ADAPTABILITY IN MOOSE (*ALCES ALCES* L.): HABITAT SELECTION IN TWO LANDSCAPES IN NEWFOUNDLAND, CANADA

by

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ABSTRACT

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Moose (*Alces alces* [L.]) exist circumglobally and in a vast array of different habitats. I explore differences in habitat selection in relation to differences in availability of forest stands by habitat type and number of foraging patches, and variation in quality of a winter forage item, balsam fir (*Abies balsamea* [L.] Mill.), used by moose in Gros Morne National Park, Newfoundland and Labrador, Canada. Adult female moose collared in 1997-1998 occupied two landscapes, the Gulf of St. Lawrence Coastal Plain ecoregion (lowlands) and the Long Range Barrens ecoregion (highlands). They followed three landscape-use strategies: year-round residence in the lowlands (n = 5), year-round residence in the highlands (n = 5), and migration from lowlands in winter to the highlands in summer (n = 2). Habitat selection at the stand scale was calculated as the likelihood of selecting a habitat type, based on its availability estimated from classification of SPOT-5 satellite imagery and on moose location data from Global Positioning System (GPS) collars, used to calculate home ranges, core-use areas and foraging patches. There was no difference in habitat selection between migrants and residents either in the lowlands in winter or in the highlands in summer. The summer season, identified as the period of higher rate of movement compared to the winter, was shorter for migrants (median 166 days) than for moose occupying the highlands (174 days) and the lowlands (173days). Foraging patches were arbitrarily defined as areas where a minimum of three consecutive GPS locations < 24 h apart occurred with distances between them of < 50 m. Straight-line distances between successive locations and between foraging patches over weekly and seasonal periods did not differ among the three landscape-use strategies in winter or in summer. Distances travelled were lower in winter than in summer and the number of foraging patches relative to the amount of forested area was higher in the highlands. Chemical analysis of terminal and lateral branches of balsam fir, collected in July 2010, was used as a surrogate for identifying site richness in foraging patches and as a means of identifying forage quality. Lateral and terminal branches had a higher carbon-to-nitrogen ratio in the lowlands, including significant variation in quality by habitat type, compared to the highlands, where variation did not occur by habitat and carbon-to-nitrogen ratio was significantly lower. This outcome suggests the lowlands offer lower quality forage items and lower average site richness compared to the highlands. The migration strategy likely evolved for moose to cope with less available forage during winter in the highlands when snow is very deep.

Keywords: *Abies balsamea*, *Alces alces*, balsam fir, habitat selection, Long Range Barrens, Gros Morne National Park, migration, moose, Northern Peninsula Forest

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INTRODUCTION

Habitat selection is how an individual animal or group of animals decides to situate itself on the landscape; this decision ultimately determines fitness. According to habitat selection theory (Fretwell and Lucas 1970), individuals distribute themselves by density, proportional to the quantity or the quality of limiting resources available in each of several foraging patches, larger habitat units, and still larger landscapes. An example of selection at the foraging-patch scale in the deer family (Cervidae) involves reindeer (*Rangifer tarandus* L.), which select patches with higher forage biomass, apparently because the greater quantity of forage returns more nitrogen (Van der Wal et al. 2000). An example for another ungulate, domestic sheep (*Ovis aries* L.), shows that stronger selection occurs for more productive habitat units when the forager is at low density than when it is at high density (Moebæk et al. 2009). Similarly, mule deer (*Odocoileus hemionus* L.) experience a higher-quality winter diet when at lower density (Nicholson et al. 2006); diet breadth for the mule deer is narrower in habitat units where they occur at higher density, as a consequence of heavy browsing.

The forage maturation hypothesis illustrates how migration may be driven by an ungulate's ability to sense and select higher quality food items; animals redistribute themselves over larger (landscape) scales as forage items mature (McNaughton 1985; Fryxell 1991). This hypothesis is based in optimal foraging theory, which describes a common strategy used by individuals to maximize net gain per unit time by balancing energy spent searching for and consuming a food item against its energetic value (MacArthur and Pianka 1966). Migrant ungulates may be able to find and exploit better-quality forage over a larger spatial scale than those adopting a resident strategy

(Hebblewhite et al. 2008). Returning to ideas of density-dependent habitat selection, a migratory strategy arises in a seasonal climate, when one of two landscapes provides higher fitness to individuals, but the difference is less during the growing season (Holt and Fryxell 2011). In this case, migrants occupy the less suitable habitat only during the growing season. A more general description of space use by ungulates invokes the home-range hypothesis (McNab 1963), a coarse-grained description of optimal foraging that predicts longer travel distances with more limited food resources.

Moose (*Alces alces* L.) are the largest members of Cervidae and are classified as browsing ungulates (Hoffmann 1973); meaning that their diet consists largely of woody fibrous material (shrubs and trees) and they are only modestly selective according to its quality (Shipley 2010). During summer months, their diet focuses on leaves of abundant shrubs and forbs available only during the growing season. During winter months, twigs (branches) dominate their diet. To maintain thermoneutrality and large body size, moose conform to predictions of optimal foraging theory (Renecker and Schwartz 1988). Any excess energy available after expenditures on activities related to thermoregulation, feeding and locomotion is allocated to reproduction, growth and maintenance of condition. Different landscapes offer variable resource amounts and distributions, variably constraining moose behaviours, including their food uptake (Belovsky 1978; Belovsky and Jordan 1981), thermoregulation (Belovsky 1981), and predation risk (Rettie and Messier 2000). Moose habitat preferences are not fixed, meaning there is considerable individual variation in space use, as well as variation among groups, when different habitats are available (Dussault et al. 2005a; Osko et al. 2004). Optimal foraging by moose is usually considered as travel between foraging patches and from one habitat unit to another.

Migration from one landscape to another is occasionally documented for moose. Moose exist in many different landscapes, in which the quality of many habitats varies according to season. Elevation provides a gradient along which habitats change seasonally in their suitability for moose. Several migratory moose populations have been described in such areas, in the southern Rocky Mountains of British Columbia (Poole and Stuart-Smith 2006), in Alaska and the Yukon (Mauer 1998), in Newfoundland (McLaren et al. 2000), and in Sweden (Ball et al. 2001). One of the strategies used by moose in Gros Morne National Park (GMNP), Newfoundland and Labrador (Canada), involves migration from higher elevations, over 400 m above sea level (a.s.l.) to the coastal plain on the Gulf of St. Lawrence (Atlantic Ocean) in winter (McLaren et al. 2000). When moose first established in the GMNP area in the 1940s, they occupied only higher elevations (Caines and Deichmann 1989). Later immigration into the coastal plain created what is now one of North America's highest densities of moose (Connor et al. 2000; Thompson 2007). This lowland population may now sustain a population of moose in the highlands.

The general question arises as to how moose adapt to meet their minimum energy requirements in such diverse landscapes with varying resources and habitat types. At their easternmost extent in North America, moose in Newfoundland consume branches of balsam fir (*Abies balsamea* [L.] Mill.) and white birch (*Betula papyrifera* Marsh.) as the majority of their winter diet (Bergerud and Manuel 1968), and are accordingly found in balsam fir dominated forest and associated mixed-conifer forest. Where forests are slower growing, moose have lower reproduction rates, lower survival, and a lower body condition (body mass, fat reserves), compared to moose in the more productive lowlands of Newfoundland (Albright and Keith 1987; McLaren et al. 2000). The most occupied foraging patches in the balsam fir-white birch habitat type of the Central Newfoundland Forest ecoregion, in terms of moose density, are associated with stands of better soil fertility (Bergerud and Manuel 1968). Extensive negative effects of moose browsing have been observed in such foraging patches, and generally on landscapes where moose reach high densities in Newfoundland (Mercer and McLaren 2002; McLaren et al. 2004). Understanding this plant-herbivore dynamic, which also introduces a management concern of "overbrowsing moose" for GMNP and the Newfoundland and Labrador government, is thus tied to understanding variation in habitat quality, including soil fertility, forage plant chemistry, and density-dependent habitat selection in moose.

Rapidly growing plants in their early phenological stages are easily digestible, and may have fewer defence compounds deterring herbivores (Crawley 1983; Hartley and Jones 1997), although exceptions have been recorded, e.g. for juvenile white birch (Bryant 1983). Slow growth rates are thought to favour selection for higher amount of defences in balsam fir, because the cost of defence is low and the potential impact for herbivory is high (Coley et al. 1985). Lower nitrogen can often indicate low digestibility due to high lignin and fibre content (Prop and Vulink 1992, Robbins 1993, Van Soest 1994). Carbon to nitrogen (C:N) ratios can substitute as a coarse measure of forage quality, and for this study were used alongside transect surveys of woody stems to investigate quality of foraging patches in GMNP (finest scale of investigation: foraging patch). Higher C:N ratios indicate lower quality, and lower C:N indicates a higher quality site (Mattson 1980). Frequency of moose GPS locations within home ranges and within core-use areas of GMNP was used in this study to compare forest stands by habitat type (next scale of investigation: stand scale to landscape scale). Finally, moose density from moose surveys (GMNP, unpublished data) and frequency of migration from more extensive tracking of moose (McLaren et al. 2000) were used to compare the lowland and highland landscapes in GMNP in terms of what they have to offer to moose (broadest scale of investigation). The central task is to explain migration across landscapes in terms of resource availability and energy expenditure by moose in obtaining these resources.

This thesis relates moose habitat selection in two distinct regions of GMNP, habitat selection that is representative of what occurs in moose habitats across Newfoundland and Labrador (Damman 1983; Meades and Moores 1994). Its purpose is to provide a description of adaptability in moose to different landscapes. This purpose also allows a test of habitat selection theory, involving questions of short- and long-distance travel in a context of optimal foraging, and provides recommendations for management of moose elsewhere in Newfoundland and Labrador. There are three main objectives associated with this study:

1) To document habitat selection by moose in GMNP in two landscapes across an environmental gradient divided into lower and higher elevation;
2) To discuss forage quality and site richness of foraging patches within these landscapes and to assess the potential use of C:N ratios in predicting habitat quality as a driving factor in habitat selection and in migration;

3) To comment on the apparent adaptability of moose to different habitats, seasons and landscapes, and on the consequent migratory strategy adopted by some moose in GMNP.

These objectives were addressed using a dataset from Global Positioning System (GPS) collars on twelve moose in GMNP during 1997-1998, which allowed calculation of home ranges, core-use areas, foraging patch locations, travel distances and resource selection functions for moose following three landscape-use strategies relative to elevation. Investigation in this study tracks: (1) year-round residence in the lowlands (coastal plain) in GMNP, (2) year-round residence in the highlands in GMNP, and (3) migration from the highlands in summer to the lowlands in winter. Predictions are as follows:

1) Landscape scale:

Differences in moose habitat selection, home-range size, and travel distances should occur across the two landscapes, the lowlands and the highlands. Shorter travel distances should occur in areas of higher forage quality within each landscape, and habitat selection should adapt according to the habitat types available in each landscape and according to season. On the other hand, habitat selection should not differ by strategy, migrant or resident, for the same landscape. Similarly, moose travel distances should differ by season, due to limiting snow depths in winter, but should not differ between landscapes for the same season. Finally, moose in the highlands, where foraging patches are likely more sparsely distributed on the landscape, should have larger home ranges than moose in the lowlands.

2) Stand scale:

Habitat selection theory suggests that stronger selection for habitats with higher resource availability should occur. Where moose density is higher, in the lowlands, habitat types with lower resource availability should be increasingly used. If lower soil fertility is indicative of lower resource availability, then C:N ratios should be on average lower in the lowlands. A further prediction is that moose in both landscapes should select habitat types that provide a better thermal environment, such as closed-canopy forests, following patterns identified as thermoregulatory requirements in moose in other parts of their range (Schwab and Pitt 1991; Poole and Stuart-Smith 2006); this preference will be more evident in winter. Travel distance between foraging patches should be less in summer than in winter, and should differ less between landscapes in summer than in winter.

3) Foraging-patch scale:

Because some moose migrate from the highlands before winter, foraging patches in the lowlands should provide access to more winter forage items. However, in the highlands, where moose density is lower, better-quality balsam fir branches, with lower C:N ratios should occur. During the summer, both more and better-quality forage might occur in the highlands, explaining migration to the highlands in summer.

STUDY AREA

Description of Gros Morne National Park

Gros Morne National Park (GMNP) is located on the Gulf of the St. Lawrence on the northern peninsula of Newfoundland (Fig. 1). The protected area encompasses 1,805 km^2. The lowlands, which include the Western Newfoundland Forest ecoregion and the Coastal Plain sub-region of the Northern Peninsula Forest ecoregion (Damman 1983), have a total area of 938 km^2, or 52% of the park (Taylor and Sharma 2010) and are 0 to 400 m a.s.l. The highlands, which comprise only the Long Range Barrens ecoregion, have a total area of 867 km^2 and are 400 m to 800 m a.s.l. The lowlands are characterized by weather influences from the Gulf of St. Lawrence, moderate annual precipitation (900-1,000 mm) and cold and snowy winters (300-350 mm of the precipitation is in the form of snow; Hare 1952). The highlands are characterized by a harsher climate with annual precipitation and snowfall on average double that of the lowlands (Watson 1974). The mean annual temperature in the highlands is 4.5 C cooler than that of the lowlands (Banfield 1983). The Coastal Plain ecoregion is thought to be the more productive of the two landscapes (McLaren et al. 2000).

Taylor and Sharma (2010) classified habitat types in the lowlands and highlands of Gros Morne National Park from a single-image subset of two 10-m multispectral SPOT-5 satellite images (recorded June 20, 2006) with a K-means unsupervised classification. Habitat types in the classification were then described using information from aerial photographs and forest inventories, and from local expert knowledge combined with confirmation through field visits (Taylor and Sharma 2010). In the in the lowlands, ten habitat types were classified (Table 1) and in the highlands, five habitat types were classified (Table 2).

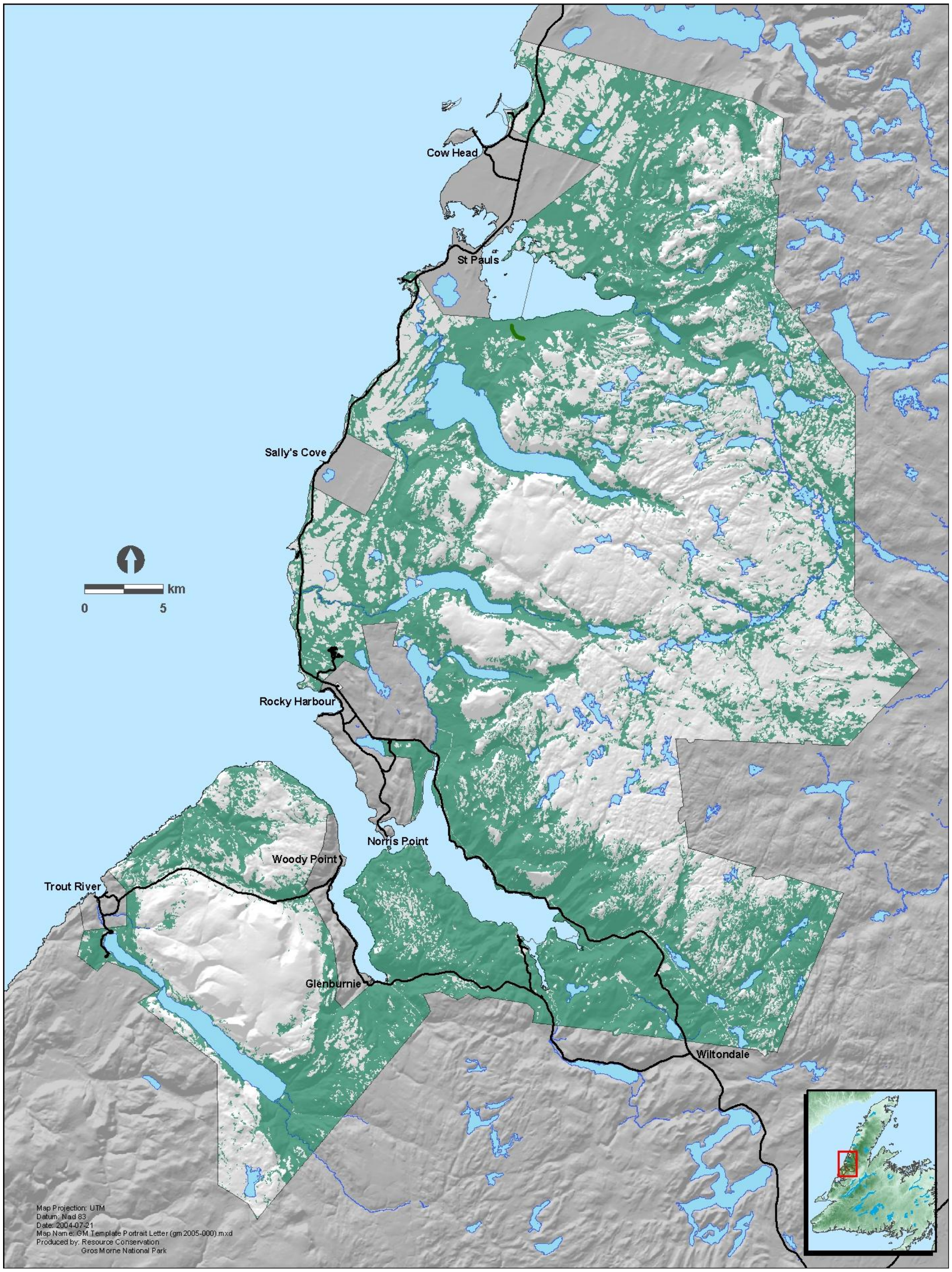

Figure 1. The study area, Gros Morne National Park, showing the forested areas (green) and non-forested areas (light gray) ecoregions (Taylor 2005).

Table 1. Habitat descriptions from a lowlands classification in Gros Morne National Park (Taylor and Sharma 2010).

Habitat type	Description	Forest status
Softwood mature	Softwood dominated (balsam fir); balsam fir dominated with some mixed stands with white birch.	Closed-canopy forest
Spruce closed	Softwood dominated (balsam fir, black spruce, *Picea mariana* [Mill]. Britt.); other species evident include tamarack (*Larix laricina* [Du Roi] Koch), trembling aspen (*Populus tremuloides* Michx.), and alder (*Alnus* spp.); site condition can be wet; some stands have scrub characteristics.	Closed-canopy forest
Mixed closed	Balsam fir dominated with some mixed stands (balsam fir, white birch, Marsh.). Stem density can be very high. Slightly younger stands (~30 years) are included.	Closed-canopy forest
Softwood young	Softwood dominated (balsam fir, white birch); high content of hardwoods; canopy open, 6-9 m height.	Closed-canopy forest
Softwood open	Balsam fir dominated; birch content can be significant. Many stands are breaking up leaving remnant spruce or birch; many openings occur throughout the stands, some with regeneration (1-4 m), while other openings have varying degrees of tree mortality.	Open-canopy forest
Softwood sparse	Softwood dominated (white birch, balsam fir, black spruce,); limited regeneration; ferns and grass very prominent (< 50% of ground cover); forest canopy is very broken consisting of mostly remnant forest from past disturbance; low density young black spruce < 6 m; pockets of balsam fir / black spruce regeneration < 4 m can be present.	Sparse-canopy forest and herb/grass dominated ground cover

Table 1 (continued)

Habitat type	Description	Forest status
Herb/ hardwood	Dominant plants include ferns, grass and raspberry (*Rubus* L.); (> 50% of ground cover); very sparse forest canopy for remnant trees (< 10%) consisting of white birch, alder, or elderberry (*Sambucus racemosa* L.). Very little balsam fir regeneration. Most sites were forested but have not regenerated after severe disturbance. Scattered spruce < 4 m.	Sparse-canopy forest and herb/grass dominated ground cover
Herb	Dominant plants include ferns and grass (> 50% of ground cover); exposed soil is common; large amounts of dead material (standing or fallen), scattered remnant trees. Little regeneration > 30 cm. Most sites forested but not regenerated after severe disturbance.	Sparse-canopy forest and herb/grass dominated ground cover

Disturbances in Gros Morne National Park

The majority of disturbances in GMNP are attributed to insect outbreaks, with some timber harvesting in the forested areas of the park (Taylor and Sharma 2010). Three major insect outbreaks occurred in 1969, 1988, and 1996, and have affected large areas of forest and domestic timber cutting areas, 76 km^2 and 28 km^2 respectively. The primary agents were spruce budworm (*Choristoneura fumiferana* Clem.) and hemlock looper (*Lambdina fiscellaria* Guen.). All of these disturbances have allowed the continued existence of young forests, primarily in the lowlands, which likely provide good foraging opportunities for moose (Connor et al. 2000; McLaren et al. 2009).

Table 2. Habitat descriptions from a highlands classification in Gros Morne National Park (Taylor and Sharma 2010).

Habitat type	Description	Forest status
Forest	Typically mature balsam fir and some black spruce forest in a closed canopy and/or mature balsam fir and black spruce forest with canopy closure of < 25%; dense pockets of krummholz (tuckamore). Open heath and fen and bog interspersed.	Forest
Scrub open	Site comprised of pockets of open scrub forest (< 4 m). Open heath, fen, and bog throughout (> 50%).	Unforested
Shrub	Predominantly low shrub (< 1m), fen/bog, with pockets of scrub. Often associated with transition from fen and tundra to scrub type. Can be wet.	Unforested
Tundra	Heath, low vegetation comprised of sedges, caribou moss (*Cladonia* L.), crowberries (*Empetrum* L.); < 20% rock, little to no scrub or trees. Fairly dry.	Unforested
Fen	Sedge meadows with fens throughout.	Unforested
Rock Barren	Boulder fields and exposed rock. Very little ground vegetation.	Unforested

Moose in Gros Morne National Park

In 1878, one female and one male moose were introduced to Newfoundland from Nova Scotia, and in 1904 two male and two female moose were introduced from New Brunswick (Pimlott 1953). Moose first inhabited the northern peninsula of Newfoundland by the 1940s (Caines and Deichmann 1989). While moose are currently found in all ecoregions in GMNP (and all ecoregions in Newfoundland), collared moose in this study primarily resided in the Long Range Barrens (highlands) ecoregion or the

Coastal Plain (lowlands) sub-region of the Northern Peninsula Forest ecoregion (Fig. 2; McLaren et al. 2000).

Moose are found at different densities in each ecoregion. Moose density over all of GMNP in 1977 was 0.5 moose/km^2 (Janes 1977), and in 1995 was 4.0 moose/km^2 (Connor et al. 2000). Moose populations have declined since 1998, although their density is still considered very high compared to other boreal regions (Thompson 2007). Population sizes were estimated in surveys during March of both 2007 and 2009 using stratified, random block sampling (Gasaway et al. 1986). Aerial helicopter counts were corrected by a factor of 1.5 for visibility bias (Taylor and Knight 2009). Both surveys were conducted in good weather conditions over the same geographic areas and survey blocks (Thompson 2007; Taylor and Knight 2009). Population size within GMNP in 2007 was estimated at 3,975 ± 1,287 standard deviation (SD) for the lowlands, and 788 ± 223 SD for the highlands (Thompson 2007). From aerial surveys of the lowlands in two adjacent moose management areas (Lowlands North and St. Paul's South) in 2009, populations extending into GMNP were as high as 2,631 ± 811 SD and 1,577 ± 670 SD for a total lowlands population estimate of 4,208 ± 1,481 SD, matching the park estimate in 2007. Based on the most recent population estimates, in 2009 for the lowlands (Taylor and Knight 2009) and in 2007 for the highlands (Thompson 2007), there are 5.9 moose/km^2 in the lowlands, and 1.1 moose/km^2 in the highlands. The lowlands support more forested area, 408 km^2, than the highlands, 185 km^2 (Taylor and Sharma 2010). The difference in moose density, using this correction factor, is 13.6 moose/km^2 of forest in the lowlands, and 5.2 moose/km^2 of forest in the highlands.

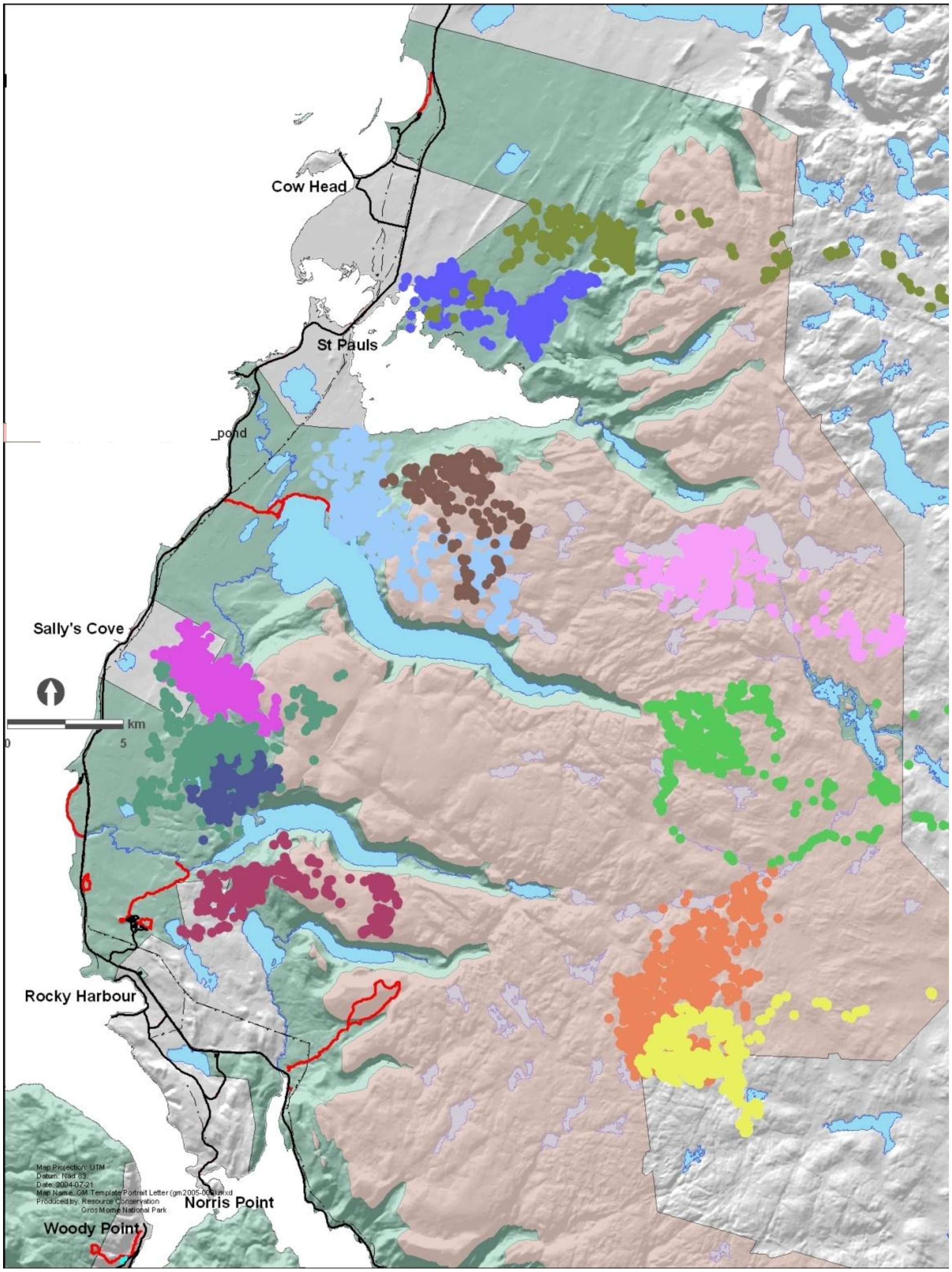

Figure 2. Moose locations in Gros Morne National Park. The Coastal Plain sub-region of the Northern Peninsula Forest ecoregion is shaded green; the Long Range Barrens ecoregion is shaded buff. Each coloured dots represents a separate moose.

METHODS

MOOSE COLLARING AND LOCATIONS

Twelve adult female moose (11 with at least one calf) were immobilized and fitted with GPS collars (Lotek Engineering, Inc.) in June 1997, under a Memorandum of Understanding between Parks Canada and the Department of Forest Resources and Agrifoods (Inland Fish and Wildlife Division), Newfoundland and Labrador. The collars were set to attempt a fix at three-hour intervals. Remote downloading occurred in September 1997, November 1997 and March 1998.

The collars were removed in November 1998, and the remaining data records were collected at that time. Test collars were deployed for 2-4 weeks in December 1997 in four different situations (in the open, under mixed forest cover, under coniferous forest cover, and on a cliff slope) to determine the fix frequency, activity and location accuracy associated with each. Location accuracy was found to be dependent on the collar position in relation to topography and canopy, but 95% of all differentially corrected data from test collars had ± 25 m accuracy (McLaren et al. 2000). Differential correction enhances the quality of location data gathered using global positioning system (GPS) receivers (Chivers 2011), and it uses a network of fixed, ground-based reference stations to detect the difference between the positions indicated by the satellite systems and known, fixed positions. Subsequently, all 2-D fixes were removed from the data recorded by the collars deployed on the study moose, and only 2-D and 3-D differentially corrected locations were used for this study.

Depending on collar functioning, locations were recorded over a 4 to 15.5 month period (Table 3). Five of the collared moose remained primarily in the lowlands, five primarily in the highlands, and the remaining two migrated from summers spent in the highlands to winter in the lowlands (Fig. 2).

Table 3. Time periods in which GPS collars recorded data for that individual moose. Landscape-use strategy of each moose is identified as: resident in the lowlands (L), resident in the highlands (H), or migrant (M), using the highlands in summer and the lowlands in winter.

Moose	Landscape-use strategy	First day collared	Last day recording	Days of recording
17	H	25-Jun-97	13-Oct-98	468
18	H	25-Jun-97	27-Feb-98	242
20	H	25-Jun-97	17-Mar-98	262
23	H	26-Jun-97	13-Oct-98	467
24	H	26-Jun-97	01-Jun-98	335
15	L	25-Jun-97	13-Oct-98	468
16	L	25-Jun-97	13-Oct-98	468
19	L	25-Jun-97	05-Nov-97	130
25	L	26-Jun-97	21-Jun-98	355
26	L	26-Jun-97	15-Nov-97	139
21	M	25-Jun-97	16-Jan-98	201
22	M	26-Jun-97	18-Jun-98	352

FIELD WORK

Foraging patches were defined as areas where a minimum of three consecutive GPS locations < 24 h apart occurred with distances between them of < 50 m. This definition was arbitrary, but based on an inference that foraging takes place with shorter travel distances. Field sites were a subset of all foraging patches that were identified as visited by moose during the 1997-98 winter season, the subset determined based on logistical constraints in accessing them. Field work was conducted during July 2010 by Krystal Kerckhoff (Dixon), Dr. Brian McLaren and Scott Taylor. At each selected foraging patch, an attempt was made to enumerate the understory trees and shrubs available as food resources for moose in winter along transects 25 m long and 2 m wide, established from the plot centre (GPS location in middle of plot), and following a north-south bearing. Shrubs were tallied based on clusters of stems. From a terminal (apical) branch and from a lateral branch of the closest available balsam fir tree to the plot centre, approximately 100 g of current growth was removed. Two additional plot locations 150 m and 300 m away from the first were chosen at random cardinal directions, where balsam fir branch collections and understory tallies were repeated. The random locations were intended to assess areas within the home ranges and core-use areas of the collared moose, but not used as foraging locations. Given the high density of moose in GMNP, and the many uncollared moose, this definition was determined from the outset to be problematic.

LABORATORY ANALYSIS

Each day, branch samples were placed into paper bags and air dried, and then frozen. A few days prior to processing, samples were dried in an oven until they no longer lost any weight between daily measurements. They were then ground using a crushing grinder and stored in plastic containers, where they were processed in a LECO® CNS 2000 (LECO Corporation; Saint Joseph, Michigan USA) located at the Forest Soils Laboratory at Lakehead University. Carbon and nitrogen content were calculated as a fraction of dry weight. Lateral and terminal branches of balsam fir were analyzed separately.

DATA ANALYSIS

All analysis used Statistical Package for the Social Sciences (SPSS), version 18. Moose locations were plotted using ArcView version 9 (ESRI, Redlands, California). Winter and summer seasons were calculated based on cumulative time and distance travelled (Vander Wal and Rodgers 2009). Each animal's location data was re-organized so that locations spanned from January 1 – December 31 to provide a complete year of locations. Only animals that had an entire year of data (n = 6) could be used for seasonal calculations. The location data for the remainder (n = 6) were divided with season boundaries determined based on the average of the calculations for the subset of the first six occupying the same ecoregion. Cumulative location times were placed into units of seconds. Cumulative elapsed time with collars collecting location data and cumulative distance travelled were standardized and plotted against one another (Appendix; Figures A3-A6). The resulting curves were used to determine seasonal transitions from the inflection points. Home ranges and core areas within these home ranges were estimated with the fixed-kernel method with Gaussian (bivariate normal) distributions, calculating a 95% and 50% isopleth for ranges and cores, respectively, using Home Range Tools (Rodgers et al. 2007). The bandwidth size was determined by finding the smallest proportion of the reference bandwidth (h_{ref}) that allowed one continuous outer line encompassing the home range (Worton 1989).

Mean daily and weekly travel distances, as well as distances between forage patches, were determined for each moose, for summer and winter separately, and then compared across seasons and strategies (resident in the lowlands, resident in the highlands, and migrant between landscapes), using Analysis of Variance (ANOVA). The weekly travel distances were compared with a repeated-measures ANOVA. Average weekly distances travelled were averaged for summer, from July 3, 1997 to August 23, 1997, and for winter, from November 16, 1997 to January 6, 1998. A second summer was used to average for moose that had recordings for the following year for the dates July 3, 1998 through August 23, 1998 (moose 15, 16, 17, and 23). This adjustment in dates was done to avoid averaging the transition periods across the strategies. Annual distances travelled were also compared by strategy using ANOVA. Minimum travel distances are reported in all cases as straight lines between successive location points.

Repeated-measures ANOVA, nesting habitat types within ecoregions, was used to compare C:N ratios in lateral and terminal branches of balsam fir with the two seasons (summer and winter) the periods of re-measurement.

Resource selection functions (Manly et al. 2002) were estimated using logistic regression for each moose (conditional models) and for each strategy by pooling individuals into populations (marginal models). Random intercepts and selection coefficients for all habitat types experiencing some use were estimated, such that selection coefficients ≥ 1 show preference for a habitat type. The fixed effects in the pooled, mixed models across moose were strategy and season. To determine the most parsimonious models with season and strategy, Akaike's Information Criteria (AIC) and model deviance were compared in different combinations, also including a random variable representing individual moose. A compound symmetric structure was assumed, meaning that covariance among all responses of an animal is assumed constant (Skrondal and Rabe-Hesketh 2004) and that availability is assumed to remain constant over time (Manly et al. 2002). These assumptions limit the applicability of the calculated resource selection functions to the time period studied.

Resource selection functions were estimated three times for each of the lowlands and highlands: first, based on coverage of habitat types within the home range compared to their coverage on the surrounding landscape; second, based on coverage of habitat types within core-use areas compared to their coverage on the surrounding landscape; third, based on frequency of locations in each habitat type within the core-use areas compared to the coverage of each habitat type on the surrounding landscape. Comparisons across these scales, the two strategies and the winter and summer seasons followed a mixed-effects model with random intercepts and coefficients (Gillies et al. 2006). Selection coefficients calculated for the lowlands used softwood open forest as a reference habitat type; coefficients for the highlands used forest as a reference habitat type. Reference habitats are needed as a reference is always required when using logistic regression. These references were the most similar habitat types across the two landscapes. A habitat type was considered selected if it was occupied more often than expected based on its availability and on a random distribution of locations, and termed avoided, or not selected, if it was occupied less than expected, relative to the reference habitat, for which the ratio of frequency of locations to habitat availability was set at 1.0.

RESULTS

Home-range size varied considerably among individual moose, such that there was no consistent size difference by landscape-use strategy for either winter ($F_{2.9} = 0.57$, $p = 0.58$) or summer ($F_{2.9} = 0.41$, $p = 0.68$; Table 4). There was a high variance noted here given the small sample size. There was also no difference in winter and summer home-range sizes for the same moose ($F_{2,9} = 0.97$, $p = 0.68$). The mean distances travelled during a one-year period were 309 km for residents in the lowlands, 267 km for residents in highlands, and 379 km for migrants. Weekly distances travelled varied according to strategy ($F_{2,148} = 6.65$, $p = 0.002$) and season ($F_{1,148} = 106.35$ $p < 0.001$; Fig. 3). The interaction between strategy and season was not significant in explaining differences in weekly travel ($F_{2,148} = 0.75$, $p = 0.47$). Moose travelled less in winter than in summer, and migrants travelled furthest each week, followed by moose residing in the highlands.

The majority of foraging patches in the lowlands were in young and disturbed forest habitat types. There were relatively more foraging patches in the highlands, per unit area, where the majority of foraging patches were in forest (Table 5). The density of potential foraging items did not vary according to habitat type in the lowlands (all $p > 0.46$) or in the highlands (all $p > 0.20$; Table 6). Distances between foraging patches were greater in summer than in winter ($F_{1,120} = 36.28$, $p = 0.01$), a consistent pattern among landscape-use strategies ($F_{2,120} = 0.08$, $p = 0.93$) with no difference in distances travelled between foraging patches by landscape-use strategy ($F_{2, 120} = 0.01$, $p = 0.99$; Appendix Figures A6-A9).

Considerable individual and seasonal variation was observed in selection of habitats, and analysis of deviance guided selection of the best resource selection functions (Table 7; additional information on resource selection functions can be found in appended Tables A1-A5). In summer, habitat types used less than expected based on their availability were a common occurrence in the lowlands. These habitat types were similar to those that were used more than expected in winter in the lowlands: young and disturbed forests including herb, herb/hardwood and softwood sparse forest. Selected habitat types were similar within home-ranges and core-use areas, but in the lowlands, softwood young forest was selected more strongly at the home-range scale than within core-use areas. In summer on the lowlands, six of seven moose occupied spruce closed forest more than expected, five of seven moose occupied mixed closed forest more than expected, and five of seven moose occupied softwood mature forests more than expected. In winter on the lowlands, three of five moose occupied spruce closed forest more than expected, and three of five moose did not occupy any habitat type significantly more than expected. All moose resident in the highlands avoided open scrub, shrub and tundra habitat types. The overall trend was use of closed forest types in summer and use of more open habitat types in the winter, for both the highlands and the lowlands. Habitat selection did not differ between migrants and residents of the lowlands in winter or between migrants and residents of the highlands in summer. Comparisons of resource selection functions among landscape-use strategies resulted in all $p > 0.07$, except for selection of the herb type in the lowlands (a disturbed type created by high density of moose; Table 1), which was stronger in migrants than in lowland residents ($p = 0.03$).

There was no difference in C:N ratios for random locations and foraging patches, comparing either lateral branches ($F_{1,61} = 0.10$, $p = 0.76$) or terminal branches ($F_{1,57} = 1.08$, $p = 0.30$) collected from the same general area. There were significant qualitative differences in the results of chemical analysis of lateral and terminal branches ($F_{1,79} = 7.19$, $p = 0.009$). Lateral branches from foraging patches in the highlands (mean = 26.09, standard deviation, SE = 0.85) were lower in C:N relative to lateral branches from foraging patches in the lowlands (mean = 33.77, SE = 1.58; $F_{1,19} = 9.20$, $p < 0.01$); the same difference occurred for terminal branches (lowlands: mean = 30.27, SE = 1.27;

highlands: mean = 21.03, SE = 1.70; $F_{1,18} = 10.84$, $p = 0.004$). The C:N ratios for laterals and terminals by habitat type and across the two landscapes did not have a significant difference ($F_{13,79} = 0.50$, $p = 0.92$). C:N ratio in lateral branches did not vary with habitat type in the lowlands ($F_{1,8} = 1.72$, $p = 0.15$), the same for thehighlands ($F_{1,5} = 0.83$, $p = 0.825$; Table 8). C:N ratios in terminals branches did not differ with habitat type either in the lowlands ($F_{1,8} = 0.87$, $p = 0.56$) or in the highlands ($F_{1,5} = 0.83$, $p = 0.55$; Table 8). The resource-poorer habitat types, where higher C:N ratios occurred, were softwood young, softwood open, and mixed forests in the lowlands, though these differences were not significant. The highest-quality balsam fir branches (lowest C:N ratios) occurred in forest, shrub, and tundra habitat types in the highlands, again not significantly different from one another.

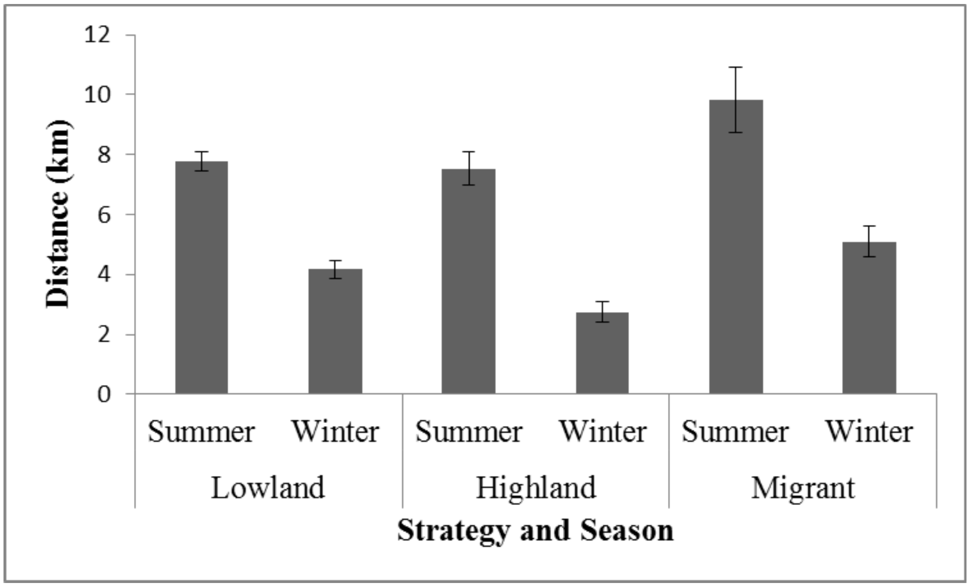

Figure 3. Mean weekly distances (km) travelled by moose, according to landscape-use strategy and Season (S = summer, W = winter) shown with standard error bars and the number of weeks used for the comparison (N). Landscape- use strategy for each moose is identified as in Table 3; seasons are summer (S) and winter (W), defined in Methods.

Table 4. Home range of moose in GMNP calculated summer and winter. The median seasonal transition dates and season lengths for three landscape-use strategies were calculated following methods of Vander Wal and Rodgers (2009). Landscape-use strategy of each moose is identified as in Table 3.

Moose and landscape-use strategy		Home-range size (ha)		Seasonal transition dates		Season length (days)	
Moose	Strategy	Summer	Winter	Winter to summer	Summer to winter	Summer	Winter
17	H	1,128	1,082	30-Apr-98	24-Oct-98	174	180
18	H	684	874				
20	H	660	816				
23	H	916	715				
24	H	701	455				
15	L	1,192	1,208	18-Apr-98	11-Oct-98	173	180
16	L	1,324	1,311				
19	L	289	175				
25	L	827	1,213				
26	L	422	237				
21	M	568	546	18-Apr-98	04-Oct-98	166	188
22	M	797	1,231				

Table 5. Winter foraging patches visited and occurring in the lowlands and the highlands by habitat type. The percent area of the landscape occupied by foraging patches is relative to all habitat types classified in the lowlands and in the highlands.

Habitat Type	Foraging patches			Availability on landscape	
	Number visited	Total Number	Percent (%)	Area (km^2)	Percent (%)
		Lowlands			
Softwood mature*	0	2	2	69.6	17
Spruce closed	1	3	2	27.6	7
Mixed closed	3	3	2	65.5	16
Softwood young	4	22	17	56.7	14
Softwood open	7	7	6	62.5	15
Hardwood open	5	16	13	39	9
Herb/hardwood	1	8	6	20	5
Herb	3	19	15	13.5	3
Mixed open	3	24	19	43.6	10
Softwood sparse	2	23	19	19.3	5
		Highlands			
Forest	3	70	44	184.7	24
Scrub open	1	47	30	133.5	18
Shrub	10	22	14	130	17
Tundra	6	18	11	130.3	17
Fen	5	2	1	62.6	8

*There were no foraging patches visited in the softwood mature habitat type

***Betula glandulosa* Michx

Table 6. Mean densities (stems per ha) with standard error of trees and shrubs identified in the understory of moose foraging patches in Gros Morne National Park.

Habitat type	Balsam fir		White birch		Black Spruce		White Spruce		Alder		Willow		Dwarf birch**	
	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE
Lowlands														
Softwood mature*	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Spruce closed	2,200	-	200	-	0	-	0	-	0	-	0	-	0	-
Mixed closed	1,867	909	67	82	400	490	0	0	0	0	0	-	0	-
Softwood young	2,571	1,647	86	131	629	535	0	0	543	520	0	-	0	-
Softwood open	1,100	535	500	205	400	221	300	245	100	82	0	-	0	-
Hardwood open	920	-	960	-	240	-	40	-	280	-	0	-	0	-
Herb/hardwood	400	-	200	-	0	-	0	-	0	-	0	-	0	-
Herb	333	216	267	216	0	0	133	163	0	0	0	-	0	-
Mixed open	2,000	510	0	0	733	163	0	0	0	0	0	-	0	-
Softwood sparse	1,100	1,556	0	0	0	0	200	0	0	0	0	-	0	-
Highlands														
Forest	2,600	616.44	0	-	733	496.66	0	-	0	-	0	0	0	0
Scrub open	1,800	-	0	-	800	-	0	-	0	-	0	-	0	-
Shrub	1,400	611.12	0	-	600	579.77	0	-	0	-	400	697	0	132
Tundra	2,700	974.47	0	-	167	104.56	0	-	0	-	1,667	1155	0	0
Fen	200	223.61	0	-	400	393.7	0	-	0	-	880	410	200	224

Table 7. Habitat types within home ranges and core-use areas in the lowlands and the highlands, ranked from highest (1) to lowest (10 lowlands, 5 highlands) selected by season, for resident moose on each landscape ($n = 5$, lowlands, $n = 4$, highlands). Habitat types that are significantly used or not used in proportion to the amount of habitat available (selected or avoided; $p < 0.05$) according to their availability are shown in boldface, relative to softwood-open forest (lowlands) and forest (highlands) habitat types, which were the references for the ranking (shown in italics and underlined). The number of locations used in the ranking is shown for analysis by home range and by core-use areas.

Summer		Winter	
		Lowlands	
Home range (n = 3,765):	Core-use area (n = 1,485):	Home range (n = 2,013):	Core-use area (n = 1,679):
(1) Spruce closed	Mixed closed	(1) **Herb**	**Herb/hardwood**
(2) Softwood young	Spruce closed	(2) **Herb/hardwood**	**Herb**
(3) Mixed closed	Softwood young	(3) **Softwood young**	**Softwood sparse**
(4) *Softwood open*	Softwood mature	(4) **Hardwood open**	**Hardwood open**
(5) Softwood mature	*Softwood open*	(5) Mixed closed	Mixed open
(6) Softwood sparse	Hardwood open	(6) Spruce closed	Spruce closed
(7) Hardwood open	Mixed open	(7) **Softwood sparse**	Softwood young
(8) Mixed open	**Softwood sparse**	(8) Mixed open	Mixed closed
(9) **Herb/hardwood**	**Herb/hardwood**	(9) Softwood mature	*Softwood open*
(10) **Herb**	**Herb**	(10) *Softwood open*	Softwood mature
		Highlands	
Home range (n = 2,954):	Core-use area (n = 1,609):	Home range (n = 1,914):	Core-use area (n = 1,619):
(1) *Forest*	**Fen**	(1) **Fen**	Fen
(2) Fen	**Tundra**	(2) **Shrub**	**Shrub**
(3) **Tundra**	Shrub	(3) **Tundra**	Tundra
(4) **Shrub**	*Forest*	(4) **Scrub open**	Scrub open
(5) **Scrub open**	Scrub open	(5) *Forest*	*Forest*

Table 8. Means and standard errors (SE) for carbon (C), nitrogen (N), and carbon to nitrogen ratio (C:N) from balsam fir lateral branches collected from winter foraging locations in habitats of the lowlands and highlands of Gros Morne National Park.

Habitat Number	Habitat Type	n	C		N		C:N	
			mean	SE	mean	SE	mean	SE
			Lowlands					
4	Spruce-Closed	1	51.53	n/a	1.67	n/a	30.78	n/a
6	Mixed-closed	3	51.55	0.21	1.32	0.23	40.78	7.22
7	Softwood, closed - mature	7	51.24	0.22	1.37	0.10	38.29	2.51
8	Softwood - open	4	50.34	0.65	1.42	0.19	37.18	5.52
9	Hardwood-open	5	49.40	1.62	1.67	0.16	30.23	2.13
10	Herb-hardwood	1	51.33	-	1.72	-	29.77	-
11	Herb	3	50.50	0.47	1.89	0.23	27.26	3.68
12	Mixed-open	3	51.39	0.10	1.41	0.12	36.74	3.27
14	Softwood, sparse	2	50.52	0.06	1.75	0.10	29.00	1.68
			Highlands					
6	Softwood open/scrub closed	3	51.03	1.17	1.90	0.26	27.57	4.00
7	Scrub open	1	51.76	-	1.80	-	28.82	-
8	Shrub	10	52.02	0.26	2.48	0.43	23.89	2.28
9	Tundra	6	51.61	0.42	1.99	0.11	26.30	1.44
11	Fen	5	52.65	0.53	1.81	0.07	29.22	1.39
12	Rock Barren	1	53.36	-	1.48	-	35.98	-

DISCUSSION

Two landscapes in GMNP provide insight into adaptability and migration in moose. Moose habitat selection in general varied in the lowlands and the highlands of GMNP according to the different habitat types presented by each landscape, supporting original predictions. There were also general similarities in habitat selection by moose in both landscapes in winter, where they used open areas more frequently than in summer. Individual variation in habitat selection at the stand scale shows that a general prediction about landscape use by individual moose is difficult to infer from any average use of habitats by a population, as found elsewhere (Gillingham and Parker 2008), and earlier for GMNP (McLaren et al. 2009). Migrant and resident moose considered as two groups or strategies also did not generally select habitat differently when they occupied the same landscape, supporting original predictions. Migrants seemed ready to adapt their habitat preferences by season, similar to migrating moose in Norway (Ball et al. 2001). A sample size for the migratory strategy ($n = 2$) in this study may be too small to infer additional population-level findings, but the exception of migrants more strongly selecting the highest-density and most disturbed habitat units during winter in the lowlands, relative to residents, is also a starting point from which to explore different habitat use strategies that are consistent initially with predictions from density-dependent habitat selection.

Migration has been observed to occur in several moose populations for areas such as the southern Rocky Mountains of British Columbia (Poole and Stuart-Smith 2006), in Alaska and the Yukon (Mauer 1998), in Newfoundland (McLaren et al. 2000), and in Sweden (Ball et al. 2001). In these areas, only a portion of moose exhibit this migratory strategy, while others remain resident, much like what is described here for GMNP. Animal populations that exhibit partial migration present a unique opportunity to understand the causes of migratory behaviour (Lundberg 1988a, Kaitala et al. 1993). Migration has been observed for several animal taxa, including birds, fish, insects and mammals. Different migratory behaviour among individuals suggests that partial migration has resulted from natural selection, perhaps favouring founder effects (Kaitala et al. 1993).

Home-range size varied considerably among individual moose, such that there was no consistent size difference by landscape-use strategy for winter or summer. There was also no difference in winter and summer home-range sizes for the same moose, not consistent with our prediction that home range sizes would differ by strategy. Home range sizes did not vary among groups of moose in this study, indicating that movement rates may be a better indicator to assess forage availability. This conclusion is consistent with Dussalt et al. (2005a), where movement rates for moose collared in Quebec, in a region where forage is widely distributed, were better indicators of forage quality than were home range sizes. Thus, forage quality influenced space use of moose in at least two studies at a smaller temporal or spatial scale (movement rates) more than at a larger scale (home-range sizes). Habitat selection cannot evolve in the complete absence of adaptability (Meeŭs et al. 1993) and must be considered at multiple scales (Mayor et al. 2009). Spatial scale is important to consider when studying habitat selection (Weins 1989). Assessing strategies (e.g., of residents versus migrants) on the landscape appears to be the appropriate scale at which to begin to understand migration.

Variation in densities of moose can also account for variation in their space use and habitat selection (Bremset Hansen et al. 2009), Moose at higher densities will select habitat differently, in part because they affect habitat quality more at higher density. To approximate local moose densities in the highlands and lowlands, the total area in habitat types strongly selected by moose, defined as having average selection likelihood >3.00 across all moose, could be substituted for total landscape area or forested area, resulting in a new density calculation. In the lowlands, if moose only used the forest stands selected in winter by the GPS-collared subset (herb, herb/hardwood, softwood mature and spruce closed forest), their density would be 20.6 moose/km^2, several times larger than the density across the landscape estimated in the 2007 survey (4.8 moose/km^2). If moose in the highlands only used those habitat types also selected in winter by the GPS-collared subset (shrub, tundra and fen), their density would be 1.7 moose/km^2, only slightly higher than the landscape density estimate (1.1 moose/km^2). A higher density of moose across a larger area of preferred habitat types in the lowlands seems consistent with habitat selection theory, where the variety or number of habitat types used by a population should increase with higher density (Pianka 1988).

Indirect competition for forage within the best habitat types and for the richest foraging patches in GMNP is likely stronger in the lowlands than in the highlands, as suggested both by the higher density of moose found in the lowlands and by the association of migrants with the lowland habitat type (the herb type) already heavily occupied by moose in winter. In the lowlands, moose also selected foraging patches supporting higher C:N ratios or lower quality forage than what was available to moose in the highlands. Migrant moose may move into the areas of poorer-quality habitat during the winter, due to snow inhibiting travel or reducing access to forage in the highlands. On the other hand, the highlands support high quality forage, at least during the sampling undertaken in July in this study, indicating that migration may be a favourable practice in the summer. In winter, travel distances for moose in the highlands were also lower, consistent with findings from Dussault et al. (2005a) in areas of Quebec, where available foraging patches similarly supported higher food quality. No differences were observed in the GMNP study between foraging and random locations within a given foraging patch, suggesting that moose occupy foraging patches that contain consistent site or forage quality. Random locations only 150 m and 300 m apart may not represent areas unavailable for foraging, and foraging patches are likely much larger than originally envisioned.

There was a consistently lower C:N ratio found in terminal branches of balsam fir, when only lateral and terminals were compared, and not nested into landscape and habitat type. This difference occurs because terminal branches are nitrogen sinks within the tree, as upward growth is important to competition for light in a forest. Lateral branches, then, should have more opportunity for variation in C:N ratio where nitrogen is a limiting factor. Highest damage from extensive moose browsing in some areas of North America coincides with high-nitrogen soils and low balsam fir density (Brandner et al. 1990, Thompson and Curran 1993). However, Albright and Keith (1987) observed that the highlands of Newfoundland offered poor nutrition for moose in the winter. In the GMNP study, moose occupied areas offering a better-quality winter diet in the highlands, based on C:N ratios measured in balsam fir branches. Plant phenology has been known to affect forage quality, such that the nitrogen content declines steadily after snowmelt (Crawley 1983). Migrant moose may be travelling to track a delayed plant phenology and get a higher return of nitrogen from their forage, as predicted by the forage maturation hypothesis (Fryxell 1991). In this study, no differences in stem densities were detected across the two landscapes, suggesting that moose in GMNP may be reducing the quantity of food in heavily browsed areas to levels that are very similar across the two landscapes. However, lack of difference may also be due to an inadequacy of stem density as a measure of actual forage biomass available seasonally. More winter foraging patches may have been predicted for the highlands only as a result of defining the patches based on moose travel distances, where deep snow inhibits long-distance travel.

Resource availability often changes according to season; therefore, resource selection functions were calculated separately for different seasons (Neilsen et al. 2003). Strong variation in summer and winter habitat selection in GMNP indicates different seasonal limiting factors for moose. In winter, moose preferred closed-canopy forests in the lowlands, likely because they offer better thermal cover to escape heat loss (McLaren et al. 2009). These closed-canopy forests may have less snow in the lowlands, resulting in easier locomotion and access to forage, consistent again with findings from Dussault et al. (2005b) in Quebec. There, the interpretation was that moose traded off food availability with the cost of travel in deep snow by decisions made at the landscape scale. Selection of open-canopy habitat types in the lowlands of GMNP, such as the herb and herb/hardwood forest types, could be explained by the need to occupy areas of highest-quality forage. On the other hand, moose overwintering in the highlands occupied open areas, possibly because compaction of snow by wind made movement easier compared to closed patches where snow may have been deeper. This interpretation contrasts original predictions and results from a previous study in GMNP, where twenty of twenty-one collared moose resident in the highlands travelled from open to forested stands during winter (McLaren et al. 2000). It is possible that the difference in winter habitat selection in GMNP occurs to reflect local climatic conditions or habitat availability, or it may be that the sample size of GPS-collared moose was too small to generalize. The sample with GPS collars also included only female moose, while McLaren et al. (2000) reported results from a juvenile and male moose among female moose with VHF collars.

In summer, avoidance of open habitat types occurs at the home-range scale for moose throughout the park, and at the core-use scale for moose resident in the lowlands. This pattern suggests that a reversal of the thermal environment takes place and moose seek shelter from heat in summer rather than seeking heat in winter, supporting original predictions. Seeking forest for predator avoidance is a less likely explanation, as predators of moose in GMNP are limited to black bear (*Ursus americanus* L.). It is also possible that moose in the lowlands move to closed forest in an attempt to escape disturbance from the presence of large numbers of human visitors to GMNP. At the core-use scale for moose occupying the highlands in summer, selection for fen and tundra may have been a result of a lower need to escape heat relative to the lowlands, or may have been a means of finding forage or escaping insects. Despite decades of work on density-dependent habitat selection (reviews in Rosenzweig 1981, 1991, Morris 2003), resource selection functions were calculated without specific regard to how differences in density contributed to variation in habitat selection; this shortfall of the study is typical of studies using GPS-collar data on just a few animals (McLoughlin et al. 2010).

Some moose in GMNP migrate from the relatively open highlands to the forested lowlands in winter. At least 17/76 VHF-collared moose monitored in GMNP concurrently with the GPS-collar study followed this migratory pattern (McLaren et al. 2000). The conditions favouring migration are common (Holt and Fryxell 2011), so it is not surprising that this strategy has evolved in moose. When populations are closely studied, a mix of migratory strategies is often observed (Lundberg 1988b). The prediction for GMNP would be that summer in the highlands offers an advantage to more moose than the number sustained in winter. The demographic costs of migration at GMNP are unlikely to include additional attack by predators than non-migrants would experience. Summer migration from the lowlands by adult female moose may be a means to avoid black bear predation on their calves, because the highlands may offer easier escape from this predator (McLaren et al. 2000). As a comparison, elk (*Cervus canadensis* Erxl.) migrating between high and low elevations in Alberta, were shown to avoid predation risks associated with resident elk (Hebblewhite and Merrill 2007; Hebblewhite et al. 2008). In GMNP, limited access to forage in winter created by large amounts of snow in the highlands may have led to evolution of the migratory strategy in moose (Coady 1974; Connor et al. 2000). It may be possible that moose overwinter in areas where population densities are higher, where they can benefit from the presence of other moose, travelling through areas of deeper snow packed down by successive travel that likely reduces the cost of locomotion (Pennyquick 1975, Telfer and Kelsall 1979).

In areas where snow is deep reducing the energy cost of travel may be more important than avoiding competition for food.

Moose densities in GMNP are on average 10 times higher than in other parts of their range in North America (Crête and Daigle 1999). High density is likely a result of few natural predators and lack of hunting pressure within the park. The occurrence of high moose densities significantly alters the landscape in Newfoundland (Thompson et al. 1992; McLaren et al. 2004). A maximum of 16 months of location data does not allow identification of changes to the classified habitat types that may have been as a result of high-density moose. While GPS locations of moose were recorded for this study during 1997-98, analysis of site quality in foraging patches was based on field work undertaken twelve years later. There is no evidence that the foraging patches predicted from the GPS records are not used by moose presently. The utility of C:N in comparing the quality of food between landscapes is high. In the future, monitoring forage abundance at the same temporal scale at which moose foraging occurs would be useful. Quantity of forage combined with measurement of C:N ratios could be useful in defining finer-scale habitat selection by moose. Future studies might also focus on habitat selection with further changes to habitat quality created by increasing or decreasing moose density, including through experimental reductions or exclosures. New collars deployed on moose in GMNP during winter 2011 may provide insight on how changes in density can affect habitat selection (Tom Knight, personal communication). Specific attention should also be given to how the migratory landscape-use strategy may change if densities of moose are changed. Currently, a conclusion from this study is that moose wintering on the lowlands may be a source population for moose on the highlands, and it is now based on a tested assumption of density-dependent habitat selection.

MANAGEMENT CONSIDERATIONS

Similarities among moose occupying the highlands and the lowlands of GMNP include home-range sizes, annual distances travelled, distances travelled between foraging patches, and habitat selection for migrants and residents in the same landscape during the same season. Some of the differences include forage quality as estimated by C:N ratio in balsam fir branches and weekly distance travelled by moose. C:N ratios were higher for the lowlands than the highlands, suggesting that the highlands offer higher soil fertility and richer foraging opportunities.

Examining habitat selection is a way to assess the importance of different habitats for a species (Mayor et al. 2009). In the case of GMNP, it is recommended that moose management consider two landscapes (the lowlands and the highlands) as separate management units for moose due to differences in the habitat types they offer to moose and in the densities of moose they support. In a park management plan, connectivity should be ensured for migrating moose to move between the highlands and the lowlands. While individual habitat selection models are difficult to extrapolate to larger moose populations, assessment of other aspects of home ranges suggests differences may be less apparent within landscapes than across them. On this note, management across Newfoundland that is both effective and adaptable need not be on different groups of moose, but on the different landscapes offered to moose.

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APPENDED TABLES AND FIGURES

Table A1. Analysis of deviance table for models of habitat use. N is the number of collared moose in the model, n the number of locations included in the model. Resource selection functions used are bolded and were constructed from log-linear models. Model significance was calculated by comparing the change in deviance (Δ D) between successive models listed using a Chi-squared distribution for the appropriate degrees of freedom (df). Akaike's Information Criteria (AIC) are shown for each model step using individual moose as the sampling unit.

Model	Deviance	df	AIC	Δ D	df	*p*
a. Habitat selection varies in winter and summer for moose resident in the lowlands (N = 5, summer n = 3,765, winter n=2,013)						
No selection of habitats	4,606.63	110	5,255.00	-	-	-
Constant selection of habitat	2,486.04	101	3,152.41	2120.59	9	<0.001
Selection varies by season	**1,694.37**	**92**	2,378.74	791.67	9	**<0.001**
Selection varies among moose	2,486.04	65	3,152.41	0	0	-
Selection varies among moose and by season (Full model)	1,694.73	56	2,378.74	791.31	9	<0.001
b. Habitat selection varies in winter and summer for moose resident in the lowlands based on core-use areas (N = 5, summer n = 1,485, winter n= 1,679)						
No selection of habitats	3,285.98	110	3,823.55	-	-	-
Constant selection of habitat	2,007.82	100	2,565.39	1,278.16	10	<0.001
Selection varies by season	**1,539.14**	**91**	2,114.71	468.68	9	**<0.001**
Selection varies among moose	1,507.04	64	2,136.61	500.78	36	<0.001
Selection varies among moose and by season	1,101.94	55	1,749.51	405.10	9	<0.001
c. Habitat selection varies in winter for migrants and residents occupying the lowlands together (resident N = 5, n = 2,013; migrant N = 2, n = 1,018)						
No selection of habitats	2,169.71	63	2,528.85	-	-	-
Constant selection of habitat	1,137.83	54	1,514.98	1,031.87	9	<0.001
Selection varies by migrants	**885.81**	**45**	1,280.95	252.02	9	**<0.001**
Selection varies among moose	1,529.35	50	2,297.72	-391.51	4	N/A

Table A1. (continued)

Model	Deviance	df	AIC	Δ D	df	*p*
d. Habitat selection varies in winter and summer for moose resident in the highlands (N = 4, summer n = 2,954, winter n = 1,914)						
No selection of habitats	2,414.58	32	2,659.2	-	-	-
Constant selection of habitat	664.26	28	916.89	1,750.31	4	<0.001
Selection varies by season	**405.00**	**24**	665.62	259.27	4	**<0.001**
Selection varies among moose	300.04	16	576.67	364.22	12	<0.001
Selection varies among moose and by season	88.38	12	373.00	211.66	4	<0.001
e. Habitat selection varies in winter and summer for moose resident in the highlands, based on core-use areas (N = 3, summer n = 1,609, winter n=1,619)						
No selection of habitats	1,807.02	24	1,980.44	-	-	-
Constant selection of habitat	348.68	20	530.09	1,458.34	4	<0.001
Selection varies by season	**231.02**	**16**	420.43	117.67	4	**<0.001**
Selection varies among moose	187.59	12	385.00	161.09	8	<0.001
Selection varies among moose and by season	56.78	8	262.2	130.80	4	<0.001
f. Habitat selection varies in summer for migrants and residents occupying the highlands together (resident N = 5, n = 3,252; migrant N = 2, n = 919)						
No selection of habitats	1,505.03	28	1,734.52	-	-	-
Constant selection of habitat	411.50	24	648.99	1,093.53	4	<0.001
Selection varies by migrants	**344.46**	**20**	589.95	67.03	4	**<0.001**
Selection varies among moose	0.00	0	285.49	411.5	24	<0.001

Table A2. Relative selection probabilities for individual moose, comparing habitat use in winter and summer of moose resident in the lowlands of Gros Morne National Park, based on 95% isopleth kernel (ΔD1) and 50% isopleth kernel (ΔD2) estimates of core areas in their home ranges and landscape coverage of habitat types listed in Table 1. Selection probabilities were derived from parameters in the resource selection functions constructed for individual moose for which habitat selection varied significantly (Table A1). The reference habitat type was softwood open forest, which has a relative selection probability of 1. Asterisks indicate cases where probabilities are derived from significant parameter estimates ($p < 0.05$).

Moose	ΔD Model diagnostics	Season	Kernel	Softwood closed mature	Spruce closed	Mixed closed	Softwood closed young	Hardwood open mature	Herb/ hardwood	Herb	Mixed open	Softwood sparse
15	ΔD1 = 125.91; $p < 0.001$	S	95	0.810	5.409*	1.400	*1.616	0.940	0.725*	0.160*	0.682*	0.560*
		W	95	8.457*	4.297*	2.829*	3.955*	2.075*	2.312*	4.870*	2.212*	2.410*
	ΔD2 = 37.93; $p < 0.001$	S	50	4.116*	4.267*	2.018*	2.754*	0.790	1.270	0.176*	0.533*	0.405*
		W	50	1.576	9.034*	2.980*	3.165*	2.759*	-	3.463*	2.465*	3.127*
16	ΔD1 = 486.34; $p < 0.001$	S	95	1.108	2.560*	1.811*	1.976*	0.635*	0.392*	0.238*	0.433*	0.386*
		W	95	5.551*	1.889*	4.993*	0.519*	4.166*	19.434*	94.538*	3.401*	10.87*
	ΔD2 = 416.62 ; $p < 0.001$	S	50	10.433*	5.254*	10.412	3.572	0.618	0.241*	0.157*	0.299*	0.112*
		W	50	0.526	3.158	0.316	0.210*	3.991*	73.995*	-	6.488*	50.400*

Table A2. (continued)

Moose	ΔD Model diagnostics	Season	Kernel	Softwood closed mature	Spruce closed	Mixed closed	Softwood closed young	Hardwood open mature	Herb/hardwood	Herb	Mixed, open	Softwood sparse
19	$\Delta D1 = 17.69$; $p = 0.039$	S	95	1.525	7.286*	1.831	2.442	0.973	0.357*	0.191*	0.681	1.415
		W	95	-	-	-	1.126	0.547	0.658	0.859	0.803	0.618
	$\Delta D2 = 6.13$; $p < 0.727$	S	50	5.871	5.382	5.507	2.748	0.834	0.344*	0.226	0.745	0.662
		W	50	-	-	-	1.996	1.006	1.029	0.850	1.347	1.759
25	$\Delta D1 = 249.87$; $p < 0.001$	S	95	2.686*	1.672*	2.052*	2.085*	0.506*	0.249*	0.567*	0.715*	1.401
		W	95	0.811	5.244*	2.030*	1.490	1.935*	4.840*	2.904*	1.293	0.453*
	$\Delta D2 = 169.01$; $p < 0.001$	S	50	-	2.413	-	2.266*	0.443*	0.276*	1.086	0.483*	0.612*
		W	50	0.00	4.336*	<0.001	1.483	0.379*	6.488*	1.323	2.522*	0.956
26	$\Delta D1 = 26.28$; $p = 0.002$	S	95	2.363*	1.690	1.876*	1.018	0.390*	0.226*	0.298*	0.576*	1.332
		W	95	1.606	-	0.928	1.242	0.389	0.537	0.385	1.438	0.265*
	$\Delta D2 = 47.62$; $p < 0.001$	S	50	7.345	2.430	2.462	0.590	0.211*	0.179*	0.406*	0.253*	0.360*
		W	50	-	-	-	-	-	-	-	-	-

Table A3. Relative selection probabilities for individual moose, comparing habitat use in winter and summer for moose resident in the highlands of Gros Morne National Park, based on 95% isopleth kernels (ΔD1) and 50% isopleth kernels (ΔD2) estimates of core areas in their home ranges and landscape coverage of habitat types listed in Table A1. Selection probabilities were derived from parameters in the resource selection functions constructed for individual moose for which habitat selection varied significantly (Table A2). The reference habitat was softwood open forest - scrub closed, which has a relative selection probability of 1. Asterisks indicate cases where probabilities are derived from significant parameter estimates ($p < 0.05$).

Moose ID	ΔD Model diagnostics	Season	Kernel	Scrub open	Shrub	Tundra	Fen
17	ΔD1 = 166.56; $p < 0.001$	S	95	0.774	0.862	1.726*	5.414*
		W	95	1.413*	4.609*	2.197*	9.217*
	ΔD2 = 101.63 ; $p < 0.001$	S	50	1.245*	1.545*	3.357*	7.768*
		W	50	1.716*	2.962	1.172	-
20	ΔD1 = 87.38; $p < 0.001$	S	95	0.443*	0.246*	0.306*	0.697
		W	95	4.140*	7.800*	43.51*	40.085*
		S	50	-	-	-	-
		W	50	-	-	-	-
23	ΔD1 = 20.80; $p < 0.001$	S	95	0.773*	1.338*	1.163	58.674*
		W	95	1.464*	1.545*	1.900*	0.708
	ΔD2 = 56.50 ; $p < 0.001$	S	50	0.668*	1.085	1.058	4.914*
		W	50	2.568*	2.375*	2.358*	6.896*
24	ΔD1 = 25.30; $p < 0.001$	S	95	0.799*	2.440*	2.337*	84.945*
		W	95	1.200	2.591*	7.614*	-
	ΔD2 = 29.46; $p < 0.001$	S	50	0.715*	7.637*	1.639*	-
		W	50	1.189	-	8.466*	-

Table A4. Relative selection probabilities for individual moose, comparing habitat use by residents and migrants during winter in the lowlands of Gros Morne National Park, based on frequency of locations within the 95% isopleth kernels (ΔD1) estimate of their home ranges and landscape coverage of habitat types listed in Table A1. Probabilities were derived from parameters in the resource selection functions constructed for individual moose for which habitat selection varied significantly (Table A2). The reference habitat was softwood open forest, which has a relative selection probability of 1. Asterisks indicate cases where probabilities are derived from significant parameter estimates ($p < 0.05$). Moose 15, 16, 19, 25 and 26 are residents. Moose 21 and 22 are migrants. Strategies are identified in Table 3.

Strategy	Moose ID	Model diagnostics	Softwood, closed	Softwood (spruce), closed	Mixed closed	Softwood, closed (immature)	Hardwood, open, mature	Herb/ hardwood	Herb	Mixed open	Softwood sparse
L	15	ΔD1 = 374.51; $p < 0.001$	6.883*	23.243*	3.963*	6.398*	1.958*	1.674*	0.773*	1.510*	1.350*
L	16	ΔD1 = 448.26; $p < 0.001$	6.153*	4.831*	9.043*	1.026	2.646*	7.614*	22.488*	1.474*	4.191*
L	19	ΔD1 = 448.26; $p < 0.001$	-	-	-	2.751	0.533	0.235*	0.169*	0.666	0.874
M	21	ΔD1 = 374.51; $p < 0.001$	7.553*	12.280*	3.784*	2.522*	5.436*	18.578*	9.593*	3.480*	7.599*
M	22	ΔD1 = 448.26; $p < 0.001$	4.428*	2.716*	6.110*	3.854*	1.493*	3.387*	4.092*	0.494*	0.834
L	25	ΔD1 = 374.51; $p < 0.001$	2.177*	8.767*	4.175*	3.105*	0.811	1.207	1.645*	0.924	0.635*
L	26	ΔD1 = 448.26; $p < 0.001$	3.792	-	1.853	1.265	0.152*	0.122*	0.115*	0.828	0.353

Table A5. Relative selection probabilities for individual moose, comparing habitat use by residents and migrants during the summer in the highlands of Gros Morne National Park, based on frequency of locations within the 95% isopleth kernels (ΔD1) estimates of their home ranges and landscape coverage of habitat types listed in Table 2. Selection probabilities were derived from parameters in the resource selection functions constructed for individual moose for which habitat selection varied significantly (Table 8). The reference habitat was softwood open forest - scrub closed, which has a relative selection probability of 1. Asterisks indicate cases where probabilities are derived from significant parameter estimates ($p < 0.05$). Strategies are identified in Table 3.

Strategy	Moose ID	Model diagnostics	Scrub open	Shrub	Tundra	Fen
H	17	ΔD1 = 301.75; $p < 0.001$	0.918	1.020	2.147*	7.822*
H	18	ΔD1 = 66.55; $p < 0.001$	0.586*	0.603*	0.698	3.655*
H	20	ΔD1 = 97.51; $p < 0.001$	0.624*	0.332*	0.419*	1.011
M	21	ΔD1 = 161.87; $p < 0.001$	0.735*	2.121*	1.083	27.385*
M	22	ΔD1 = 271.14; $p < 0.001$	1.018	2.168*	3.589*	37.151*
H	23	ΔD1 = 243.02; $p < 0.001$	0.773*	1.338*	1.163	8.037*
H	24	ΔD1 = 363.19; $p < 0.001$	0.799	2.440*	2.337*	84.945*

Table A6. Weekly movements' comparison by season (factor1) and the interaction of season and strategy (group), with repeated measures with season as repeat.

Tests of Within-Subjects Effects

Measure:MEASURE_1

Source		Type III Sum of Squares	df	Mean Square	F	Sig.
factor1	Sphericity	1.142E9	1	1.142E9	106.346	.000
	Greenhouse-	1.142E9	1.000	1.142E9	106.346	.000
	Huynh-Feldt	1.142E9	1.000	1.142E9	106.346	.000
	Lower-bound	1.142E9	1.000	1.142E9	106.346	.000
factor1 * Group	Sphericity	1.619E7	2	8097402.500	.754	.472
	Greenhouse-	1.619E7	2.000	8097402.500	.754	.472
	Huynh-Feldt	1.619E7	2.000	8097402.500	.754	.472
	Lower-bound	1.619E7	2.000	8097402.500	.754	.472
Error(factor1)	Sphericity	1.589E9	148	1.074E7		
	Greenhouse-	1.589E9	148.000	1.074E7		
	Huynh-Feldt	1.589E9	148.000	1.074E7		
	Lower-bound	1.589E9	148.000	1.074E7		

Table A7. Weekly movement's comparison by ecosystem group (repeated measures).

Tests of Between-Subjects Effects

Measure:MEASURE_1
Transformed Variable:Average

Source	Type III Sum of Squares	df	Mean Square	F	Sig.
Intercept	9.349E9	1	9.349E9	963.000	.000
Group	1.291E8	2	6.455E7	6.649	.002
Error	1.437E9	148	9708235.885		

Table A8. ANOVA results for distance between foraging patches by season and by strategy (group) and season.

Tests of Within-Subjects Contrasts

Measure:MEASURE_1

Source	Season		Type III Sum of Squares	df	Mean Square	F	Sig.
Season	dimension2	Linear	36.276	1	36.276	8.047	.005
Season * Group	dimension2	Linear	.676	2	.338	.075	.928
Error(Season)	dimension2	Linear	540.948	120	4.508		

Table A9. ANOVA results for distances between foraging patches according to landscape strategy (MEASURE_1).

Univariate Tests

Measure:MEASURE_1

	Sum of Squares	df	Mean Square	F	Sig.
Contrast	.047	2	.023	.010	.990
Error	292.050	120	2.434		

The F tests the effect of Group. This test is based on the linearly independent pairwise comparisons among the estimated marginal means.

Table A10. ANOVA results for densities of potential foraging types for lowlands.

Univariate Tests

Dependent Variable		Sum of Squares	df	Mean Square	F	Sig.
Balsam	Contrast	1.822E7	10	1822320.448	.606	.793
	Error	6.916E7	23	3006766.046		
B. Spruce	Contrast	4628224.090	10	462822.409	1.014	.461
	Error	1.049E7	23	456215.321		
Alder	Contrast	1476033.613	10	147603.361	.579	.814
	Error	5865142.857	23	255006.211		
W.birch	Contrast	3391389.356	10	339138.936	1.007	.466
	Error	7743904.762	23	336691.511		
W. spruce	Contrast	358980.392	10	35898.039	.678	.734
	Error	1218666.667	23	52985.507		

The F tests the effect of Habitat. This test is based on the linearly independent pairwise comparisons among the estimated marginal means.

Table A11. ANOVA results for densities of potential foraging items for highlands.

Univariate Tests

Dependent Variable		Sum of Squares	df	Mean Square	F	Sig.
Balsam	Contrast	2.529E7	5	5058276.923	1.618	.201
	Error	6.254E7	20	3127200.000		
Willow	Contrast	1.256E7	5	2512656.410	.619	.687
	Error	8.114E7	20	4057066.667		
Black spruce	Contrast	982461.538	5	196492.308	.653	.663
	Error	6016000.000	20	300800.000		
scrub birch	Contrast	161538.462	5	32307.692	.808	.558
	Error	800000.000	20	40000.000		

The F tests the effect of Habitat. This test is based on the linearly independent pairwise comparisons among the estimated marginal means.

Table A12. Repeated ANOVA results for comparing lateral and terminal branches, nested in landscape (refer to factor *latera1 1terminal2 for the model of interest.

Multivariate Tests[c]

factor	Pillai's Trace	.994	6527.320[a]	2.000	76.000	.000
	Wilks' Lambda	.006	6527.320[a]	2.000	76.000	.000
	Hotelling's Trace	171.772	6527.320[a]	2.000	76.000	.000
factor * IDSPSS	Pillai's Trace	.374	1.365	26.000	154.000	.127
	Wilks' Lambda	.658	1.363[a]	26.000	152.000	.128
	Hotelling's Trace	.472	1.360	26.000	150.000	.130
factor * Lowlands1highlands2	Pillai's Trace	.000	.[a]	.000	.000	.
	Wilks' Lambda	1.000	.[a]	.000	76.500	.
	Hotelling's Trace	.000	.[a]	.000	2.000	.
factor * lateral1terminal2	Pillai's Trace	.275	14.404[a]	2.000	76.000	.000
	Wilks' Lambda	.725	14.404[a]	2.000	76.000	.000
	Hotelling's Trace	.379	14.404[a]	2.000	76.000	.000
factor * IDSPSS * Lowlands1highlands2	Pillai's Trace	.000	.[a]	.000	.000	.
	Wilks' Lambda	1.000	.[a]	.000	76.500	.
	Hotelling's Trace	.000	.[a]	.000	2.000	.
factor * IDSPSS * lateral1terminal2	Pillai's Trace	.167	.538	26.000	154.000	.967
	Wilks' Lambda	.840	.531[a]	26.000	152.000	.970
	Hotelling's Trace	.182	.525	26.000	150.000	.972
	Roy's Largest Root	.102	.602[b]	13.000	77.000	.846
factor * Lowlands1highlands2 * lateral1terminal2	Pillai's Trace	.000	.[a]	.000	.000	.
	Wilks' Lambda	1.000	.[a]	.000	76.500	.
	Hotelling's Trace	.000	.[a]	.000	2.000	.
factor * IDSPSS * Lowlands1highlands2 * lateral1terminal2	Pillai's Trace	.000	.[a]	.000	.000	.
	Wilks' Lambda	1.000	.[a]	.000	76.500	.
	Hotelling's Trace	.000	.[a]	.000	2.000	.
	Roy's Largest Root	.000	.000[a]	2.000	75.000	1.000

a. Exact statistic

b. The statistic is an upper bound on F that yields a lower bound on the significance level.

c. Design: Intercept + IDSPSS + Lowlands1highlands2 + lateral1terminal2 + IDSPSS * Lowlands1highlands2 + IDSPSS * lateral1terminal2 + Lowlands1highlands2 * lateral1terminal2 + IDSPSS * Lowlands1highlands2 * lateral1terminal2

Within Subjects Design: factro

Table A13. Terminal branch comparison of C:N between lowlands and highlands.

Tests of Between-Subjects Effects

Dependent Variable:C:N Ratio

Source	Type III Sum of Squares	df	Mean Square	F	Sig.
Corrected Model	409.721[a]	1	409.721	10.838	.004
Intercept	12634.926	1	12634.926	334.212	.000
Lateral1terminal2	.000	0	.	.	.
Lowlands1Highland2	409.721	1	409.721	10.838	.004
Foragingsite1random2	.000	0	.	.	.
Lateral1terminal2 * Lowlands1Highland2	.000	0	.	.	.
Lateral1terminal2 * Foragingsite1random2	.000	0	.	.	.
Lowlands1Highland2 * Foragingsite1random2	.000	0	.	.	.
Lateral1terminal2 * Lowlands1Highland2 * Foragingsite1random2	.000	0	.	.	.
Error	680.493	18	37.805		
Total	15216.692	20			
Corrected Total	1090.215	19			

a. R Squared = .376 (Adjusted R Squared = .341)

Table A14. Lateral branch comparison of C:N between lowlands and highlands.

Tests of Between-Subjects Effects

Dependent Variable:C:N Ratio

Source	Type III Sum of Squares	df	Mean Square	F	Sig.
Corrected Model	302.886[a]	1	302.886	9.203	.007
Intercept	18429.191	1	18429.191	559.972	.000
Lateral1terminal2	.000	0	.	.	.
Lowlands1Highland2	302.886	1	302.886	9.203	.007
Foragingsite1random2	.000	0	.	.	.
Lateral1terminal2 * Lowlands1Highland2	.000	0	.	.	.
Lateral1terminal2 * Foragingsite1random2	.000	0	.	.	.
Lowlands1Highland2 * Foragingsite1random2	.000	0	.	.	.
Lateral1terminal2 * Lowlands1Highland2 * Foragingsite1random2	.000	0	.	.	.
Error	625.307	19	32.911		
Total	20436.731	21			
Corrected Total	928.193	20			

a. R Squared = .326 (Adjusted R Squared = .291)

Table A15. ANOVA results of C:N for lateral branches comparison of foraging and random locations.

Tests of Between-Subjects Effects

Dependent Variable:C:N Ratio

Source	Type III Sum of Squares	df	Mean Square	F	Sig.
Corrected Model	5.439[a]	1	5.439	.096	.758
Intercept	53092.064	1	53092.064	934.052	.000
Foragingsite1random 2	5.439	1	5.439	.096	.758
Error	3467.277	61	56.841		
Total	63604.993	63			
Corrected Total	3472.716	62			

a. R Squared = .002 (Adjusted R Squared = -.015)

Table A16. ANOVA results of C:N for terminal branches comparison of foraging and random locations.

Tests of Between-Subjects Effects

Dependent Variable:C:N Ratio

Source	Type III Sum of Squares	df	Mean Square	F	Sig.
Corrected Model	57.544[a]	1	57.544	1.080	.303
Intercept	40341.042	1	40341.042	757.401	.000
Foragingsite1random 2	57.544	1	57.544	1.080	.303
Error	3035.961	57	53.262		
Total	49203.722	59			
Corrected Total	3093.505	58			

a. R Squared = .019 (Adjusted R Squared = .001)

Table A17. ANOVA results for C:N lateral comparisons between habitats of the lowlands.

Tests of Between-Subjects Effects

Dependent Variable:c_n

Source	Type III Sum of Squares	df	Mean Square	F	Sig.
Corrected Model	607.731[a]	8	75.966	1.723	.154
Intercept	21993.878	1	21993.878	498.967	.000
habitats	607.731	8	75.966	1.723	.154
Error	881.577	20	44.079		
Total	36025.881	29			
Corrected Total	1489.308	28			

a. R Squared = .408 (Adjusted R Squared = .171)

Table A18. ANOVA results for laterals C:N comparisons between habitats of the highlands.

Tests of Between-Subjects Effects

Dependent Variable:c_n

Source	Type III Sum of Squares	df	Mean Square	F	Sig.
Corrected Model	204.272[a]	5	40.854	1.438	.254
Intercept	10538.826	1	10538.826	371.073	.000
habitat	204.272	5	40.854	1.438	.254
Error	568.019	20	28.401		
Total	19099.225	26			
Corrected Total	772.291	25			

a. R Squared = .265 (Adjusted R Squared = .081)

Table A19. ANOVA results for C:N terminal comparisons between habitats of the lowlands.

Tests of Between-Subjects Effects

Dependent Variable:c_n

Source	Type III Sum of Squares	df	Mean Square	F	Sig.
Corrected Model	303.307[a]	8	37.913	.869	.558
Intercept	17932.887	1	17932.887	410.880	.000
habitat	303.307	8	37.913	.869	.558
Error	872.900	20	43.645		
Total	29918.707	29			
Corrected Total	1176.208	28			

a. R Squared = .258 (Adjusted R Squared = -.039)

Table A20. ANOVA results for C:N terminal comparisons between habitats of the highalnds .

Tests of Between-Subjects Effects

Dependent Variable:c_n

Source	Type III Sum of Squares	df	Mean Square	F	Sig.
Corrected Model	143.309[a]	5	28.662	.825	.549
Intercept	6344.320	1	6344.320	182.673	.000
habitats	143.309	5	28.662	.825	.549
Error	590.418	17	34.730		
Total	12504.270	23			
Corrected Total	733.727	22			

a. R Squared = .195 (Adjusted R Squared = -.041)

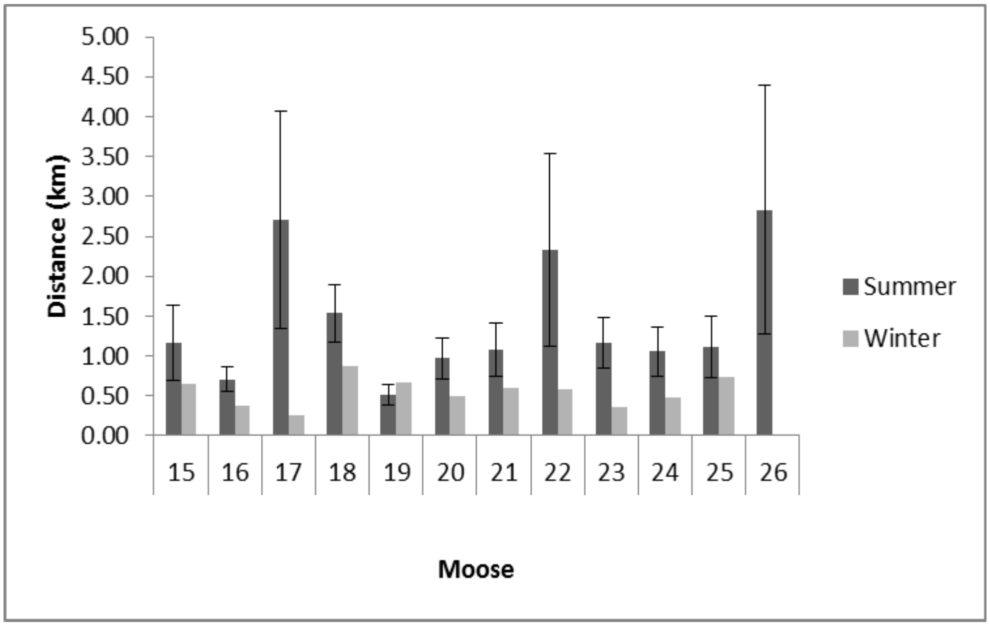

Figure A1. Distances (km) travelled between foraging patches by moose in winter and summer. Error bars show the standard errors.

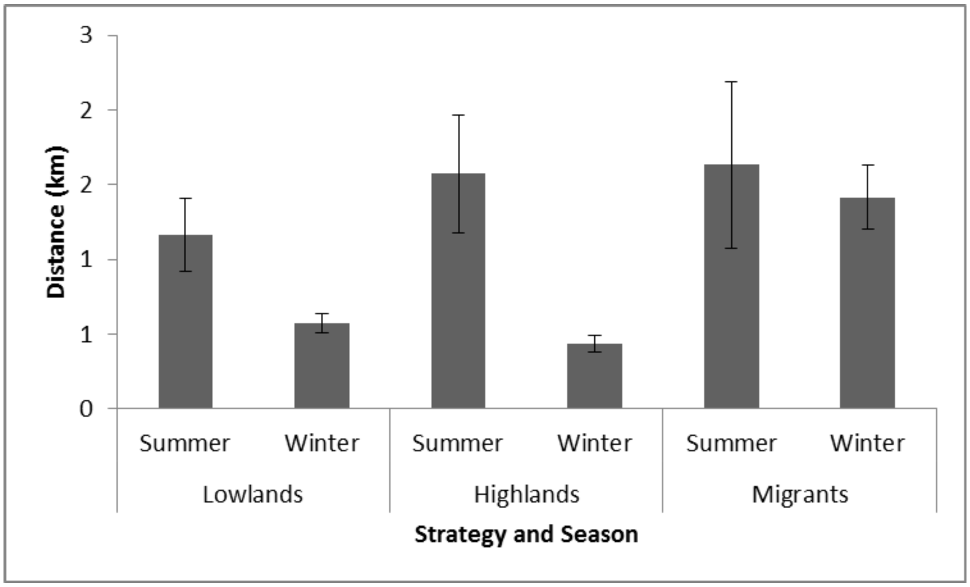

Figure A2. Distances (km) travelled between foraging patches by moose, according to strategy, in summer and winter. Strategies are identified in Table 3. Error bars show the standard error.

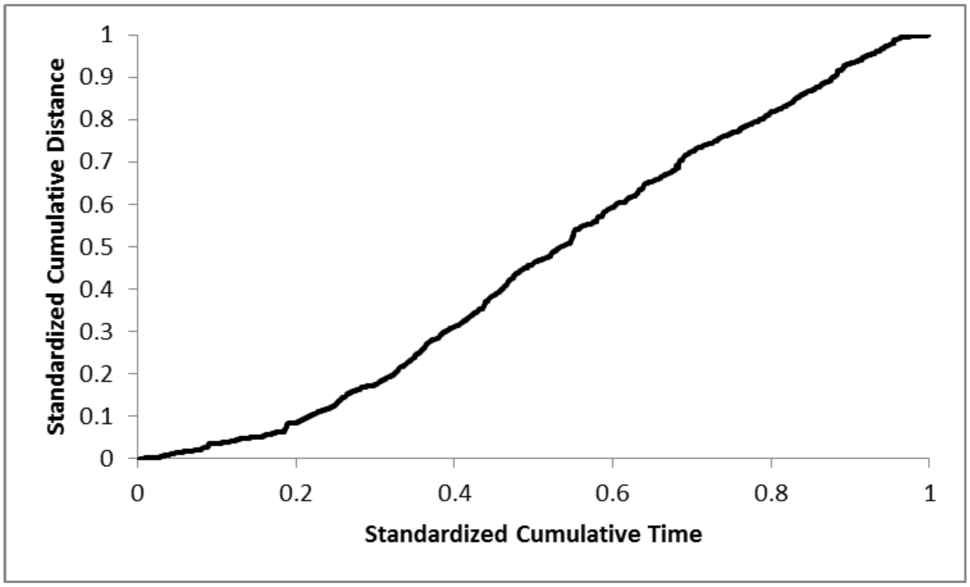

Figure A3. The movement rate of moose 15 (lowland moose) in the study based on the standardized cumulative movement and the standardized cumulative distance.

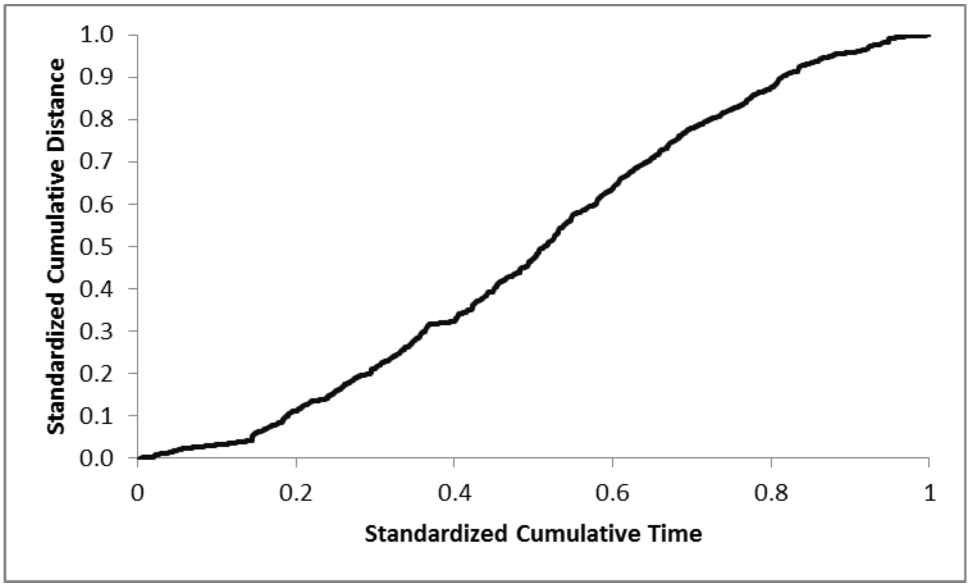

Figure A4. The movement rate of moose 16 (lowland moose) in the study based on the standardized cumulative movement and the standardized cumulative distance.

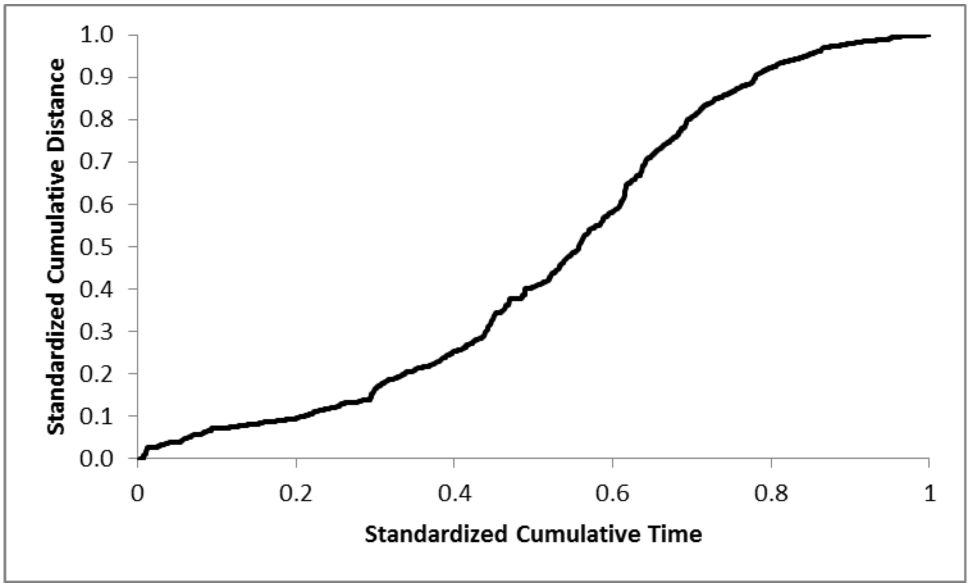

Figure A5. The movement rate of moose 17 (highland moose) in the study based on the standardized cumulative movement and the standardized cumulative distance.

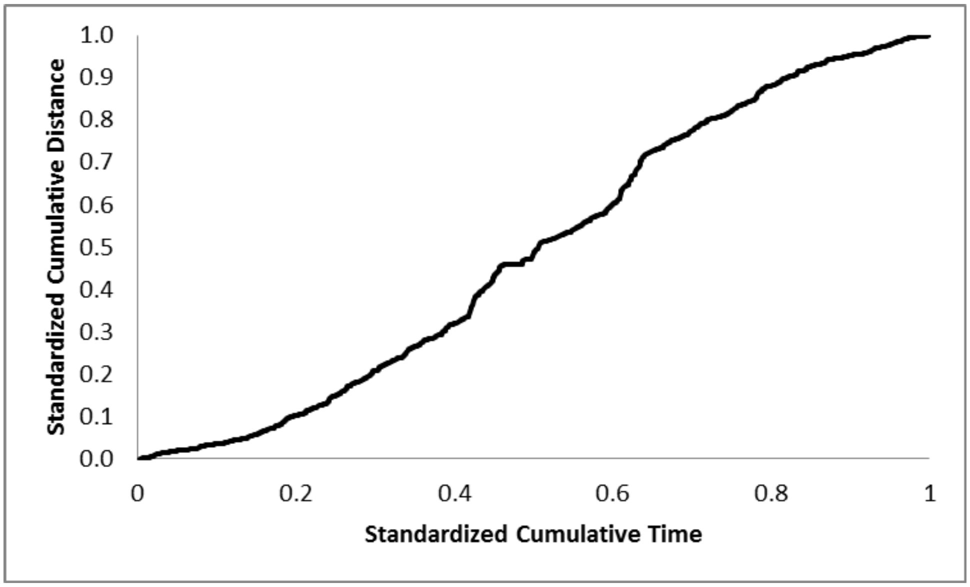

Figure A6. The movement rate of moose 22 (migrant moose) in the study based on the standardized cumulative movement and the standardized cumulative distance.

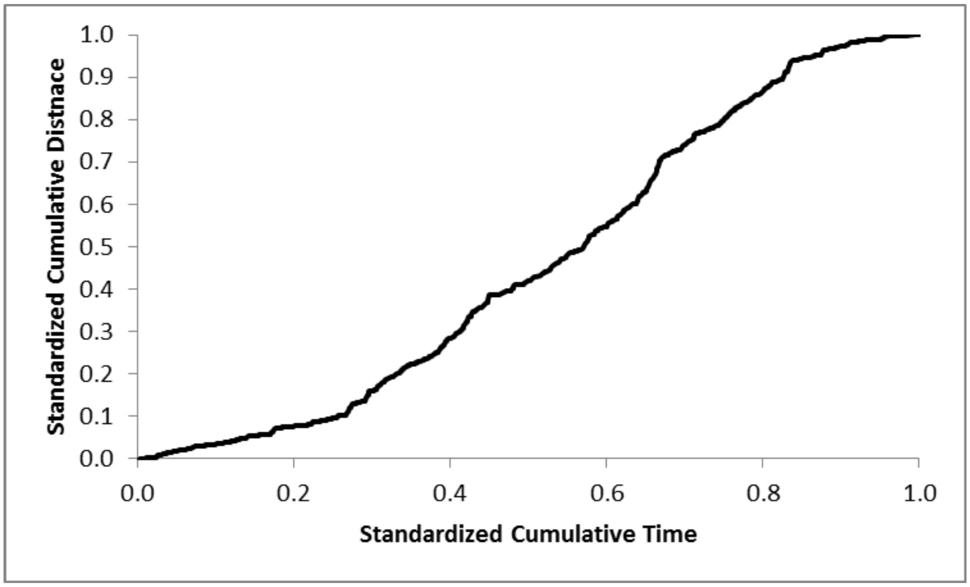

Figure A7. The movement rate of moose 23 (highland moose) in the study based on the standardized cumulative movement and the standardized cumulative distance.

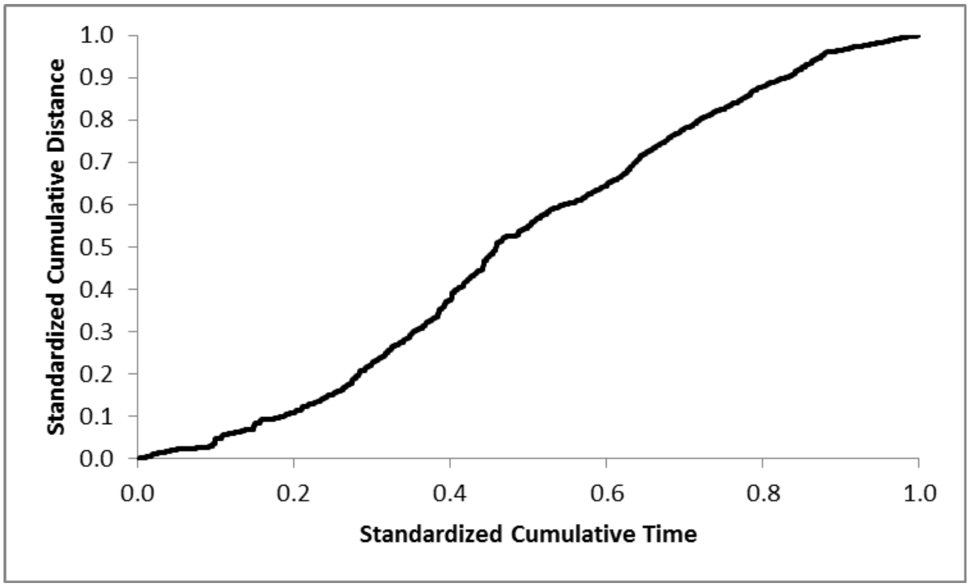

Figure A8. The movement rate of moose 25 (lowland moose) in the study based on the standardized cumulative movement and the standardized cumulative distance.