EXTREME MOOSE DEMOGRAPHICS IN GROS MORNE NATIONAL PARK, NEWFOUNDLAND

Brian McLaren[1], Christopher McCarthy[2], and Shane Mahoney[1]

[1]Government of Newfoundland & Labrador, Department of Forest Resources & Agrifoods, Inland Fish & Wildlife Division, P. O. Box 8700, St. John's, NF, Canada A1B 4J6; [2]Gros Morne National Park, P. O. Box 130, Rocky Harbour, NF, Canada A0K 4N0

ABSTRACT: We compare demographics and migration between 2 distinct ecoregions within Gros Morne National Park (GMNP) on Newfoundland's Great Northern Peninsula: the highland Long Range Barrens (LRB) and the lowland Coastal Plains (CP). Both ecoregions are well represented in the Park and also in a large portion of managed moose areas in the Province. Concurrent with Park establishment in 1973, hunting closure was followed by a local increase in the moose population, which first populated the Great Northern Peninsula in the late 1940's. While no change has been measured in densities of LRB moose in the Park during the past 25 years, densities of 14.6 moose per km^2 in 4% (very high stratum) and 6.1 moose per km^2 in 29% (high stratum) of the 1998 census area represent a substantial increase for the CP habitat. Calf production and yearling recruitment into GMNP were consistently higher in 1995 - 99 in CP relative to LRB habitat; evidence from herd composition surveys for the emigration of bull moose from the Park is also becoming apparent. For the same period, survival and migration were investigated with the use of VHF collars ($n = 76$) on calves and adults, and GPS collars ($n = 12$) on adults (total $n = 48$ LRB and $n = 40$ CP). Calf survival to 1 year differed significantly between the 2 habitats, lower in LRB (0.557) than in CP (0.718). In both habitats, the main cause of calf mortality was black bear predation (18% of all collared calves). Yearling survival to 2 years (0.793 LRB and 0.902 CP) and annual adult survival (0.817 LRB and 0.920 CP) also differed significantly between the 2 habitats. Several VHF-animals (at least 17) left the Park boundary, with extreme migration distances (>147 km) in some cases. Four GPS-collared moose left the Park boundary from highland areas in winter. GPS-ranges were consistently larger in LRB than in CP, and LRB ranges were more commonly used in summer. The habitats within the greater Park ecosystem apparently present very different carrying capacities, and GMNP area moose can be considered a single, dynamic population that crosses habitat and management boundaries. As a result, moose experience highly variable survival rates and migration patterns.

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Key words: carrying capacity, census, Gros Morne National Park, habitat, migration, moose, Newfoundland, protected area, ranging characteristics, survival

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Moose (*Alces alces*) populations have the ability to increase rapidly (Murie 1934, Pimlott 1959), especially in the absence of hunting, and also when faced with limited natural predation. On the island of Newfoundland, wolves (*Canis lupus*) became extinct in the early part of the century (Pimlott 1953, Ferguson and Messier 1996). Moose were successfully introduced into Newfoundland in 1904 (Pimlott 1953) and colonized the entire island, including Gros Morne National Park (GMNP) on the Great Northern Peninsula by the late 1940's (Caines and Deichmann 1989). Permanent closure of moose hunting in the Park and its residential enclaves in 1974 led to a rapid increase in moose numbers over the next 2 decades, particularly in low-elevation Coastal Plains (CP) areas (Janes 1976, Taylor 1991). Census information before 1974 documented small numbers, about 1,000 animals, generally restricted to the less accessible, higher-elevation Long Range Barrens (LRB), where hunting was less common (Gillespie *et al.* 1971, Wentzell 1974, Prescott 1978). This paper provides updated demographic and migration information for a now much larger moose population of about 7,700 animals. This study was initiated in 1995 to investigate long-term moose and vegetation dynamics in GMNP, with recognition of a rapidly increased moose population potentially near habitat carrying capacity (KCC) (Mawhinney *et al.* 1996). Included here is baseline progress toward a study goal of understanding long-term moose and vegetation dynamics in the greater GMNP ecosystem that contrasts forested, CP, and barren, LRB, ecoregions.

Long-term monitoring cultivates a greater understanding of moose population demographics at or near KCC and also toward answering management questions related to moose at KCC (Mawhinney *et al.* 1996). Because the 2 ecoregions in this study are representative of moose habitat in hunted areas of Newfoundland (Damman 1983, Meades and Moores 1994), the Newfoundland & Labrador Inland Fish & Wildlife Division (NLWD) benefits from information on moose demographics in 2 different habitat areas. An assessment of the ecological and social effects of a non-native species in the Park addresses management concerns of the Canadian Parks Service. Documentation of migration outside the boundary of the Park helps assess the extent to which moose demographics in GMNP are influenced by the hunting season in areas surrounding the Park.

STUDY AREA

GMNP is situated on the western coast of the Great Northern Peninsula of Newfoundland, and encompasses an area of 1,945 km^2, including 12 timber harvest blocks totalling 193 km^2 and 6 community enclaves totalling 140 km^2. The Park is divided by land area into 24% Northern Peninsula Ecoregion, 51% Long Range Barrens (LRB) Ecoregion, and 25% Western Newfoundland Forest (WNF) Ecoregion (Damman 1983, Fig. 1). The LRB ecoregion extends from about 425 m above sea level (a.s.l.) elevation to the highest elevations of the mountains, about 800 m a.s.l. The Northern Peninsula Ecoregion includes the coastal plains and the mid-elevation (<425 m a.s.l.) western slopes of the Long Range Mountains, known also as the Coastal Plain (CP) Subregion of the Northern Peninsula Ecoregion (Meades and Moores 1994). Upland areas of the LRB ecoregion are covered with sparsely forested heath and dwarf shrub barrens; where more productive forest occurs it is usually restricted to river valleys. Productive conifer stands are also restricted in the CP subregion mainly to the slopes of the mountain range, and support balsam fir, spruce, and white birch mixed forests. Other tree species of the boreal forest may be occasionally present or locally abundant, but the CP habitat is generally the more productive in this study. Numerous ponds and bogs occur in both areas. Mean annual temperatures are about 4.5°C cooler in the LRB habitat, and winter snow cover has a longer duration by about 1 month in the higher elevations.

METHODS

A stratified random block survey modified from Gasaway *et al.* (1986) was carried out in March 1995 to survey moose in GMNP. The Park was divided into a low-density stratum of 932 km^2 and a high-density stratum of 986 km^2 based on classification of 2 x 2 km blocks. An understanding of habitat potential based on 1:50,000 topographic map information and observer experience in GMNP were used in stratification. For the survey, 16 blocks were

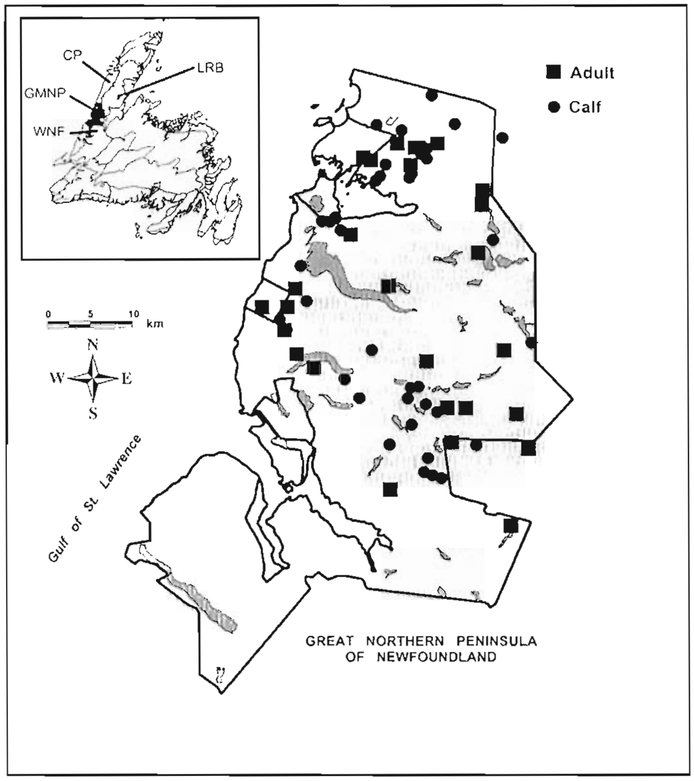

Fig. 1. Location of Gros Morne National Park (GMNP) relative to the Western Newfoundland Forest (WNF), the Long Range Barrens (LRB), and the Coastal Plain (CP) of the Great Northern Peninsula of Newfoundland (insert map). The larger-scale map shows the separation of the LRB (lightly shaded) and CP (unshaded) habitats within the Park boundary (heavy line) at the 425 m a.s.l. contour line. Moose collaring locations (1995 - 1998) within both habitats are plotted by age.

randomly chosen from the low-density stratum, and 40 blocks were randomly chosen from the high-density stratum. The total area sampled was 11.6% of GMNP, and an average of 14 minutes was spent surveying each block in parallel flight strips of about 0.25 km width. All observations were made using a Bell 206L helicopter with 2 rear-seat observers and a front-seat navigator-recorder. Moose were classified as bulls, cows with calves, cows without calves, calves alone, and "unknown" during the census. Correction factors for unseen moose were based on observer ratings for visibility assigned after each survey block, based on tree canopy closure, weather conditions, and amount of flying time over each block. Confidence intervals at 90% were constructed for population estimates within each stratum and for the total survey area. These confidence intervals accounted for variance between block counts only, assuming a normal distribution within a stratum; they did not include estimates of variance in moose sightability (see below for assignment of correction factors, following the 1998 survey). High and low density estimates were compared with cluster analysis and a *t*-test.

A similar survey was conducted in March 1998 with a more complete stratification of the Park into low, medium, high, and very high density, using the above determinants and 8 hours of fixed-wing survey in a Cessna 185, with 2 rear-seat observers and a front-seat observer-navigator-recorder. Snow conditions on the LRB were assessed during the fixed-wing stratification, and moose tracks and sightings were recorded along all flight lines. Relative assessments of density based on fixed-wing observations, previous experience drawn from the 1995 survey and other field work, and a revised 1:12,500 map showing forest cover from the GMNP forest inventory were used to stratify the Park. Resulting areas by stratum were 723 km^2 low, 523 km^2 medium, 535 km^2 high, and 77 km^2 very high moose density, of which 5%, 7%, 12%, and 90% were sampled in a total of 58 2x2 km blocks (11.2% of GMNP). The 1998 survey was conducted using 2 helicopters, a Bell 206B and an AS 350 B2, for portions of 3 days total.

During the day prior to counting 1998 survey blocks, an aerial monitoring flight of all radio-collared moose locations was flown in a Cessna 185, locating collared moose with on-board GPS. These animals were intended to be used as a blind assessment of moose sightability, such that several survey blocks were non-randomly assigned to include marked animals. This partial non-random assignment was unknown to observers during the survey. Blocks were checked again by helicopter radio-monitoring, after completing each count, for the inclusion of 1 or more marked animals, according to a list consulted only after counting. Of 7 radio-collared moose in survey blocks at the time of the survey, all 7 were observed before their signal was re-recorded. However, these animals all occurred in blocks given a fair visibility rating. Thus, in both the 1995 and 1998 surveys, blocks with a "fair" rating were uncorrected for sightability, while blocks given a "poor" rating were corrected by a factor of 2.0, based on the minimum number of unseen moose in a comparison of similar stratified survey techniques and a mark recapture study conducted by Oosenbrug and Ferguson (1992).

Spring herd composition surveys took place in June 1995, 1997, and 1999. Moose were classified as male and female adults, and unclassified yearlings and calves. All observations were made from a Bell 206L or Bell 206B helicopter, and sex determination was based on presence of the vulva patch and/or the presence or absence of antlers. Individuals were recorded in groups and their locations recorded using GPS coordinates or landmarks. Sampling attempted totals of >100 moose and complete aerial coverage of the LRB and CP ecoregions, but this goal was not always achieved during surveys of higher elevations due to unfavourable weather. Calf production was calculated as calves per 100 cows and percent calves in the total sample. Recruitment was calculated as percent yearlings in the adult plus yearling sample. Sex ratios were calculated as adult bulls per 100 cows. In November 1997, moose were again classified using the same criteria as spring, with the exception that yearlings were not distinguished from older adults. Herd composition was also summarized from aerial survey estimates in March 1995 and March 1997, although no attempt was made during those surveys for complete aerial coverage of the Park.

Fourteen adult female moose (n = 11, LRB; n = 3, CP) were radio-collared with VHF collars (Lotek Engineering Inc., Newmarket, ON) during May - June 1995. Moose were immobilized by darting from helicopter with 6 mL of 300 mg/cc xylazine, weighed, measured, and ear-tagged. An incisor (I4) was extracted for *cementum* ageing, and reproductive status was recorded. After collaring, animals were released with an intramuscular injection of 3 mg RX82100 2A. Aerial monitoring flights were conducted every 2 - 4 weeks using a Cessna 185 to identify mortality signals and to determine moose locations using the on-board GPS recorder. The Park was also patrolled by helicopter during the calving periods (20 May - 1 June) of 1995 - 1999 in search of 1 - 3-day-old calves. Calves (*n* = 76) were captured, weighed, measured, sexed, ear-tagged, and collared with expandable VHF radio-collars (Lotek Engineering Inc.). Collared calves were visually checked from helicopter within 48 hours of capture to determine if rebonding with their dams occurred, and then remotely monitored with fixed-wing aircraft every 3 - 5 days thereafter until mid- to late-June, and every 2 - 4 weeks through the remainder of their first year. Transmitters in mortality mode were retrieved as soon as feasible and the site and remains examined to determine the cause of death. Capture method and cause of death determination followed Ballard *et al.* (1979). Test VHF collars (*n* = 6) were placed in a stationary position and locations were recorded with a hand-held GPS recorder. The same pilot monitored moose locations during most of this study, and accuracy of his locations was rated by comparison to these test collar locations and to the recorded positions of retrieved dead animals.

In June 1997, 12 adult female moose (11 with at least 1 calf) were also immobilized and fitted with GPS collars (Lotek Engineering Inc.). Resulting GPS location records for this study were corrected with base station fixes from Corner Brook, NF (West Viking College, College of the North Atlantic). Fix attempt schedule was set at every 3 hours beginning at 0300 h NST, to allow 6 months of continuous data reception between downloading sessions. Remote downloading of GPS collars occurred in September 1997, November 1997, and March 1998. Collars were removed to provide the remaining data records in November 1998. Test GPS collars (*n* = 5) were placed in a stationary position in 4 habitats (open, mixed forest cover, coniferous forest cover, and cliff slope) to determine fix frequency, activity, and location accuracy under variable cover types using the same fix schedule (Moen *et al.* 1997). These collars were retrieved and downloaded after 2 - 4 weeks of recording in December 1997, and corrected data were compared to a control location determined from the hand-held GPS recorder.

Proportions of all collared animals surviving to the end of May 31 of each year of study were calculated, and mortality causes were classified by cohort, for both VHF- and GPS-moose. Linear survival estimates were based on the number of monitoring days summed across all collared animals for a given cohort, within a biological year, defined as June 1 in the year of collaring, to May 31 of the following calendar year (Heisey and Fuller 1985). An animal was assumed alive either from June 1 - May 31 (365 days), or from June 1 to the midpoint between the last date the collar was heard in live mode and the date of the next monitoring flight before May 31 (for censored animals or animals dying before 1 year elapsed).

Home ranges were calculated using the 95% minimum convex polygon method, based on an algorithm written for MapInfo software (MapInfo Inc., Troy, NY), by Nolan and Taylor (1998). Annual and seasonal ranges were calculated separately for each VHF-collared moose, and seasonal and monthly ranges were calculated for each GPS-collared moose, to determine shifts in range size (Doerr 1983). Home ranges were compared by comparing median sizes (Wilton and Bisset 1988). Seasons were classified as summer from June - November and as winter from December - May. Calves monitored into their second and third years were used to test the model of juvenile dispersal of moose by calculating range overlap (Gasaway *et al.* 1981). Distances between successive locations <30 days apart were used to calculate straight-line (minimum) rates of movement for calves, yearlings, and adults monitored >300 consecutive days including $\geq$10 locations in 1 year. Distances moved immediately following collaring were excluded from movement rate calculations to avoid the possibility of introducing error caused by intrusion at the time of contact of cows and calves. Total distances moved were compared within and between 2 groups, calf-cow pairs and yearlings, by season and habitat, using Wilcoxon's rank sum test, $\alpha = 0.05$ (Wilton and Bisset 1988).

RESULTS

In the 1995 winter survey, 35 moose were observed in the low-density stratum and 544 moose were observed in the high-density stratum, equivalent to sightability-corrected densities of 0.6 and 6.4 moose per km^2 respectively, and an overall corrected population estimate of 6,893 ± 1,543 (± 22.4%). The 2 strata had significantly different densities ($t = 3.66$, 54 df, $P < 0.001$); however, cluster analysis of blocks in the high-density stratum indicated 2 additional distinct density groups (1.7 ± 1.2 and 7.9 ± 1.7 moose per km^2), and the need for the more detailed stratification in the 1998 survey work.

During the March 1998 survey, 935 moose were counted in 4 strata. The density of the low stratum in 1998, 2.2 moose per km^2, was more than 3 times the low-density estimate in 1995, but areas stratified as medium and high density were estimated at 3.3 and 5.5 moose per km^2 in 1998, below the comparable high-density estimate in 1995. Comparison of 10 blocks which sampled the same 2 x 2 km areas in 1995 and 1998 also showed that the total number of moose observed had declined slightly in high-density areas. However, identification of an area of very high density, 14.1 moose per km^2, compensated for this change, and a corrected estimate of 7,377 ± 1,249 (± 16.9%) moose suggested no overall population change since 1995. The higher degree of stratification resulted in a higher level of precision in the 1998 census. The strata were statistically distinct in all cases, with contrasted densities between the low and medium strata ($t = 1.74$, 18 df, $P < 0.05$), between the low and high strata ($t = 4.20$, 25 df, $P < 0.05$), between the medium and high strata ($t = 2.81$, 25 df, $P < 0.05$), and between the high and very high strata ($t = 4.55$, 33 df, $P < 0.05$).

Survey work also showed that calf production and survival to midwinter were 32 and 36 calves per 100 cows in 1995 and 1998, respectively (Table 1). Spring composition surveys showed that calf production was consistently higher in CP habitat than in LRB habitat (tests of proportions, $\alpha = 0.01$), and that the percent calves has increased over time in both subpopulations. Spring recruitment of yearlings was also higher in the CP than the LRB subpopulations in 1997 and 1999, but not in 1995 (tests of proportions, $\alpha = 0.01$). Calves per 100 cows and percent yearlings in the CP subpopulation declined slightly during the study period, but the difference was not significant, nor was the same trend evident in the LRB subpopulation. In the fall survey, calf classifications in the LRB subpopulation were higher than in spring of the same year (test of proportions, $\alpha = 0.01$), possibly indicating a later birth date for some calves in this habitat than the time when the spring surveys were conducted. Sex ratios were variable, but proportionately more bulls were found in LRB surveys than in CP surveys in 1997 and 1999 (tests of proportions, $\alpha = 0.01$). Comparing the 3 spring surveys of the CP habitat, bulls appear to be a declining proportion of this subpopulation; again, this trend is not evident in the LRB subpopulation.

Among radio-collared moose dying dur-

Table 1. Summary of moose herd composition surveys in Gros Morne National Park (GMNP), 1995-1999.

Survey Date	Area Surveyed[1]	Number Classified	Calves per 100 Cows	Percent Calves	Percent Yearlings	Sex Ratio (♂:♀)[2]
March 18, 1995	GMNP	579	32	13	-	1 : 1.2
June 2, 1995	CP	123	44	15	27	1 : 1.5
June 10, 1995	LRB	11	20	9	40	1 : 9.0
June 4, 1997	CP	147	46	22	13	1 : 2.8
June 5, 1997	LRB	95	20	13	7	1 : 2.7
November 11, 1997	CP	130	40	21	-	1 : 1.9
November 15, 1997	LRB	83	38	16	-	1 : 0.9
March 18, 1998	GMNP	935	36	19	-	1 : 2.3
May 29, 1999	CP	90	33	25	18	1 : 3.2
May 30, 1999	LRB	45	20	15	15	1 : 2.4

[1] GMNP surveys are conducted during random block counts in the Park censuses, and are not necessarily representative of a population; CP = Coastal Plain, LRB = Long Range Barren habitats.

[2] Sex ratio is calculated with combined classification of yearlings and adults.

ing this study, adult deaths were attributed to 1 legal hunter kill, 1 case of poaching in the Park, 1 accidental death due to a fall over a steep cliff, and 1 winter-related death (Table 2). Three collared yearlings were poached outside the Park boundary, and among the known causes of death for adults and yearlings, poaching was the most frequent explanation. Most calf deaths were attributed to black bear (*Ursus americanus*) predation in June and July. Calf deaths designated as winter-related in 2 cases were described as starvation due to immobilization in deep snow in the LRB habitat. Proportionately more calf deaths occurred in the LRB habitat. When annual survival rates were combined over all years of study, estimates for each of the 3 cohorts examined were statistically lower (Heisey and Fuller 1985, $P < 0.05$) in LRB than in CP habitat (Table 3). Calf survival between habitats in individual years was not statistically distinguishable, and survival was similar among the 4 years of study.

Range sizes for VHF-collared moose were dependent on the number of locations. Fixed-wing monitoring was infrequent through fall and winter. Therefore, categorization of range size variability due to season, sex, age, or habitat was confounded by low sample size in many instances. However, accuracy was fairly good on fixed-wing locations from the test collar results and the locations of retrieved mortality cases: a median error of 2.0 km, a mean error of 2.4 km, and maximum error of 6.1 km were recorded between pilot and ground GPS co-ordinates. Ranges were smaller (Wilcoxon test of medians, $T = 64$, $n_1 = 12$, $n_2 = 11$, $P < 0.01$) in winter (median 4.8 km^2) than in summer (median 10.6 km^2) for both sexes and all ages (seasonal VHF data are not shown). Maximum winter range was 60 km^2 and maximum summer range was 67 km^2. Sex and age could not be used to predict annual (nor seasonal) range sizes (Table 4). Larger ranges were generally found on LRB habitat than on CP habitat,

Table 2. Observations of mortality among collared moose by cohort, 1995-1999.

	Monitoring Years				
Cohort	1995-96	1996-97	1997-98	1998-99	Total (%)
Calves (sample size)[1]	*n* = 14	*n* = 12	*n* = 18	*n* = 13	*n* = 57
Total dying within year (%)	5 (36)	3 (25)	5 (28)	3 (23)	16 (28)
Probable causes:					
Dam abandonment[2]	1	1	2	1	5 (-)
Black bear predation	2	3	4	1	10 (18)
Winter related	3	0	0	0	3 (5)
Unknown	0	0	1	2	3 (5)
Yearlings (sample size)		*n* = 6	*n* = 9	*n* = 13	*n* = 28
Total dying within year (%)		2 (33)	0 (0)	3 (23)	5 (18)
Probable causes:					
Poached		1	0	2	3 (11)
Unknown		1	0	1	2 (7)
Adults (sample size)[3]	*n* = 14	*n* = 11	*n* = 26	*n* = 19	*n* = 44
Total dying within year (%)	3 (21)	0 (0)	2 (8)	4 (21)	9 (20)
Probable causes:					
Accident	1	0	0	0	1 (2)
Legally hunted	1	0	0	0	1 (2)
Poached	1	0	0	0	1 (2)
Winter related	0	0	0	1	1 (2)
Unknown	0	0	2	3	5 (12)

[1] Sample sizes for calves exclude cases of collar slip <2 days following handling.

[2] Dam abandonment cases are not included in calf mortality totals or survival calculations in Table 3.

[3] Annual adult sample size is the number of animals monitored during each year; total adult sample size is the number of independent animals collared through the study duration.

for calves (LRB, 43.4 km^2; CP, 18.3 km^2: $T = 45$, $n_1 = 9$, $n_2 = 5$, $P < 0.01$), yearlings (LRB, 35.1 km^2; CP, 28.6 km^2: $T = 42$, $n_1 = 9$, $n_2 = 5$, $P < 0.01$), and 2-year-olds (LRB, 10.1 km^2; CP, 1.5 km^2: $T = 21$, $n_1 = 5$, $n_2 = 5$, $P < 0.05$). Many yearling ranges calculated for moose of both sexes (Animals 7, 12, 15, 16, 19, 20, and 22) extended further onto the LRB than calf ranges for the same animal, including 3 of 5 cases of calves collared on the CP (Fig. 2). Yearling ranges overlapped the corresponding cow-calf ranges of the previous year in the 10 cases shown, with a median of only 36% overlap (range, 12 - 94%).

Adults or cow-calf pairs moved more frequently from the LRB to the CP habitat or *vice versa* in 1 year (16 of 24 cases) than the similar movement monitored for yearlings (5 of 12 cases). The adult sample also included the most erratic movements: 11 of 24 cases changed habitats more than once per year. Mean straight-line distances moved by moose did not differ for adults (0.25 km per day) and yearlings (0.17 km per day) ($F = 0.25$, 1 df, $P = 0.62$). In the complete analysis of variance, there were also no differences in distances moved between seasons ($F = 0.12$, 1 df, $P = 0.83$) or between animals collared in LRB relative to

Table 3. Survival estimates for collared moose by cohort, year, and subpopulation, 1995 - 1999.

Cohort and Subpopulation	Year	Collared Sample Size	Monitoring Days	No. of Deaths	Survival Estimate	95% C.I.
Calves						
LRB	1995-96	11	2,732	4	0.586	0.475-0.722
	1996-97	8	1,604	3	0.505	0.335-0.761
	1997-98	9	1,731	3	0.531	0.369-0.764
	1998-99	4	809	1	0.637	0.363-1.000
	Total	32	6,875	11	0.557	0.509-0.610
CP	1995-96	3	877	1	0.659	0.386-1.000
	1996-97	4	1,184	0	1.000	
	1997-98	9	1,559	2	0.626	0.454-0.863
	1998-99	9	1,894	2	0.680	0.536-0.862
	Total	25	5,514	5	0.718	0.664-0.777
Park Total	1995-96	14	3,608	5	0.603	0.517-0.703
	1996-97	12	2,788	3	0.675	0.570-0.800
	1997-98	18	3,290	5	0.574	0.480-0.687
	1998-99	13	2,702	3	0.667	0.559-0.795
	Total	57	12,388	16	0.624	0.597-0.652
Yearlings						
LRB	Total	17	4,503	4	0.723	0.657-0.795
CP	Total	14	3,549	1	0.902	0.847-0.962
Park Total	Total	31	8,052	5	0.797	0.763-0.833
Adults						
LRB	Total	23	12,640	7	0.817	0.796-0.838
CP	Total	21	13,216	3	0.92	0.907-0.935
Park Total	Total	44	25,855	10	0.868	0.859-0.878

CP habitats ($F = 3.07$, 1 df, $P = 0.09$). A greater relative number of moose in the LRB habitat left the Park boundary (12 of 27 cases) than in the CP habitat (5 of 25 cases) in 1 year. Extreme migration distances occurred in some cases. For example, 1 calf-cow pair moved >147 km in 1 year, likely crossing the 425 m elevation contour between habitats at least 4 times. The range of straight-line distances moved in 1 year by cow-calf pairs was 18.7 - 183.8 km (median 42.4 km), higher (Wilcoxon test, $T = 253$, $n_1 = 22$, $n_2 = 12$, $P < 0.01$) than for yearlings (range, 23.0 - 102.5 km; median, 40.3 km). The median distance travelled in LRB habitat (63.2 km) did not differ from the median distance travelled in CP habitat (41.2 km) for adults ($T = 69$, $n_1 = 10$, $n_2 = 12$, $P > 0.10$), or for yearlings (LRB, 45.5 km; CP, 38.7 km: $T = 14$, $n_1 = 5$, $n_2 = 7$, $P > 0.10$).

GPS-collared moose produced much more accurate locations and range estimates. Test collar location accuracy was found to be dependent on collar position with respect to topography and forest

Table 4. Annual range sizes (km^2) for moose collared as newborn calves and monitored during the following 2 - 3 years, by age, cohort, sex, and subpopulation. Number of locations from fixed-wing and helicopter flights is given as n, and range sizes are calculated only for $n \geq 5$. A yearling range calculation begins with points located in June of the year following collaring, and an adult range begins in June of the next year.

Sub-Population	Sex	Cohort Year	Animal Code	Calf Size	Calf n	Yearling Size	Yearling n	Adult Size	Adult n
LRB	Female	1995	MC05	6.6	12	6.3	11	40.0	11
			MC12	43.4	14	48.6	11		
			MC14	188.3	13	3.8	6		
		1996	MC20	112.6	18	35.1	11	4.9	5
			MC23	83.8	16	43.3	9		
	Male	1995	MC04	107.4	14	96.0	13	151.3	11
			MC15	15.1	16	68.5	14	10.1	9
			MC17	14.5	15	1.6	9		
			MC22	24.0	16	16.0	10	2.1	5
CP	Female	1995	MC07	18.0	16	64.3	13	13.7	6
			MC08	15.9	16	28.9	14	1.5	6
		1996	MC16	62.3	19	28.6	10	0.3	5
			MC19	30.3	16	15.8	10	1.4	5
	Male	1996	MC24	18.3	17	15.4	11	3.2	5

canopy, but 95% of all differentially corrected data from test collars had ± 25 m accuracy. Monthly ranges for GPS moose were seasonally variable, and were consistently larger through summer for LRB moose than for CP moose (Fig. 3, $T = 24$, $n_1 = 8$, $n_2 = 6$, $P < 0.05$). Seasonal shifts in range use were much more clearly distinguished for GPS-moose, where summer ranges were very often located over more upland areas than winter ranges (Fig. 4).

DISCUSSION

Identification of several areas in the Park with very high winter moose density in 1998 resulted in a new census calculation confirming that moose may be locally more numerous (14.1 per km^2) than in nearly any other recorded location in the world. On the other hand, more barren areas in the Park, especially in LRB habitat, do not show any change in moose density between the 1995 and 1998 census estimates, consistent with other observations over the past 25 years (Prescott 1978, Taylor 1991). If this portion of the Park, in the low-density stratum, has habitat comparable to the barren areas in south-central Newfoundland studied in the 1970's, which do not typically support hunted moose densities above 0.5 per km^2 (Albright and Keith 1987), and 1.1 - 3.4 moose per km^2 is representative of the equivalent densities in an unhunted situation, then it may be possible to suggest that KCC applies here. In the high-density stratum of the Park, the overall population also shows no increase from 1995 to 1998, suggesting that moose density is stabilising. It is likely from the tracking of VHF- and GPS-collared animals to date that this stabilisation is due in part to emigration of longer-ranging LRB animals from the Park.

Fig. 2. Calf (—) and yearling (- - - - - -) ranges from VHF fixed-wing monitoring of moose in GMNP. Numbers refer to animal codes in Table 4 and are positioned in the region of annual range overlap for the same moose. Ranges are plotted only when monitoring frequency $n \geq 10$. The map on the left shows males, and maps on the right show females. Animals 7, 8, 16, 19, and 24 were collared in CP habitat; the lightly shaded region on each map is LRB habitat.

Spring and fall survey results, supported by radio telemetry, indicate moose within GMNP seasonally disperse outside the Park boundary. From the high recruitment rates observed, particularly in spring 1995 and fall 1997, GMNP should have shown increases in the period of the study. The best way to account for the lack of increase in the census results then, is movement outside the Park boundary. Fall sex ratios, especially on the CP habitat, reflect generally poorer yearling and adult male survival rates in the Park relative to the female component, possibly due to hunting and poaching of bulls, but more likely due to male dispersal from high-density to low-density areas within the Park (*cf.* Miquelle *et al.* 1992). Survival calculations, telemetry monitoring, and range calculations support this latter conclusion.

Hunter statistics are shown in Table 5 for areas surrounding GMNP, relative to the most recent population estimates for those areas. This table is included to show that moose survival outside the Park is very heavily influenced by hunting. Hunters are harvesting mostly the adult component of populations in Areas 2, 4, 5, and 6, usually in more accessible CP or WNF habitats (NLWD, *unpubl. data*). The resulting survival rate for adult moose outside the Park is clearly lower than adult survival in

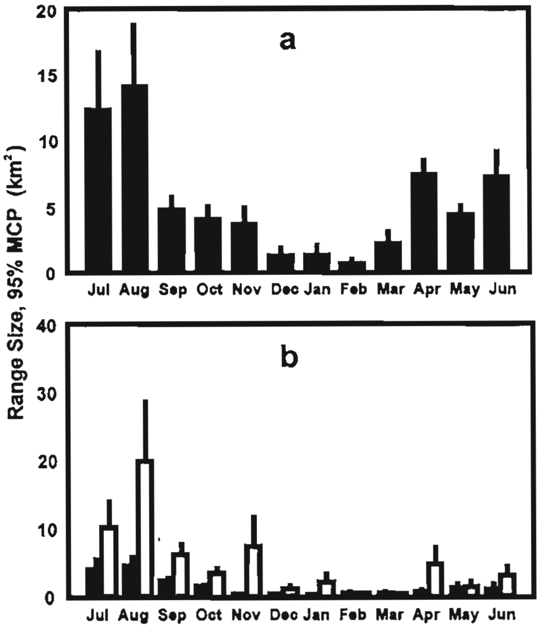

Fig. 3. Monthly range sizes calculated (a) for all GPS-collared moose in GMNP, and (b) separately for LRB (unshaded bars) and CP (shaded bars) subpopulations. July to October samples combine 1997 and 1998 ranges for some moose; monthly sample sizes range from 6 - 16 moose (a) and from 4 - 8 moose (b) for the separate subpopulations. Vertical lines above each bar are 95% confidence intervals.

the Park, much lower than the 92% annual survival in CP habitat, and likely lower than the 82% calculated for the LRB habitat (Table 3). This comparison does not take into account the fact that many adult losses recorded for the Park population were actually incurred by hunting or poaching outside the Park boundary. Moose poaching violations are also among the most frequent law enforcement occurrences for wardens of GMNP, where a minimum of 25 - 60 violations can occur each year (GMNP Law Enforcement Plan 1998).

Assessing moose KCC demands multi-year monitoring and the acceptance of a broad range of values for KCC because the moose-vegetation equilibrium is not constant, but rather, dependent on variations in snow depth or forage availability, variations in forage quality, the influence of forest succession on forage production (Crête 1989), and changes in predation on moose (McLaren and Peterson 1994). Fire, insect outbreaks, and logging can substantially increase (or decrease) KCC. Higher survival, smaller ranges, and fewer cases of extreme dispersal in CP versus LRB moose still suggest better habitat for CP moose. Yet, the LRB habitat presents a seasonally

Table 5. Population indices for hunting areas adjacent to GMNP, from most recent aerial survey data[1] and annual hunter questionnaires[2].

Hunting Area	Population Estimate	Census Year	Moose Harvest by Hunting Season 1995	1996	1997	1998	Mean Harvest, 1995-98	Harvest / Population (%)
2	5,300	1990	688	748	1,068	1,172	919	17.3
4	3,280	1997	749	791	779	639	740	22.6
5	2,040	1993	603	651	711	708	668	32.8
6	2,250	1994	732	642	708	690	690	30.8
Total	12,870		2,213	2,832	3,266	3,209	2,880	22.4

[1] Aerial survey technique follows method described for GMNP 1995 survey (see Methods).
[2] Mail-in response to the NLWD as a proportion of all questionnaires attached to moose licences (Mercer and Manuel 1974), has been consistently >50%, or >75% following a post-season reminder, since 1989. Respondents to the reminder are used to adjust hunter success and harvest estimates.

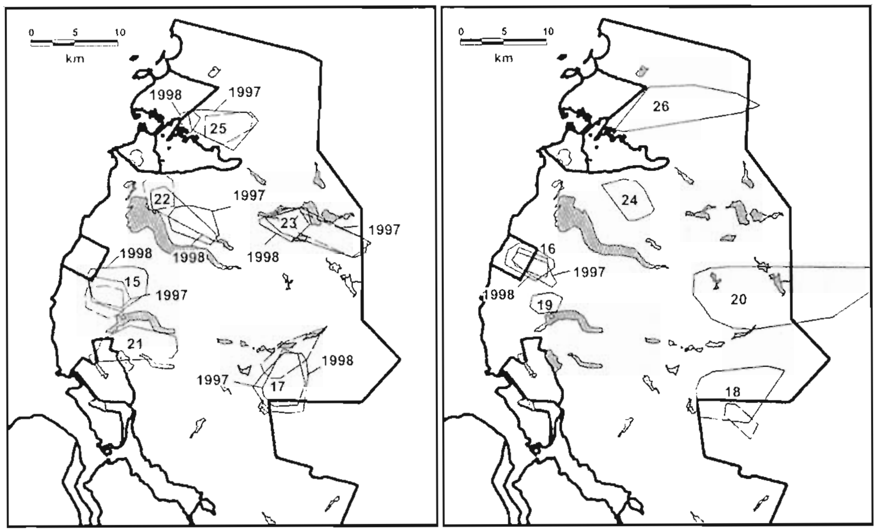

Fig. 4. Summer (—) and winter (- - - - - -) ranges for GPS-collared moose relative to the LRB (lightly shaded) and CP (unshaded) habitats. Seasonal ranges overlap for the same moose; summer ranges are shown separately for 1997 and 1998 for some moose.

important area to moose collared on the CP. In contrast to many other studies showing more juvenile than adult dispersal (Gasaway *et al.* 1981, Wilton and Bisset 1988), this study determined that migration between habitats, and also into hunted areas outside the Park, where survival is reduced, are possibly more common for the reproducing component of the population than for yearlings. Consistent with the findings of Cederlund and Sand (1994), yearling moose dispersal and home range size were not different between sexes.

While acknowledging that the understanding of reasons for extreme moose demographics and movements from 1 habitat up a steep elevation change to another habitat in GMNP may better come from a later paper, which will make more detailed use of habitat information for the Park and the greater accuracy of the GPS-moose locations, we offer here several possible explanations for what this paper documents. The most probable explanation for the movement between habitats comes by comparison to the several previously published descriptions of seasonal elevation changes for moose (Miller and Litvaitis 1992, Miquelle *et al.* 1992, Cederlund and Sand 1994, Van Dyke *et al.* 1995). The suggestion that moose are optimizing their energy intake by following plant phenological delays with increasing elevation is consistent with the suggestion that all ranges within the Park have experienced declined availability of preferred forage (Connor *et al.* 2000). This decline in habitat suitability can explain the larger ranges in summer, when moose are maximizing their intake during a short growing season, especially at the higher Park elevations. An alternative explanation for the energy costs that may be associated with moose moving long distances is the possibility that predation by black bear poses a threat to calves. Dams may seek security by moving to higher elevations or by moving less predictably (Garner and Porter 1990, Miquelle *et al.* 1992). The absence of wolves in Newfoundland may allow greater freedom of movement for cow-calf pairs across barren areas in the Park. Finally, it is possible that moose ranges are still equilibrating with habitat in Newfoundland, especially at a distance from their original point of introduction. That is, dispersal and elevation changes monitored in this study may simply be a result of the rapid increase recently observed in the GMNP moose population.

Very different population dynamics occur within habitats of the greater Park ecosystem separated by abrupt elevation changes, but also due to different management of moose by the partner agencies in this study. The GMNP research speaks well for interagency co-operation in resolving concerns for a locally very abundant - and broadly very dynamic - species, through long-term research plans. Park officials and local residents have expressed concern over the management of domestic forest cutting areas in the Park, because the creation of younger forest by harvesting activities may be contributing to moose population increase, while preferential browsing by moose in harvested stands may also be restricting forest regeneration. Information on moose habitat preferences and their effect on forest regeneration in GMNP are to be reported in a later paper. Knowledge of the demographics of moose in GMNP assists management planning in Hunting Areas 2, 4, 5, and 6 by the NLWD (*cf.* Garner *et al.* 1990), and understanding habitat use by this dominant herbivore assists the long-term strategy for Park protection of 2 of Newfoundland's unique ecoregions.

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