HOW MOOSE SELECT FORESTED HABITAT IN GROS MORNE NATIONAL PARK, NEWFOUNDLAND

Brian. E. McLaren[1], S. Taylor[2] and S. H. Luke[1]

[1]Lakehead University, Faculty of Forestry and the Forest Environment, 955 Oliver Road, Thunder Bay, ON, Canada P7B 5E1; [2]Gros Morne National Park, P.O. Box 130, Rocky Harbour, NL, Canada A0K 4N0.

ABSTRACT: Current Parks Canada policy does not allow moose (*Alces alces*) to be hunted in National Parks in Newfoundland and Labrador; combined with the extirpation of wolves (*Canis lupus*), this policy creates a situation where introduced moose (*A. a. americana*) are relatively predator-free in Gros Morne National Park. Forested areas of this park are frequently disturbed by defoliating insects resulting in extensive young conifer forest; increasingly, more areas are identified as failing to regenerate to normal tree densities or "not sufficiently restocked" (NSR). We used data from GPS-collared moose that occupy areas of the park where limited timber cutting is allowed for domestic purposes and a very detailed and current forest inventory exists; such areas are still dominated by insect and wind disturbance, including a large designation of NSR forest. We hoped to determine whether moose are found preferentially in disturbed forest *versus* other landscape patches during summer or winter, during day or night, and under certain temperature conditions. Variability in habitat availability and habitat use by moose appears to preclude forest management options directed at specific habitat types.

When moose (*Alces alces*) face fewer predators they can reach higher densities (Peterson et al. 2003). Moose (*A. a. americana*) were first introduced to central Newfoundland, Canada in 1878 with the release of a male and female from Nova Scotia (Pimlott 1953). A second release of 2 males and 2 females from New Brunswick into western Newfoundland followed in 1904. Gray wolves (*Canis lupus*), their only potential predator, were extirpated in 1932 (Pimlott 1959). Therefore, for most of their occupation of the island province, Newfoundland moose were preyed on only by human hunters, with black bear (*Ursus americana*) predating only calves. Consequently, their density averages about tenfold higher than in other parts of their range in North America (Crête and Daigle 1999). Newfoundland moose experience large population fluctuations even where heavily hunted in central areas of the island, an effect that the limited

functional response of human predation and delayed density dependence in hunter kill have been implicated (Ferguson and Messier 1996). Relationships with their food source during extreme population peaks were first described by Bergerud and Manuel (1968); declines in population following such peaks identified by Mercer and McLaren (2002) suggest that food availability is often the only limiting factor for moose in Newfoundland.

Moose are not hunted in the National Parks in Newfoundland, creating a situation where populations are predator-free in 1,805 km^2 of western Newfoundland (Gros Morne National Park) and 404 km^2 of eastern Newfoundland (Terra Nova National Park). The resulting extreme moose demographics in both parks (McLaren et al. 2000), the fact that moose are not native to Newfoundland, and the potential for their high densities to alter natural ecosystem processes (McLaren

et al. 2004), add up to policy and management challenges for Parks Canada (Corbett 1995). In Canada, the response to hyperabundant species in protecting the ecological integrity within and by means of national parks follows a definition that very explicitly requires relating the reasons for hyperabundance to human impacts (PCA 2000). Examples of acceptable reasons to control large herbivores include artificial introductions and the loss of key predator species like carnivores, both of which have occurred in Newfoundland. However, to institute any control program, Parks Canada also demands confirmation that the reasons for hyperabundance are well understood and the program is conducted under an adaptive management framework where the original assumptions are subject to review. Moreover, control is better justified when "ecological integrity" is compromised by the large herbivore; according to the Canada National Parks Act, ecological integrity means "…a condition that is determined to be characteristic of its natural region and likely to persist, including…rates of change and supporting processes." It is in this context that we embarked on a review of how moose exploit areas of forest disturbance in Gros Morne National Park (GMNP).

It has been hypothesized that the Gros Morne moose population expanded as its range expanded into new habitat created by insect, wind, and timber cutting disturbances in GMNP (Connor et al. 2000). We argue that forecasts for forest regeneration and moose habitat in GMNP depend on how much the cause for high moose densities can be ascribed to forest disturbance, and how confident we are that moose generally select and occupy disturbed areas. Therefore, we matched the forest inventory and disturbance database to information from a series of collars with global positioning system (GPS) capability placed on adult female moose in 1997-1998 (McLaren et al. 2000). While the sample size is small (N = 4), we focus on a subset of collared moose that occupy areas of the park where timber

cutting is allowed for domestic purposes (home and boat construction and fuelwood) and, therefore, a very detailed and current forest inventory exists. The sample size and inventory data quality are sufficient to determine whether moose are found preferentially in disturbed forest *versus* other landscape patches during summer or winter, during day or night, and under certain temperature conditions. We explored these expected differences against a null hypothesis that selection within the home range varies among individual moose to an extent that general prediction about their use of landscape patches is not possible.

STUDY AREA

Gros Morne National Park is situated on the Gulf of St. Lawrence in Newfoundland, encompassing parts of the Northern Peninsula, Long Range Barrens, and Western Newfoundland Forest ecoregions (Damman 1983). Moose likely invaded the area now protected by GMNP in 1925 and became common by the 1950s, with modest population increases until the 1970s. Surveys in the late 1970s indicated that after GMNP became established (and human hunting was excluded), moose population density increased much more rapidly (GMNP, unpublished data). Increases first occurred in upland areas, but by the 1980s moose density increased throughout the park (Connor et al. 2000). In a 1998 survey, approximately 8,000 animals occurred in <1,000 km^2 of potential habitat (GMNP unpublished data). Some survey units in 2007 and 2008 had densities >15 moose/km^2 in lowland areas, where the average density remains ~ 4 moose/km^2.

Gros Morne National Park includes an allowance for domestic timber cutting in 12 "cutblocks" (193 km^2), but excludes 6 adjacent community enclaves (140 km^2). The cutblocks used by moose in this study were located in the Coastal Plain sub-region of the Northern Peninsula ecoregion, east of the flat coastal areas of the Gulf and including the western slopes of the Long Range Mountains. At elevations

<425 m, these areas experience a cool boreal climate with a relatively long growing season of 110-150 days (Damman 1983). Forests consist mostly of balsam fir (*Abies balsamea*), with some spruce (*Picea* spp.) and a mix of pioneer (mostly *Betula* spp.) and tolerant (mostly *Acer* spp. and *Sorbus* spp.) hardwoods; a more detailed description is found in Connor et al. (2000). Insect outbreaks, primarily of spruce budworm (*Choristoneura fumiferana*) in 1977 and hemlock looper (*Lambdina fiscellaria*) in 1969, 1988 and 1996 affected a large area of the forest: 7,550 ha in total (2,800 ha in the cutblocks) with individual areas of canopy disturbance up to 49 ha in extent (GMNP unpublished data). A study just east of GMNP on the northern peninsula concluded that insects caused defoliation and death of the forest canopy in >60% of the landscape, plus an additional canopy break-up and gap regeneration in >10% of the forest (McCarthy and Weetman 2007). In contrast, domestic timber cutting entails manual tree removal from small patches (maximum 2.2 ha); to an extent within the higher areas of this range, 'high-grading' may occur where large, dominant trees are preferentially cut leaving smaller trees in place. At the local level then, cutting, wind disturbance, and insect outbreaks create very similar forest structures. The disturbance types also frequently occur in combination; for example, cutting has occurred in 340 ha of defoliated forest following insect outbreaks in the cutblocks, and windfall is frequently associated with defoliation. Timber cutting, on the other hand, is a relatively minor contributor to new disturbances in GMNP, amounting to approximately 20 ha per year, equivalent to just over 1% of the total forested areas within the cutblocks since records began in the mid-1990s.

METHODS
Forest Inventory
A new, detailed forest inventory for GMNP was completed in 1997. Forest stand information was delineated using data on colour, 1:12,500 scale aerial photographs taken in 1995. This information included age, height, and crown density estimates, and the approximate species composition of each forested stand >0.5 ha; the disturbance type and year (if known) were tagged to disturbed forest stands identified on these photographs. If disturbed forest was interpreted as failing to regenerate to normal tree densities at the time of interpretation, based on absence of crown closure, stands in this category were tagged "not sufficiently restocked" (NSR). In addition, non-forest vegetation types such as barren, bog, scrub, residential areas and water were mapped.

In 2004, black-and-white, 1:10,000 scale aerial photographs were acquired to update and classify more accurately the forest disturbances limited to the cutblocks. Forest stands that were labelled in the 1995 inventory as disturbed, NSR, or regenerating forest were re-evaluated to determine their status. If regeneration had partly or completely failed, they were labelled (or re-labelled) NSR; stands with sufficient regeneration were labelled with the appropriate regenerating forest label from the original age of disturbance. Approximately half of these stands were labelled in the "0-20 year" age category and half in the "20-40 year" category. New disturbances, such as recent cutting or insect outbreaks (~ 1996-2004) were also delineated in 2004.

Moose Locations
We used location data collected from 4 adult, female moose collared and monitored 26 June 1997-13 October 1998. Collars were set to record differentially correctable GPS locations every third hour (Lotek Engineering Inc., Newmarket, Ontario, Canada). Details of the collaring and of accuracy testing of the location data are found in McLaren et al. (2000). Only locations with 3D accuracy and differential correction were used in this study; these locations had a 95% accuracy

of <25 m.

A night location dataset was created approximately equal in size to a daytime location dataset for each moose by first choosing from the 3D locations recorded closest to 0300 and 1500 hr each monitoring day. The night location datasets were supplemented in 13-21% of cases with locations recorded at approximately 0000 hr when no 3D location occurred at 0300 hr, and the daytime datasets were supplemented similarly in 18-25% of cases with locations recorded at approximately 1200 hr. The resulting datasets covered 91-97% of possible night locations and 96-99% of possible day locations during a 351-402 day monitoring period, depending on the moose.

The monitoring periods were further divided into summer and winter seasons following a method developed by Vander Wal (2005). For each moose, cumulative distance moved was calculated in ArcView version 9 (ESRI, Redlands, California) beginning with the first 3D location on 1 January 1998, and ending with either 26 June 1998 (2 cases) or 13 October 1998 (2 cases). The time series were completed with data beginning on 26 June 1997 or 13 October 1997 and ending 31 December 1997. Winter was defined as the period when slope of cumulative distance over cumulative time was less than the annual mean slope; summer was when movement within the home range was faster. Each time series was closest matched to a logistic curve, using regression with statistical software (SPSS, version 16). Summer fell between 8-28 April and 17 September-18 October, ranging from 158-186 days in length, depending on the moose. For 3 of the 4 moose, 2 nearly complete summer seasons (1997 and 1998) could be quantified in the GPS database. The fourth moose was sufficiently monitored only during the 1998 summer season.

Data Analysis

Summer (1997 and 1998) and winter (1997-1998) home ranges were calculated using 100% minimum convex polygons. Size of seasonal ranges was compared across all 4 moose by *t*-test. Areas outside the cutblocks and large areas of open water were then excluded from each of the seasonal ranges. The remaining area was divided into a) young NSR forest ≤ 20 years since disturbance, b) older NSR forest, c) young (regenerating) conifer forest ≤ 20 years since disturbance, d) older conifer forest, e) mixed forest and deciduous forest of all ages, f) scrub forest, and g) barren (non-forested) areas. The first 2 categories were defined according to information in both the original forest inventory (1995) and the update (2004); disturbances that were labelled NSR in either database (or both databases) were re-categorized as "young" or "older" NSR forest. Recognizing that the moose locations were recorded during 1997-1998, we classed "young" NSR based either on a date in the inventory indicating ≤20 years since disturbance by 1997, or on a forest age class in the 1995 inventory of "0-20 years." Areas of NSR first identified in the 2004 update were counted as NSR habitat only if they were classed as "0-20 years" of age (or older) at that time, because most insect outbreaks occurred before 1997; new areas of NSR in the update were not counted as NSR areas in the habitat analysis if they were assigned to a date after 1998. The reason 2 of the habitat categories refer to "young" forest is that forage for moose in Newfoundland has long been estimated to be highest in regenerating balsam fir forest at 8-10 years of age (Parker and Morton 1978), where the amount of browsing by moose increases with the fraction of balsam fir among trees <3 m in height (Thompson 1988). Thus, "young" forest is a special and desired habitat for foraging by moose, while older forest may serve largely as cover, but not foraging habitat.

Habitat selection was tested for all 7 of the categories in 4 separate resource selection functions (RSF), one for each moose. RSFs are statistical tools that describe the relative

probability of occurrence of animals based on their response to their habitat (Boyce 2006). In this study, each observed moose location was linked to 10 random locations within a 700-m radius circle, an area that encompassed approximately 50% of the distances between 2 successive locations during any season for all moose. Thus, the observed moose locations were considered "selected" among random areas within 700 m, a distance chosen to assume that moose selected the habitat class recorded by the GPS collar as their location among random locations to which they would have been capable of moving, but were not found. In other words, locations are tracked relative to the patches of habitat immediately available to a moose at any given time.

The RSF typically distinguishes among observed locations and available habitats using log-linear modelling, for this study constructed in SPSS (version 16). Comparisons among resulting RSF models were made using a combination of the significance of change in deviance in an analysis of deviance table (Manley et al. 2002) and the Akaike's Information Criterion (AIC, Burnham and Anderson 2002). Relative habitat selection was calculated, setting the probability of selection of young NSR forest at 1.000. Reporting relative rather than absolute habitat selection probabilities follows the recommendation of Arthur et al. (1996), for situations when availability of habitats is not constant and comparisons among habitats may be affected by the choice of which habitats to include.

Variation in habitat selection among individual moose was compared to 1) variation in habitat selection between summer and winter and between day and night in each season, 2) variation in habitat selection when the collar recorded cold ($\leq 0^\circ$ C) *versus* warm ($>0^\circ$ C) winter temperatures, 3) variation in habitat selection when the collar recorded cool ($\leq 8^\circ$ C) *versus* warm ($>8^\circ$C) summer temperatures, and 4) variation in habitat selection between summers (1997 and 1998) only when warm

($>8^\circ$ C) collar temperatures were recorded (limited by data availability). The temperature thresholds were chosen as close as possible to the temperatures at which heat stress may begin for moose, -5° C in winter and 15° C in summer (Renecker and Hudson 1986), while also dividing the 3D locations approximately evenly among cold, warm, and cool categories. Young NSR forest was considered the best choice for a standard against which to compare habitat selection in the other 6 categories, both because it serves as a theoretical target for foraging by moose, and because it provides the highest actual likelihood among the other young forest categories that it was visited by moose due to its NSR designation and the likelihood that regeneration failure is linked to moose overabundance.

RESULTS

Seasonal range sizes varied from 135-1,692 ha (Table 1), and were larger ($P = 0.002$) in winter ($1,200 \pm 257$ ha, $N = 4$) than in summer (419 ± 101 ha, $N = 7$). Range composition also varied considerably among individual moose (Table 1); 3-86% of a seasonal range occurred outside a cutblock. In 3 of 4 cases, the proportion of range outside cutblocks was greater in winter than in summer. For Moose 15 and 16, old and young NSR forest made up more than one-third of all range area within the cutblocks, whereas scrub forest filled a dominant proportion of every range for Moose 22 and 25. By contrast, non-forested (barren) areas comprised anywhere from 1-33%, mixed and deciduous forest 4-33%, and older conifer forest 2-32% of ranges.

Habitat selection was significant and varied significantly for all tested factors (Table 2). Variation in habitat selection among individual moose was significant and larger than variation in habitat selection by season, by temperature, by time of day, or by year for the summer season.

Table 1. Characteristics of seasonal ranges for adult female moose captured (Moose 15, 16, 22 and 25) in Gros Morne National Park (GMNP). Monitoring occurred from collars set to record Global Positioning System (GPS) locations every third hour; records began on 26 June 1997 and were censored at the end of the second summer, 26 September 1998. Range size and composition were calculated from Minimum Convex Polygons (MCPs) encompassing 100% of 3D differentially corrected locations. Sample sizes in subsequent analyses are shown as the number of locations, divided into categories of day and night, and cool- or cold- versus warm-temperature locations. A dashed line indicates a censored category in comparative analyses due to low sample size.

Moose I.D. Number	Season & Year	Percent of Total Range			Percent Range Composition (Excluding Water and Areas Outside Cutblocks)							Number of Points			
		100% MCP Range Size (ha)	In Water	Outside Cut Block	Young NSR Forest	Older NSR Forest	Young Conifer Forest	Older Conifer Forest	Mixed Forest	Scrub Forest	Barren	Day	Night	Cool/Cold	Warm
15	Summer 1997	303	10	7	29	5	3	8	4	16	33	–	–	–	70
	Winter 1997-98	1,196	22	15	27	5	5	11	6	22	23	159	149	426	515
	Summer 1998	582	17	13	30	5	4	8	5	25	23	98	120	126	499
16	Summer 1997	135	4	54	29	6	14	4	23	12	11	–	–	–	36
	Winter 1997-98	614	0	86	25	15	16	2	33	7	1	–	–	98	71
	Summer 1998	325	3	72	25	10	15	3	32	10	5	–	–	–	193
22	Winter 1997-98	1,300	2	37	9	5	4	13	26	35	9	116	114	343	390
	Summer 1998	894	2	26	9	4	4	12	28	34	10	35	38	77	33
25	Summer 1997	358	10	3	14	3	6	30	14	30	2	–	–	–	353
	Winter 1997-98	1,692	18	36	14	4	9	12	19	40	3	116	112	284	470
	Summer 1998	338	6	47	18	3	4	32	8	33	2	44	25	55	152

Table 2. Analysis of deviance table for models of habitat use. N is the number of collared, adult female moose using cutblocks. Resource selection functions (RSFs) were constructed from one log-linear model for each moose from n locations and 10n additional random locations. Model significance was calculated by comparison of the difference in deviance (Δ D) between successive models with the $\chi 2$ distribution for df degrees of freedom. Akaike's Information Criteria (AICs) are shown for each model step.

Model	Deviance	df	AIC	Δ D	df	P
a. Habitat selection by day and by night in winter 1997-98 and summer 1998 (N = 3; n = 1,081)						
No selection of habitats	640.0	72	978.8	—	—	—
Constant selection of habitats	430.0	66	780.8	110.0	6	< 0.001
Selection varies among moose	176.8	54	551.5	253.2	12	< 0.001
Selection varies among moose by season	115.4	36	526.1	61.4	18	< 0.001
Selection varies among moose between day and night	92.8	36	503.6	84.0	18	< 0.001
Full model (including seasonal and diurnal variation)	0	0	482.7	92.8	36	< 0.001
b. Habitat selection by temperature ($\leq$ 0°C and > 0°C) in winter 1997-98 (N = 4; n = 2,448)						
No selection of habitats	1,340.4	48	1,625.0	—	—	—
Constant selection of habitats	805.7	42	1,102.3	534.7	6	< 0.001
Selection varies among moose	192.3	24	524.9	613.4	18	< 0.001
Full model (including variation by temperature)	0	0	380.6	192.3	24	< 0.001
c. Habitat selection by temperature ($\leq$ 8°C and > 8°C) in summer 1998 (N = 3; n = 979)						
No selection of habitats	532.3	36	720.9	—	—	—
Constant selection of habitats	245.7	30	446.3	286.6	6	< 0.001
Selection varies among moose	52.2	18	276.8	193.5	12	< 0.001
Full model (including variation by temperature)	0	0	260.6	52.2	18	< 0.001
d. Habitat selection by year (1997 and 1998) in summer with temperature > 8°C (N = 3; n = 1,246)						
No selection of habitats	724.0	36	917.7	—	—	—
Constant selection of habitats	292.0	30	497.7	432.0	6	< 0.001
Selection varies among moose	42.7	18	272.4	249.3	12	< 0.001
Full model (including variation by year)	0	0	265.7	42.7	18	0.001

Young NSR forest was the most selected among all habitat types, although less selected by Moose 22 (Table 3). Among winter, day-time locations for Moose 15, young NSR forest was selected more than any other habitat type. The same pattern, although not significant, held at all times except on summer nights when scrub forest was slightly, but not significantly, more selected than young NSR forest. For Moose 25 the same pattern held for winter day-time locations, with young NSR forest selected more often than 4 of the 6 other habitat types. In contrast, Moose 22 selected only barren areas significantly less than young NSR forest, while mixed forest and scrub forest were generally more selected than young NSR forest. Moose 25 had the largest shift in selection between winter and summer; both older conifer forest and scrub forest were less selected than young NSR forest on winter days, but more selected on summer days. In contrast to young NSR forest, older NSR forest did not appear to be selected.

There was a significant difference in winter habitat selection during cold *versus* warm periods for all moose. Conclusions about these differences were difficult, due to the higher variation in selection among individual moose (Table 2). For 3 moose (16, 22, and 25), mixed and deciduous forest was either the most selected habitat type or the second most selected throughout winter, next to young NSF forest; however, Moose 15 selected significantly less mixed and deciduous forest and significantly more older coniferous forest in colder periods during winter, relative to young NSF forest (Table 4). On the other hand, coniferous forest was significantly less selected in colder periods by Moose 22 and Moose 25, relative to young NSR forest. During warmer periods in winter, selection among moose was more constant when conifer forest was less selected than young NSR forest. There was a smaller, but significant difference in summer habitat selection during cool *versus* warm periods for the 3 moose with sufficient records for this comparison. As in winter, Moose 15 selected significantly less mixed and deciduous forest than young NSR forest during the cooler period; the same pattern held for Moose 25 for the summer period. Moose 25 selected scrub forest significantly more than NSR forest on warm summer days, but significantly less scrub forest was selected on cool summer days.

Table 3. Relative selection probabilities when comparing habitat use by season and time of day. Relative selection was assessed using 1.000 as the probability of selection for young (≤20 year-old) NSR forest. Probabilities were derived from parameters in RSFs constructed for individual moose for which habitat selection varied significantly (Table 2a). Resource selection varied for the other factors, season and time of day, for moose 15 and 22, but not for moose 25. For these conclusions, Δ D is compared to the χ2 distribution for 6 degrees of freedom. Asterisks indicate cases where probabilities are derived from significant parameter estimates (P <0.05).

Moose I.D. Number	Δ D₂ Model Diagnostics	Season (Factor 1)	Time of Day (Factor 2)	Older NSR Forest	Young Conifer Forest	Older Conifer Forest	Mixed Forest	Scrub Forest	Barren
15	Season:	Winter 1997-98	Day	* 0.345	* 0.150	* 0.624	* 0.213	* 0.490	* 0.072
	Δ D = 23.4; *P* = 0.001		Night	0.369	0.185	0.649	0.092	0.888	* 0.725
	Time of Day:	Summer 1998	Day	0.227	0.230	0.587	0.189	0.656	* 0.251
	Δ D = 52.7; *P* < 0.001		Night	0.946	0.194	0.864	0.079	2.347	0.043
22	Season:	Winter 1997-98	Day	0.815	0.705	0.752	* 5.703	* 2.273	* 0.000
	Δ D = 13.2; *P* = 0.040		Night	0.590	0.263	0.421	2.818	* 0.715	* 0.538
	Time of Day:	Summer 1998	Day	2.630	0.266	0.000	1.684	1.914	* 0.267
	Δ D = 19.9; *P* = 0.003		Night	0.341	7.599	>1,000	22.399	2.307	0.000
25	Season:	Winter 1997-98	Day	* 0.406	* 0.355	* 0.399	0.856	* 0.550	0.000
	Δ D = 23.4; *P* = 0.423 (n.s.)		Night	0.331	0.404	0.411	1.130	0.351	0.000
	Time of Day:	Summer 1998	Day	0.303	0.152	* 1.239	0.283	* 1.988	0.000
	Δ D = 11.5; *P* = 0.074 (n.s.)		Night	0.209	0.776	0.199	0.564	* 0.084	0.000

Table 4. Relative selection probabilities comparing habitat use on cold and warm days in winter (Δ D1), cool and warm days in summer (Δ D2), and for warm summer days, 2 monitoring seasons in 1997 and 1998 (Δ D3). Other definitions and calculations are as in Table 3.

Moose I.D. Number	Model Diagnostics	Temperature (Factor 1)	Season within Year (Factor 2)	Older NSR Forest	Young Conifer Forest	Older Conifer Forest	Mixed Forest	Scrub Forest	Barren
15	$\Delta D_1 = 28.0$; $P < 0.001$	≤ 0°C (cold)	Winter 1997-98	* 0.527	* 0.347	* 1.634	* 0.194	0.844	* 0.596
		> 0°C (warm)		* 0.234	0.212	* 0.355	0.189	0.691	0.460
	$\Delta D_2 = 23.2$; $P = 0.001$	≤ 8°C (cool)	Summer 1998	* 0.193	0.000	* 0.161	* 0.000	* 0.351	0.760
		> 8°C (warm)		0.122	0.160	0.235	0.145	* 0.638	0.741
	$\Delta D_3 = 11.8$; $P = 0.067$ (n.s.)	> 8°C (warm)	Summer 1997	* 0.128	* 0.000	* 0.123	* 0.127	* 0.537	* 0.293
16	$\Delta D_1 = 18.4$; $P = 0.005$	≤ 0°C (cold)	Winter 1997-98	0.374	2.795	0.000	* 6.787	* 4.600	0.000
		> 0°C (warm)		0.722	0.826	0.292	* 0.968	2.179	0.100
	insufficient cool records	> 8°C (warm)	Summer 1998	* 0.335	0.542	* 0.257	* 0.000	* 0.238	* 0.240
	$\Delta D_3 = 20.7$; $P = 0.002$	> 8°C (warm)	Summer 1997	0.161	0.710	0.096	* 0.575	0.482	0.075
22	$\Delta D_1 = 49.4$; $P < 0.001$	≤ 0°C (cold)	Winter 1997-98	* 0.503	* 0.106	* 0.567	* 3.149	* 0.558	* 0.119
		> 0°C (warm)		0.441	* 0.803	0.795	19.434	* 1.725	* 0.619
	$\Delta D_2 = 16.6$; $P = 0.011$	≤ 8°C (cool)	Summer 1998	* 0.433	* 0.375	0.623	0.726	0.543	0.526
		> 8°C (warm)		0.739	0.349	0.236	1.471	0.949	0.166
25	$\Delta D_1 = 56.5$; $P < 0.001$	≤ 0°C (cold)	Winter 1997-98	* 0.674	* 0.420	* 0.318	0.843	* 0.210	0.000
		> 0°C (warm)		* 0.143	0.282	0.296	0.799	* 0.548	0.000
	$\Delta D_2 = 12.5$; $P = 0.052$	≤ 8°C (cool)	Summer 1998	0.434	* 0.289	0.700	* 0.350	* 0.490	* 0.000
		> 8°C (warm)		0.132	0.320	0.649	0.247	* 1.279	* 0.033
	$\Delta D_3 = 10.2$; $P = 0.116$ (n.s.)	> 8°C (warm)	Summer 1997	* 0.181	* 0.314	* 0.501	* 0.179	* 0.629	* 0.010

The difference in summer habitat selection between 1997 and 1998 was significant for only 1 (Moose 16) of the 3 moose with a long enough monitoring record to allow comparison. In this case, the least selected habitat in 1997 was mixed and deciduous forest, while in 1998 it was either older conifer forest or barren areas. Except for scrub forest on warm summer days, young NSR forest was the most selected habitat type throughout the summer in both years, while older NSR forest was among the least selected habitat types.

DISCUSSION

For GMNP we conclude that selection within the home range varies among individual moose to an extent that general prediction about use of landscape patches by even 4 moose, let alone the population, is not possible. This conclusion is not different from that made recently by Gillingham and Parker (2008) for northern British Columbia, and it may be a general caution about the interpretation of RSFs, as well as guidance for managers in the management of moose

We also garnered additional information from the GPS-collared moose that differed from conclusions made from VHF-collared moose in the same area (McLaren et al. 2000). For example, migrations did not occur from cutblocks during the early months of summer among the 4 moose reported in this study. Even though local movement rates increase in summer months, moose residing in the cutblocks may be less prone to long-distance migrations if food can be found in young forest, even in young NSR forest. If this condition describes the current situation, it likely also explains smaller summer home ranges, while ranges sufficiently larger to include older coniferous forest in colder periods, for example, were likely required during winter. The observation of higher daily movement rates in summer *versus* winter, the only uniform pattern among the moose in this study, is consistent with Vander Wal's (2005) conclusion that winter is a period of energy conservation and limited daily movement.

Variation in snow conditions in the Coastal Plain subregion of Newfoundland is probably the source for variation in habitat selection by moose in winter. Except for warmer summer days, young NSR forest appears generally the most selected habitat type in the cutblocks.

However, overall high variability in habitat selection during winter and summer suggests that conclusions drawn to assist moose or moose habitat management in GMNP will not be general ones. One possibile generalization is that in 20 years, when young NSR forest converts to older NSR forest, foraging opportunities for moose may be depleted. Even with modestly high densities, moose habitat in Newfoundland demonstrably declines over a few decades (Mercer and McLaren 2002). However, this study is unable to show that moose are food limited in GMNP. Variability in habitat availability and habitat use by moose appears to preclude forest management options directed at specific habitat types.

Concern with high-density moose populations in national parks arises from the possibility that forests will not regenerate naturally. A study in Terra Nova National Park detailed that even after moose are removed from the ecosystem, alteration of forest dynamics by hyperabundant moose can persist at least 2 decades (McLaren et al. 2009). Only circumstantial evidence of altered forest composition in GMNP was found by Connor et al. (2000). However, in extreme cases in GMNP, persistent invasive plants, including coltsfoot (*Tussilago farfara*) and Canada thistle (*Cirsium arvense*), as well as native grasses (e.g., *Calamagrostis canadensis*), become widespread problems as a result of moose browsing and trampling in disturbed areas (Rose and Hermanutz 2004). We recommend continued monitoring in GMNP to evaluate impacts by moose on forested habitats relative to forest regeneration and composition.

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REFERENCES

ARTHUR, S. M., B. F. J. MANLY, L.L. McDONALD, and G. W. GARNER. 1996. Assessing habitat selection when availability changes. Ecology 77: 215-227.

BERGERUD, A. T., and F. MANUEL. 1968. Moose damage to balsam fir-white birch forests in central Newfoundland. Journal of Wildlife Management 32: 729-746.

BOYCE, M. S. 2006. Scale for resource selection functions. Diversity & Distributions 12: 269-276.

BURNHAM, K. P., and D. R. ANDERSON. 2002. Model Selection and Multi-Model Inference: A Practical Information-Theoretic Approach. Springer-Verlag, New York, New York, USA.

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.

CORBETT, G. N. 1995. Review of the history and present status of moose in the national parks of the Atlantic region: management implications? Alces 31: 255-268.

CRÊTE, M., and C. DAIGLE. 1999. Management of indigenous North American deer at the end of the 20th century in relation to large predators and primary production. Acta Veterinaria Hungarica 47: 1-16.

DAMMAN, A. W. H. 1983. An ecological subdivision of the island of Newfoundland. Pages 163-205 *in* G. R. South (ed.) Biogeography and Ecology of the Island

of Newfoundland. W. Junk Publishers, Boston, MA, USA.

FERGUSON, S. H., and F. MESSIER. 1996. Can human predation of moose cause population cycles? Alces 32: 149-161.

GILLINGHAM, M. P., and K. L. PARKER. 2008. The importance of individual variation in defining habitat selection by moose in northern British Columbia. Alces 44: 7-20.

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, The Netherlands.

MCCARTHY, J. W., and G. WEETMAN. 2007. Stand structure and development of an insect-mediated boreal forest landscape. Forest Ecological Management 241: 101-114.

MCLAREN, B., L., HERMANUTZ, J. GOSSE, B. COLLET, and C. KASIMOS. 2009. Broadleaf competition interferes with balsam fir regeneration following experimental removal of moose. Forest Ecological Management 257: 1395-1404.

_____, B. A. ROBERTS, N. DJAN-CHÉKAR, and K. P. LEWIS. 2004. Effects of overabundant moose on the Newfoundland landscape. Alces 40: 45-59.

_____, C. MCCARTHY, and S. P. MAHONEY. 2000. Extreme moose migrations in Gros Morne National Park, Newfoundland. Alces 36: 217-232.

MERCER, W. E., and B. E. MCLAREN. 2002. Evidence of carrying capacity effects in Newfoundland moose. Alces 38: 123-141.

PARKER, G. R., and L. D. MORTON. 1978. The estimation of winter forage and its use by moose on clearcuts in northcentral Newfoundland. Journal of Range Management 31: 300-304.

PCA (PARKS CANADA AGENCY). 2000. Managing hyperabundant species. Pages 5-12 and 5-13 in Panel of the Ecological Integrity of Canada's National Parks. Unimpaired for Future Generations? Protecting Ecological Integrity with Canada's National Parks. Volume II. Setting a New Direction for Canada's National Parks. Ottawa, Ontario, Canada.

PETERSON, R. O., J. A. VUCETICH, R. E. PAGE, and A. CHOUINARD. 2003. Temporal and spatial aspects of predator-prey dynamics. Alces 39: 215-232.

PIMLOTT, D. H. 1959. Reproduction and productivity of Newfoundland moose. Journal of Wildlife Management 23: 381-401.

_____. 1953. Newfoundland moose. Transactions North American Wildlife Conference 18: 563-581.

RENECKER, L. A., and R. J. HUDSON. 1986. Seasonal energy expenditure and thermoregulatory response of moose. Canadian Journal of Zoology 64: 322-327.

ROSE, M., and L. HERMANUTZ. 2004. Are boreal ecosystems susceptible to alien plant invasion? Evidence from protected areas. Oecologia 139: 467-4776.

THOMPSON, I. D. 1988. Moose damage to precommercially thinned balsam fir stands in Newfoundland. Alces 24: 56-61.

VANDER WAL, E. J. 2005. Core areas of habitat use: the influence of spatial scale of analysis on interpreting summer habitat selection by moose (*Alces alces*). M. Sc. Thesis, Lakehead University, Thunder Bay, Ontario, Canada.