MOOSE HABITAT USE THROUGHOUT GROS MORNE NATIONAL PARK

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ABSTRACT: Previous research indicated high variability in availability and habitat use by female moose in the lowlands of Gros Morne National Park (GMNP), Newfoundland and Labrador, an area dominated by bogs and forest. Here, we extend the earlier analysis with an additional 7 female moose (*Alces alces americana*) occupying the Park highlands, a region dominated by heath and shrub vegetation with forest limited to sheltered valleys, typical of interior and highland parts of the province. Resource selection function (RSF) models with differences in habitat use between moose resident in the 2 regions and 2 moose that migrated from the lowlands in winter to the highlands in summer were rejected. In summer, more use of closed-canopy forest types occurred on the lowlands, while more use of non-forest habitat types occurred on the highlands. As before, we found that selection of disturbed forest is a winter phenomenon on the lowlands of GMNP; the same series of habitat types associated with disturbance were avoided in summer. Summer migration by about 20% of GMNP moose to the highlands suggests that foraging opportunities are better during that season than in winter, a motivation for migration perhaps augmented by an overabundance of moose on the lowlands and unfavourable temperatures in disturbed areas that might otherwise serve as lowland foraging areas. An observation of more clustered relocations of moose on the highlands than on the lowlands of GMNP is consistent with our conclusion that moose use habitats within the highlands and lowlands of Newfoundland and Labrador very differently. We recommend 2 approaches to moose management for these different landscapes, both within GMNP and elsewhere in Newfoundland and Labrador.

ALCES VOL. 49: 1–13 (2013)

Key words: Gros Morne National Park, habitat selection, moose, Newfoundland and Labrador, resource selection functions.

According to habitat selection theory (Fretwell and Lucas 1970), individuals distribute themselves in a manner proportional to the quantity or quality of limiting resources available in each of several foraging patches, larger habitat units, and still larger landscapes. For ungulates, habitat selection should be driven by an individual's ability to sense and select higher-quality food items or foraging areas (McNaughton 1985, Fryxell 1991). Habitat selection that involves migration between 2 different landscapes can arise in a seasonal climate where different fitness opportunities (or forage availability) are offered by each landscape, but where the difference is less during the growing season (Holt and Fryxell 2011). Moose (*Alces alces americana*) in Newfoundland and Labrador, Canada presumably distribute themselves optimally according to habitat selection theory in each of 2 typical landscapes in this province, the "highlands" and the "lowlands." We explore this idea with analysis of summer and winter location data from GPS-collared moose, using the assumption that more forested, lowland landscapes are, on average (i.e., throughout the year), superior to the highlands where some moose migrate during summer.

This paper is motivated by previous study of Gros Morne National Park (GMNP), an area of 1,805 km^2 in western Newfoundland, where approximately 20% of the female moose population migrates within the Park from forested, coastal lowlands (< 400 m above sea level) in winter to relatively open highlands (between 400 and 800 m) during summer (McLaren et al. 2000). Our interpretation is that spending summer in a highland landscape offers an advantage to this fraction of the moose population. We compared seasons of activity of the resident moose in the highlands and lowlands of GMNP, and described their finer-scale activity in terms of frequency of smaller movements and the densities in which these smaller movement clusters occur throughout, by comparing the 2 landscapes.

During winter, snow limits accessibility to forage more on the highlands than in the coastal lowlands (Martin 2004), a motivation for migration that is consistent with empirical evidence from other studies of moose (reviewed by Ball et al. 2001). As an additional explanation for the moose migration within GMNP, as suggested in McLaren et al. (2000), summer migration from the lowlands may be a means to avoid black bear (*Ursus americana*) predation on calves, because the highlands may offer easier escape from this predator given the longer sightlines in open habitats. This second idea would be similar to the explanation for why woodland caribou (*Rangifer tarandus caribou*) often migrate up mountain slopes (Bergerud et al. 1984), and for why elk (*Cervus canadensis*) migrate between high and low elevations in Alberta (Hebblewhite and Merrill 2007, Hebblewhite et al. 2008). However, because moose densities are about tenfold higher in Newfoundland than in other parts of their range in North America (McLaren et al. 2004), creating obvious effects on hampering regeneration in the forests of the coastal plain of GMNP (Connor et al. 2000, McLaren et al. 2004, Gosse et al. 2011, Humber and Hermanutz 2011), and because only a fraction of the population migrates, we favour limited forage availability in the lowlands as the primary factor for summer moose migration. To explore this hypothesis, which is consistent with the Holt and Fryxell (2011) model for migration, we compare the frequency of the fine-scale summer movement on the lowlands and the highlands, and compare resource selection functions (RSFs) for highland and lowland moose in GMNP.

STUDY AREA

GMNP is located on the Gulf of the St. Lawrence on the northern peninsula of Newfoundland. Its lowlands, which encompass parts of the Western Newfoundland Forest and the Coastal Plain sub-region of the Northern Peninsula Forest (Damman 1983), are characterized by weather influences from the Gulf, producing moderate levels of annual precipitation (900–1000 mm) and cold and snowy winters (300–350 mm is in the form of snow; Hare 1952). Its highlands, which are situated in the Long Range Barrens (Damman 1983), are similarly influenced by the Gulf, but with an orographic effect that creates a harsher climate, having annual precipitation and snowfall on average double that of the lowlands (Watson 1974). The mean annual temperature on the highlands is 4.5 °C colder than that of the lowlands (Banfield 1983).

In 1878, one female and one male moose were introduced to Newfoundland from Nova Scotia, and in 1904, 2 male and 2 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 of Newfoundland, their density varies considerably. In the late 1970s when GMNP was being established, moose increased first on the highlands and by the 1980s moose had increased throughout the Park (Connor et al. 2000). At the time of the GPS collaring, surveys using stratified random blocks estimated the moose population at 7,377 ± 1,249 (4.1 ± 0.7 moose/km^2; McLaren et al. 2000; GMNP, unpublished data). In 2007, population size was estimated separately for the two landscapes, at 3,975 ± 1,287 in the lowlands (4.2 ± 1.4 moose/km^2) and 788 ± 223 SD in the highlands (0.9 ± 0.3 moose/km^2); densities in partial surveys of the park were estimated in 2009 at 5.9 moose/km^2 on the lowlands and 1.1 moose/km^2 on the highlands (GMNP, unpublished data).

METHODS

Habitat Classification

Taylor and Sharma (2010) classified habitat types on the lowlands and highlands of GMNP from a single-image subset of 2, 10-m multispectral SPOT-5 satellite images (recorded 20 June 2006) with a K-means unsupervised classification. Classes were reorganized and described using information from aerial photographs and forest inventories, and local expert knowledge and field visits. Ten habitat types resulted for the lowlands (Table 1), and 6 for the highlands (Table 2). Collectively, the lowlands comprise 938 km^2 or 52% of the Park, of which 417 km^2 or 44% is moose habitat in forest or disturbed forest types; the highlands comprise 867 km^2 or 48% of the Park, 641 km^2 or 74% of which is moose habitat, but only a fraction of which is forest (Table 3). The classifications in Table 1 and 2 are the reference for our description of habitat use by moose.

Moose Locations

In June 1997, 12 adult female moose (11 with at least one calf) were immobilized and fitted with GPS collars (Lotek Engineering, Inc.; McLaren et al. 2000; Table 4). The collars were set to attempt a fix at 3-h 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. Location accuracy was found to be dependent on collar position in relation to topography and canopy, but 95% of all differentially corrected data from test collars had ± 25 m accuracy (Moen et al. 1997, McLaren et al. 2000). All 2-dimensional fixes were removed from the dataset, and only differentially corrected locations were used in the current analysis. Depending on collar functioning, locations were recorded over a 4–15.5 month period (Table 4). Five of the collared moose were year-round residents in the lowlands, 5 were year-round residents in the highlands, and the remaining 2 migrated seasonally between the 2 landscapes.

Data Analysis

The dataset was divided into summer and winter seasons following Vander Wal and Rodgers (2009). Six moose were used for calculation of seasonal transition dates; 3 in the lowlands and 3 in the highlands with sufficient data records to span most of a calendar year. For these moose, cumulative distance travelled was calculated in ArcView version 9 (ESRI, Redlands, California) and plotted against time beginning with 1 January. Winter was defined as the period when rate of travel was less than the mean rate, estimated from the points of inflection of the best-fit logistic curves to the plots, where the estimated changes from winter to summer and from summer to winter are symmetric around the inflection points. Curve-fitting used the logistic regression program in the Statistical Package for the Social Sciences (SPSS), version 18 (also used for all subsequent analysis). The median dates

Table 1. Habitat descriptions from a lowlands classification of Gros Morne National Park, Newfoundland, Canada.

Habitat type	Description	Category
Mature softwood forest	Softwood dominated, especially balsam fir (*Abies balsamea*); some mixed stands with white birch (*Betula papyrifera*).	Closed-canopy forest
Closed spruce forest	Softwood dominated (balsam fir and black spruce, *Picea mariana*); other species include tamarack (*Larix laricina*), trembling aspen (*Populus tremuloides*) and alder (*Alnus* spp.); site condition can be wet. Some stands of scrub forest.	Closed-canopy forest
Closed mixed forest	Balsam fir dominated with some mixed stands (balsam fir, white birch). Stem density can be very high. Younger mixed stands (~30 years since disturbance) are included.	Closed-canopy forest
Young softwood forest	Softwood dominated with high content of hardwoods; canopy > 50% and 6–9 m in height.	Closed-canopy forest
Open softwood forest	Balsam fir dominated with 25–50% open canopy; white birch can be significant; some tree regeneration (heights of 1–4 m).	Open-canopy forest
Open mixed forest	Softwood dominated with 25–50% open canopy. Sometimes wet. Trees shorter than in closed mixed forest; some tree regeneration.	Open-canopy forest
Open hardwood forest	Hardwood dominated with 25–50% open canopy. Often originally a mixed forest where regeneration of balsam fir does not occur.	Open-canopy forest
Sparse softwood forest	Softwood dominated (balsam fir, black spruce) with < 25% canopy; 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 height; pockets of conifer regeneration < 4 m height can be present.	Disturbed forest: sparse canopy with herb/grass ground cover
Herb-hardwood forest	Dominant plants include ferns, grass and raspberry (*Rubus* spp.) > 50% of ground cover; very sparse forest canopy; some remnant white birch with alder or elderberry (*Sambucus racemosa*). Very little balsam fir. Scattered spruce < 4 m height. Includes forested areas that have not regenerated after severe disturbance.	Disturbed forest: sparse canopy with herb/grass ground cover
Herb forest	Dominant plants include ferns and grass (> 50% of ground cover); exposed soil is common; large amounts of dead material (standing or fallen) and scattered remnant trees. Little regeneration > 30 cm height. Mostly forested areas that have not regenerated after severe disturbance.	Disturbed forest: sparse canopy with herb/grass ground cover

for the start and end of winter were estimated from the 3 curves for each of the 2 landscapes and used to define the seasons for all subsequent analysis.

Summer and winter home ranges and core-use areas were calculated using the fixed-kernel method in Home Range Tools (Rodgers et al. 2007) with Gaussian (bivariate normal) distributions, reporting the 95% and 50% isopleths for ranges and cores, respectively. The bandwidth size was determined by finding the smallest proportion of the reference bandwidth that allowed one continuous outer line to encompass the

Table 2. Habitat descriptions from a highlands classification of Gros Morne National Park, Newfoundland, Canada.

Habitat type	Description	Category
Open softwood forest	Balsam fir and some black spruce in a closed canopy ranging to < 75% open; dense pockets of *krummholz* (locally known as tuckamore). Open heath and fen and bog interspersed.	Closed- to open-canopy forest
Scrub forest	Trees < 4 m height. Open heaths, fens, and bogs throughout (> 50% of area).	Open-canopy forest
Shrub	Predominantly low shrubs (< 1 m height), interspersed with fens, bogs, and small pockets of scrub forest. Associated with transition from fen and tundra to scrub forest. Can be wet.	Non-forest
Tundra	Low heath vegetation comprised of sedges (*Carex* spp.), caribou moss (*Cladonia* spp.) and crowberries (*Empetrum* spp.); < 20% rock, but few shrubs or trees. Fairly dry.	Non-forest
Fen	Sedge meadows with fens throughout.	Non-forest
Rock barren	Boulder fields and exposed rock. Very little vegetation.	Non-forest

Table 3. Habitat availability in Gros Morne National Park, Newfoundland, Canada.

	Availability on landscape	
Habitat type	Area (km^2)	Percent
Lowlands		
Mature softwood forest	69.6	7
Closed spruce forest	27.6	3
Closed mixed forest	65.5	7
Young softwood forest	56.7	6
Open softwood forest	62.5	7
Open mixed forest	43.6	5
Open hardwood forest	39.0	4
Sparse softwood forest	19.3	2
Herb-hardwood forest	20.0	2
Herb forest	13.5	1
Highlands		
Open softwood forest	184.7	21
Scrub forest	133.5	15
Shrub	130.0	15
Tundra	130.3	15
Fen	62.6	7

polygons (Worton 1989). Areas of open water, wetlands, and rock barrens were excluded from each of the resulting polygons and the remaining area was divided into the habitat types appropriate to the landscape. Fine-scale habitat use examined areas where a minimum of 3 consecutive GPS locations < 24 h apart occurred, with distances between them of < 50 m. This definition of an important habitat patch was arbitrary, but based on an inference that foraging and other activities such as bedding take place with shorter travel distances. Mean weekly travel distances, as well as distances between the habitat patches, were calculated for each moose, for summer and winter separately, and then compared across seasons using repeated-measures Analysis of Variance (ANOVA). Minimum travel distances were calculated in all cases as straight lines between successive location points.

RSFs (Manly et al. 2002) were modelled 6 times each using logistic regression from pooled locations of all individuals: 1) based on number of locations in each habitat type within the home range, compared to its area on the surrounding landscape, for describing summer habitat use by residents and migrants using the highlands in a marginal model; 2) in a similar marginal model for describing winter habitat use by residents and migrants using the lowlands; 3) in a conditional model based on number of locations for each moose in each habitat type within its

Table 4. First and last dates of collaring, record length, and home range area in summer and winter from fixed-kernel estimates using a 95% isopleth for 12 GPS-collared moose. This table also shows median seasonal transition dates, and lengths of summer and winter for moose using the two landscapes year-round in Gros Morne National Park, Newfoundland, Canada. Migrating moose are identified by an asterisk.

					Home range size (km^2)		Median seasonal transition dates		Median season length (days)	
ID	Landscape	First day collared	Last day recording	Record length (days)	Summer	Winter	Winter to summer	Summer to winter	Summer	Winter
15	Lowlands	25-Jun-97	13-Oct-98	468	11.9	12.1	18-Apr-98	11-Oct-98	173	181
16	Lowlands	25-Jun-97	13-Oct-98	468	13.2	13.1	18-Apr-98	11-Oct-98	173	181
19	Lowlands	25-Jun-97	05-Nov-97	130	2.9	1.8	18-Apr-98	11-Oct-98	173	181
21*	Lowlands	25-Jun-97	16-Jan-98	201	—	5.5	18-Apr-98	11-Oct-98	173	181
22*	Lowlands	26-Jun-97	18-Jun-98	352	—	12.3	18-Apr-98	11-Oct-98	173	181
25	Lowlands	26-Jun-97	21-Jun-98	355	8.3	12.1	18-Apr-98	11-Oct-98	173	181
26	Lowlands	26-Jun-97	15-Nov-97	139	4.2	2.4	18-Apr-98	11-Oct-98	173	181
17	Highlands	25-Jun-97	13-Oct-98	468	11.3	10.8	30-Apr-98	24-Oct-98	174	180
18	Highlands	25-Jun-97	27-Feb-98	242	6.8	8.7	30-Apr-98	24-Oct-98	174	180
20	Highlands	25-Jun-97	17-Mar-98	262	6.6	8.2	30-Apr-98	24-Oct-98	174	180
21*	Highlands	25-Jun-97	16-Jan-98	201	5.7	—	30-Apr-98	24-Oct-98	174	180
22*	Highlands	26-Jun-97	18-Jun-98	352	8.0	—	30-Apr-98	24-Oct-98	174	180
23	Highlands	26-Jun-97	13-Oct-98	467	9.2	7.2	30-Apr-98	24-Oct-98	174	180
24	Highlands	26-Jun-97	01-Jun-98	335	7.0	4.6	30-Apr-98	24-Oct-98	174	180

home range, compared to its area on the surrounding landscape, for describing summer and winter habitat use by residents of the lowlands; 4) in a similar conditional model for describing summer and winter habitat use by residents of the highlands; 5) in a conditional model based on number of locations for each moose in each habitat type within its core-use area, compared to its area in the home range, for describing finer-scale summer and winter habitat use by residents of the lowlands; and 6) in a similar conditional model for describing summer and winter habitat use within the core-use areas of residents of the highlands. In the first 2 (marginal) models, one moose resident on the highlands was removed because of too few locations (ID 18, Table 4).

Habitat use by residents in the 2 landscapes, habitat use by the 2 migrant moose, and differences in habitat use between the winter and summer seasons were statistically compared in a mixed-effects model with random intercepts and coefficients (Gillies et al. 2006). To determine the most parsimonious regression models, corrected Akaike's Information Criteria (AICc) and model deviance were compared to a model with random variables for each individual moose. A compound symmetric structure was assumed, meaning that covariance among all responses of an animal was assumed constant (Skrondal and Rabe-Hesketh 2004) and habitat availability was also assumed constant over time (Manly et al. 2002). These assumptions limit the applicability of the RSFs to the time period studied. Random intercepts and coefficients for all habitat types experiencing some use were estimated, and coefficients significantly > 1 were defined as selection of a habitat type. Calculations were all relative to open softwood forest as a reference habitat type, which was defined similarly for both landscapes.

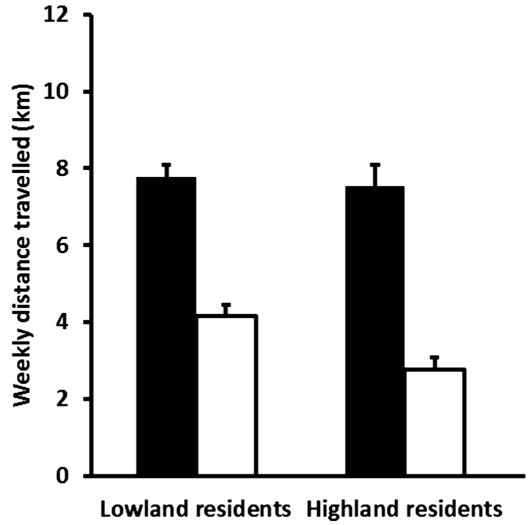

Fig. 1. Weekly distance travelled (km) for moose in Gros Morne National Park, Newfoundland, Canada.

RESULTS

Home-range size varied considerably among individual moose, and there was no consistent size difference by landscape for either winter ($F_{1,11}$ = 0.57, P = 0.58) or summer ($F_{1,11}$ = 1.53, P = 0.06; Table 4). There was also no difference in winter and summer home-range sizes on either the lowlands ($F_{1,11}$ = 0.26, P = 0.88) or the highlands ($F_{1,11}$ = 0.33, P = 0.67). The mean distances travelled during a one-year period were 309 km for residents on the lowlands and 267 km for residents on the highlands. Moose travelled less in winter than in summer. Weekly travel distances varied according to season ($F_{1,11}$ = 106.35, P < 0.001; Fig. 1). There was no difference in weekly travel distances by landscape ($F_{1,11}$ = 0.75, P = 0.47). The summer season differed in length between the 2 landscapes, but only by a day (Table 4). Summer, defined by moose travel rates, started and ended close to 2 weeks earlier on the lowlands.

The best-fit marginal RSF models describing habitat use by residents and migrants showed consistent selection of

Table 5. Ranking of habitat types, from most to least selected, for highland residents (N = 5; n = 3,252) and migrants (N = 2; n = 2,919) during summer on the highlands, and lowland residents (N = 5; n = 2,013) and migrants (N = 2; n = 1,018) during winter on the lowlands, where lower-case n refers to total number of locations in home ranges used to calculate resource selection functions (RSFs); Gros Morne National Park, Newfoundland, Canada. Habitat types significantly selected (*P* < 0.05) by at least 4 of 5 residents or both of the migrants are shown in boldface. The open softwood forest is a reference habitat (shown in italics).

Residents	Migrants
Summer on the highlands	
(1) **Fen**	**Fen**
(2) Tundra	Tundra
(3) **Shrub**	**Shrub**
(4) *Open softwood forest*	*Open softwood forest*
(5) Scrub forest	Scrub forest
Winter on the lowlands	
(1) **Closed spruce forest**	**Herb-hardwood forest**
(2) Herb forest	**Closed spruce forest**
(3) **Closed mixed forest**	**Herb forest**
(4) **Mature softwood forest**	**Mature softwood forest**
(5) Young softwood forest	**Closed mixed forest**
(6) **Herb-hardwood forest**	Sparse softwood forest
(7) Sparse softwood forest	**Open hardwood forest**
(8) Open hardwood forest	**Young softwood forest**
(9) Open mixed forest	**Open mixed forest**
(10) *Open softwood forest*	*Open softwood forest*

habitats in summer when they occupied the highlands together, and variable selection of habitats in winter when they occupied the lowlands together (Table 5); however, for both seasons, models with differences in habitat use between residents and migrants were rejected. For the remaining 4 RSFs, conditional models with residents and migrants pooled, the best-fit were those including seasonal differences. In summer, habitat types used less than expected based on availability at both the home-range and core-use scales were herb-hardwood forest and herb forest (Table 6). Closed spruce forest, closed mixed forest, and young softwood forest were among the top habitat types selected in summer relative to open softwood forest, but were not selected more than expected. The pattern was generally reversed in winter on the lowlands; herb-hardwood forest and herb forest, along with open hardwood forest and sparse softwood forest, were all selected by resident moose at both the home-range and core-use scales. At the home-range scale, young softwood forest and both closed forest types were also selected in winter. In the RSFs calculated for moose resident on the highlands, the fen, tundra, and shrub habitat types were selected in summer at the home-range scale, while only the fen and tundra types were selected at the core-use scale. The pattern was similar in winter, but scrub forest was also selected at the home-range scale and shrub, not tundra, was selected at the core-use scale. The overall trend in summer was more use of closed-canopy forest types on the lowlands and more use of non-forest habitat types on the highlands. Selection of disturbed forest is a winter phenomenon on the lowlands of GMNP; the same category of habitat types is avoided in summer.

Defined by repeated occupation of an area with travel distances < 50 m apart, most fine-scale habitat patches on the lowlands were categorized as disturbed forest (50/127) or as open-canopy forest (47/127). There were an additional 22 fine-scale habitat patches identified in young softwood forest, while only 8 of the 127 fine-scale habitat selections on the lowlands were in closed-canopy forest. There were 13.5 habitat patches per 100 km^2 on the lowlands, but more on the highlands (18.3/100 km^2) where the majority were in open softwood forest (70/159). Straight-line distances travelled between fine-scale habitat patches were

Table 6. Ranking of habitat types, from most to least selected, within home ranges and core-use areas for resident moose in Gros Morne National Park, Newfoundland, Canada: 5 moose in lowlands and 4 moose in highlands; lower-case n refers to total number of locations in home ranges or in core-use areas used to calculate RSFs. Habitat types selected or avoided (P < 0.05) in proportion to their available area are shown in boldface. The open softwood forest is a reference habitat (shown in italics).

Summer habitat ranking		Winter habitat ranking	
		Lowlands	
Home range (n = 3,765)	Core-use area (n = 1,485)	Home range (n = 2,013)	Core-use area (n = 1,679)
(1) Closed spruce forest	Closed mixed forest	(1) **Herb forest**	**Herb-hardwood forest**
(2) Young softwood forest	Closed spruce forest	(2) **Herb-hardwood forest**	**Herb forest**
(3) Closed mixed forest	Young softwood forest	(3) **Young softwood forest**	**Sparse softwood forest**
(4) *Open softwood forest*	Mature softwood forest	(4) **Open hardwood forest**	**Open hardwood forest**
(5) Mature softwood forest	*Open softwood forest*	(5) **Closed mixed forest**	Open mixed forest
(6) Sparse softwood forest	Open hardwood forest	(6) **Closed spruce forest**	Closed spruce forest
(7) Open hardwood forest	Open mixed forest	(7) **Sparse softwood forest**	Young softwood forest
(8) Open mixed forest	**Sparse softwood forest**	(8) Open mixed forest	Closed mixed forest
(9) **Herb-hardwood forest**	**Herb-hardwood forest**	(9) Mature softwood forest	*Open softwood forest*
(10) **Herb forest**	**Herb forest**	(10) *Open softwood forest*	Mature softwood forest
		Highlands	
Home range (n = 2,954)	Core-use area (n = 1,609)	Home range (n = 1,914)	Core-use area (n = 1,619)
(1) **Fen**	**Fen**	(1) **Fen**	**Fen**
(2) **Tundra**	**Tundra**	(2) **Shrub**	**Shrub**
(3) **Shrub**	Shrub	(3) **Tundra**	Tundra
(4) *Open softwood forest*	*Open softwood forest*	(4) **Scrub forest**	Scrub forest
(5) Scrub forest	Scrub forest	(5) *Open softwood forest*	*Open softwood forest*

greater in summer than in winter ($F_{1,120}$ = 36.28, P = 0.01), a consistent pattern for moose in both landscapes ($F_{1,120}$ = 0.08, P = 0.93); there was no difference in travel distances between patches by landscape ($F_{1,120}$ = 0.01, P = 0.99).

DISCUSSION

Despite variation among individual moose in habitat selection in the Park's more diverse and forested lowlands, as reported earlier (McLaren et al. 2009), we are able to show with RSFs that more use of closed-canopy forest occurs in summer, likely as a means of heat avoidance. Conversely, selection of disturbed and open-canopy forest is a winter phenomenon on the lowlands; the same category of habitat types is avoided during summer. In the cooler highlands, selection of non-forest habitat types may reflect less need to escape heat in the summer relative to the lowlands, and perhaps a means to escape insects. In winter, where moose populations are locally at higher densities according to both aerial surveys (GMNP, unpublished data) and the frequency of our identified winter habitat patches, selecting disturbed and open-canopy forest on the lowlands may be matched to optimal foraging, while selecting fen and shrub on the highlands may be matched to travel through areas where snow is packed along trails that reduces the energy cost of locomotion (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.

The most straightforward way of describing habitat use is in terms of density (Holt and Fryxell 2011). To approximate local moose densities, the total area in habitat types selected by moose could be substituted for an average density over the entire landscape areas. If habitat types selected during winter, based on the core-use areas of GPS-collared moose occupying the lowlands in this season, are used to represent the best habitat types (herb-hardwood, herb, sparse softwood, and open hardwood forests), winter density would be 20.6 moose/km^2, almost 5 x larger than the density estimate across the lowlands in the March 2007 survey (4.2 moose/km^2). If moose remaining on the highlands in winter similarly used only those habitat types selected in core-use areas by the GPS-collared subset (fen and shrub), their density would be 1.7 moose/km^2, about twice the landscape density estimate (0.9 moose/km^2) for the highlands. The lowland winter habitat types are essentially abandoned during summer in favour of habitat types providing thermal cover (closed-canopy forest); this change, combined with 20% of the population migrating to the highlands (McLaren et al. 2000), reduces effective summer density on the lowlands. Meanwhile, summer migrants, according to the 2007 winter lowland population estimate, should double the corresponding winter estimate for the highlands, where tundra, roughly equal in area to shrub, is simply substituted as a preferred habitat in summer. Presumably, seasonal abundance of forage is one benefit to spending the summer on the highlands.

Thus, 2 landscapes in GMNP provide insight into habitat selection by moose in Newfoundland and Labrador. We find that moose adapt seasonally to the Park's lowlands and highlands. Moose adopting either of 2 strategies, year-round residence in one landscape or migration between landscapes, do not appear to select habitat differently when they occupy the same landscape. This point parallels the consensus for migration in a review and study in Sweden (Ball et al. 2001) that concluded that snow depth is the likely driver for moose migration. What differs in our study is insight into the advantages in summer for the fraction of moose opting to return to an otherwise less hospitable landscape, that being the snowy highlands. If we accept a conclusion from a Québec study that movement rates for moose are better indicators of forage availability than home range size (Dussault et al. 2005), and that the habitat patches in open softwood forest on the highlands offer more forage in summer than that provided on average in the disturbed or open-canopy forest on the lowlands, we are describing a situation similar to what has been described for predator-free Svaldbard reindeer (*Rangifer tarandus platyrhynchus*) (Bremset Hansen et al. 2009). In this case, populations in overgrazed range move to areas of higher forage biomass, not higher forage quality. Further, although plant phenology from spring through early summer is generally associated with increasing forage quality (Klein 1990), the nitrogen content in forage declines initially after snowmelt (Van der Wal et al. 2000). Thus, migrant moose may travel upland in GMNP to maximize biomass consumption while tracking delayed plant phenology in the cooler highlands climate.

It is recommended that moose management in GMNP consider 2 landscapes (the lowlands and the highlands) as separate management units due to differences both in habitat types they offer and densities of moose they support. Park management plans should ensure landscape connectivity for moose migrating between the highlands and lowlands. On this note, management across Newfoundland and Labrador that is both effective and adaptable need not be dependent on defining discrete populations of moose, but should be in the context of the 2 very different landscapes the Province offers to moose.

ACKNOWLEDGEMENTS

Dr. A. Rodgers, Centre for Northern Forest Ecosystem Research, Ontario Ministry of Natural Resources, and Dr. D. Eastman, University of Victoria, provided advice and constructive criticism on portions of this paper submitted by its lead author as a MSc thesis in Forestry at Lakehead University. Two anonymous reviewers and *Alces* editor Dr. E. Addison provided helpful comments to improve this manuscript. S. Taylor, GMNP, provided invaluable assistance in interpreting habitat types and in analyzing GPS data. This project was funded and coordinated by the Institute for Biodiversity, Ecosystem Science and Sustainability of the Government of Newfoundland and Labrador, with additional funding and in-kind support provided by Parks Canada and Lakehead University. The original fieldwork and preliminary data analysis occurred under the guidance of the Inland Fish and Wildlife Division of the Government of Newfoundland and Labrador, with assistance by D. Anions and C. McCarthy (formerly of GMNP) and technical advice from Dr. A. Rodgers.

REFERENCES

Ball, J. P., C. Nordengren, and K. Wallin. 2001. Partial migration by large ungulates: characteristics of seasonal moose *Alces alces* ranges in northern Sweden. Wildlife Biology 7: 39–47.

Banfield, C. E. 1983. Climate. Pages 37–106 *in* G. R. South, editor. Biogeography and Ecology of the Island of Newfoundland. W. Junk Publishers, Boston, Massachusetts, USA.

Bergerud, A. T., H. E. Butler, and D. R. Miller. 1984. Anti-predator tactics of calving caribou: dispersion in mountains. Canadian Journal of Zoology 62: 1566–1575.

Bremset Hansen, B., I. Herfindal, R. Aanes, B.-E. Sæther, and S. Henriksen. 2009. Functional response in habitat selection and the trade-offs between foraging niche components in a large herbivore. Oikos 118: 859–872.

Caines, P., and H. Deichmann. 1989. Resource Description and Analysis: Gros Morne National Park. Gros Morne National Park, Parks Canada, Rocky Harbour, Newfoundland, Canada.

Connor, K. J., W. B. Ballard, T. Dilworth, S. Mahoney, and D. Anions. 2000. Changes in structure of a boreal forest community following intense herbivory by moose. Alces 36: 111–132.

Damman, A. W. H. 1983. An ecological subdivision of the island of Newfoundland. Pages 163–205 *in* G. R. South, editor. Biogeography and Ecology of the Island of Newfoundland. W. Junk Publishers, Boston, Massachusetts, USA.

Dussault, C., R. Courtois, J.-P. Ouellet, and I. Girard. 2005. Space use of moose in relation to food availability. Canadian Journal of Zoology 83: 1431–1437.

Fretwell, S. D., and H. L. Lucas. 1970. On territorial behaviour and other factors influencing habitat distribution in birds. Acta Biotheoretica 19: 16–36.

Fryxell, J. M. 1991. Forage quality and aggregation by large herbivores. American Naturalist 138: 478–498.

Gillies, C. S., M. Hebblewhite, S. E. Nielsen, M. A. Krawchuk, C. L. Aldridge, J. L. Frair, D. J. Saher, C. E. Stevens, and C. L. Jerde. 2006. Application of random effects to the study of resource selection by animals. Journal of Animal Ecology 75: 887–898.

Gosse, J., L Hermanutz, B. McLaren, P. Deering, and T. Knight. 2011. Degradation of boreal forests by non-native herbivores in Newfoundland's National Parks: recommendations for ecosystem restoration. Natural Areas Journal 31: 331–339.

Hare, F. K. 1952. The climate of the island of Newfoundland: a geographical analysis. Geographic Bulletin 2: 36–88.

Hebblewhite, M., and E. H. Merrill. 2007. Multiscale wolf predation risk for elk: does migration reduce risk? Oecologia 152: 377–387.

———, ———, and G. McDermid. 2008. A multi-scale test of the forage maturation hypothesis in a partially migratory ungulate population. Ecological Monographs 78: 141–166.

Holt, R., and J. Fryxell. 2011. Theoretical reflections on the evolution of migration. Pages 17–31 *in* E. Milner-Gulland, J. Fryxell, and A. Sinclair, editors. Animal Migration: A Synthesis. Oxford University Press, Oxford, United Kingdom.

Humber, J. M., and L. Hermanutz. 2011. Impacts of non-native plant and animal invaders on gap regeneration in a protected boreal forest. Biological Invasions 13: 2361–2377.

Klein, D. R. 1990. Variation in quality of caribou and reindeer forage plants associated with season, plant part, and phenology. Rangifer Special Issue 3: 123–130.

Manly, B. F. J., L. L. McDonald, D. L. Thomas, T. L. McDonald, and W. P. Erickson. 2002. Resource Selection by Animals, Second Edition. Kluwer Academic Publishers, Dordrecht, Netherlands.

Martin, C. 2004. Climatology and historical snowcover of the Big Level Plateau, Gros Morne National Park, Newfoundland. MSc Thesis, Memorial University of Newfoundland, St. John's, Newfoundland, Canada.

McLaren, B., C. McCarthy, and S. Mahoney. 2000. Extreme moose migrations in Gros Morne National Park, Newfoundland. Alces 36: 217–232.

———, B. A. Roberts, N. Djan-Chékar, and K. P. Lewis. 2004. Effects of overabundant moose on the Newfoundland landscape. Alces 40: 45–59.

———, S. Taylor, and S. H. Luke. 2009. How moose select forested habitat in Gros Morne National Park, Newfoundland. Alces 45: 125–135.

McNaughton, S. J. 1985. Ecology of a grazing ecosystem: the Serengeti. Ecological Monographs 55: 259–294.

Moen, R., J. Pastor, and Y. Cohen. 1997. Accuracy of GPS telemetry collar locations with differential correction. Journal of Wildlife Management 61: 530–539.

Pimlott, D. H. 1953. Newfoundland moose. Transactions of the North American Wildlife Conference 18: 563–581.

Rodgers, A. R., A. P. Carr, L. B. Hawthorne, L. Smith, and J. G. Kiem. 2007. Home Range Tools for ArcGIS. Version 1.1. Ontario Ministry of Natural Resources, Centre for Northern Forest Ecosystem Research, Thunder Bay, Ontario, Canada.

Skrondal, A., and S. Rabe-Hesketh. 2004. Generalized Latent Variable Modeling: Multilevel, Longitudinal, and Structural Equation Models. Chapman and Hall, New York, New York, USA.

Taylor, S., and R. Sharma. 2010. Assessing the Status of Forest Recovery in Disturbance Affected Areas Using SPOT 5 Imagery in Gros Morne National Park. Gros Morne National Park, Parks Canada, Rocky Harbour, Newfoundland, Canada.

Telfer, E. S., and J. P. Kelsall. 1979. Studies of morphological parameters affecting ungulate locomotion in snow. Canadian Journal of Zoology 57: 2153–2159.

Vander Wal, E., and A. R. Rodgers. 2009. Designating seasonality using rate of movement. Journal of Wildlife Management 73: 1189–1196.

Van der Wal, R., N. Madan, S. V. Lieshout, C. Dormann, R. Langvatn, and S. D. Albon. 2000. Trading forage quality for quantity? Plant phenology and patch choice by Svalbard reindeer. Oecologia 123: 108–115.

Watson, W. B. 1974. The Climate of Gros Morne National Park, Newfoundland. Atmospheric Environmental Service, Department of Environment, St. John's, Newfoundland, Canada.

Worton, B. J. 1989. Kernel methods for estimating the utilization distribution in home range studies. Ecology 70: 164–168.