rates became abruptly minimal in late December or early January (corresponding with the onset of late winter), there was a period of punctuated movement directed away from wintering areas beginning in early April (corresponding with spring dispersal), and this was immediately followed by an abrupt halt in movement for a relatively short period of time associated with calving.

The distributions of seasonal onset dates (pooled across years) determined via individual-based recursive partitioning are shown in **Figure 1.5.** Peak onset of late winter occurred on January 5th (+/- 5.2 days (SE), n = 50, s = 18.64), spring dispersal on April 1nd (+/- 2.5 days (SE), n = 55, s = 9.73), and calving on May 23th (+/- 2.0 days (SE), n = 62, s = 7.78). In all three cases, Anderson-Darling tests of residual values indicated no significant departure from normality. Sample 95% confidence intervals ranged from Dec. 04 – February 05 for winter, March 13 – April 19 for spring dispersal, and May 10 – June 10 for calving. Peak onset times over three years varied from Dec. 28 (2007) to Jan. 17 (2005) for winter (20 days), from March 28 (2006) to April 02 (2005) for spring (5 days), and from May 21 (2006) to May 25 (2004) for calving (4 days) (**Table 1.1**). Winter was the longest season at $\bar{x}$ = 78.6 days, followed by spring dispersal at $\bar{x}$ = 50.6 days, and finally calving at $\bar{x}$ = 20.2 days (**Table 1.2**). Based on the statistics of unique individuals, the longest period observed for winter behaviour was 130 days, for spring dispersal behaviour 80 days, and for calving behaviour 58 days. Minima and maxima were Nov. 9 and February 24 for winter (107 days), March 8 and April 22 for spring dispersal (45 days), and May 6 and June 13 for calving (38 days). Results of individual time-series analyses can be found in **Appendix I**, along with mean and maximum observed movement rates (km/day) and the estimated lengths of each season.

The onset of late winter (2005 vs. 2007: $F_{12,15} = 9.70$, $p < 0.01$) and spring dispersal (2004 vs. 2006: $F_{11,20} = 15.0$, $p < 0.001$) tended to be progressively earlier from 2004 to 2007 (**Figures 1.6-1.7**). Despite the significant range in latitudes occupied by our sample population, no significant difference was observed in seasonal onset dates between caribou at high versus low latitudes. Finally, although age and experience can influence the timing of ovulation and therefore calving (Bergerud 1975; Flydal &

Reimers 2002; Langvatn et al. 2004), morphometric (and therefore age) data available for our population were not complete enough to support or refute this.

3.3 Population-based model

Adding progressive polynomial terms to the prospective regression model continued to substantially reduce AIC_c until a twelfth term was added, at which time the net change in AIC_c became positive (**Figure 1.8**). Therefore the final population-based model contained eleven polynomial terms and took the following form (jd = Julian day):

$$\hat{Y} = 1.08 - 0.301 + 2.16\times10^{-2}\,(jd)^2 - 8.18\times10^{-4}\,(jd)^3 + 1.71\times10^{-5}\,(jd)^4 - 2.11\times10^{-7}\,(jd)^5 + 1.63\times10^{-9}\,(jd)^6 - 7.97\times10^{-12}\,(jd)^7 + 2.51\times10^{-14}\,(jd)^8 - 4.92\times10^{-17}\,(jd)^9 + 5.44\times10^{-20}\,(jd)^{10} - 2.60\times10^{-23}\,(jd)^{11} + Z_i b_i + \varepsilon_i$$

Pearson's correlation coefficient (adjusted R^2) for the fitted model was 0.167. The non-negligible degree of variability in the random intercepts for individual and individual-year vis-à-vis the fixed intercept (16.6% and 18.1%, respectively) indicates that both blocking factors contributed necessary improvements to the model. Solving for x=0 in the second derivative of the fixed effects component of the regression equation allowed us to determine the estimated peak onset dates of the three biological seasons of interest: late winter (January 20), spring dispersal (March 24) and calving (May 20) (**Figure 1.9**).

3.4 Comparison of Methods

Figure 1.10 portrays the difference between onset dates determined using the individual-based method and those estimated using mixed polynomial regression with pooled data (population model). Estimates of winter were 16.6 days apart (p = 0.20), with the pooled estimate occurring later. Estimates of spring dispersal were 7 days apart (p = 0.21), with the individual-based estimate occurring earlier. The least difference occurred among estimates of peak onset for calving, with the pooled estimate preceding the individual-based estimate by only 1.6 days.

Figure 1.11 portrays the difference between onset dates determined using the individual-based method and those based on expert consensus (conventional estimates) currently for our particular study area. Estimates of winter differ greatly, with the conventionally defined period occurring close to a full month (26.6 days) later than it was found to occur by recursive partitioning. Conventional estimates for the onset of spring dispersal, likewise, precede the observed mean date by over two weeks (16.9 days). Again the least amount of difference between estimates was observed for peak calving time, with conventional dates preceding individual-based results by just over a week (8.6 days). The conventional estimate for winter was outside the 90% confidence intervals (p = 0.08) of the individually-fitted distribution; the estimate for spring was outside the 95% confidence intervals (p = 0.03).

DISCUSSION

Our results reveal considerable variation in the seasonal onset behaviour of woodland caribou as captured by variation in movement parameters. Calving was by far the most synchronous event, yet it spanned up to 38 days in length from the earliest recorded observation (May 6) to the last (June 13). Over three years, estimated annual peak onset varied by up to 20 days for winter, although only 4-5 days for spring and calving. These findings, particularly with respect to calving, corroborate with what has been documented elsewhere for woodland caribou (Bergerud 1975; Rettie & Messier 1998; Ferguson & Elkie 2004a), barren-ground caribou (Cameron et al. 1993; Post & Klein 1999), and Eurasian reindeer (Eloranta & Nieminen 1986; Flydal & Reimers 2002).

Calving may be the most synchronous event in the annual life cycle of large herbivores (Moen 1978), yet even the timing of calving may vary considerably as a function of age and reproductive history (Guiness et al. 1978; Gaillard et al. 2000; Langvatn et al. 2004), maternal body condition (Skogland 1984; Cameron et al. 1993), and/or genetic make-up (Skogland 1983), not to mention the timing of oestrus (Langvatn et al. 2004). In turn, population density, environmental variation due to climatic variability, and external factors such as disease, disturbance, and predator abundance can influence these parameters (Skogland 1983; Gaillard et al. 2000). With this in mind, our results indicate that the timing of other biological seasons may be even less predictable, as we observed increasing variability in the timing of seasons preceding calving. There were, however, strong modes and individually-estimated onset dates for all three seasons were normally distributed. Notwithstanding, consensus-based estimates of the timing of these seasons were outside the observed 90% and 95% confidence intervals for winter and spring, respectively. This suggests that researchers should use caution when adopting conventionally accepted seasonal periods in biological investigations of seasonal phenomena. A quantitative approach using pooled data in this case would have rendered considerably more accurate estimates of peak shifts in seasonal behaviour.

Seasonal changes in movement rates have been documented for a great number of species (Moen 1978; Jingfors 1982; Garner et al. 1990; Covell et al. 1996; Schneider et al. 2000; Brito 2003). Ferguson & Elkie (2004a) analyzed movement rates of woodland caribou to identify seasonal shifts in behaviour using polynomial regression. Dyke (2008) did the same using locally-weighted scatter plot (LOESS) analysis. We proposed a simple and intuitive approach based on recursive partitioning of smoothed time-series using analysis of variance (ANOVA) and biologically-informed decision rules. When conducted on an individual basis (i.e. one model per individual animal or time-series), this can generate fine-scale information on seasonal shifts in individual movement behaviour. Researchers may optionally include any number of additional variables in the model (e.g. temperature, altitude, snow depth, vegetation; Shuter 2010). Results can then be used to create a composite data set for a given season of interest by subsequently varying the temporal window used to extract observations for each unique animal (e.g. Apps et al. 2001). In the case where a fixed temporal window is deemed adequate, one may also obtain population-level estimates (peak onset dates) using a random effects-expectation maximization (RE-EM) tree (Galimberti & Montanari 2002; Sela & Simonoff 2010).

CONCLUSION

Animals such as woodland caribou exhibit marked trends in movement behaviour that reflect seasonal variation in the relative importance of foraging, reproduction, energy conservation, and predator avoidance. For this reason the study of animal space use patterns tends to be inherently seasonal in nature. However, the timing of seasonal events in the life cycle of animals may vary considerably from year to year and/or among individuals. This raises concern as to the prudence of adopting fixed time periods in the analysis of seasonal space use behaviour (e.g. habitat selection), for they may introduce unwanted bias in the form of observations that are not strictly representative of the biological activity under investigation (e.g. late winter behaviour is associated with spatial stability and energy conservation, whereas spring dispersal/migration behaviour is associated with energy expenditure and trade-offs between optimal foraging and predation risk) (Chapter 2).

Our study has demonstrated that dates determined by expert consensus and conventionally used to differentiate seasonal periods may not always be representative of the biological phenomena for which they were intended. We recommend researchers consult the biological signal of their study population using quantitative methods and other first-hand knowledge in order to verify the accuracy of the dates, and consequently the appropriateness of the data, used. Furthermore, because of the inevitable behavioural variation exhibited by free-ranging animals, we recommend both an individual-based approach to delineating seasonal periods and a temporally variable observation window in order to reduce sources of unnecessary and potentially erroneous bias in studies of habitat selection.

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FIGURES: ARTICLE 1

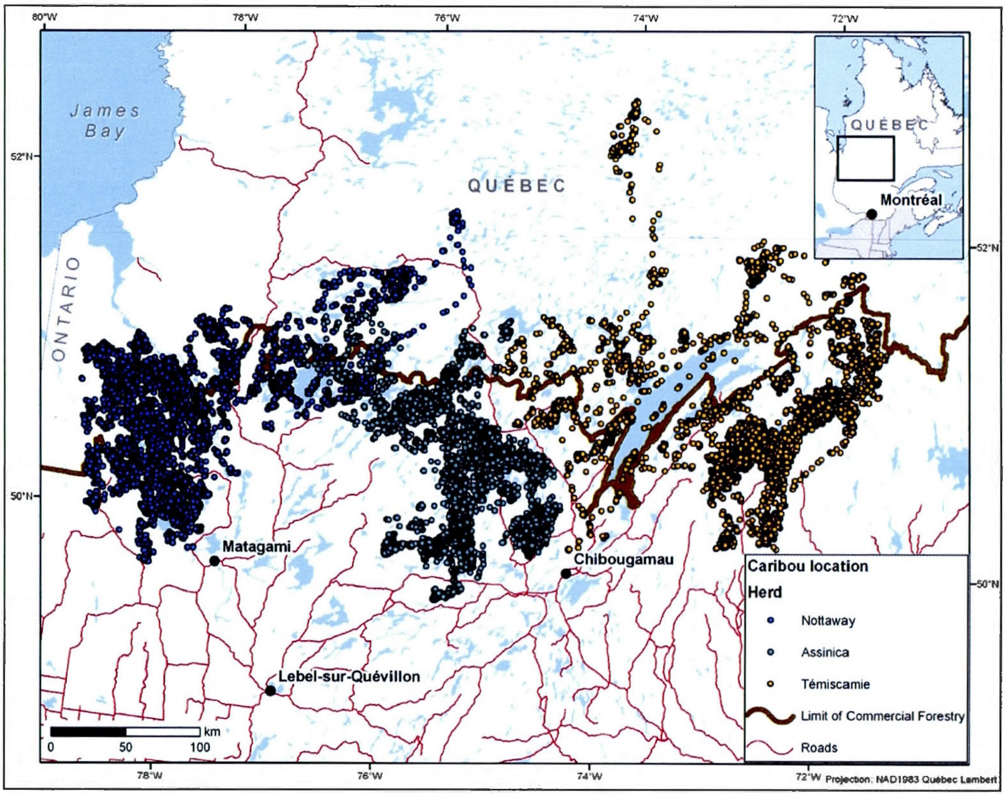

Figure 1.1: Location of study area in Northern Quebec. Points represent caribou locations obtained via GPS telemetry; purple denotes the Nottaway herd, blue the Assinica herd, and orange the Témiscamie herd. The brown line indicates the northern limit of commercial wood allocation.

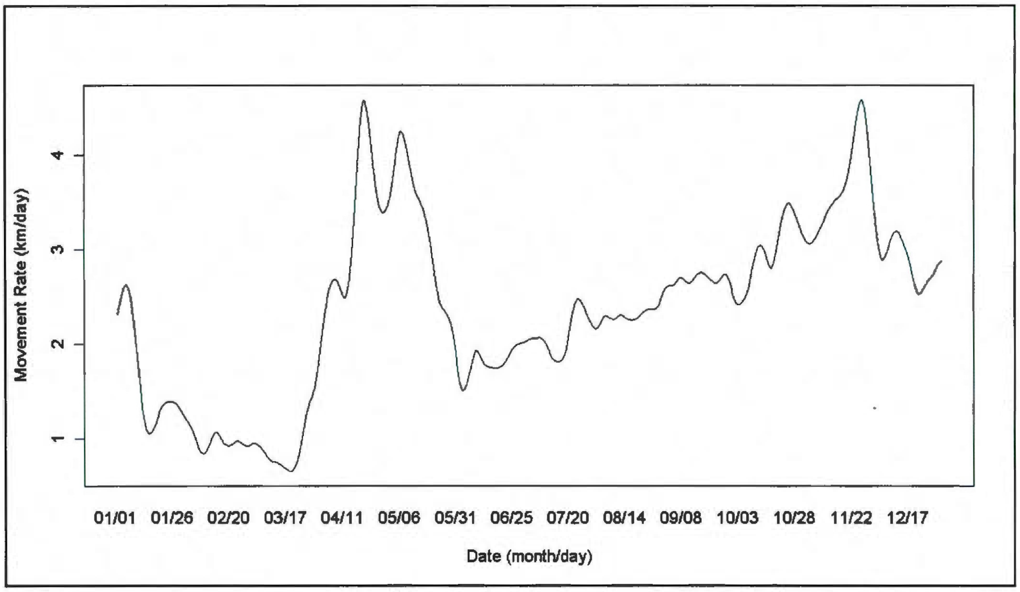

Figure 1.2: Smoothed mean daily movement rate per calendar day observed for 26 female woodland caribou in northern Quebec. Corresponding with the onset of late winter, a significant drop in movement rate takes place in early January. The sudden increase in movement rate in early April corresponds with the onset of spring dispersion, followed by a substantial drop in movement rate which indicates the start of calving in late May.

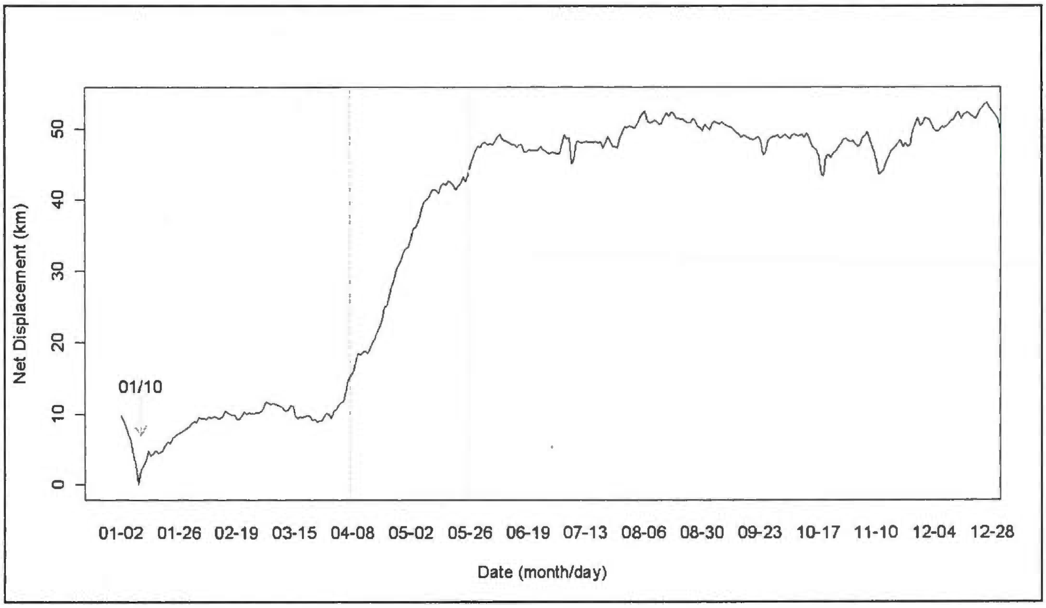

Figure 1.3: Pooled averages of net displacement per calendar day observed for 26 female woodland caribou in northern Quebec. Net displacement was defined as the Euclidean distance between an animal's location on any given day and its location on January 10 of the same year, the majority of individuals having established their wintering areas by this time. Dashed grey lines indicate the beginning and end of spring dispersal.

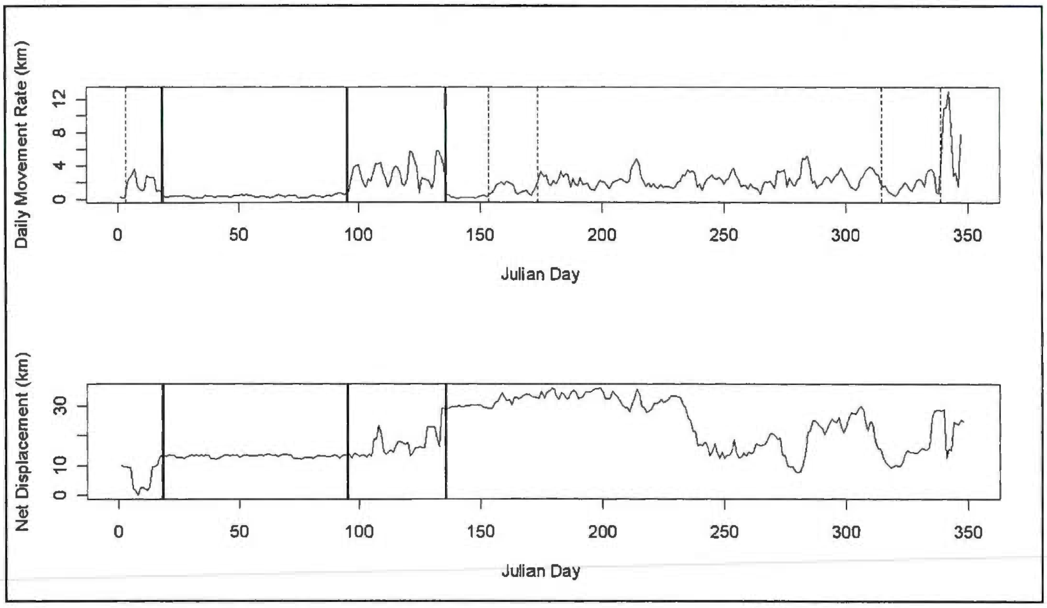

Figure 1.4: Example output from an individual-based recursive partitioning exercise (model = log(distance)~Julian day) for one individual (2002013) for the year 2005. As in a simple analysis of variance, time-series data were partitioned so as to maximize the between-groups sum-of-squares. A complexity parameter (ΔR2 >= 0.01) ensured that only worthwhile splits were accepted. Dashed grey lines represent candidate splits of the univariate regression tree and solid black lines represent splits chosen to delimit the onset of (from left) winter, spring dispersal, and calving. The migratory nature of spring dispersal is evident in the lower graphic showing net displacement as a function of time.

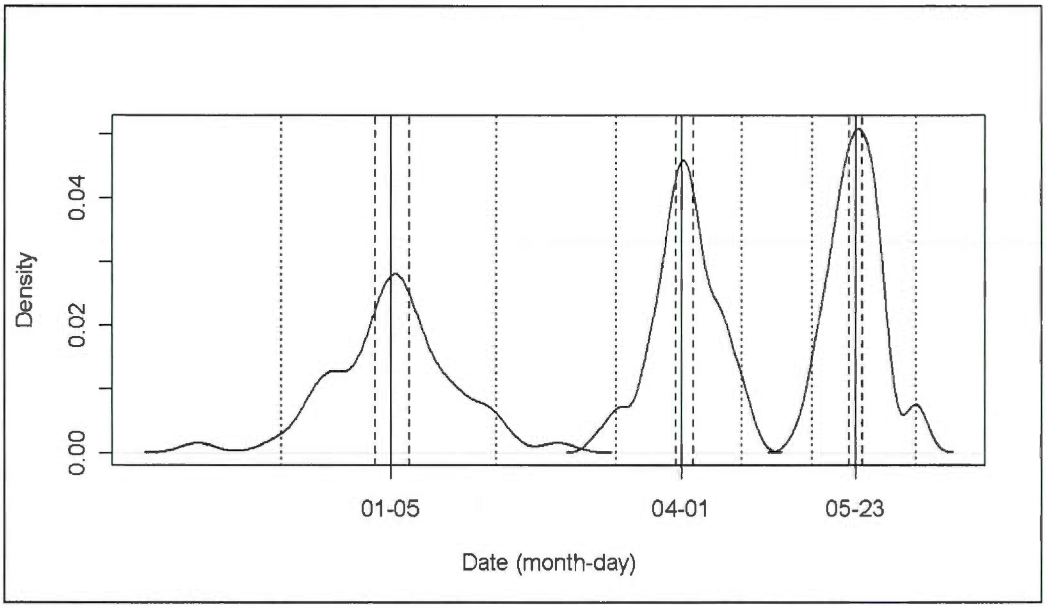

Figure 1.5: Distribution of individual onset dates determined via individual-based recursive partitioning (all years combined). Solid lines indicate peak onset dates for the winter (Jan. 5; n=50), spring dispersal (April 1; n=55), and calving (May 23; n=62) periods. Dashed lines indicate the 95% confidence intervals about the means (peak dates) and dotted lines indicate the 95% sample confidence intervals.

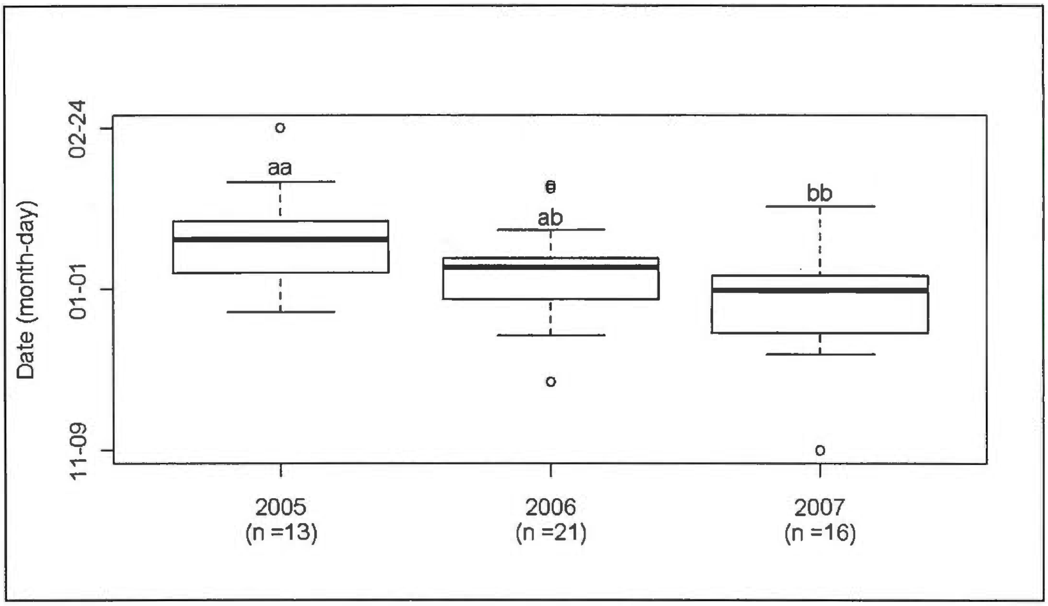

Figure 1.6: Boxplots of individual onset dates by year for the winter period. Letter notation indicates significantly different groups.

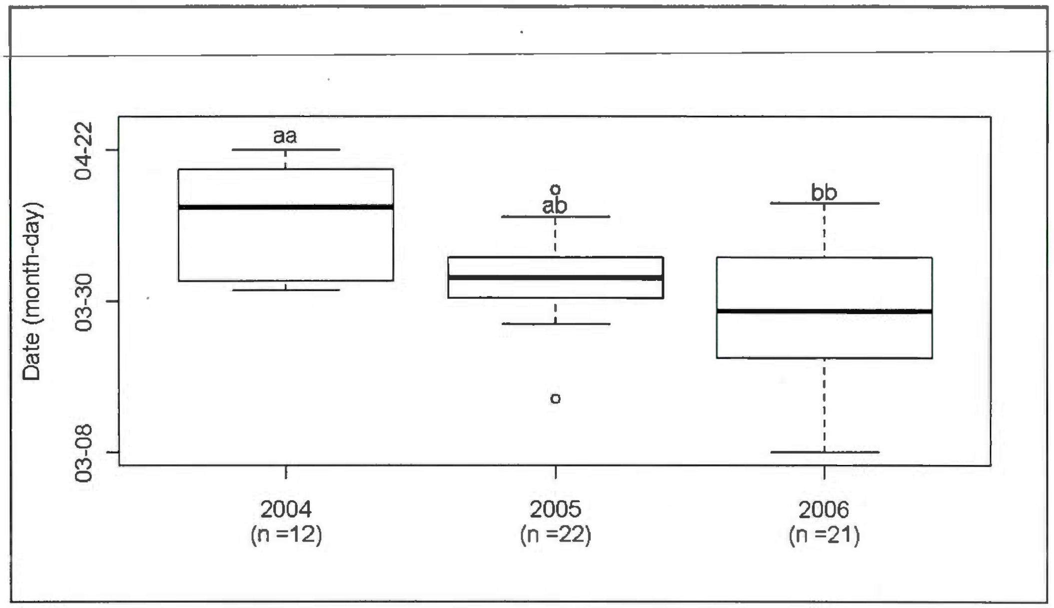

Figure 1.7: Boxplots of individual onset dates by year for the spring dispersal period. Letter notation indicates significantly different groups.

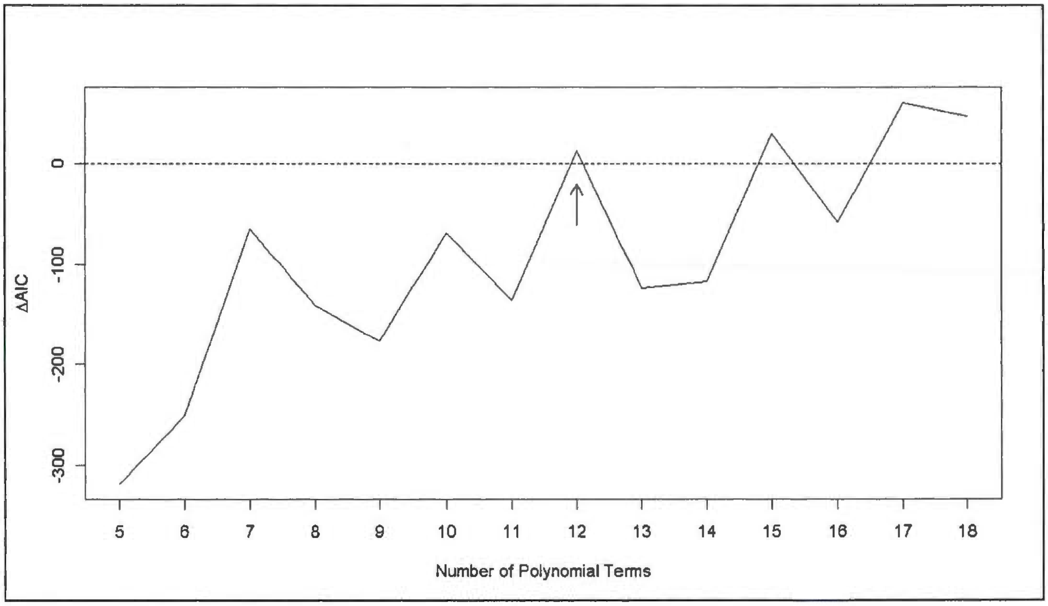

Figure 1.8: Change in AIC_c brought about by increasing the number of polynomial terms in a mixed-effects regression model of distance (in km, log-transformed) over time (Julian day, origin=January 1st). The net change in AIC_c becomes positive with the addition of a 12th term; therefore 11 terms were retained in the final population-based model.

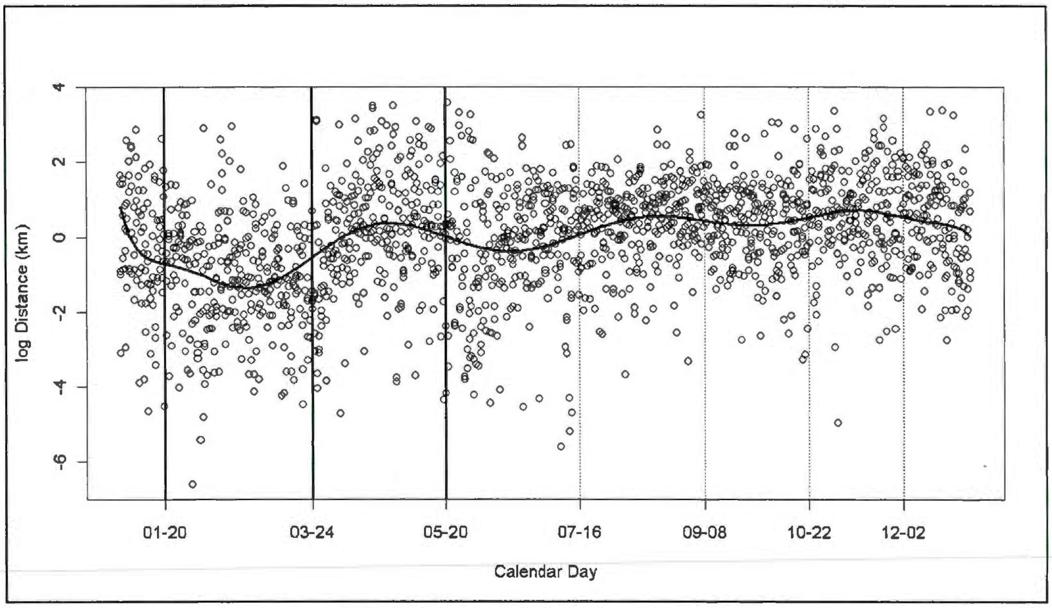

Figure 1.9: Plot showing raw data and the fitted curve from an 11th order polynomial regression model of distance (in km, log-transformed) over time. Inflection points were obtained by solving for x=0 in the second derivative of the fixed effects component of the regression equation. Solid lines indicate the estimated peak onset of the winter (January 10), spring dispersion (March 24), and calving (May 20) periods, while dotted lines indicate latter seasons of potential biological interest (most likely summer, fall, rut, and early winter).

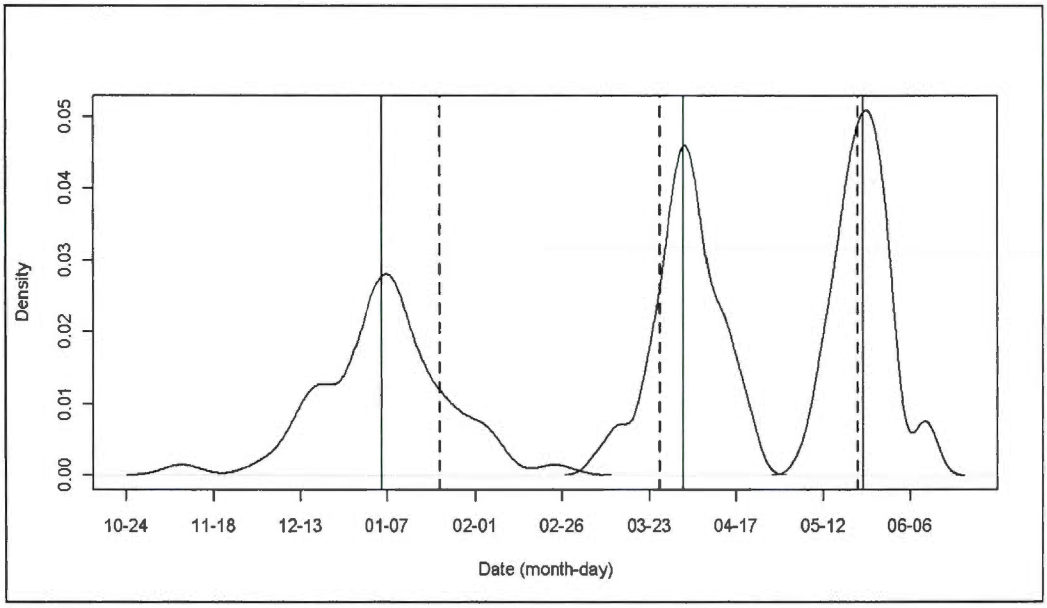

Figure 1.10: Comparison of individual-based estimates of peak onset dates (solid lines) for (from left to right) the winter, spring dispersal, and calving periods with estimates obtained using mixed polynomial regression with pooled data (dashed lines).

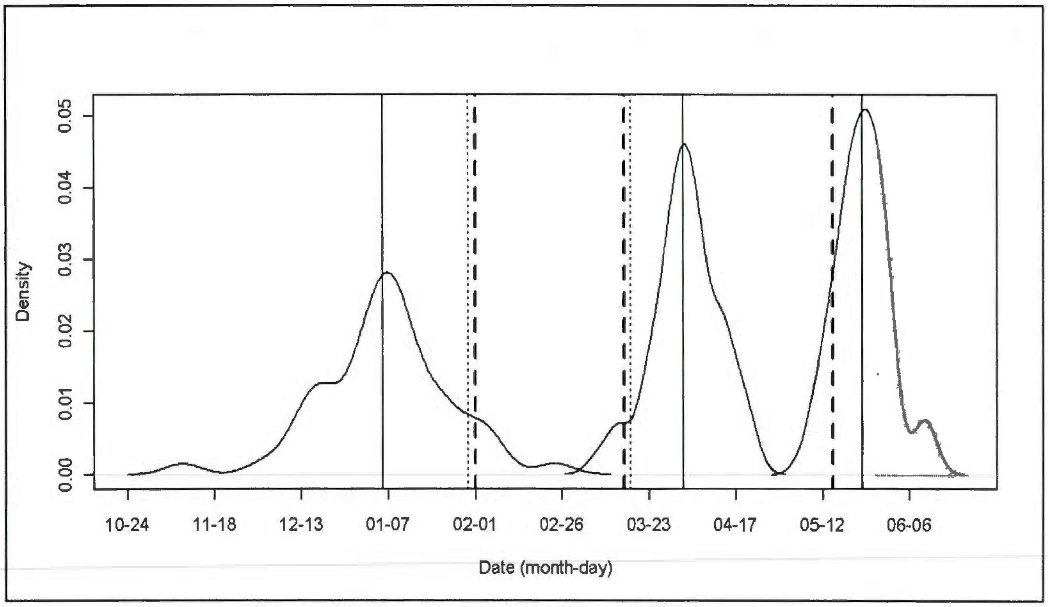

Figure 1.11: Comparison of individual-based estimates (solid lines) with consensus-based estimates (dashed lines) used in our study region. 90% (left) and 95% (right) sample one-tailed confidence intervals are shown for the winter and spring dispersal periods, respectively (dotted lines).

TABLES: ARTICLE 1

Table 1.1: Peak annual onset dates by season by year as determined by individual-based recursive partitioning. Also provided are sample sizes (n = number of individuals) and 95% confidence intervals (CI).

Year	Season	n	Lower CI	Peak onset Date	Upper CI
2005	winter	13	Jan-09	Jan-17	Jan-27
2006	winter	21	Dec-30	Jan-05	Jan-11
2007	winter	16	Dec-19	Dec-28	Jan-06
2004	spring	12	Apr-06	Apr-11	Apr-15
2005	spring	22	Mar-31	Apr-02	Apr-05
2006	spring	21	Mar-24	Mar-28	Apr-02
2004	calving	18	May-22	May-25	May-29
2005	calving	25	May-20	May-23	May-26
2006	calving	19	May-18	May-21	May-25

Table 1.2: Estimated length (in days) of the winter, spring, and calving seasons by year, with sample size (n = number of individuals) and 95% confidence intervals (CI).

Year	**Season**	**n**	**Lower CI**	**Length**	**Upper CI**
2005	winter	13	66.8	74.5	81.7
2006	winter	20	73.0	81.2	90.0
2004	spring	12	38.8	44.4	50.7
2005	spring	22	46.8	50.0	53.7
2006	spring	19	49.4	55.0	61.0
2004	calving	17	12.4	15.0	17.7
2005	calving	25	16.9	20.4	24.1
2006	calving	15	19.6	25.8	33.1

ARTICLE 2

SPRING DISPERSAL AND HABITAT SELECTION OF BOREAL CARIBOU IN NORTHERN QUEBEC

Tyler Rudolph[1,2] and Pierre Drapeau[1,2]

[1]Université du Québec à Montréal, Département des Sciences Biologiques
[2]Chaire industrielle CRSNG UQAT-UQAM en aménagement forestier durable,
Université du Québec en Abitibi-Témiscamingue

Abstract: Recovery strategies for woodland caribou invariably recognize the need to maintain functional connectivity between seasonal ranges, yet little is actually known about factors influencing caribou dispersal behaviour. We investigated movement parameters and habitat selection of boreal caribou during the highly mobile spring dispersal period. Individual movements were directional overall but there was no predominant direction at the population level. There was little interannual overlap in travel routes used although caribou did exhibit fidelity to traditional calving site locations. Caribou traveling within 30 km on average of highly roaded areas (> 0.5 km/km^2) were more likely to circle about extensively with little net displacement (i.e. random movements), whereas caribou beyond the 30 km threshold were more likely to exhibit quasi-linear (i.e. directed) movements. This indicates that roads may represent semi-permeable barriers to caribou dispersal. Second, we use a Brownian bridge movement model to estimate the probability of occurrence of boreal caribou during spring dispersal and conducted linear regression with mixed effects to estimate a Resource Selection Probability Function. Caribou space-use patterns revealed apparent trade-offs between optimal foraging, predator avoidance and energy conservation. In general caribou stayed close to waterways when they were within 500m and were slightly less likely to be found at higher elevations. Caribou selected lichen woodlands and all forms of wetlands, particularly herb-dominated, and they were less likely to be found in zones of higher road and cutblock densities. This being said, caribou were less selective during spring dispersal than they are known to be at other times of the year. Our primary recommendation for forest management is to reduce harvesting and road network development in areas still occupied by caribou. Where harvesting is permitted in zones occupied by woodland caribou we suggest localized small-scale interventions (e.g. partial or selective cutting) with permanent retention using temporary winter roads. Road deactivation and rehabilitation is of critical importance in conserving caribou on managed landscapes.

Keywords: woodland caribou, boreal ecotype, spring dispersal, landscape connectivity, semi-permeable barriers, Brownian bridge movement model (BBMM), habitat selection, resource selection probability function (RSPF), functional response.

INTRODUCTION

Conserving highly dispersed, wide-ranging species on increasingly fragmented landscapes is a particular challenge for resource managers. In the boreal forest of Canada, woodland caribou (*Rangifer tarandus caribou*) are considered threatened and particularly sensitive to habitat alteration and anthropogenic disturbance. Forest management in particular is believed to have had a deleterious effect on range occupancy due in part to changes in forest composition that have indirectly altered predator-prey relationships (Bergerud 1974a, 1988; Seip 1991b). In parallel, infiltration of road and other linear networks has improved accessibility to hunters and other predators (James 1999; James & Stuart-Smith 2000; Courtois et al. 2003b; McCutcheon 2007). The cumulative effects of disturbance, habitat loss, and predation can consequently extirpate caribou from such systems (Bergerud 1974a; McLoughlin et al. 2003; Wittmer et al. 2007).

Strategies intended to mitigate the undesired impacts of forest management on woodland caribou generally consist of maintaining a continuous supply of suitable winter habitat while permitting harvesting to occur in adjacent areas (Arsenault 2003; Manitoba Conservation 2006; MRNF 2008; OMNR 2009). There is widespread recognition of the need to protect calving areas also (Darby & Duquette 1986; Lantin et al. 2003; Environment Canada 2008; Metsaranta 2008), but the highly dispersed nature of forest-dwelling caribou at this time of year make such measures unpalatable to the forest industry. A third essential element in the conservation of threatened species such as caribou is the maintenance of habitat connectivity (Fahrig & Merriam 1985; Bennett 2003). For example, interim woodland caribou recovery guidelines from several Canadian provinces have proposed maintaining travel corridors of various widths to facilitate movements between seasonal ranges (Cumming 1992; Simpson et al. 1997; Racey et al. 1999; Courtois et al. 2004; Manitoba Conservation

2006). However the functional connectivity of managed landscapes cannot be ensured without an understanding of factors influencing woodland caribou dispersal behaviour (Lima & Zollner 1996; Tischendorf & Fahrig 2000; Bélisle 2005; Chetkiewicz et al. 2006).

Although generally characterized as "sedentary" (Bergerud 1988, 1996), the majority of forest-dwelling caribou exhibit relatively synchronous and punctuated semi-annual migrations between wintering and summering areas (Brown et al. 1986; Bergerud et al. 1990; Ferguson et al. 1998; Brown et al. 2000). In accordance with Turchin (1998) and White & Garrott (1990), we define dispersal as a form of one-way migration that leads to spatial spread or dispersion in a population. The particular importance of spring dispersion as an anti-predator spacing-out strategy has been well demonstrated in both mountain (Bergerud & Page 1987; Bergerud et al. 1990; Seip 1992) and boreal caribou (Bergerud 1985; Cumming & Beange 1987; Bergerud et al. 1990). Leaving their winter ranges in search of safe calving locations, parturient females are especially vulnerable during spring dispersal. Their primary winter food being lichen, which is high in digestible carbohydrates but low in protein (Bergerud 1972; Parker et al. 2005), caribou commonly lose up to 20% of their body mass over winter (Jacobsen & Skjenneger 1975). Moreover, the energetic demands of pregnancy near their maximum late in the third trimester (Moen 1978; Reimers et al. 1983) (Chapter 1). Females are therefore both burdened and energetically deficient at the onset of spring dispersal, during which time they expend considerable resources traveling through numerous and often unfamiliar environments, hence considerably elevating their risk of predation (Johnson et al. 2002b; McLoughlin et al. 2005b; Kauffman et al. 2007; *see also* Zollner & Lima 2005; Hebblewhite & Merrill 2007). Given that caribou populations are approximately three times more sensitive to adult female mortality than to changes in rates of juvenile recruitment (Fancy et al. 1994; Wittmer et al. 2005b; Haskell & Ballard 2007), it stands to reason that spring dispersal be considered a critical period in the annual life cycle of woodland caribou, one which merits greater biological investigation. Furthermore, because caribou are highly mobile at this time, an appreciation of factors influencing space use during spring dispersal should improve our notions of functional landscape connectivity for this species-at-risk.

Studies of resource selection by woodland caribou tend to emphasize the winter and, to a lesser degree, calving periods when caribou are relatively sedentary (Terry et al. 2000; Lantin et al. 2003; Gustine 2005; Dyke 2008; Fortin et al. 2008). In contrast, very few studies have specifically addressed habitat selection during migratory phases of boreal woodland caribou. It has been posited that caribou follow natural relief features corresponding with direction of travel such as waterways or ridge lines, preferentially selecting conifer habitats (Racey et al. 1999). However, while this appears to hold true in mountainous regions (Bergerud 1974c; Apps et al. 2001; Johnson et al. 2002b; Mahoney & Schaefer 2002b; Saher 2005), this may be less important in boreal regions characterized by minimal topographical relief. Ferguson & Elkie (2004b) compared travel routes during spring and early winter with Euclidean paths connecting the midpoints of late winter and post-calving ranges. They concluded that woodland caribou in northwestern Ontario did not show a strong selection for particular travel habitat, although they did note a greater use of wetland/fen areas and a slight aversion to deciduous forest. They also found, contrary to expectations (Stuart-Smith et al. 1997; Rettie & Messier 2000), that caribou did not noticeably avoided disturbed areas (Ferguson & Elkie 2004b). Saher & Shmiegelow (2005) examined habitat selection of eight mountain caribou during spring migration in west-central Alberta and east-central British Columbia. They differentiated travel phases from resting/foraging phases (Sibly et al. 1990; Johnson et al. 2002a) and determined that caribou traveled through less rugged terrain that was closer to water than random locations.

We examined the space-use patterns of female forest-dwelling woodland caribou during spring dispersal in the northern boreal forest of Quebec. First, we investigated animal trajectories for evidence of consistency in orientation, directionality, and tortuosity. Second, in order to assess the effectiveness of fixed travel corridors as a means of facilitating seasonal displacements, we evaluated the degree to which boreal caribou in northern Quebec exhibited fidelity to traditional routes during spring dispersal. Lastly, we asked whether the probability of a given site being used by caribou during spring dispersal was dependent on the relative abundance of certain habitats or habitat attributes. We predicted that dispersal behaviour would reflect trade-offs between predation risk, foraging opportunities, and energetic travel costs. For example, given the importance of spring dispersion as an anti-predator spacing-out behaviour (Bergerud 1990), we expected caribou to be positively associated with lowland (bog/fen) habitats less likely to be used by wolves (*Canis lupus*) or moose (*Alces alces*) (James 2004). However, as their prime source of winter forage, we also expected caribou to select upland habitats where terrestrial lichens were abundant (Klein 1982). Finally, because woodland caribou are widely known to avoid roads and recently disturbed areas (cutblocks, burns) (Darby & Duquette 1986; Cumming & Beange 1993; Dyer et al. 2002; Schaefer & Mahoney 2007; Courtois et al. 2008; Courbin et al. 2009), we predicted that relative increases in such features would significantly reduce the probability of use by caribou during spring dispersion.

1.1. Study Area

The present study comprises a 109,116 km^2 tract of boreal forest in northern Quebec situated between 49°52' and 51°46' N and 71°17' and 79°31' W (**Figure 2.1**). Part of the black spruce-feathermoss bioclimatic domain, it is dominated by black spruce (*Picea mariana*) in association with feathermoss (*Pleurozium schreberi*) and/or various lichen species. Jack pine (*Pinus banksiana*) and balsam fir (*Abies balsamea*) occur to a lesser extent, in addition to trembling aspen (*Populus tremuloides*), paper birch (*Betula papyrifera*), tamarack (*Larix laricina*), and (rarely) balsam poplar (*Populus balsamifera*) **(Table 2.1)**. Forest understory is dominated by mosses and ericaceous shrubs with few herbaceous species. The western flank of the region forms part of the Clay Belt and is dominated by large sphagnum bog and fen complexes. Terrain is broad and mildly sloping with occasional topographic relief (45-825m AMSL) and there are numerous rivers and waterways interconnecting the region. Treed wetlands and upland forest intersperse with bog/fen complexes and lichen or shrub-dominated uplands with occasional rock barrens. The region receives approximately 960 mm of precipitation annually with monthly average temperatures ranging from -19° (January) to + 16° (July) Celsius.

Constituting Québec's second-largest timber supply region, the study area encompasses both the northern limit of commercial forestry activity and the southern limit of continuous woodland caribou distribution (Courtois 2003). Primary disturbances include forest fire (100-500 year fire cycle; Bergeron et al. 2001) and forest harvesting, which is presently concentrated in the southern portion of the study area. Large mammal species include forest-dwelling woodland caribou, moose, gray wolf and black bear (*Ursus americanus*). Reliable population estimates are unavailable, but caribou densities are estimated to be between 1.5 and 2.1/100 km^2, with individuals occupying average annual home ranges of ~4386 km^2 (St-Pierre et al. 2006). In the northern sector, infrequent range overlap takes place with populations of the tundra-forest ecotype of woodland caribou (Rangifer tarandus caribou) (Courtois et al. 2003d).

MATERIALS & METHODS

2.1 Caribou Capture and GPS Telemetry

Animal relocation data were obtained via GPS (Global Positioning System) collar transmitters (Telonics model TGW 3680) fitted on 26 female caribou by members of the Québec Ministry of Natural Resources and Wildlife in March 2004 and January 2005. Captures were conducted using ASTAR 350BA or EC120 helicopters and a net gun (Potvin & Breton 1988). Individuals sampled were evenly distributed among three regional populations: the Nottaway (west), Assinica (central), and Témiscamie (east) (**Figure 1.1**). Satellite transmissions were uploaded three times daily (7-hr fix interval) between January 2005 and March 2007. While a more frequent GPS fix interval (e.g. 1-4 hour) may be desirable under certain sampling designs, 7 hours between relocations is considered adequate for detecting habitat selection (Girard et al. 2006).

Relocations were filtered for positional accuracy in order to remove large location errors: those based on 4 or more satellites (3-D) were eliminated if they had corresponding horizontal dilution of precision (HDOP) values greater than or equal to 25, whereas those based on 3 satellites (2-D) were eliminated if they had HDOP values greater than or equal to 8 (Dussault et al. 2001; D'eon & Delparte 2005; Lewis et al. 2007). The Horizontal Dilution of Precision reflects the horizontal accuracy (latitude/longitude) of GPS position fixes by adjusting the error estimates according to the geometry of the satellites used. This resulted in a roughly 4% data reduction per individual. GPS fix rate can be biased against closed canopy habitat types (Rempel et al. 1995; Dussault et al. 1999; D'eon 2003; Lewis et al. 2007), which can in turn affect biological inference (Visscher 2006; Bradshaw et al. 2007). While there are sophisticated approaches to mitigating this bias (Nielson et al. 2009; Frair et al. 2010), we largely circumvented this issue by employing probabilistic estimations of space use that incorporate GPS relocation error (described in detail in **Section 2.4**). Finally, although animal movements have been known to vary among female caribou according to reproductive status (Paré & Huot 1985; Fancy & Whitten 1991; Ferguson et al. 1998; Barten et al. 2001; Rettie & Messier 2001), high pregnancy rates are pervasive in woodland caribou populations so we assumed no error due to variation in reproductive condition (Parker 1981; Rettie 1998). Spatial relocations were projected from the World Geodesic coordinate system (WGS 84) into Quebec Lambert Conformal Conic (1983) prior to spatial analyses.

2.2 Timing of Spring Dispersion

We estimated the start and end dates of spring dispersion for each unique individual (n=26) / year (n=3) combination using recursive partitioning (Chapter 1). Cut-off dates were determined by maximizing the between-groups sums-of-squares along a smoothed time series distribution of distance travelled (logarithmically transformed) per day (Chapter 1). This resulted in 53 unique cases (data sets) of spring dispersion, each possessing their own unique start and end dates.

2.3 Dispersal trajectory characteristics

2.3.1 Directionality

Some authors have noted a directional trend in migratory movements of woodland caribou (Fuller & Keith 1981; Mahoney & Schaefer 2002; Ferguson & Elkie 2004a). We tested for directionality in spring dispersal trajectories at the population level using Moore's non-parametric second-order test of directionality based on sample means of both absolute and relative (turning) angles (Zar 1974). Although direction is inherently circular, a movement trajectory is in fact a combination of an angle (direction) and a distance (scalar), and is therefore a vector (Klink 1998). Indeed, analysis of direction alone would mask the relative influence of net displacement, a property of considerable interest (Turchin 1998). Recognizing this to be a bivariate problem, we proceeded to calculate the mean vector (or "center of mass") associated with each unique case of spring dispersal. Using the mean resultant lengths r_i we then conducted Moore's procedure, a rank-based non-parametric modification of the Rayleigh test. Using the sample derived from absolute mean angles, the critical value D^* of the test statistic reveals whether or not there was a mean direction at the population level. Using the sample derived from relative (turning) angles, D^* reveals whether or not individual dispersal paths were oriented. We also tested for significant directionality on a separate basis for each regional population (i.e. Nottaway, Assinica, and Témiscamie).

2.3.2 Path tortuosity

The extent to which forest management activities influence woodland caribou dispersal behaviour has received very limited attention (Dyer et al. 2002). Because we were aware of their tendency to avoid anthropogenic disturbances (Darby & Duquette 1986; Dyer et al. 2001), we asked whether differences in movement patterns existed between caribou in undisturbed zones and those in zones subject to forest harvesting. We hypothesized that proximity of highly developed road networks would stifle or inhibit female caribou in their movement to a safe calving site, resulting in seemingly random movements. Preliminary observation of individual migration paths revealed a tendency whereby some trajectories were spatially extensive and quasi-linear whereas others were locally concentrated and highly sinuous. We measured this phenomenon using the straightness index SI = D/L, where D is the net displacement or Euclidean distance between start and end locations and L is the sum of step lengths (Batschelet 1981). For example, SI = 1 represents a perfectly straight line (highly oriented) whereas SI → 0 tends toward randomness. Benhamou (2004) showed SI to be an exact estimator of the orientation efficiency of a path used by an animal to reach a goal located at a finite distance; however, it tends to be biased high when recording frequency is low (Benhamou 2004); therefore SI is overestimated for paths with missing relocations. We modeled this relationship using Monte Carlo methods with simulated animal trajectories. We were interested in a) estimating SI via randomization for paths with missing relocations, and b) correcting these estimates for the bias associated with unknown path lengths. We therefore proceeded to create 1000 random paths based on movement parameters observed within our sample population. We began with a full-circle radian sampled from a uniform circular distribution. Pairs of step lengths and turning angles were then sampled without replacement from observed relocations within our sample population to construct a continuous random path consisting of 175 7-hr relocations, as 51 days was the average length of spring dispersion (Chapter 1). After calculating true SI based on the complete trajectory, we proceeded to iteratively rarify simulated datasets (5-100%) and subsequently re-estimate SI using randomization with replacement (n=1000). Because differences in omitted relocations may influence bias (Nielson et al. 2009), we performed this sub-routine 500 times for each level of rarification.

We used the results of Monte Carlo simulations to obtain corrected estimates of SI (i.e. to account for paths with missing relocations). We then asked if proximity to areas of high road density could explain observed variation in the tortuosity (1-SI) of caribou movements using mixed effects linear regression. We chose road over cutover density because linear features are known to represent semi-permeable barriers to dispersal (Dyer et al. 2002); furthermore, preliminary analysis revealed a stronger relationship between path tortuosity and road density as measured by Akaike's Information Criterion (AIC).

We proceeded to generate explanatory matrices for the years 2004-2006 representing distances to the nearest cell value meeting or exceeding 0.5 km of road per square kilometre within a 25-km radius. Nellemann & Cameron (1998) reported 87% reductions in the densities of calving caribou where road densities averaged 0.45 km/km^2 as measured within 10.5-km^2 quadrats. We expanded our search window to a 25-km radius in order to account for the much larger home ranges of female caribou during spring dispersion vs. calving. We modeled SI (bias-corrected) as a function of mean distance from the probability-weighted centroid of dispersal areas to the nearest location where road density met or exceeded 0.5 km/km^2 (probabilistic methods are discussed in **Section 4.2**). We tested for the significance of a random effect for individual by comparing the mixed effect model with a second model estimated by generalized least squares with identical fixed effects but no random component. To prevent bias in variance estimation, both models were estimated using restricted maximum likelihood and tested for significance using a likelihood ratio test. Inclusion of a nested structure for individual caribou accounts for correlation among observations of SI (bias-corrected) for the same individuals in successive years. Finally, we tested whether a quadratic term was warranted using maximum likelihood and AIC.

2.4 Spatial Distribution and Extent of Spring Dispersal

A central issue in studies of habitat selection is how to objectively define the domain available to a given animal or population at a given period of time (Garshelis 2000; Buskirk & Millspaugh 2006). In terms of home range delineation, kernel density estimators are certainly an improvement over the traditional Minimum Convex Polygon (MCP) approach (White & Garrott 1990); however, they can be sensitive to the choice of smoothing parameter and technique used (Seaman & Powell 1996; Kernohan et al. 2001; Gitzen et al. 2006). Furthermore, kernel methods may estimate the bivariate probability distribution of spatial point-patterns, but they do not account for the temporal relationship between subsequent animal relocations (Moorcroft et al. 1999; Benhamou & Cornélis 2010). In fact, animal distributions are generated by movement processes that are of primary biological interest (Turchin 1998; Benhamou & Cornélis 2010). For example, individual animals tend to have more tortuous pathways in good quality habitat and move further and faster over unfavorable terrain (Crist et al. 1992; Johnson et al. 1992; With 1994b). Bullard (1991) demonstrated how such processes can be intuitively accommodated by incorporating Brownian motion into probabilistic estimates of space use. The continuous counterpart of a random walk (Turchin 1998), many natural phenomena are represented mathematically as Brownian motion (Bullard 1991). Though animal movements are rarely random, without a priori knowledge of underlying mechanisms it is appropriate to model the stochastic process linking two known relocations as a Brownian bridge (Horne et al. 2007). In this case the bivariate probability surface becomes a function of a) the spatial arrangement of consecutive points (b_1, b_2), b) the time elapsed (T) between relocations, c) the Brownian motion variance ($\sigma^2{}_1$), which is proportional to the speed at which the animal is travelling, and d) the spatial error associated with the endpoint location ($\sigma^2{}_2$). Horne et al. (2007) derived a maximum likelihood approach for empirically estimating the Brownian motion variance and demonstrated the utility of the Brownian bridge movement model (BBMM) for estimating migration routes and resource selection. After Horne (2007) and Sawyer et al. (2009), we considered a 7-hour fix interval adequate to meet the assumptions of Brownian motion.

Because we were interested in obtaining a probabilistic measure of space use and deriving associated habitat preferences during spring migration of woodland caribou (Marzluff et al. 2004; Sawyer et al. 2009), we estimated one utilization distribution (UD; Van Winkle 1975) for each unique case of spring dispersion observed (n=53) based on the Brownian bridge movement model. Brownian motion variance (σ^2m) was estimated separately for each UD (individual-year combination) using the maximum likelihood approach described by Horne et al. (2007). In order to avoid undue bias in estimates of σ^2m, data sets containing relocations based on sampling intervals greater than 21 hours apart (3 missed locations) were split into constituent parts. Separate UDs were then estimated for each component distribution on a common spatial grid, after which UDs were combined based on a temporally weighted average. Specifically, grid cell values were multiplied by the proportion of the total time represented by each UD, as recommended by Horne (2010, personal communication). UD cell resolution was 50m.

In the BBMM, positional errors of the estimated locations are assumed to be isotropic and normally distributed about the true location. After Horne (2007), we estimated the spatial error about each true location using the relationship between the recorded PDOP value and mean location error for 2-D and 3-D fixes described by Lewis et al. (2007). First the expected distance $\hat{d}$ was modeled from each estimated location to its corresponding true location using the following:

2-D fixes: $= 12.98 * \text{PDOP} + 12.43$

3-D fixes: $= 4.07 * \text{PDOP} + 1.15$.

Standard deviations δ of $\hat{d}$were then estimated using $\hat{\delta} = \hat{d}/\sqrt{\pi/2}$. Using the grid cell values of the resulting BBMM, we calculated the cumulative 99% probability density contours of each BBMM based on the height values within each UD.

2.5 Travel Route Fidelity

We measured fidelity to traditional travel routes by calculating the proportion of spatial overlap in pairs of polygons representing the 99% probability contours of BBMMs from consecutive years. Specifically, for each unique individual i we calculated the proportion of overlap *POL* between each pair of consecutive year polygons (i_1,i_2) as:

$$POL_{i1,i2} = A_{i1,i2} - (A_{i1} + A_{i2} - A_{i1,i2}),$$

where $A_{i1,i2}$ is the area of overlap between i_1 and i_2, and A_{i1} and A_{i2} are the areas of i_1 and i_2, respectively (Dahl 2005; Faille et al. 2010). A somewhat similar metric (static territorial interaction, *S*) was proposed by White & Garrott (1990) to assess spatial associations between animals. However as a measure, *S* is necessarily contingent on a reference animal, or in our case, year. *POL*, rather, is a static measure of the proportion of overlapping area (or static territorial overlap) between home ranges of two equally weighted years. From an applied perspective we preferred *POL* over probabilistic metrics (Fieberg & Kochanny 2005) because it is simple and intuitive and we were primarily interested in determining to what general spatial extent migrating individuals traveled through the same geographic areas interannually. Furthermore, by using polygons based on the 99% probability contours of the BBMM surface, we circumvented two issues raised by Kernohan et al. (2001) relating to the use of MCPs in measures of shared space use; namely, a) the correlation of sample size to range size and b) the inability of MCPs to conform to irregularly shaped ranges (Kernohan et al. 2001).

Given that spring dispersal paths are also a function of the relative locations of the onset and terminus of each dispersal event, we also examined fidelity to late winter (onset) and calving (terminus) locations. We did this by calculating Euclidean distances between interannual pairs of locations associated with the onset and terminus of spring dispersal for the years 2004/2005 and 2005/2006.

2.6 Habitat selection

Using the pixel coordinates of each BBMM UD, we extracted spatial attribute data in order to associate UD probabilities with particular habitat characteristics in a tabular format (Millspaugh et al. 2006). This resulted in extremely large datasets, thus requiring us to subsample as follows: in a format similar to the classic RSF (Resource Selection Function; Manly et al. 2002) approach, we sampled every unique pixel coinciding with observed GPS points and paired these with randomly chosen pixels (1:5 ratio) found within the 99% contours of each unique Brownian bridge UD. We then combined the tables from the subsetted UDs to form a composite dataset for habitat selection analyses.

We examined habitat selection by caribou during spring dispersion at the scale of the seasonal home range (3rd order habitat selection; Johnson 1980). Numerous methods have been developed for analyzing animal space use with telemetry data (Aebischer & Robertson 1993; Cooper & Millspaugh 1999; Manly et al. 2002; Nielsen et al. 2002; Fortin et al. 2005b; Gillies et al. 2006; Forester et al. 2007; Koper & Manseau 2009). Marzluff (2004) demonstrated how variation in the height of the utilization distribution can be associated with any set of independent spatial variables to estimate a Resource Utilization Function (Young & Ruff 1982). One drawback of this individual-based approach is the difficulty of population-level inference when certain individuals have never been exposed to a given habitat condition (Fieberg et al. 2010). Given that we were working with individuals from a very large geographic area, we encountered this particular problem with several habitat types of interest (e.g. harvest blocks, dense broadleaf/mixedwood forest). However we retained the advantage of working with a continuous response variable (based on a modeled space use pattern and not a collection of static points) by way of generalized linear mixed effects regression modeling (GLMM; Gillies et al. 2006). As inferred by Millspaugh et al. (2006), this is equivalent to estimating the Resource Selection Probability

Function (RSPF; Manly et al. 2002; Lele & Keim 2006). The model includes both a linear predictor and a random component and takes the following form:

$$w^{*}(x) = f\,(\beta_0 + \beta_1 x_{1ij} + \ldots + \beta_n x_{nij} + \gamma_{nj}\, x_{nj} + \gamma_{0j} + \varepsilon_n)$$

where $f(x)$ is the link function, x_n are the model covariates, β_n are the estimated coefficients, γ_{nj} is the random coefficient of covariate x_n for group j, and ε_n is the residual error. We tested for the significance of a random effect for a) UD and b) id nested by year in order to reflect the grouped structure of the data set and thus permit variation in the intercept for unique levels of these factors. To prevent bias in variance estimation, models were estimated using restricted maximum likelihood and random effects were tested for significance using a likelihood ratio test. Zuur et al. (2009, pg. 116) demonstrated that the inclusion of a random effect in mixed models is equivalent to specifying a compound symmetric working correlation using generalized least squares. This allows for uniform serial correlation among observations from within the same UD and adjusts parameter estimates accordingly. In this way the individual animal is accounted for as the sample unit and the population estimates are unaffected by variable sample sizes (Gillies et al. 2006). We considered this to be an adequate treatment of autocorrelation given the already implicit smoothing of the BBMM and our intention to model relatively fine-scale spatio-temporal variation in caribou dispersal behaviour.

The importance of functional responses to changes in resource availability is often neglected in studies of resource selection (Mysterud & Ims 1998). For example, an individual may not appear to select a given resource until it is relatively scarce, or it may use it less than its relative availability when it is abundant (Mysterud & Ims 1998; Mauritzen et al. 2003; Osko et al. 2004; Gillies et al. 2006; Fortin et al. 2008). Including quadratic terms may allow us to better model such relationships (Boyce et al. 2003). Another technique is to allow the slope to vary for a covariate of interest through constrained adjustments to random-level coefficients (or shrinkage estimates). We pursued this by examining the relationship between individual responses to covariates and the degree of individual exposure to those covariates (relative abundance/importance) as measured by the mean observed value within each UD. This informed our choice of three candidate variables exhibiting the most visible non-linearity in individual response over the range of observed values. We conducted likelihood ratio tests for random coefficients for the top variables using models estimated by REML.

2.7 Habitat Attributes

2.7.1 Categorical variables

Forest resource inventories were not available for the entirety of our study area, part of which lies north of the current limit of commercial forestry. We therefore evaluated habitat conditions over a broad geographic area using Landsat images classified by the Canadian Forest Service (Wulder 2000). We aggregated habitat units to obtain a 50 m cell resolution using the nearest neighbor rule; this grain was considered adequate to capture variation in lichen abundance yet reasonable enough to accommodate demanding computational procedures. We subsequently updated the image to account for all forest fires, harvest blocks, and roads having arisen between 2000 and each year of our study period, 2004-2007, using spatial data from annual forest management reports (RAIFs, *rapports annuels d'intervention forestière*). Detailed descriptions of habitat types and acronyms are provided in **APPENDIX II-1**.

2.7.2 Continuous variables

Although most habitat selection analyses occur at discrete spatial scales, the most parsimonious models may include covariates measured at multiple spatial scales (Johnson et al. 2004c; Bowyer 2006; Gustine et al. 2006b). It may therefore be advantageous to measure the response of organisms to variables measured across several spatial scales. We were particularly interested in quantifying the influence of road and cutblock networks on caribou dispersal behaviour as modeled by the BBMM. As a means of exploring caribou response to anthropogenic landscape features at several spatial scales, we first generated road and cutblock density matrices based on a range of moving window sizes: 2.5, 5, 10, 15, 20, and 25km. We did not distinguish between primary, secondary and tertiary roads nor did we attempt to control for landscape context. In order to determine the optimal scale at which to characterize road and cutblock density, we estimated six RUF models per unique UD, i.e. one for each scale of measure (radius length of the circular moving window). Specifically, we modeled the probability of occurrence of individual caribou during spring dispersal (based on UD height) as a function of road or cutblock density measured at six spatial scales. Distributions of the standardized coefficients of the fitted models were then compared in order to select the measure which elicited the most uniform response among caribou (i.e. positive or negative; Bring 1994). In order to reduce correlation within individual datasets, we estimated an additional parameter for the spatial covariance at observed locations within the UD by optimizing a Matérn autocorrelation function by way of maximum likelihood (Handcock & Stein 1993). The autocorrelation function estimates 2 parameters, spatial range (θ_1) and smoothness (θ_2). Range (θ_1) controls the decay of the correlation as distances between observations increase, and θ_2 controls the behaviour of the autocorrelation function where observations are separated by small distances (Hoeting et al. 2006). We estimated the Resource Utilization Function (Young &

Ruff 1982) using the `ruf.fit` function of the `R` package ruf developed by Mark Handcock (2004).

In addition to anthropogenic variables, we included a distance matrix for waterways (20m resolution) and a digital elevation (DEM) model.

2.8 Model selection

As a preliminary means of assessing the relative importance of the different categorical habitat types of interest, we calculated the sum of UD heights by variable for each unique UD, i.e. $\sum z_{i1 \ldots in_j}$ where z_{i1} is UD height at observation 1 of UD *i* and *j* is an independent variable. We then contrasted the proportion of the total sums of UD heights ($\sum_{jn,in} \sum z_{i1 \ldots in_j}$) with the relative frequency of each habitat type to compare used vs. available proportions (**Figure 2.2**). For numerical variables, we inspected distributions of standardized coefficients from simple linear regression models fitted for each variable/individual combination. We used this information to inform our priority of covariates in candidate models.

Using a suite of potential covariates including quadratic terms for certain numeric variables (in order to model potentially non-linear relationships), we developed a series of candidate models and performed model selection using Akaike's Information Criterion as per Burnham & Anderson (2002). The response variable was log-transformed to improve normality; the link function therefore became $f(x) = \exp(x) / (1 + \exp(x))$. Candidate models were grouped into several categories (relative canopy closure, protective cover, forage potential, terrain, and disturbance features) and variables were subsequently combined to form composite models estimated by maximum likelihood. Models were inspected for multicollinearity using variance inflation factors (VIF); in cases where VIF was greater than 7 we iteratively removed the variable responsible for the largest value and re-estimated the model until all VIF values were below 7. The best approximating model was subsequently re-estimated by restricted maximum likelihood (REML). We used Monte Carle methods to iteratively simulate data from a normal distribution based on variable means and standard deviations, and subsequently re-estimate model parameters (n=5000) in order to assess model fit. Residuals of both fixed and random effects were inspected for normality and homoscedasticity of variances.

RESULTS

3.1 Spatial Extent of Migration

The total surface beneath the 99% probability contours of estimated BBMMs ranged from 79 km^2 to 2,378 km^2 ($\bar{Y}$ = 728.5 km^2, $s_{\bar{Y}}$ = 74.6) (**Appendix II**). Spring home ranges were smallest among the Assinica herd, followed by the Nottaway and the Témiscamie herds (**Figure 2.3**). Maximum likelihood estimates of the Brownian motion variance (σ_1^2) ranged from 0.5 to 27.9 ($\bar{Y}$ = 11.5, $s_{\bar{Y}}$ = 0.55), and mean estimates of the location errors (σ_2^2) ranged from 15.3 to 34.7 m ($\bar{Y}$ = 22.82, $s_{\bar{Y}}$ = 0.44). Eleven out of the 53 spring dispersal trajectories (20.8 %) had greater than 3 consecutive missing relocations and were therefore split into two separate BBMMs that were subsequently joined based on temporally-weighted mean pixel values.

3.2 Migration Route Fidelity

Interannual overlap in 99% home range polygons was minimal overall between pairs of years (**Figure 2.4**); bootstrap estimates of the median POL were 11.52 +/- 4.8 % for 2004/2005 (n=17), and 6.74 +/- 4.44 % for 2005/2006 (n=20) (**Table 2.2**). This being said, calving site (terminus) locations were 23.5 km closer on average between years than were late winter (onset) locations (t_{36}=2.806, p=0.004) (**Table 2.3**). Furthermore, the median interannual distance between calving locations was minimal at 5.3 km (CI_{95}: 0, 23.8 km) for 2004/2005 and 10.9 km (CI_{95}: 4.9, 24.5 km) for 2005/2006 (**Figure 2.5**). Given the relatively vast areas covered by animals during spring dispersal, this indicates that boreal caribou of northern Quebec do exhibit fidelity to traditional calving site locations, if not to spring travel routes themselves.

3.3 Dispersal Characteristics

3.3.1 Directionality

There was no evidence of a predominant direction in spring dispersal movements, whether by year, herd, or population-at-large (α = 330.9° (ESE), ρ = 0.12, σ^2 = 0.99, $D^*(\alpha)$ = 0.352, p > 0.1) (**Figure 2.6**). However, examination of turning angle distributions revealed conclusive directionality at the individual level (α = -16.7°, ρ = 0.64, σ^2 = 0.59, $D^*(\alpha)$ = 2.93, p < 0.001). Mean distance-weighted turning angles approximated a Von Mises distribution with maximum likelihood estimates κ = 2.07 and μ = -16.4° +/- 12.52° (**Figure 2.7**).

3.3.2 Path Tortuosity

Monte Carlo simulations revealed that estimations of the straightness index (*SI*) by randomization were positively biased and proportional to the amount of missed relocations in individual datasets (**Figure 2.8**). Estimations based on spring dispersal paths missing more than 17% of total observation time were outside the 95% confidence intervals of the true value. This resulted in bias corrections to estimations of *SI* that ranged from 0 to -0.02. Resulting bias-corrected estimates of the straightness index (*SI*) ranged from $9.5e^{-3}$ to 0.48; these values were subsequently scaled from 0 to 1 (i.e. divided by the maximum value) for interpretation purposes.

A likelihood ratio test determined that inclusion of a random component for individual was warranted ($L = 3.95$, $p < 0.05$). Linear mixed effects regression revealed that orientation efficiency, or linearity, of spring dispersal movements decreased with increasing proximity to high density road networks ($L = 16.13$, $p < 0.01$). In other words, movements of caribou in closer proximity to highly developed road networks were more likely to be interpreted as random, where animals retrace their steps ad nauseam (high path tortuosity) without actually traveling very far over the course of spring dispersal (as SI and net displacement were highly correlated based on Spearman's rank correlation: rho = 0.92). When a quadratic term was added to improve model fit (lower AIC), the resulting fitted curve implied the strongest effect within a 30 km threshold distance of highly roaded zones (**Figure 2.9**). The fitted model equation for fixed effects was as follows, where y is SI and x is the distance from the probability-weighted UD centroid to the nearest location where road density met or exceeded 0.5 km/km^2:

$$y = 3.03\text{ e-}2 + x\,(5.94\text{ e-}3) + x\,(-3.78\text{ e-}5)$$

3.4 Habitat Selection

3.4.1 Scale of Measure (Anthropogenic Variables)

Using 2-dimensional optimization, the `ruf.fit` algorithm consistently converged on a spatial smoothness parameter (θ_2) of 0.5, which is equivalent to an exponential model in the Matérn family (Hoeting et al. 2006). Corresponding estimates of the spatial range (θ_2) were identically distributed for both road and cutblock density models and these varied from 50 to 753 metres with a strong mean at 372.5 m.

Based on t-tests of standardized RUF coefficients (grouped by spatial scale of measure), the probability of caribou occurrence was negatively associated with road density at spatial scales of up to 15 km (t = -1.99, df = 51, $p < 0.05$). The same relationship held true for cutblock density at spatial scales of up to 10 km (t = -2.2, df = 43, $p < 0.05$) (**Table 2.4**). However, in order to optimize the trade-off between sample size and effect size (response uniformity), we chose road and cutblock density measured within a 5-km circular radius as covariates for future model selection (**Figures 2.10** & **2.11**).

3.4.2 Model Selection

Log-likelihood tests of models estimated by REML supported the inclusion of a random intercept for both id (individual) and year nested within id (L = 1334.4, $p < 0.0001$). This being said, a model with the same fixed effects but only one random intercept for UD was more parsimonious (Δ AIC = 2.92); we therefore chose the latter of the two. These results suggest that with so little overlap in dispersal routes between years, UDs from the same individual but different years were independent.

Fixed effects that were not retained in the final model included categorical variables for 0-5 year and 6-20 year cutblocks, as well as dense mixed and broadleaf forest; the latter were likely too scarce to contribute much to the explained variation. Barren and exposed bedrock cover types were also rare and therefore not retained in the best approximating model. The most common habitat category, open coniferous forest, was strongly collinear with numerous other variables; this type was therefore excluded, although it did appear to be mildly selected on the whole. All of the anthropogenic variables (road and cutblock density, road surface) elicited variance inflation factors below 7 except the quadratic term for road density ("rdense05"), which naturally is collinear with its root. Orthogonal polynomials circumvent such issues but these measures are used more for computational efficiency than for obtaining statistical independence as such (Wishart & Metakides 1953).

Parameters of the best approximating model (based on AIC) are listed in **(Table 2.5)**. The observed sum of squared residuals (SSE) fell well outside the 95% confidence limits of the simulated Monte Carlo distribution; we therefore deferred to bootstrap methods to obtain better precision in parameter estimates (Efron 1987). Inspection of observed versus fitted values indicated that while caribou on the whole did select certain features while avoiding others, the amount of variation explained by the best approximating model was fairly minimal overall (Spearman's rho = 0.290). Despite the influence of numerous factors, no variable had a dramatic impact on the probability of occurrence. In terms of relative importance based on fitted curves, lichen woodlands and herb-dominated wetlands were most strongly selected by caribou during spring dispersal. Shrub- and tree-dominated wetlands were also somewhat strongly selected, which indicates that wetland environments are relatively important habitats during spring dispersal. Low and tall shrub-dominated environments were selected to a lesser degree, presumably for the fresh browse they would begin to offer at this time of year. Sparse coniferous forest was mildly selected, and response to open mixed and deciduous forest was benign. In contrast, 6-20 year old fires were avoided by caribou as were 0-5 year old fires, though to a much lesser degree. Dense coniferous forest was likewise avoided during spring dispersal.

In general, animals avoided higher altitudes and selected areas in closer proximity to water than what was otherwise available to them during the course of spring dispersal (as measured within the boundaries of their respective 99% BBMM probability contours). Shorelines are an important form of escape habitat for woodland caribou (Bergerud 1985). In terms of anthropogenic disturbances, caribou avoided road surfaces during spring dispersal as well as zones characterized by higher road and cutblock densities.

Examination of individually fitted regression coefficients revealed considerable non-linearity in response to changing importance of three variables: a) proximity to water ("h20prox"), b) cutblock density ("cutdense05"), and c) road density ("rdense05"). For example, animals dispersing within 300-500m of waterways on average tended to spend greater amounts of time in closer proximity to the shoreline; however beyond 500m the response at the population level was more-or-less neutral (**Figure 2.12**). We tested for a random coefficient for this variable and found it to be highly significant ($L = 1175.4$, $p < 1e-4$). We subsequently observed that inclusion of the random coefficient for h20prox simultaneously altered the predicted response to cutblock density from mildly negative to extremely positive. Inspection of individual model responses to the cutdense05 variable revealed that individuals dispersing within 5 km of relatively low cutblock densities appeared to more unanimously space away from roads, whereas individuals dispersing in more intensely harvested areas did not appear to respond as strongly (**Figure 2.13**). The scarcity of observations at the tail end of this distribution may partially explain why the quadratic term in the new model projected substantial increases in the probability of occurrence at high cutblock densities, when in actual fact observations were scarce at higher densities because no caribou were found to occur there. Although we tried to allow a random coefficient to alleviate this imbalance the model would not converge.

Functional response to variations in road density elicited a signal altogether similar to that of cutblock density (**Figure 2.14**), although we were able to substantially improve the model by adding this variable to h20prox as a second random coefficient ($L = 693.3$, $p < 1e-4$). This consequently corrected the aberrant positive response to cutblock density. Two UDs elicited excessively negative responses in individual regression models, UD 48 for cutblock density ($\beta = -174.3$) and UD 34 for road density ($\beta = -72.1$), which we corrected in both cases by making all within-UD observations for these variables non-positive.

DISCUSSION

4.1 Fidelity and directionality

The degree to which caribou exhibit interannual fidelity to certain parts of their range has been a matter of interest for many years (Brown & Theberge 1985; Cumming & Beange 1987; Gunn 2000; Schaefer et al. 2000a; Rettie & Messier 2001; Hinkes et al. 2005; Wittmer et al. 2006; Metsaranta 2008; Faille et al. 2010; Tracz et al. 2010). Generally speaking, the more predictable an animal's movements over space and time, the easier it is to manage from a conservation standpoint. In describing the migratory patterns of woodland caribou, some authors have found little consistency in travel routes used (Darby & Pruitt 1984; Cumming & Beange 1987; Stuart-Smith et al. 1997), whereas others have identified recurring tendencies (Stardom 1977; Edmonds & Bloomfield 1984; Mahoney & Schaefer 2002; Brown et al. 2003; Ferguson & Elkie 2004a). Our research in northern Quebec reveals that while individual caribou do exhibit directional movements during spring dispersal (a form of one-way migration), there does not appear to be any predominant direction of travel at this time. This is likely due in part to the nature of the landscape, for although the probability of occurrence was marginally higher at lower elevations, topographic relief of any importance is fairly uncommon in our study area. This may also serve to explain why we observed little interannual overlap in spring dispersal routes (median = 8.5 %). In regions such as ours, boreal caribou may have a selective advantage over caribou living in mountainous regions, as the latter are generally constrained to valley bottoms during migration due to the high energetic costs of alternative routes (Apps et al. 2001; Mahoney & Schaefer 2002; Saher 2005). At an individual level, by alternating their dispersal patterns from one year to the next, boreal caribou are considerably less predictable, so they may incur a lower risk of predation (Hebblewhite & Merrill 2007). At the population level, the relatively accessible terrain ensures a multitude of route options and allows boreal caribou to optimize their antipredator spacing out strategy. This being said, since dispersal was directional on the whole (quasi-linear), it may largely be seen as a function of where the dispersal event began (i.e. late winter range) and where the dispersal event ended (i.e. calving site). As has been documented elsewhere (Shoesmith & Storey 1977; Darby & Pruitt 1984; Edmonds 1988; Stuart-Smith et al. 1997; Brown et al. 2000; Bergerud 2006), caribou in our study area showed little interannual fidelity to wintering areas (Bergeron & Drapeau, unpublished data), although they did show considerable interannual fidelity to calving site locations (median interannual distance = 8.1 km for calving vs. 33.2 km for late winter). As a behavioural trait, site fidelity may be partially attributed to individual experience and memory (Gunn & Miller 1986; Metsaranta 2008; Van Moorter et al. 2009), which in the context of landscape alteration could have undesirable consequences for individual fitness (Wittmer et al. 2006; Faille et al. 2010). For example, highly disturbed landscapes may mean reduced travel route options for caribou and thus increased fidelity to what routes do remain functionally available, rendering seasonal movements more predictable and thus caribou more vulnerable to predation. In our study area, it would be of particular interest to examine travel route fidelity during late fall/early winter movements of woodland caribou when they are more gregarious.

4.2 Probabilistic Framework

Under normal circumstances, animals occupying heterogeneous landscapes are known to alternate between intensive (area-concentrated) and extensive (ranging and relocation) search modes (Barraquand & Benhamou 2008). Various methods have been developed for identifying such shifts in movement behaviour (Benhamou 1992; Johnson et al. 2002a; Fauchald & Tverra 2003; Morales et al. 2004; Jonsen et al. 2005; Nams 2005; Jerde et al. 2006), perhaps the most intuitive of which consists of contrasting zones of high vs. low probability along an animal's trajectory based on a

Brownian bridge movement model (Sawyer et al. 2009). We did observe more intensively used neighbourhoods along spring dispersal paths presumed to coincide with higher quality habitat, and we recognize that in our case the RSPF is a measure of variables influencing this pattern. However, we agree with Sawyer et al. (2009) that the conservation of stopover sites for rest and foraging is likely more important than that of movement corridors on the condition that there are no anthropogenic barriers to dispersal.

4.3 Functional Responses

There are likely two elements responsible for the observed functional response to variations in road and cutblock densities. One is bias due to a paucity of observations where densities are greater than zero, which may lead to erroneous conclusions that there is a strong avoidance of anthropogenic features when in fact there is none (Type I error). The second element is behavioural and context-dependent: clearly caribou have an aversion to roads, whether due to noise, predation risk, or a combination of factors (Dyer et al. 2001). During spring dispersion, caribou in less roaded areas can more easily avoid roads because there are less of them; in such cases roads may have a minimal impact on dispersal itself, and the avoidance effect is measurable. However caribou in highly roaded areas may be severely inhibited by these features, as examination of path tortuosity has revealed. In these cases the avoidance effect may appear weak or insignificant (Type II error) since animals are in some respects confined and therefore unable to space away further. Alternatively, if unable to cross they may disperse in a parallel direction or pass long periods of time in proximity to roads, thereby causing the model to infer selection when in fact there is avoidance. Movement models that take barrier effects into account may better address this particular problem (Benhamou & Cornélis 2010). In general, however, our experience demonstrates that it is essential to examine the mechanisms behind the inferences prior to adopting a given model.

4.4 Anthropogenic disturbance

Caribou may respond in different ways to habitat alteration and disturbance, which may in turn influence population fitness. For example, increasing movement rates and reducing fidelity to traditional ranges may increase encounters with predators and/or displace animals into less optimal habitats (Nellemann & Cameron 1998; Courtois 2003; Courtois et al. 2007; Faille et al. 2010; Sebbane et al. 2011). Indeed, Johnson et al. (2002b) found that short-term occupancy of risk-prone cover types led to highest risk of predation during interpatch movements of mountain caribou. On the other hand, anthropogenic landscape features and associated disturbances may impose a barrier effect which alters or inhibits dispersal of woodland caribou (Curatolo & Murphy 1986; Smith et al. 2000; Dyer et al. 2002; Mahoney & Schaefer 2002; Weclaw & Hudson 2004; *but see* Reimers et al. 2007). This may cause reductions in home range size, which in turn may compromise the ability of populations to space out from predators (Bergerud 1990; Seip 1991b), potentially resulting in an ecological trap (Courbin et al. 2009).

We did not specifically examine whether caribou were less likely to cross roads than expected, although between late winter and calving Dyer et al. (2002) reported an approximate 1:4 ratio among woodland caribou of Alberta and considered roads to represent semi-permeable barriers to dispersal. Our results indicate that caribou dispersing in spatial proximity to highly roaded zones (> 0.5 km/km^2) may be functionally inhibited by such features, and that this effect may be most pronounced within 30 km of such zones on average. Considering that the theoretical goal of spring dispersal is to space away from conspecifics to avoid predation (Bergerud et al. 1990), and given that predation mortality is higher in proximity to roads (James & Stuart-Smith 2000), this lends credence to the notion that caribou choosing to remain in areas encroached upon by industrial development may be the ultimate victims of an ecological trap (Courbin et al. 2009; Bowman et al. 2010; Faille et al. 2010).

It may be argued that due to the confounding influence of forest cutovers, road density may not entirely account for the trend in path tortuosity observed. We concur that road density is a proxy for development and associated disturbance on the landscape. However, although road density and cutover density were marginally correlated (Spearman's rho = 0.46), contrary to our expectation they were not collinear (Variance Inflation Factors = 1.5); this is likely because road developments often precede harvesting on the landscape, so higher road densities are not always associated with higher cutblock densities. Further investigation is needed in order to better elucidate the relationship between road density and other landscape variables such as forest harvesting and fire as they influence woodland caribou dispersal behaviour. In addition, a better understanding of the relative influence of road class (width, grade) and traffic levels would greatly improve our ability to forecast the likelihood of success of proposed mitigation measures.

4.5 Habitat Selection

To our knowledge, this is the first time a BBMM has been used to infer habitat selection at the scale of the seasonal home range (3rd order, Johnson 1980). Horne (2007) demonstrated the use of the BBMM to infer resource selection at highway crossing locations by one female black bear in northern Idaho, yet thus far BBMMs have mainly been used to estimate individual home ranges (Bullard 1991; Horne 2005; Huck et al. 2008) and/or population-level migration routes (Horne et al. 2007; Sawyer et al. 2009; White et al. 2010). Furthermore, very few studies have explicitly quantified and characterized the migratory behaviour and dispersal patterns of forest-dwelling woodland caribou (Ferguson & Elkie 2004b; Saher & Schmiegelow 2005). Numerous authors have identified a spring season, however, in analyses of seasonal resource selection, in which case results are likely to reflect at least some portion of the active dispersal period. Hins et al. (2009), for example, studied spring habitat selection by woodland caribou in the Saguenay-Lac St-Jean region of Quebec using compositional analysis. Among their findings was that caribou selected open lichen woodlands and avoided regenerating stands (0-5 years old). Using Resource Selection Functions (RSF, Manly et al. 2002), Fauteux & St-Laurent (2009) made the same conclusions for spring habitat selection of caribou in Quebec's Côte-Nord region. These results concur with our findings for spring movements of caribou in northern Quebec and suggest that lichens continue to be an important food source while spring vegetation is emerging.

Another finding reported by Hins et al. (2009) was selection for 6-20 year old cutblocks in spring, which is perhaps not surprising given the highly managed nature of their study area (~25% cutover); prior to green-up caribou are known to browse on the buds and twigs of white birch (*Betula papyrifera*), trembling aspen (*Populus tremuloides*), pin cherry (*Prunus pensylvanica*) and willow (*Salix* spp.) and such browse is generally readily accessible within regenerating stands (Simkin 1965). This may also explain mild selection of shrub-dominated environments by our study population. Likewise, Fauteux & St-Laurent (2009) reported selection of roads by caribou in spring, for roadsides are among the first locations to offer leafy browse at this time. In our case, however, cutblocks were not very common within BBMM UDs (~2% cutover) so neither categorical variable for cutblock (i.e. 0-5 and 6-20 years old) was retained in the final model; however caribou were found to select areas with lower densities of harvest blocks as well as roads. Although we did not measure traffic levels or distinguish between road classes, Leblond & St-Laurent (2010) observed avoidance of roads by woodland caribou during the spring period in

Quebec, with maximum effect at distances of 1.25 km for primary roads and 750m for secondary and tertiary roads.

We observed a disproportionate use of wetlands by caribou during spring dispersal. In terms of diet, wetland sedges may serve as a protein supplement for caribou (Skoog 1968; Klein 1982; Bradshaw et al. 1995), whose main winter food consists of protein-poor lichen (Klein 1990; Dannell et al. 1994). Bergerud (1972) found evergreen shrubs such as Labrador tea (*Ledum groenlandicum*), leatherleaf (*Chamaedaphne calyculata*), bog rosemary (*Andromeda glaucophylla*) and creeping snowberry (*Gaultheria hispidula*) to be important sources of food in early spring for Newfoundland caribou. Bog and fen complexes are frequently selected during calving as well (Brown et al. 1986; Hirai 1998; Lantin et al. 2003) and may provide a form of refuge from predators (Ferguson et al. 1988; Stuart-Smith et al. 1997). James (2004) demonstrated that by selecting lowland habitats caribou were able to spatially separate themselves from wolves and moose and sustain reduced mortality. Along similar lines, predator avoidance is likely what drives caribou in our study area to spend more time in closer proximity to shorelines than expected, as water is known to be a vital form of escape habitat (Bergerud 1985; Ferguson et al. 1988; Bergerud et al. 1990; Carr et al. 2007).

Dense coniferous forest was mildly avoided during spring dispersal, likely because such environments would offer little in the way of food and would be difficult to traverse for a dispersing animal. The same can be conjectured for 6-20 year old fires, as fallen trees and thick regeneration tend to characterize these sites.

Overall our results support that caribou space-use patterns during spring dispersal reflect trade-offs between optimizing forage opportunities while minimizing both predation risk and energetic costs. However our results corroborate with those of Ferguson & Elkie (2004b) in that at the population level, boreal caribou of northern Quebec did not show a particularly strong tendency to select or avoid particular features or habitat types during spring dispersal. Part of this is due to fairly strong variation in individual selection behaviour as witnessed by the significance of the random effects. Also, since habitat selection is hierarchical and multi-scalar (Wiens 1989; Johnson 2000), it is possible that we omitted some determinant factor acting at a scale beyond that of the effective dispersal range or at a finer resolution yet. For example a higher GPS fix interval may be combined with information on temporal changes in environmental conditions such as snow melt and vegetation emergence over the course of the spring dispersal period. Other aspects of interest include foraging energetics (Owen-Smith et al. 2010), correlated movements (Boyce et al. 2010), and even memory processes (Smouse et al. 2010; Van Moorter et al. 2010) of individual animals.

CONCLUSIONS

We examined the movement characteristics and space-use patterns of boreal woodland caribou during spring dispersal, a particularly critical period in the annual life cycle of this species-at-risk. Spring dispersal is an evolutionary trait permitting caribou populations to space out at low densities in order to reduce the risk of predation during the calving period when newborns are most vulnerable (Bergerud & Page 1987; Bergerud et al. 1990). Because they are also highly mobile at this time, knowledge of factors influencing spring dispersal behaviour of caribou may be particularly applicable when considering landscape connectivity.

Our results show that while travel paths were directional (quasi-linear) at the individual level, there was no predominant orientation to spring dispersal at the population level. Interannual overlap between travel routes was minimal, although animals did show fidelity to travel destinations (calving sites).

Based on evaluations of path tortuosity (1-*SI*), movements of caribou travelling within 30 km of highly roaded areas (> 0.5 km/km^2) were substantially more likely to be interpreted as random than oriented (Benhamou 1992), indicating that roads may inhibit the functional dispersal of woodland caribou. This has profound implications for the survival of caribou populations if it compromises their ability to space out from each other and thus reduce detection by predators (Bergerud & Page 1987; Seip 1991b; James 2004). Gray wolves and black bears are by far the most important predators of woodland caribou and both are positively associated with roads and cutover environments in spring (Bergerud 1988; Schwartz & Franzmann 1991; Thomas 1995; Rettie & Messier 1998; James & Stuart-Smith 2000; James 2004; Brodeur et al. 2008; Courbin et al. 2009; Bastille-Rousseau et al. 2010); caribou unable to disperse away from such features may therefore be victims of an ecological trap, which could have important consequences at the population level (Sutherland 1996).

We used a Brownian bridge movement model (BBMM) to quantify space use and estimate habitat selection by female woodland caribou during spring dispersal in northern Quebec. Estimates of the BBMM explicitly incorporate uncertainty between consecutive locations based on the animal's mobility and the associated GPS location error (Frair et al. 2010); they are therefore particularly suited to revealing fine-scale variation in the space use of mobile animals. Our results indicate that overall caribou select wetlands and lichen uplands during spring dispersal and are less likely to occur in zones associated with higher road and cutblock densities. They may also favour shorelines as escape habitat providing they are reasonably accessible (e.g. within 500m). This being said, caribou did not appear to be as strongly selective during spring dispersal as they may be at other times of the year (Ferguson & Elkie 2004b).

5.1 Management Implications

Given that caribou showed little interannual fidelity to spring dispersal routes in our study area, we conclude that retention of fixed travel corridors may not be a particularly effective conservation strategy where the goal is to maintain connectivity between seasonal ranges of woodland caribou. It is worthwhile to note that connectivity is likely to decrease as landscapes become more disturbed, which may result in more predictable seasonal movements (and therefore higher fidelity to travel routes) by woodland caribou. However, this is not a solution in itself, since such conditions are likely to coincide with increased mortality and population declines (Environment Canada 2008). A more effective strategy would be to minimize harvesting in areas still occupied by caribou, and to invest considerable effort in the decommission and rehabilitation of forest roads, using temporary winter roads wherever possible and minimizing road densities as a general rule. Where harvesting is foreseen in zones occupied by caribou, we suggest localized small-scale interventions (e.g. partial or selective cutting) with permanent retention using temporary winter roads. In terms of habitat, our research supports that protection of wetland environments may be advantageous as a source of food and refuge habitat for caribou, particularly in the spring. Retention of habitats supporting terrestrial lichen growth is also essential as a key food source both during winter and spring (Klein 1982).

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FIGURES: ARTICLE 2

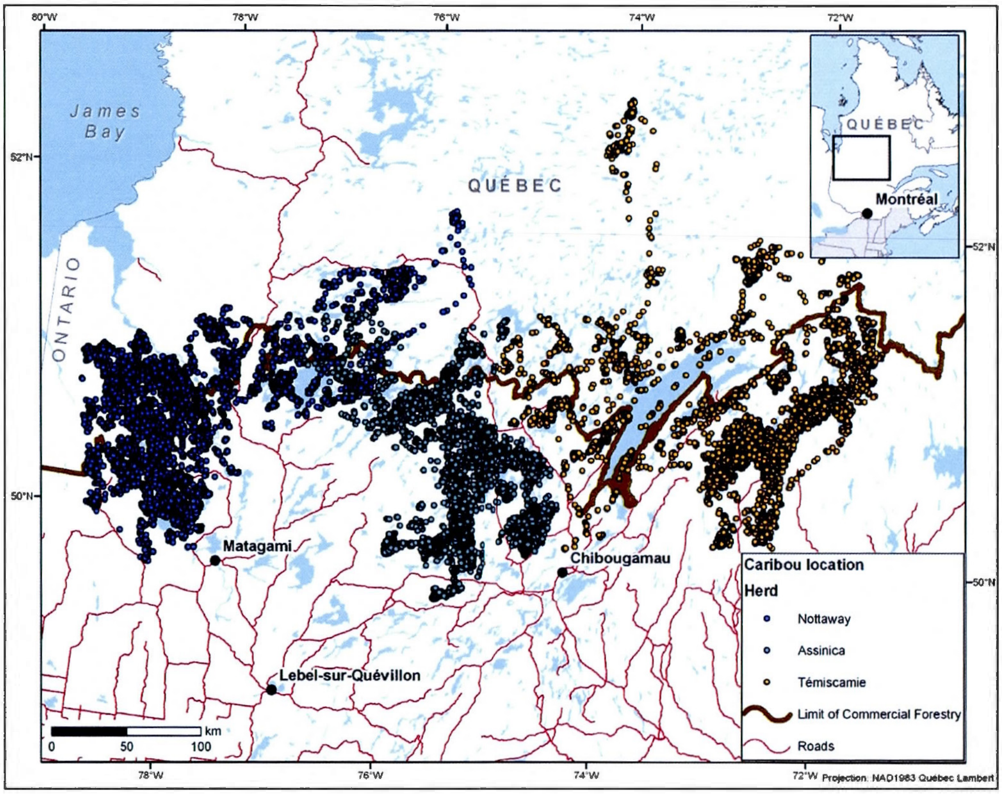

Figure 2.1: Location of study area in Northern Quebec. Points represent caribou locations obtained via GPS telemetry; purple denotes the Nottaway herd, blue the Assinica herd, and orange the Témiscamie herd. The brown line indicates the northern limit of commercial wood allocation.

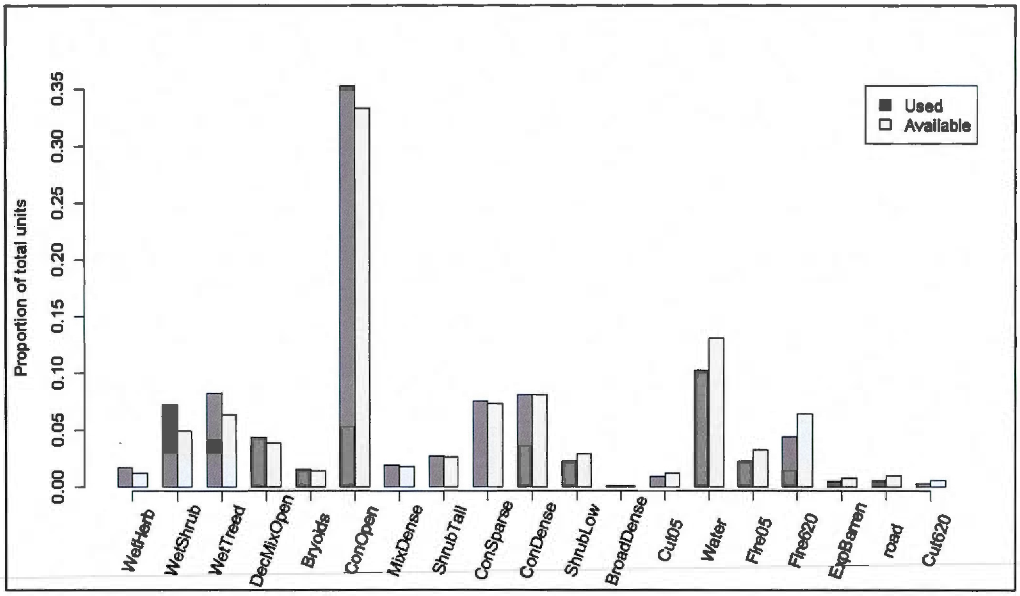

Figure 2.2: Comparison of used vs. available proportions of categorical habitat types found in study area. Proportions available are based on % area whereas proportions used are based on the mean of the cumulative sum of probability values (UD heights) falling within each habitat type.

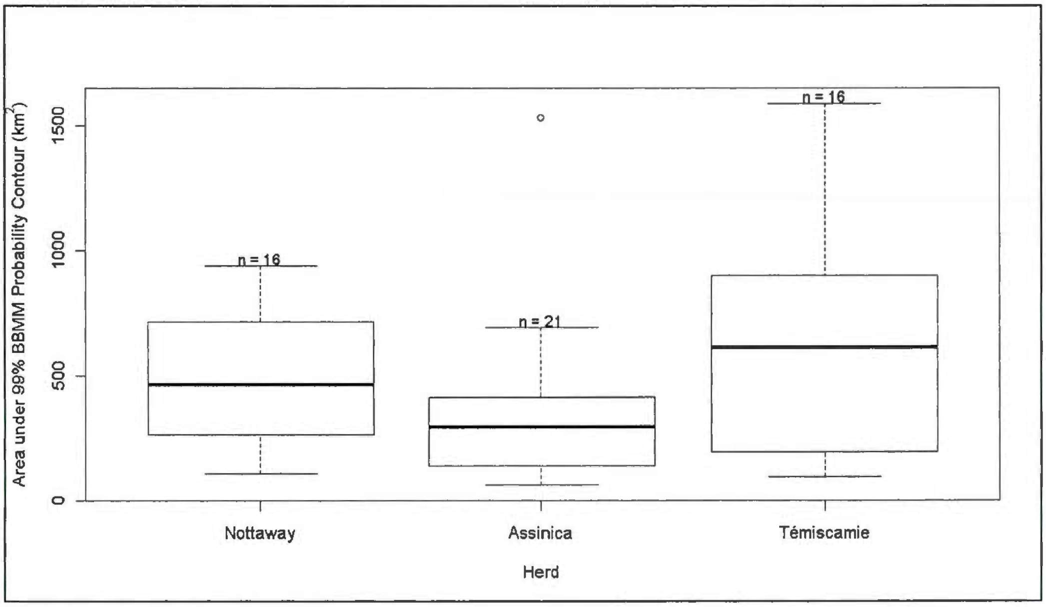

Figure 2.3: Extent (in km^2) of spring dispersal paths ("seasonal home range") for three populations in northern Quebec as estimated using a Brownian bridge movement model (BBMM).

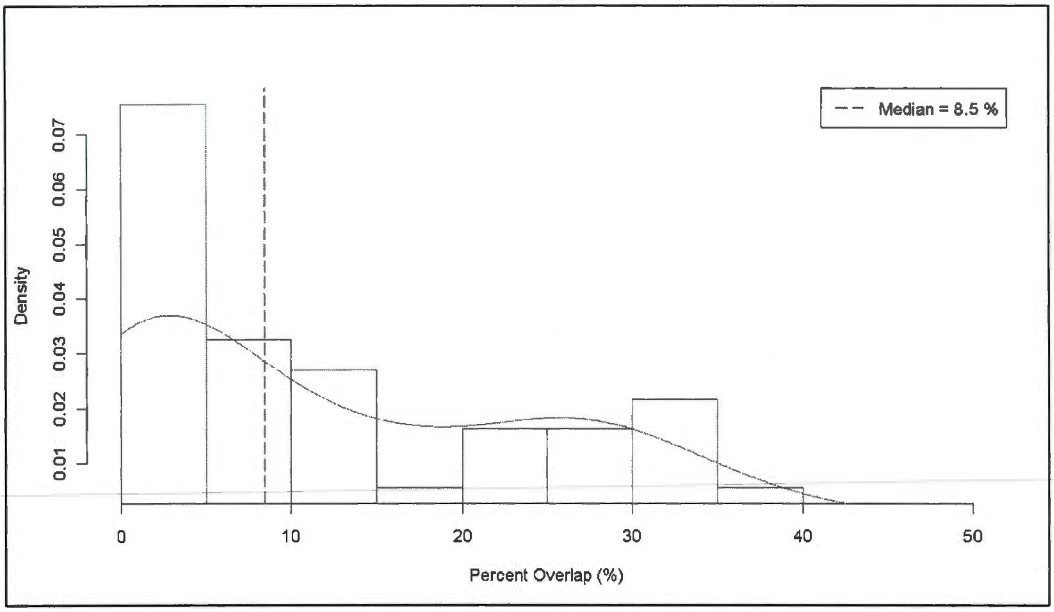

Figure 2.4: Interannual overlap in consecutive-year (2004/2005, 2005/2006) spring dispersal routes by individual woodland caribou in northern Quebec.

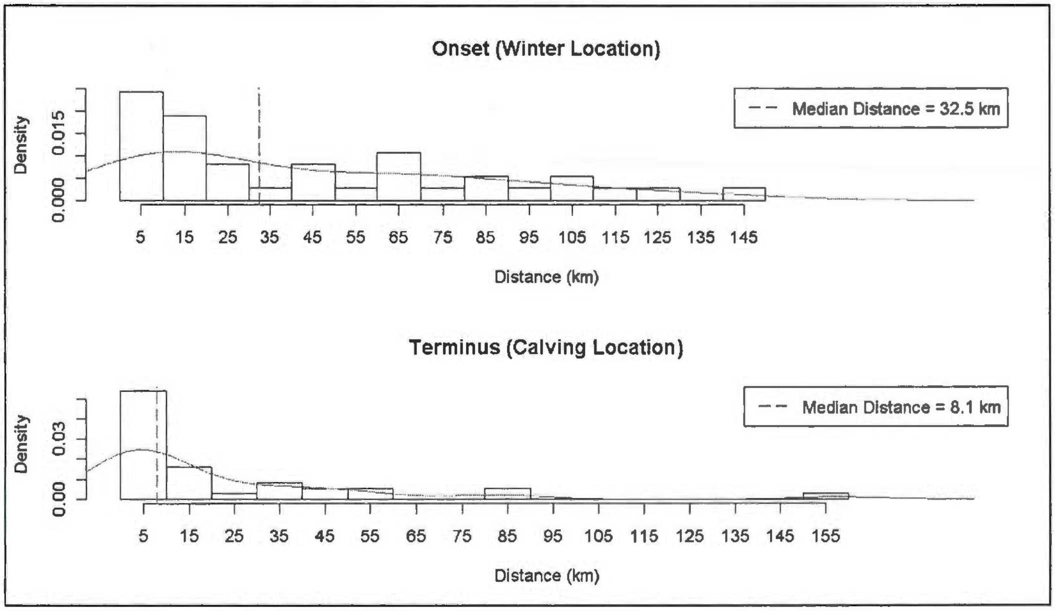

Figure 2.5: Interannual fidelity to winter vs. calving locations (2004/2005, 2005/2006) as measured at the onset and terminus of spring dispersal among woodland caribou in northern Quebec.

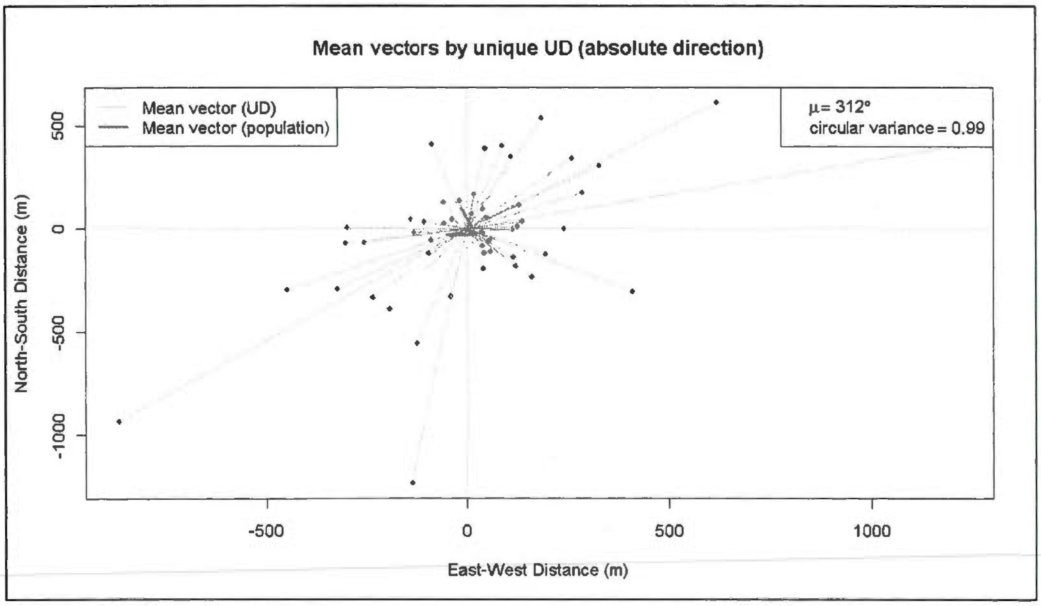

Figure 2.6: Absolute mean vectors corresponding with 53 unique cases of spring dispersal of woodland caribou in northern Quebec.

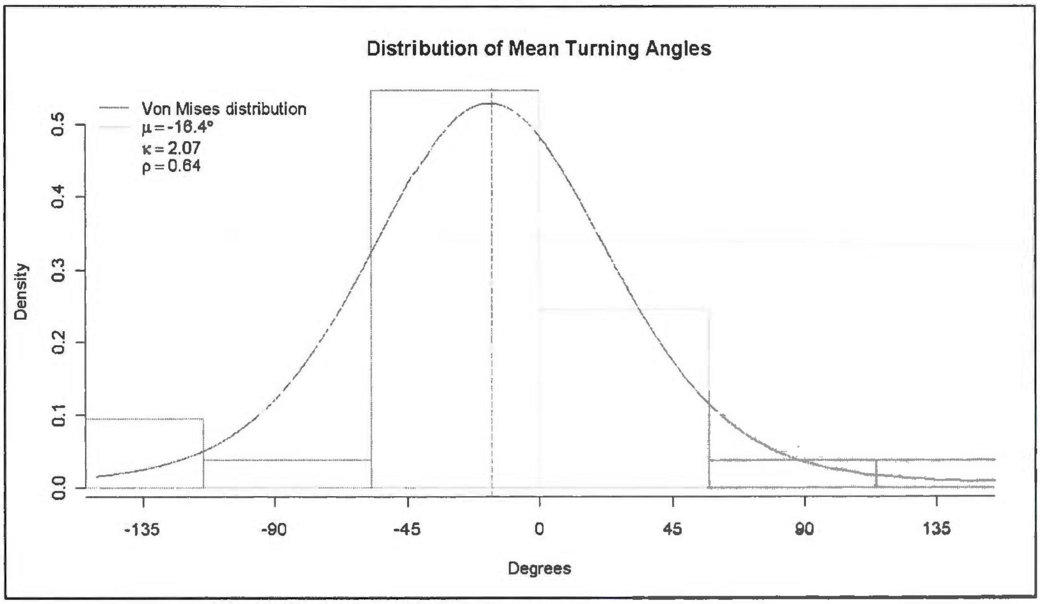

Figure 2.7: Distribution of mean vector turning angles for 53 cases of spring dispersal showing Von Mises curve and parameters estimated by maximum likelihood.

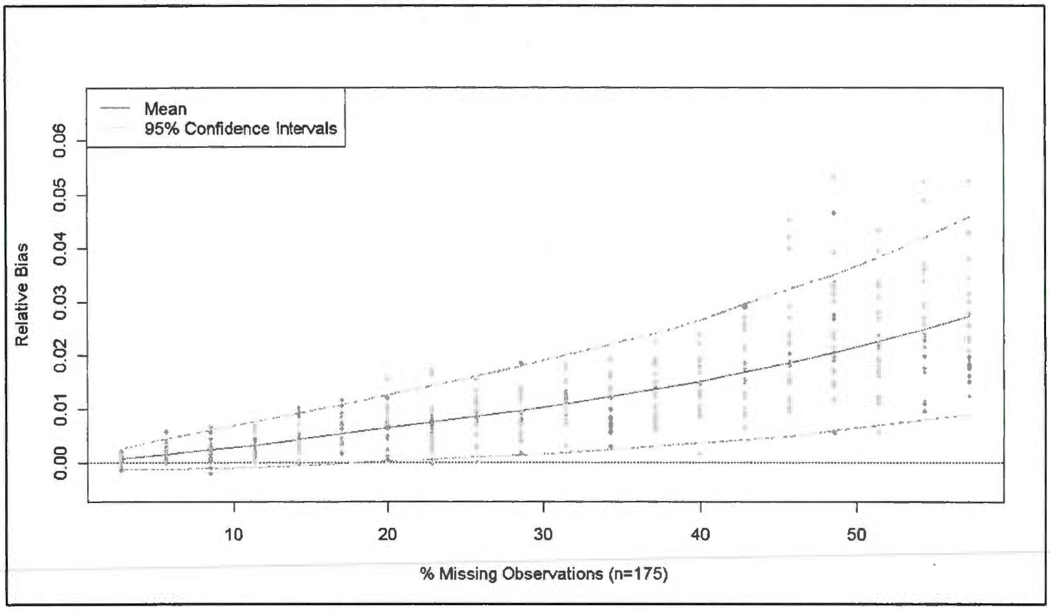

Figure 2.8: Effect of missing data on the estimation of the Straightness Index (*SI*). Estimations of *SI* were subsequently corrected by subtracting the mean bias from the estimated value.

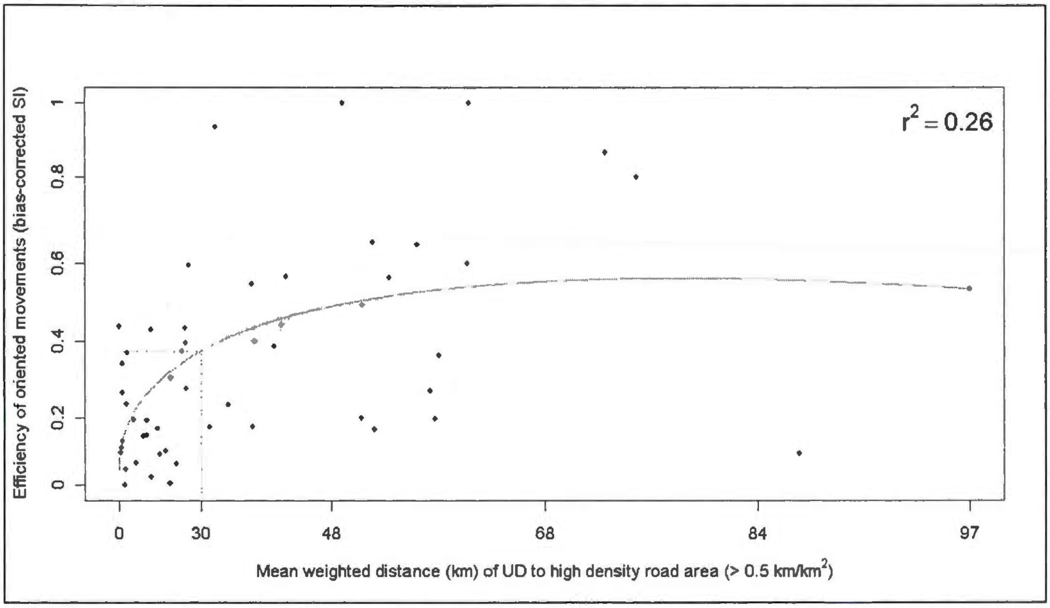

Figure 2.9: Effect of proximity to densely roaded zones on the spring dispersal of boreal caribou in northern Quebec as measured by the path tortuosity (1-*SI*). Movements of animals in close proximity to densely roaded zones tended toward randomness, whereas movements of caribou dispersing further away from roaded zones tended to be directional (quasi-linear). The inflection point at 30 km indicates a potential threshold distance within which movements are more strongly inhibited due to the semi-permeable effect of roads on caribou dispersal.

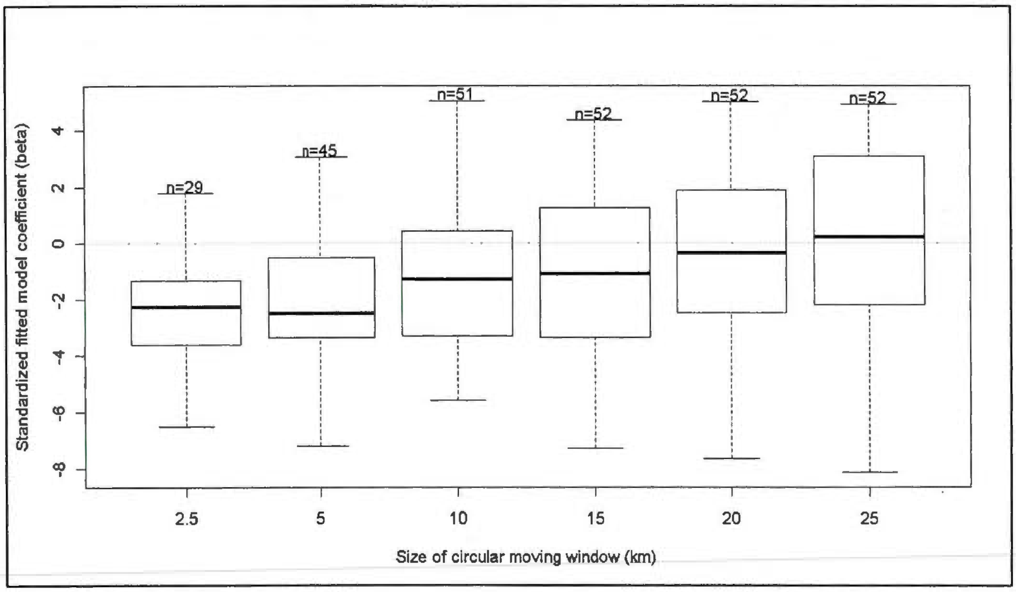

Figure 2.10: Boxplots of standardized regression coefficients from a series of individually-fitted RUFs modeling the probability of occurrence during spring dispersal as a function of **road density** measured at 6 spatial scales. Standard errors about the mean indicated a significant negative response to road densities measured at distances of up to 15 km.

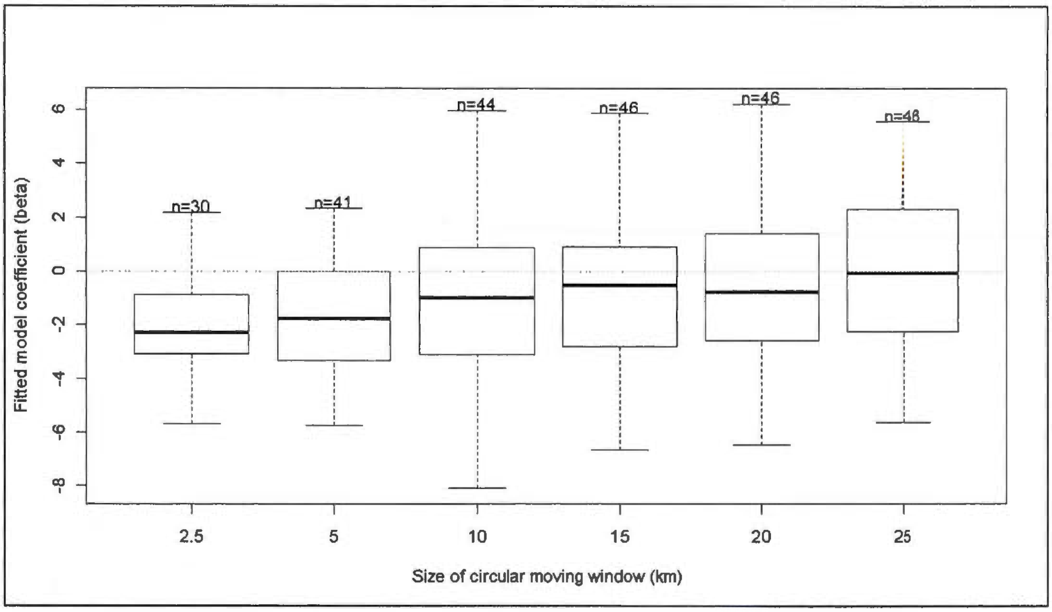

Figure 2.11: Boxplots of standardized regression coefficients from a series of individually-fitted RUFs modeling the probability of occurrence during spring dispersal as a function of **cutblock density** measured at 6 spatial scales. Standard errors about the mean indicated a significant negative response to cutblock densities measured at distances of up to 10 km.

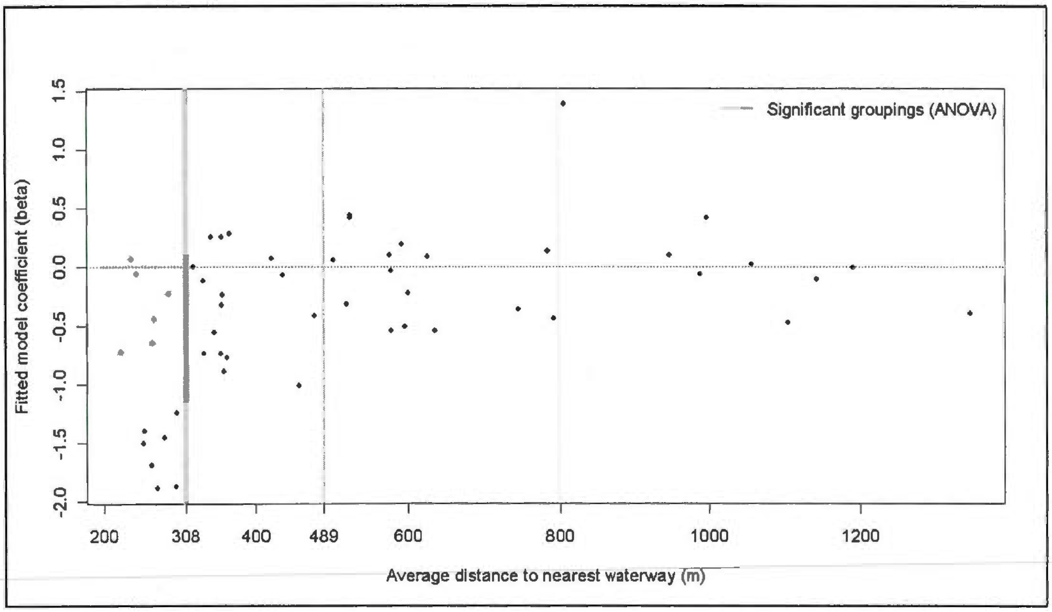

Figure 2.12: Functional response of individual caribou to varying distances to the nearest waterway. Grey lines indicate significant clusters estimated using recursive partitioning. Animals dispersing within 308m of a waterway were considerably more likely to favour shoreline locations. Animals dispersing within 489m were still likely to select shoreline locations, whereas beyond this distance the response at the population level is essentially negligible.

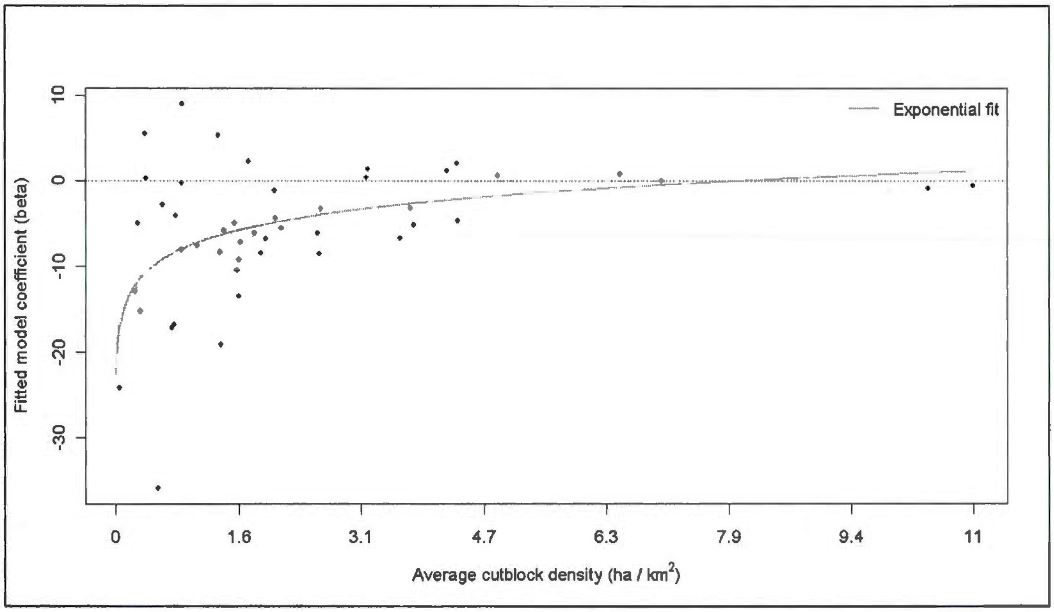

Figure 2.13: Functional response of individual caribou to varying cutblock densities. Where little harvesting had taken place within a 78.5 km^2 area, caribou showed a marked avoidance of these features. However the more abundant these features the less caribou appeared to respond positively or otherwise. The exponential curve demonstrates how allowing non-linear relationships may lead to erroneous conclusions (e.g. in this case that caribou select areas with high cutblock densities when it reality there were simply none observed beyond a given threshold).

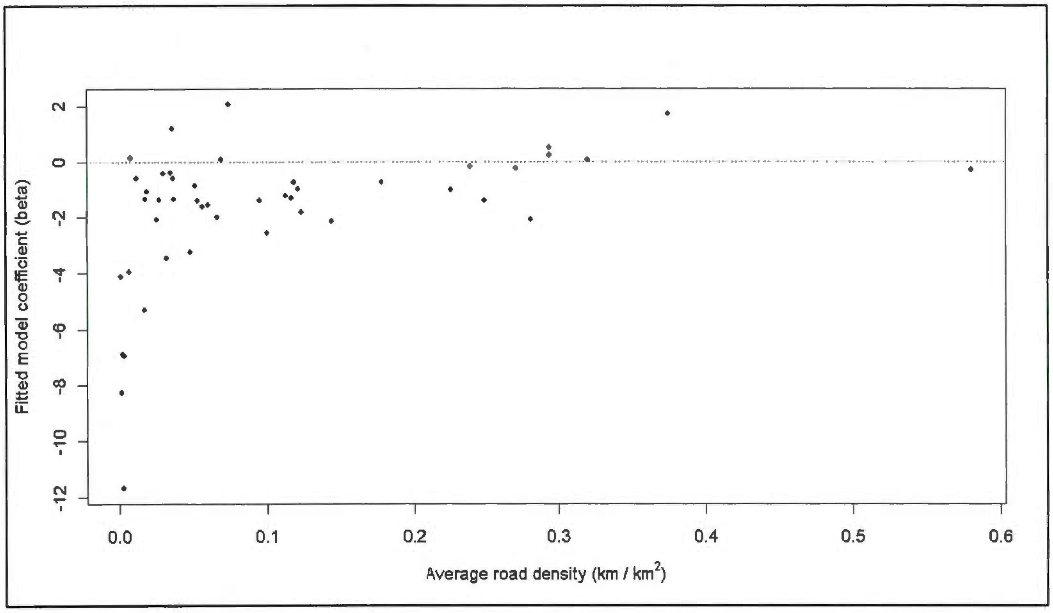

Figure 2.14: Functional response of individual caribou to varying road densities. Where few roads were measured within a 78.5 km^2 area, caribou showed a marked avoidance of these features. However the more abundant roads became, the less caribou were able to strongly avoid them.

TABLES: ARTICLE 2

Table 2.1: Summary of categorical habitat types and their relative abundances within 99% probability contours of 53 different utilization distributions estimated during spring dispersal using a Brownian bridge movement model.

Variable Name	**Description**	**Area** (km^2)	**Relative abundance**
ConOpen	Open coniferous forest	10482	0.332
Water	Open water / water bodies	4200	0.133
ConDense	Dense coniferous forest	2485	0.079
ConSparse	Sparse coniferous forest	2279	0.072
Fire620	Fire (6-20 years old)	2103	0.067
WetTreed	Treed wetland	1878	0.059
WetShrub	Shrub-dominated wetland	1591	0.050
DecMixOpen	Open deciduous or mixed forest	1196	0.038
Fire05	Fire (0-5 years old)	1172	0.037
ShrubLow	Low shrub dominated	849	0.027
ShrubTall	Tall shrub dominated	836	0.026
MixDense	Dense mixed forest	543	0.017
Bryoids	Lichen woodland	472	0.015
Cut05	Cutblock (0-5 years old)	380	0.012
WetHerb	Herb-dominated wetland	353	0.011
road	Road surface	334	0.011
ExpBarren	Barren / exposed bedrock	215	0.007
Cut620	Cutblock (6-20 years old)	203	0.006
BroadDense	Dense deciduous forest	35	0.001

Table 2.2: Bootstrap estimates of median percent overlap between spring dispersal BBMMs by unique individual for two pairs of years. Standard errors about the estimates are provided along with lower and upper 95% confidence intervals.

Year	n	Lower 95	Median POL (%)	Upper 95	S.E.
04/05	17	4.77	11.52	22.23	4.80
05/06	20	1.15	6.74	19.07	4.44

Table 2.3: Bootstrap estimates of median Euclidean distances (km) separating departure (winter) and arrival (calving) locations of spring dispersal events by unique individual for two pairs of years. Standard errors about the estimates are provided along with lower and upper 95% confidence intervals.

Season	Year	n	Lower 95	Median distance	S.E.	Upper 95
Winter	04/05	17	12.88	34.41	16.59	67.60
Winter	05/06	20	12.54	34.79	16.95	74.32
Calving	04/05	17	0.40	5.26	6.65	23.77
Calving	05/06	20	4.89	10.93	4.95	24.52

Table 2.4: Bootstrap estimates of the means of standardized beta coefficients derived from individual RUF models. Regression models included Matérn spatial covariates for range (θ_1) and smoothness (θ_2) and regressed the probability of caribou occurrence against road and cutblock density measured at six different spatial scales (i.e. within a circular window of 2.5, 5, 10, 15, 20, and 25 km centered on each pixel). Below are presented the bootstrap estimates of the mean coefficient for each variable and spatial scale along with respective standard errors and 95% confidence intervals.

Variable	Scale (km)	n	Lower 95	Mean	Upper 95	S.E.
Road density	**2.5**	29	-3.00	-2.41	-1.77	0.31
	5	45	-2.58	-1.99	-1.39	0.31
	10	51	-2.02	-1.26	-0.56	0.37
	15	52	-1.71	-0.83	-0.07	0.42
	20	52	-1.23	-0.39	0.46	0.43
	25	52	-1.00	-0.01	0.95	0.49
Cutblock density	**2.5**	30	-2.57	-1.90	-1.28	0.33
	5	41	-2.44	-1.76	-1.04	0.36
	10	44	-2.07	-1.08	-0.09	0.50
	15	46	-1.42	-0.60	0.23	0.43
	20	46	-1.48	-0.52	0.39	0.46
	25	46	-0.87	-0.04	0.76	0.40

Table 2.5: Parameters of the best approximating RSPF model. Quadratic terms are indicated with ".sq".

Variable	Beta	Std.Error
(Intercept)	-2.04	0.06
rdense05	-1.01	0.29
h20prox	-0.22	0.09
WetHerb	0.54	0.05
Bryoids	0.58	0.05
WetTreed	0.24	0.02
WetShrub	0.23	0.03
Fire620	-0.19	0.03
ConDense	-0.08	0.02
cutdense05	-1.26	0.34
cutdense05.sq	0.40	1.32
rdense05.sq	-0.42	0.10
topo.sq	0.01	0.01
ShrubTall	0.15	0.04
ConSparse	0.10	0.02
ShrubLow	0.15	0.04
road	-0.22	0.07
Fire05	-0.05	0.04
DecMixOpen	0.03	0.03
topo	-0.15	0.02
h20prox.sq	-0.04	0.01

CONCLUSION

General

Woodland caribou are especially vulnerable in the early spring due to winter weight loss and nutrient deficiencies caused by a prolonged lack of protein- and vitamin-rich foods (Chan-M^{c}Leod et al. 1999; Parker et al. 2005). Energetic demands are high for female caribou at this late stage of parturition leading into lactation (Moen & Boomer 2005). However they typically travel large distances from their wintering areas at this time in order to space away from conspecifics and thereby reduce the risk of predation (Bergerud et al. 1990).

Forest management has been shown to have a negative impact on caribou populations through habitat alteration, fragmentation and disturbance (Cumming 1992). Road networks may represent semi-permeable barriers to caribou dispersal (Dyer et al. 2002), and this behavioural avoidance alone could represent the most important form of functional habitat loss for this species-at-risk (Nellemann & Cameron 1998; Smith et al. 2000; Dyer et al. 2001; Weclaw & Hudson 2004). Increases in the proportion of early seral habitats on the landscape create favourable conditions for other ungulates and their predators (Vors & Boyce 2009), compromising the ability of caribou to spatially separate themselves from zones of unnaturally high predation risk (James 2004).

Temporal Variability in Seasonal Onset Behaviour

The life history strategies of free-ranging animals are closely tied to the bioclimatic environments in which they live. Animals such as woodland caribou exhibit marked trends in movement behaviour that reflect seasonal variation in the relative importance of foraging, reproduction, energy conservation, and predator avoidance. Consequently the study of animal space use patterns tends to be inherently seasonal in nature. The results of Chapter 1, however, indicate that the timing of seasonal events in the life cycle of animals may vary considerably from year to year and/or among individuals. This raises concern as to the prudence of adopting fixed time periods in the analysis of seasonal space use behaviour, for they may introduce unwanted bias in the form of observations that are not strictly representative of the biological activity under investigation. Chapter 1 demonstrates that dates determined by expert consensus and conventionally used to differentiate between seasonal periods may not always be representative of the biological phenomena for which they were intended. We therefore recommend that researchers consult the biological signal of their study population using quantitative methods in order to verify the accuracy of dates used. Furthermore, because of the inevitable behavioural variation exhibited by free-ranging animals, we recommend both an individual-based approach to delineating seasonal periods and a temporally variable observation window in order to reduce misclassification and therefore erroneous sources of variation.

Dispersal Behaviour

Dispersal movements of woodland caribou populations may appear oriented in nature or essentially random (Stuart-Smith et al. 1997; Ferguson & Elkie 2004a). Our examination of individual movement trajectories (Chapter 2) indicates that while spring dispersal movements were oriented for boreal caribou of northern Quebec, there was no predominant direction either at the herd or population levels. There was also negligible interannual overlap in travel routes used: locations corresponding with the onset of spring dispersal (i.e. winter ranges) shifted from year-to-year, although female caribou did exhibit fidelity to traditional calving locations (termini). The mean area of spring dispersal ranges was 730 km^2 and the mean net displacement of dispersal paths was 47 km.

Analysis of path tortuosity revealed that caribou dispersing within 30 km of highly roaded zones (>5 km/km^2) were substantially more likely to retrace their steps continuously with little net displacement over the course of the period. These paths appeared random in nature, whereas caribou dispersing at greater distances from roads were more likely to exhibit directed (quasi-linear) movements. This has profound implications for the survival of caribou populations if it compromises their ability to space out from each other and thus reduce detection by predators (Bergerud & Page 1987; Seip 1991b; James 2004). Gray wolves and black bears are by far the most important predators of woodland caribou and both are positively associated with roads and cutover environments in spring (Bergerud 1988; Schwartz & Franzmann 1991; Thomas 1995; Rettie & Messier 1998; James & Stuart-Smith 2000; James 2004; Courbin et al. 2009; Bastille-Rousseau et al. 2010); caribou unable to disperse away from such features may therefore be particularly vulnerable to predation, which could have important consequences for threatened populations (Sutherland 1996).

Habitat Selection

We used a Brownian bridge movement model (BBMM) to quantify space use and estimate habitat selection by female woodland caribou during spring dispersal in northern Quebec. Estimates of the BBMM explicitly incorporate uncertainty between consecutive locations based on the animal's mobility and the associated GPS location error (Frair et al. 2010); they are therefore particularly suited to revealing fine-scale variation in the space use of mobile animals. Our work (Chapter 2) indicates that overall caribou select wetlands and lichen uplands during spring dispersal and are less likely to occur in zones associated with higher road and cutblock densities. They may also favour shorelines as escape habitat providing they are reasonably accessible (e.g. within 500m). We conclude therefore that space-use patterns during spring dispersal appear to reflect trade-offs between optimizing forage opportunities while minimizing both predation risk and energetic costs. This being said, caribou did not appear to be as strongly selective during spring dispersal as they may be at other times of the year (Ferguson & Elkie 2004b).

Management Recommendations

Given that caribou showed little interannual fidelity to spring dispersal routes in our study area, we conclude that retention of fixed travel corridors may not be a particularly effective conservation strategy where the goal is to maintain connectivity between seasonal ranges of woodland caribou. Nevertheless, fidelity to travel routes may increase as landscapes become more disturbed; therefore we do not rule out the possibility that this could work in a different landscape context. We do contend, however, that a more effective strategy would be to strictly minimize harvesting in areas still occupied by caribou, and to invest considerable effort in the decommission and rehabilitation of forest roads, using temporary winter roads wherever possible and minimizing road densities as a general rule. Where harvesting is foreseen in zones occupied by woodland caribou we suggest localized small-scale interventions (e.g. partial or selective cutting) with permanent retention using temporary winter roads. Finally, in terms of habitat, our research supports that protection of wetland environments may be advantageous as a source of food and refuge habitat for caribou, particularly in the spring. Retention of habitats supporting terrestrial lichen growth is also essential as a key food source both during winter and spring (Klein 1982).

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APPENDIX I

APPENDIX I-1: Onset dates determined via individual-based recursive partitioning for the winter period in the years 2005 and 2006. Where available, estimated end dates and season lengths are also provided along with mean and maximum recorded movement rates within the period.

ID	Year	Season	Onset	Estimated Finish	Estimated Length (days)	Mean Movement Rate (km/day)	Maximum Movement Rate (km/day)
2002007	2005	winter	Feb-06	Apr-04	57	0.56	4.95
2003008	2005	winter	Jan-23	Apr-07	74	1.66	14.75
2003009	2005	winter	Jan-24	Apr-02	68	0.19	0.68
2003017	2005	winter	Jan-24	Apr-02	68	0.58	8.14
2003018	2005	winter	Jan-08	Mar-28	79	1.52	19.72
2004017	2005	winter	Jan-07	Mar-31	83	0.58	9.29
2004019	2005	winter	Jan-13	Mar-27	73	0.29	2.96
2004020	2005	winter	Feb-24	Apr-08	43	0.70	3.28
2004021	2005	winter	Jan-18	Apr-05	77	0.36	1.41
2004023	2005	winter	Feb-01	Apr-12	70	0.22	1.48
2003009	2006	winter	Jan-10	Mar-29	78	0.45	1.64
2003010	2006	winter	Jan-13	Mar-30	76	0.72	3.48
2003011	2006	winter	Jan-16	Apr-06	80	0.86	4.91
2003012	2006	winter	Jan-09	Mar-25	75	0.57	2.25
2003013	2006	winter	Jan-21	Mar-22	60	0.66	4.15
2003014	2006	winter	Feb-05	Apr-08	62	0.37	1.98
2003017	2006	winter	Jan-02	Mar-22	79	1.27	9.29
2003021	2006	winter	Jan-06	Mar-26	79	0.94	4.10
2004017	2006	winter	Jan-09	Mar-22	72	0.58	2.44
2004020	2006	winter	Jan-09	Mar-13	63	0.54	4.06
2004024	2006	winter	Jan-12	Mar-08	55	0.73	6.08
2005025	2006	winter	Feb-04	Apr-06	61	0.65	6.83
2005027	2006	winter	Jan-12	Mar-14	61	0.87	9.06
2005028	2006	winter	Jan-02	Mar-23	80	0.92	9.47
2005030	2006	winter	Jan-09	Apr-13	94	1.07	9.41
2003020	2006	winter	Dec-18				

APPENDIX I-2: Onset dates determined via individual-based recursive partitioning for the spring dispersal period in the year 2004. Estimated end dates and season lengths are also provided along with mean and maximum recorded movement rates within the period.

ID	Year	Season	Onset	Estimated Finish	Estimated Length (days)	Mean Movement Rate (km/day)	Maximum Movement Rate (km/day)
2002007	2004	spring	Apr-21	May-26	34	2.69	19.47
2003011	2004	spring	Apr-14	May-20	35	5.05	24.59
2003013	2004	spring	Apr-16	May-26	39	4.10	29.86
2003017	2004	spring	Apr-02	May-21	48	4.68	22.57
2003018	2004	spring	Apr-02	May-20	47	4.62	28.38
2003020	2004	spring	Apr-03	Jun-12	69	3.75	22.25
2003021	2004	spring	Apr-20	May-25	34	5.89	39.68
2004018	2004	spring	Apr-04	Jun-01	54	2.91	15.60
2004019	2004	spring	Apr-20	May-27	36	3.83	15.85
2004022	2004	spring	Apr-15	May-19	33	6.90	31.12
2004023	2004	spring	Apr-23	Jun-14	51	5.23	33.05
2004024	2004	spring	Apr-07	May-18	40	1.94	19.86

APPENDIX I-3: Onset dates determined via individual-based recursive partitioning for the spring dispersal period in the year 2005. Estimated end dates and season lengths are also provided along with mean and maximum recorded movement rates within the period.

ID	Year	Season	Onset	Estimated Finish	Estimated Length (days)	Mean Movement Rate (km/day)	Maximum Movement Rate (km/day)
2002007	2005	spring	Apr-05	May-24	48	2.38	9.22
2002008	2005	spring	Mar-28	May-30	62	3.61	32.73
2003008	2005	spring	Apr-08	May-28	49	6.73	36.49
2003009	2005	spring	Apr-03	May-23	49	2.70	14.72
2003010	2005	spring	Apr-06	May-19	42	2.77	18.40
2003011	2005	spring	Apr-17	May-30	42	3.92	28.98
2003012	2005	spring	Apr-05	May-23	47	3.47	21.01
2003013	2005	spring	Apr-07	Jun-09	62	4.69	30.96
2003014	2005	spring	Apr-03	May-29	55	4.02	54.62
2003017	2005	spring	Apr-03	May-07	33	6.18	30.58
2003018	2005	spring	Mar-29	May-17	48	3.94	23.52
2003021	2005	spring	Mar-31	May-20	49	4.27	26.61
2004017	2005	spring	Apr-01	May-22	50	4.29	26.11
2004018	2005	spring	Apr-02	May-18	45	2.51	12.65
2004019	2005	spring	Mar-28	May-16	48	3.07	25.66
2004020	2005	spring	Apr-09	May-28	48	4.84	27.28
2004021	2005	spring	Apr-06	May-16	39	3.13	14.10
2004023	2005	spring	Apr-13	May-26	42	2.44	16.21
2005025	2005	spring	Mar-17	Jun-02	76	4.04	31.60
2005027	2005	spring	Apr-05	May-26	50	2.64	14.51
2005028	2005	spring	Apr-02	May-21	48	3.19	19.07
2005030	2005	spring	Apr-13	May-31	47	4.27	33.22

APPENDIX I-4: Onset dates determined via individual-based recursive partitioning for the spring dispersal period in the year 2006. Where available, estimated end dates and season lengths are also provided along with mean and maximum recorded movement rates within the period.

ID	Year	Season	Onset	Estimated Finish	Estimated Length (days)	Mean Movement Rate (km/day)	Maximum Movement Rate (km/day)
2002007	2006	spring	Apr-15	May-22	36	3.07	13.78
2002008	2006	spring	Apr-12	May-28	45	6.25	38.54
2003008	2006	spring	Mar-31	May-24	53	6.00	34.61
2003009	2006	spring	Mar-30	May-16	46	1.73	17.21
2003010	2006	spring	Mar-31	May-27	56	2.82	17.00
2003012	2006	spring	Mar-26	May-27	61	3.22	16.75
2003013	2006	spring	Mar-23	May-11	48	3.22	29.15
2003017	2006	spring	Mar-23	May-29	66	3.93	23.26
2003018	2006	spring	Apr-01	May-22	50	3.47	12.94
2003021	2006	spring	Mar-27	May-14	47	4.38	35.72
2004017	2006	spring	Mar-23	May-13	50	4.56	30.55
2004020	2006	spring	Mar-14	May-31	77	3.51	23.56
2004023	2006	spring	Apr-09	May-15	35	6.20	24.64
2004024	2006	spring	Mar-09	May-12	63	1.61	6.98
2005025	2006	spring	Apr-07	May-30	52	4.82	46.76
2005027	2006	spring	Mar-15	Jun-03	79	2.11	15.62
2005028	2006	spring	Mar-24	May-31	67	4.06	22.97
2005029	2006	spring	Mar-28	May-25	57	5.54	26.41
2005030	2006	spring	Apr-14	May-24	39	5.11	36.44
2003011	2006	spring	Apr-06				
2003014	2006	spring	Apr-08				

APPENDIX I-5: Onset dates determined via individual-based recursive partitioning for the calving period in the year 2004. Estimated end dates and season lengths are also provided along with mean and maximum recorded movement rates within the period.

ID	Year	Season	Onset	Estimated Finish	Estimated Length (days)	Mean Movement Rate (km/day)	Maximum Movement Rate (km/day)
2002007	2004	calving	May-26	Jun-18	22	0.37	1.50
2003008	2004	calving	May-30	Jun-24	24	3.34	14.11
2003009	2004	calving	May-21	May-31	9	0.48	2.55
2003011	2004	calving	May-20	Jun-05	15	0.13	0.27
2003012	2004	calving	May-25	Jun-10	15	0.20	1.20
2003013	2004	calving	May-26	Jun-04	8	0.12	0.45
2003017	2004	calving	May-21	May-29	7	0.08	0.18
2003018	2004	calving	May-20	Jun-08	18	0.51	2.77
2003020	2004	calving	Jun-12	Jul-03	20	0.44	0.98
2003021	2004	calving	May-25	Jun-10	15	0.16	0.42
2004017	2004	calving	May-25	Jun-06	11	0.85	4.25
2004018	2004	calving	Jun-01	Jun-25	21	1.24	3.54
2004019	2004	calving	May-27	Jun-09	12	0.38	1.39
2004021	2004	calving	May-21	Jun-01	10	0.52	4.79
2004022	2004	calving	May-19	May-29	9	2.10	9.63
2004023	2004	calving	Jun-14	Jun-24	9	0.52	2.02
2004024	2004	calving	May-18	May-29	10	0.46	1.03

APPENDIX I-6: Onset dates determined via individual-based recursive partitioning for the calving period in the year 2005. Estimated end dates and season lengths are also provided along with mean and maximum recorded movement rates within the period.

ID	Year	Season	Onset	Estimated Finish	Estimated Length (days)	Mean Movement Rate (km/day)	Maximum Movement Rate (km/day)
2002007	2005	calving	May-24	Jun-15	21	0.33	1.26
2002008	2005	calving	May-30	Jun-16	16	0.36	2.28
2003008	2005	calving	May-28	Jun-06	8	0.69	1.37
2003009	2005	calving	May-23	Jun-08	15	0.33	2.24
2003010	2005	calving	May-19	Jun-05	16	0.30	2.17
2003011	2005	calving	May-30	Jun-25	25	0.34	0.88
2003012	2005	calving	May-23	Jun-09	16	0.57	2.01
2003013	2005	calving	Jun-09	Jul-23	42	0.83	2.48
2003014	2005	calving	May-29	Jun-11	12	0.18	0.49
2003017	2005	calving	May-07	May-20	12	0.38	1.61
2003018	2005	calving	May-17	May-29	11	0.23	0.43
2003020	2005	calving	Jun-02	Jun-24	21	0.32	1.38
2003021	2005	calving	May-20	Jun-04	14	0.24	1.42
2004017	2005	calving	May-22	Jun-07	15	0.53	2.79
2004018	2005	calving	May-18	Jun-13	25	0.66	2.37
2004019	2005	calving	May-16	Jun-08	22	0.85	4.12
2004020	2005	calving	May-28	Jun-08	10	0.16	0.58
2004021	2005	calving	May-16	Jun-03	17	0.28	1.17
2004023	2005	calving	May-26	Jun-03	7	0.18	0.83
2004024	2005	calving	May-12	Jun-19	37	0.97	3.14
2005025	2005	calving	Jun-02	Jul-06	33	0.73	4.06
2005027	2005	calving	May-26	Jun-12	16	0.35	1.47
2005028	2005	calving	May-21	Jun-14	23	0.28	1.36
2005029	2005	calving	Jun-11	Jul-01	19	0.99	4.49
2005030	2005	calving	May-31	Jul-01	30	0.58	5.52

APPENDIX I-7: Onset dates determined via individual-based recursive partitioning for the calving period in the year 2006. Where available, estimated end dates and season lengths are also provided along with mean and maximum recorded movement rates within the period.

ID	Year	Season	Onset	Estimated Finish	Estimated Length (days)	Mean Movement Rate (km/day)	Maximum Movement Rate (km/day)
2002007	2006	calving	May-22	Jun-06	14	0.28	1.20
2002008	2006	calving	May-28	Jun-15	17	0.39	2.11
2003008	2006	calving	May-24	Jul-18	54	1.54	9.91
2003009	2006	calving	May-16	Jun-04	18	0.38	1.75
2003010	2006	calving	May-27	Jun-14	17	1.16	3.19
2003013	2006	calving	May-11	Jun-06	25	0.40	1.75
2003018	2006	calving	May-22	Jun-03	11	0.42	1.37
2003021	2006	calving	May-14	May-28	13	0.10	0.66
2004017	2006	calving	May-13	Jun-06	23	1.36	10.06
2004020	2006	calving	May-31	Jun-26	25	0.68	3.26
2004024	2006	calving	May-12	Jun-15	33	0.70	3.75
2005025	2006	calving	May-30	Jun-26	26	1.34	4.28
2005028	2006	calving	May-31	Jul-28	57	1.43	4.74
2005029	2006	calving	May-25	Jun-10	15	0.20	1.65
2005030	2006	calving	May-24	Jun-18	24	0.38	2.53
2004020	2004	calving	May-31				
2003012	2006	calving	May-26				
2003017	2006	calving	May-28				
2004023	2006	calving	May-14				
2005027	2006	calving	Jun-02				

APPENDIX II

APPENDIX II-1: Description of land cover classes in the original EOSD image mosaic (Wulder 2000) and the habitat categories they were grouped into for habitat selection analyses.

EOSD CLASS	HABITAT CATEGORY	DESCRIPTION
Exposed Land	**ExpBarren**	River sediments, exposed soils, pond or lake sediments, reservoir margins, beaches, landings, burned areas, road surfaces, mudflat sediments, cutbanks, moraines, gravel pits, tailings, railway surfaces, buildings and parking, or other non-vegetated surfaces.
Rock / Rubble	**ExpBarren**	Bedrock, rubble, talus, blockfield, rubbley mine spoils, or lava beds.
Herbs	**ExpBarren**	Vascular plant without woody stem (grasses, crops, forbs, gramminoids); minimum of 20% ground cover **or** one-third of total vegetation must be herb.
Water	**Water**	Lakes, reservoirs, rivers, streams, or salt water.
Shrub – Tall	**ShrubTall**	At least 20% ground cover which is at least one-third shrub; average shrub height greater than or equal to 2 m.
Shrub – Low	**ShrubLow**	At least 20% ground cover which is at least one-third shrub; average shrub height less than 2 m.
Bryoids	**Bryoids**	Bryophytes (mosses, liverworts, and hornworts) and lichen (foliose or fruticose; not crustose); minimum of 20% ground cover **or** one-third of total vegetation must be a bryophyte or lichen.

APPENDIX II-2: Description of land cover classes in the original EOSD image mosaic (Wulder 2000) and the habitat categories they were grouped into for habitat selection analyses (cont.).

EOSD CLASS	HABITAT CATEGORY	DESCRIPTION
Wetland – Treed	**WetTreed**	Land with a water table near/at/above soil surface for enough time to promote wetland or aquatic processes; the majority of vegetation is coniferous, broadleaf, or mixed wood.
Wetland – Shrub	**WetShrub**	Land with a water table near/at/above soil surface for enough time to promote wetland or aquatic processes; the majority of vegetation is tall, low, or a mixture of tall and low shrub.
Wetland – Herb	**WetHerb**	Land with a water table near/at/above soil surface for enough time to promote wetland or aquatic processes; the majority of vegetation is herb.
Coniferous – Dense	**ConDense**	Greater than 60% crown closure; coniferous trees are 75% or more of total basal area.
Coniferous – Open	**ConOpen**	26-60% crown closure; coniferous trees are 75% or more of total basal area.
Coniferous – Sparse	**ConSparse**	10-25% crown closure; coniferous trees are 75% or more of total basal area.
Broadleaf – Dense	**BroadDense**	Greater than 60% crown closure; broadleaf trees are 75% or more of total basal area.
Broadleaf – Open	**DecMixOpen**	26-60% crown closure; broadleaf trees are 75% or more of total basal area.
Broadleaf – Sparse	**DecMixOpen**	10-25% crown closure; broadleaf trees are 75% or more of total basal area.

APPENDIX II-3: Description of land cover classes in the original EOSD image mosaic (Wulder 2000) and the habitat categories they were grouped into for habitat selection analyses (cont.).

EOSD CLASS	HABITAT CATEGORY	DESCRIPTION
Mixed Wood – Open	**DecMixOpen**	26-60% crown closure; neither coniferous nor broadleaf tree account for 75% or more of total basal area.
Mixed Wood – Sparse	**DecMixOpen**	10-25% crown closure; neither coniferous nor broadleaf tree account for 75% or more of total basal area.
N/A	**Cut05**	0-5 year-old cutover
N/A	**Cut620**	6-20 year-old cutover
N/A	**Fire05**	0-5 year-old fire
N/A	**Fire620**	6-20 year-old fire
N/A	**Road**	Road surface (includes highway, primary, secondary, and tertiary classes)

APPENDIX II-4: Parameters of Brownian bridge movement models estimated for spring dispersal trajectories in 2004. In cases where more than 3 consecutive fixes failed, trajectories were split and recombined after separate BBMM estimations using a temporally-weighted average. Provided are estimates of the Brownian motion variance (sig1), the location error (sig2), and the home range area based on three probability density contours (95, 99, 100).

UD	id	year	# BBMM	n	sig1	sig2	hr_95	hr_99	hr_100
UD1	2002007	2004	1	102	13.91	15.33	128.75	198.25	612.75
UD4	2003011	2004	2	76	13.51	16.26			
				26	15.82	16.53	195.00	235.75	646.00
UD6	2003013	2004	1	110	13.71	18.51	149.25	221.75	784.75
UD7	2003017	2004	1	137	25.23	19.28	258.75	498.00	8977.50
UD8	2003018	2004	1	140	13.81	17.66	1207.00	1823.25	43454.50
UD9	2003020	2004	2	168	11.71	26.90			
				24	27.93	25.83	1107.50	1651.25	31085.25
UD10	2003021	2004	1	98	25.43	24.67	962.50	1609.75	30899.25
UD12	2004018	2004	1	152	9.21	19.87	163.50	272.75	2201.00
UD13	2004019	2004	1	104	13.51	21.89	80.75	129.75	1480.50
UD16	2004022	2004	1	96	18.22	16.18	137.75	197.75	1617.00
UD17	2004023	2004	2	58	14.31	19.91			
				82	14.41	29.76	127.50	188.75	1645.00
UD18	2004024	2004	1	113	9.71	20.24	414.00	661.75	9310.00

APPENDIX II-5: Parameters of Brownian bridge movement models estimated for spring dispersal trajectories in 2005. In cases where more than 3 consecutive fixes failed, trajectories were split and recombined after separate BBMM estimations using a temporally-weighted average. Provided are estimates of the Brownian motion variance (sig1), the location error (sig2), and the home range area based on three probability density contours (95, 99, 100).

UD	id	year	# BBMM	n	sig1	sig2	hr_95	hr_99	hr_100
UD19	2002007	2005	1	160	7.01	22.52	324.50	541.00	16684.50
UD20	2002008	2005	1	191	9.31	28.46	293.25	484.25	10471.50
UD21	2003008	2005	1	159	14.71	22.08	274.50	430.00	4050.00
UD22	2003009	2005	1	156	8.61	25.94	313.25	559.50	7905.00
UD23	2003010	2005	2	126	7.91	24.13			
				7	8.71	21.62	691.25	1178.00	17226.00
UD24	2003011	2005	1	142	9.11	22.36	280.50	549.25	7560.00
UD25	2003012	2005	1	161	9.31	23.29	692.50	1135.00	13140.00
UD26	2003013	2005	1	193	13.51	25.11	938.50	1389.50	8694.00
UD27	2003014	2005	1	183	13.01	24.66	913.00	1318.00	13727.50
UD28	2003017	2005	1	103	12.61	23.92	461.25	728.50	7367.25
UD29	2003018	2005	1	159	11.61	22.93	466.25	726.00	9852.75
UD31	2003021	2005	1	167	12.81	18.82	350.75	487.50	2121.00
UD32	2004017	2005	1	164	10.41	24.09	288.00	414.00	3325.00
UD33	2004018	2005	2	53	8.31	24.63			
				82	7.21	20.03	374.25	597.75	3565.00
UD34	2004019	2005	1	161	13.51	23.61	1534.25	2377.50	14520.00
UD35	2004020	2005	1	152	13.81	24.26	493.50	810.00	7482.25
UD36	2004021	2005	1	118	9.61	28.73	591.50	889.50	4437.50
UD37	2004023	2005	1	138	7.01	23.90	601.50	899.50	10539.50
UD39	2005025	2005	1	224	10.41	22.79	741.25	1184.25	14400.00
UD40	2005027	2005	1	154	9.01	26.04	204.00	314.50	3366.00
UD41	2005028	2005	1	163	8.51	22.00	107.75	166.75	1138.50
UD43	2005030	2005	1	159	10.11	24.12	233.00	355.50	3545.25

APPENDIX II-6: Parameters of Brownian bridge movement models estimated for spring dispersal trajectories in 2006. In cases where more than 3 consecutive fixes failed, trajectories were split and recombined after separate BBMM estimations using a temporally-weighted average. Provided are estimates of the Brownian motion variance (sig1), the location error (sig2), and the home range area based on three probability density contours (95, 99, 100).

UD	id	year	# BBMM	n	sig1	sig2	hr_95	hr_99	hr_100
UD44	2002007	2006	2	96	10.11	20.48			
				19	5.21	34.72	357.50	564.00	4450.50
UD45	2002008	2006	1	146	14.81	27.19	668.75	1016.25	6927.25
UD46	2003008	2006	2	163	13.01	24.44			
				4	0.50	24.41	335.75	495.25	4380.75
UD47	2003009	2006	1	152	8.21	26.12	193.50	294.50	2814.00
UD48	2003010	2006	1	182	7.71	27.29	1590.50	2321.75	41615.00
UD50	2003012	2006	1	209	9.11	22.95	594.25	926.25	13770.00
UD51	2003013	2006	2	26	15.52	17.39			
				136	7.81	18.76	93.25	141.75	1740.00
UD52	2003017	2006	1	212	10.91	23.12	765.50	1180.75	12614.00
UD53	2003018	2006	1	161	8.41	20.23	66.25	112.00	510.00
UD54	2003021	2006	1	156	12.31	22.89	60.25	79.25	250.00
UD55	2004017	2006	2	125	15.52	17.45			
				34	12.81	22.43	834.75	1229.25	9106.00
UD56	2004020	2006	1	248	7.81	24.10	628.25	1101.00	8610.75
UD57	2004023	2006	2	39	10.11	27.36			
				72	17.62	22.54	229.50	329.25	1763.00
UD58	2004024	2006	1	201	5.31	25.15	116.25	183.25	1044.00
UD59	2005025	2006	2	161	15.12	24.39			
				5	0.60	25.12	188.25	324.50	3607.50
UD60	2005027	2006	1	245	8.01	25.81	565.75	870.75	15997.50
UD61	2005028	2006	1	230	9.61	17.82	788.50	1182.00	42608.75
UD62	2005029	2006	1	198	11.91	17.32	302.75	459.25	2053.25
UD63	2005030	2006	1	126	11.31	23.36	412.00	583.00	2980.00

APPENDIX II-7: Probability-weighted UD centroid locations and individual identifiers for the Assinica caribou herd. Also indicated are maximum and final net displacements along with bias-corrected estimates of the Straightness Index (*SI*).

id	year	herd	UD	n	x	y	pttag	eartag	max R2n	final R2n	SI_bc
2003011	2004	Assinica	UD4	102	-496416	712645	4	913	80.95	25.88	0.08
2003013	2004	Assinica	UD6	110	-525535	794087.2	10	18	91.90	87.10	0.31
2003020	2004	Assinica	UD9	192	-487110	812280.8	22	922	51.08	26.42	0.05
2003021	2004	Assinica	UD10	98	-470925	767262.5	2	923	112.10	92.19	0.28
2004024	2004	Assinica	UD18	113	-488543	700101.5	11	8	15.97	14.84	0.11
2003009	2005	Assinica	UD22	156	-518315	692721.4	9	911	38.84	31.04	0.16
2003010	2005	Assinica	UD23	133	-441769	704332.8	7	912	21.48	21.48	0.12
2003011	2005	Assinica	UD24	142	-500580	759882.1	4	913	103.13	99.27	0.48
2003012	2005	Assinica	UD25	161	-550987	795862.9	5	17	59.71	57.59	0.31
2003013	2005	Assinica	UD26	193	-555372	798520	10	18	95.42	93.33	0.27
2003021	2005	Assinica	UD31	167	-453152	736962.9	2	923	51.96	6.46	0.02
2005027	2005	Assinica	UD40	154	-436676	705769.4	3	13	20.61	14.32	0.06
2005030	2005	Assinica	UD43	159	-488919	721403.6	15	16	43.21	14.41	0.05
2003009	2006	Assinica	UD47	152	-499464	682061.1	9	911	27.47	27.36	0.21
2003010	2006	Assinica	UD48	182	-437607	702431.4	7	912	24.22	17.30	0.06
2003012	2006	Assinica	UD50	209	-507252	762988.8	5	17	29.69	26.86	0.09
2003013	2006	Assinica	UD51	162	-484202	727706.8	10	18	43.40	39.32	0.20
2003021	2006	Assinica	UD54	156	-460964	748789.1	2	923	32.28	28.48	0.11
2004024	2006	Assinica	UD58	201	-489963	701093.1	11	8	10.66	2.59	0.01
2005027	2006	Assinica	UD60	245	-440390	696757.9	3	13	23.91	15.28	0.05
2005030	2006	Assinica	UD63	126	-479454	720572	15	16	40.61	4.59	0.01

APPENDIX II-8: Probability-weighted UD centroid locations and individual identifiers for the Nottaway caribou herd. Also indicated are maximum and final net displacements along with bias-corrected estimates of the Straightness Index (*SI*).

id	year	herd	UD	n	x	y	pttag	eartag	SI_bc	max R2n	final R2n
2003018	2004	Nottaway	UD8	140	-688585	737814.2	8	19	0.14	54.19	50.35
2004018	2004	Nottaway	UD12	152	-695818	754783.1	22	2	0.13	45.67	45.67
2004019	2004	Nottaway	UD13	104	-685483	776300.9	22	3	0.19	51.07	47.59
2003014	2005	Nottaway	UD27	183	-622599	786744.8	22	916	0.26	80.34	61.24
2003017	2005	Nottaway	UD28	103	-689672	795930.4	6	919	0.21	58.22	47.07
2003018	2005	Nottaway	UD29	159	-709548	780694.8	8	19	0.08	39.55	19.49
2004017	2005	Nottaway	UD32	164	-711202	798147.4	17	1	0.09	79.71	22.35
2004018	2005	Nottaway	UD33	135	-701418	755323.4	22	2	0.08	23.98	15.84
2004019	2005	Nottaway	UD34	161	-693481	768653.4	22	3	0.18	53.37	49.72
2005028	2005	Nottaway	UD41	163	-668757	736837.7	13	14	0.17	50.22	37.79
2003017	2006	Nottaway	UD52	212	-694371	714651.5	6	919	0.09	50.71	33.17
2003018	2006	Nottaway	UD53	161	-708160	791165.5	8	19	0.13	50.98	31.55
2004017	2006	Nottaway	UD55	159	-720509	791135.7	17	1	0.23	82.88	66.48
2005028	2006	Nottaway	UD61	230	-658452	762924.5	13	14	0.28	108.25	91.22
2005029	2006	Nottaway	UD62	198	-536908	844546.3	12	15	0.25	97.61	97.61

APPENDIX II-9: Probability-weighted UD centroid locations and individual identifiers for the Nottaway caribou herd. Also indicated are maximum and final net displacements along with bias-corrected estimates of the Straightness Index (*SI*).

id	year	herd	UD	n	x	y	pttag	eartag	SI_bc	max R2n	final R2n
2004022	2004	Témiscamie	UD16	96	-356903	770830.5	22	6	0.45	148.76	141.51
2004023	2004	Témiscamie	UD17	140	-270986	738067.9	14	7	0.17	64.93	64.01
2002007	2005	Témiscamie	UD19	160	-303476	748512.9	20	1005	0.03	19.80	5.31
2002008	2005	Témiscamie	UD20	191	-265477	770971.3	18	1006	0.42	117.11	116.36
2003008	2005	Témiscamie	UD21	159	-355903	811451.5	19	76	0.48	195.65	193.17
2004020	2005	Témiscamie	UD35	152	-308462	770516	16	4	0.05	49.70	18.26
2004021	2005	Témiscamie	UD36	118	-284022	757911.7	22	5	0.18	40.15	39.88
2004023	2005	Témiscamie	UD37	138	-264827	794984	14	7	0.17	27.57	24.98
2005025	2005	Témiscamie	UD39	224	-284019	756473.1	21	11	0.20	66.04	66.04
2002007	2006	Témiscamie	UD44	115	-298207	749941.4	20	1005	0.07	14.49	11.21
2002008	2006	Témiscamie	UD45	146	-322205	817964.9	18	1006	0.39	157.53	142.50
2003008	2006	Témiscamie	UD46	167	-264956	768479.5	19	76	0.27	104.84	90.78
2004020	2006	Témiscamie	UD56	248	-285629	737736.2	16	4	0.07	46.59	26.62
2004023	2006	Témiscamie	UD57	111	-288595	760076	14	7	0.04	85.03	9.50
2005025	2006	Témiscamie	UD59	166	-299530	721226.9	21	11	0.09	66.67	28.30

APPENDIX II-10: Mean vectors and associated parameters by unique case of spring dispersal (year 2004). Alpha is the mean direction in radians, r is the mean resultant length, and corr is the bivariate correlation coefficient ($\mathrm{Cov}_{(x,y)}/s_x s_y$).

id	year	UD	alpha	r	corr
2002007	2004	UD1	4.93	199.23	0.81
2003008	2004	UD6	3.73	538.78	0.55
2003009	2004	UD9	1.17	103.93	0.23
2003012	2004	UD17	0.75	448.25	0.46
2003013	2004	UD20	1.78	416.68	-0.36
2003017	2004	UD24	5.64	511.63	-0.14
2003018	2004	UD27	5.06	126.36	0.01
2003021	2004	UD32	1.99	140.20	-0.32
2004017	2004	UD35	2.73	59.65	0.51
2004019	2004	UD40	5.16	92.80	0.53
2004021	2004	UD45	0.78	871.11	0.13
2004022	2004	UD47	5.18	127.14	-0.42
2004023	2004	UD48	0.73	174.21	0.30
2004024	2004	UD51	4.25	437.46	0.55

APPENDIX II-11: Mean vectors and associated parameters by unique case of spring dispersal (year 2005). Alpha is the mean direction in radians, r is the mean resultant length, and corr is the bivariate correlation coefficient ($Cov_{(x,y)}/s_x s_y$).

id	year	UD	alpha	r	corr
2002008	2005	UD4	4.49	571.57	0.45
2003008	2005	UD7	3.40	269.50	-0.48
2003009	2005	UD10	4.60	1244.85	0.40
2003010	2005	UD12	6.28	241.46	-0.40
2003012	2005	UD18	5.32	284.45	-0.82
2003013	2005	UD21	0.32	1283.39	0.25
2003014	2005	UD23	0.11	125.63	0.65
2003017	2005	UD25	5.72	231.37	0.29
2003018	2005	UD28	3.37	314.46	-0.47
2003020	2005	UD31	5.61	75.66	0.01
2003021	2005	UD33	1.70	137.51	-0.29
2004017	2005	UD36	0.55	336.41	0.36
2004018	2005	UD39	4.65	9.93	0.39
2004019	2005	UD41	3.28	134.17	0.15
2004020	2005	UD43	1.46	168.86	0.17
2004021	2005	UD46	1.24	566.90	0.01
2004024	2005	UD52	5.45	80.93	-0.42
2005025	2005	UD54	2.85	148.53	-0.39
2005027	2005	UD56	0.81	68.68	0.31
2005028	2005	UD58	2.25	57.24	-0.18
2005029	2005	UD60	5.79	46.54	0.51
2005030	2005	UD62	4.09	408.63	0.62

APPENDIX II-12: Mean vectors and associated parameters by unique case of spring dispersal (year 2006). Alpha is the mean direction in radians, r is the mean resultant length, and corr is the bivariate correlation coefficient ($Cov_{(x,y)}/s_x s_y$).

id	year	UD	alpha	r	corr
2003008	2006	UD8	3.14	302.08	0.05
2003010	2006	UD13	1.35	410.47	-0.33
2003011	2006	UD16	3.97	1275.46	0.19
2003012	2006	UD19	5.75	41.50	0.32
2003013	2006	UD22	2.86	109.92	0.18
2003017	2006	UD26	5.29	220.77	-0.20
2003018	2006	UD29	6.23	114.20	-0.55
2003021	2006	UD34	1.45	393.55	-0.13
2004017	2006	UD37	5.40	182.07	-0.20
2004020	2006	UD44	0.25	143.25	0.57
2004023	2006	UD50	1.39	70.45	0.00
2004024	2006	UD53	4.05	150.30	-0.20
2005025	2006	UD55	0.92	430.34	-0.24
2005027	2006	UD57	3.87	437.92	0.73
2005028	2006	UD59	4.59	331.61	0.54
2005029	2006	UD61	1.27	364.85	0.17
2005030	2006	UD63	3.73	104.70	0.24