The Ninth North American Caribou Workshop,
Kuujjuaq, Québec, Canada,
23–27 April, 2001.

Winter range drift in the George River Caribou Herd: a response to summer forage limitation?

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Abstract: Space use by the George River caribou herd (GRCH) changes in correspondence with migration patterns. The traditional range of this herd encompasses an area of approximately 900 000 km^2. Range use is seasonal and includes travel to traditional calving grounds. Winter range use however, is more variable. The GRCH has grown rapidly from 5000 animals in 1954 to approximately 775 000 in 1993. Beginning in the mid 1980s, the calving and summer range habitats of the GRCH have deteriorated, resulting in a decline in physical condition and subsequent poor calf survival and low pregnancy rates. We assessed the importance of the winter range as a food source compensating for poor summer range quality through an evaluation of winter range drift and use intensity. We hypothesized that if winter ranges provide a compensatory source of forage, then George River caribou should avoid sites heavily used during the previous winter at a population level. Winter ranges for the GRCH were calculated using 4300 caribou locations obtained 1986-2000. We found that in spite of a doubling in net range area, the size of annual winter ranges did not increase, indicating the occurrence of range drift. Further, George River caribou exhibited avoidance of wintering areas at several spatial scales. Avoidance occurred across a use threshold, where the degree of use (or density) during the previous winter determined the level of avoidance during the subsequent winter. As the spatial scale decreased, the degree of avoidance increased. Caribou significantly avoided areas used the previous winter at spatial scales below and including 245 km^2 (corresponding to a 75% use distribution). Results suggest winter foraging allows caribou suspend the effects of density-dependent summer forage limitation on herd productivity. As such, analysis of GRCH population trends should be considered in light of both summer and winter range resources.

Key words: habitat, Labrador, Nunavik, population ecology, range fidelity, Rangifer tarandus, spatial, telemetry.

Rangifer, Special Issue No. 14: 113-122

Introduction

The migratory George River caribou (Rangifer tarandus) herd (GRCH) is a vital wildlife species of the taiga of Labrador and Northern Québec, and has been an integral component of the way of life for aboriginal peoples for many centuries. In modern times, caribou meat remains an important food resource for many residents, particularly those residing in isolated northern communities. Currently, the GRCH provides the basis for a lucrative sports-hunting industry and developing commercial hunt.

A combination of traditional knowledge, historical records, and scientific censes suggest that this herd has undergone at least 2 population cycles, and that these have incorporated both periods of rapid increase and great abundance and precipitous declines (Couturier et al., 1990; Messier et al., 1988; Russell et al., 1994). Historical records suggest that caribou were abundant in the mid and late 1800s (Elton, 1942), but became rare beginning early in the 19th century. This lasted for a period of approximately 40 years, an event that resulted in widespread starvation of native peoples (Messier et al., 1988; Bergman, 1998). In 1958, a systematic aerial census indicated a population size of around 15 000 caribou

(Bergerud, 1967). For the next 30 years, the herd increased rapidly (annual rate of increase of 0.11 estimated from census data; Messier et al., 1988), eventually peaking at 775 891 (plus or minus 13.4%) caribou, including calves, in 1993 (Couturier et al., 1996; Russell et al., 1996). At that level of abundance, the herd was considered to be the largest in the world (Williams & Heard, 1986; Couturier et al., 1996).

During the late 1980s, several demographic indices including low pregnancy rates, poor adult survival, and declining physical condition, indicated that herd size had stabilized or begun to decline by the time of the 1993 census (Messier et al., 1988; Huot, 1989; Hearn et al., 1990). In 1985, Huot and Goudreault documented an unusual phenomenon for a northern ungulate: female caribou appeared to increase their fat reserves over the winter. However, they believed that the surprisingly poor fall condition of females was related to a sampling bias. Couturier et al. (1988) also presented data confirming that the fat reserves of female caribou were better in the spring than in the fall in during the 1980s. Their explanation for this unique phenomenon among caribou was based on the deterioration of the calving grounds of the GRCH. Generally, caribou increase their protein and fat reserves during summer, when forage is plentiful, and lose fat and protein during the long winters. Documented erosion of the quality of summer calving grounds (Couturier et al. 1990; Manseau et al., 1996) was a likely cause of the poor summer physical condition observed in the latter studies. The fact that caribou were nutritively stressed during summer led Messier et al. (1988) to suggest that forage limitation on the summer range may be an important component of population regulation in the large GRC herd. Expanding on that theory, Couturier et al. (1990) proposed that caribou might be using the winter range to compensate for the poor quality of the summer range.

The goal of this study was to test the importance of the winter range as a component of forage-dependent population regulation in the GRCH. If winter ranges provide a compensatory source of forage, then George River caribou should avoid sites heavily used during the previous winter. Our hypothesis was based on the assumption that the removal of terricolous lichens, the main winter food of caribou (Thomas & Hervieux, 1986), exceeds annual production on any given winter range (Arsenault et al., 1997; Couturier et al., 1990). We evaluated avoidance as a function of range drift, a spatial behaviour in which expansion occurs on one front while contraction occurs on another, and animal density. Specific objectives in our assessment of interannual winter range use in the GRCH included 1) determining changes in total (or cumulative) winter range size 1986 to 2000, 2) assessing long-term changes in annual winter range size, and 3) evaluating winter range fidelity (or avoidance) at the population level as a function of use intensity during the previous winter.

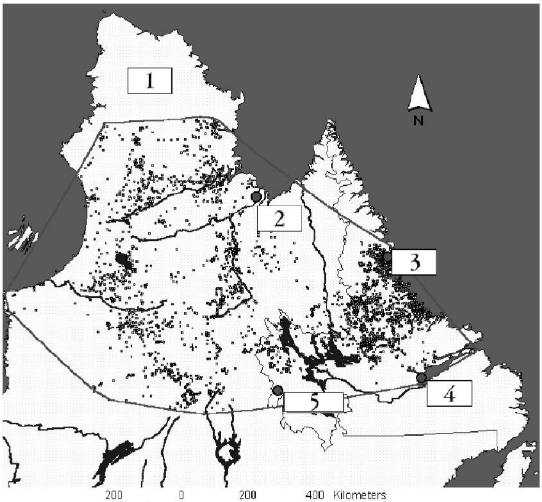


Fig. 1. Map of Labrador and Northern Québec showing the total winter range (Dec.-Mar. inclusive) of the George River Caribou Herd. Range boundaries are delineated based on 4306 locations (NQ 1-3) of 61 radio-collared animals, tracked from 1986-2000. 1: Ungava Peninsula, 2: Kuujjuaq, 3: Nain, 4: Goose Bay and 5: Labrador City.

Methods

Study Area

The George River caribou herd occupies much of the Ungava peninsula of Northern Québec and Labrador encompassed between the latitudes 54° and 61°N, an area extending from Hudson Bay to the Labrador Sea, approximately 900 000 km^2 (Fig. 1). The southern latitudes of this range are characterized by open lichen woodland composed of black (Picea mariana) and white spruce (P. glauca) and larch (Larix laricina) with a continuous lichen carpet (mostly fruticose species such as Cladina) or peatlands. Moving north, the taiga gives way to forest tundra that consists of stands of ericaceous plants (Ledum groenlandicum, Vaccinium spp.), dwarf birch (Betula glandulosa) and willow (Salix spp.). Most of the area north of 58° in Québec and 56° in Labrador consists of arctic tundra, a treeless area dominated by mosses, graminoids, lichens and water, although forest tundra persists in many river valleys. Elevation rises to approximately

1600 m a.s.l. on the height of land east of the George River and toward the Torngat Mountains in the east. Snow cover lasts from mid October to early May in the taiga, and approximately half of the annual precipitation falls as snow. Goose Bay receives an average annual snowfall of 440 cm (Goose Bay, 1951-1980 average), while forest and Arctic tundra receive about 224 cm of snow per year (30 year average ending 1980). The daily mean temperature during January for the villages of Kuujjuaq, Schefferville and Goose Bay, respectively, are -23.4, -22.7 and -13.4 °C, respectively.

Data Collection and Preparation

The study was conducted over a 14-year period for winters beginning 1 December 1986 and ending 1 March 2000. GR caribou belong to the migratory Rangifer ecotype (Bergerud, 1996), and their space use and movement changes in correspondence with sub-annual time periods. Bergman (1998) and Bergman et al. (2000) identified 6 such periods on the basis of mean daily travel rates and direction of travel. The winter period was characterized by low daily travel rates and hence reduced space use for the period December through April. As GR caribou tend to move north toward the calving grounds beginning in April (Bergman et al., 2000; NFWD unpubl. data), we restricted use of locations to the period January through March for each winter. We captured adult (≥ 1-year-old females) using chemical restraint agents, administered by dart fired from helicopter (1986-1997), or by using nets also fired from a helicopter (1998-2001). Captured caribou were fitted with satellite-tracked (Service Argos, Landover, Maryland, USA) ultra high frequency Platform Terminal Transmitters (PTTs; Telonics, Mesa, Arizona, USA). PTTs were set to 3 or 4-day transmissions cycles, and were replaced or removed prior to battery exhaustion. We tracked the movements of a total of 61 different animals over the study period. Service Argos Inc. provides 6 location quality classes based on the number of signals received by the satellite. These classes range from -2 (poorest) to 3 (highest, about 150 meters), and provide users with an estimate of location precision (Keating et al., 1991; Rodgers 2001). PTT locations belonging to location quality (NQ) classes 1 to 3 were selected on a basis of one location per transmission day for one particular collar. We discarded locations with NQ ≤ 0 due to their inherent imprecision (Keating et al., 1991; Rodgers 2001). In addition, data were plotted using a GIS and visually screened within each winter season and among individual animals per season, and any outliers were removed unless another nearby location of NQ 1-3 (equivalent to an accuracy of £ 1 km; Rodger 2001: 100) within the same transmission period could confirm them. Otherwise, the location was discarded. The resulting dataset contained a total of 4306 individual locations over 14 winter seasons. Table 1 summarizes the number of individual caribou, and the number of locations by quality class, for each of the 14 winters of the study.

Table 1. A summary of George River caribou winter location data, showing the number of individual caribou, and the number of locations by quality class (NQ), for each of the 14 winters of the study.

Winter season	Number of locations NQ = 3	NQ = 2	NQ = 1	n
1986-1987	135	12	43	4
1987-1988	28	170	55	8
1988-1989	4	59	44	4
1989-1990	6	55	35	5
1990-1991	12	186	133	13
1991-1992	18	188	150	16
1992-1993	20	138	128	12
1993-1994	30	169	153	14
1994-1995	85	171	129	13
1995-1996	127	182	102	15
1996-1997	187	272	143	13
1997-1998	238	248	110	15
1998-1999	114	106	59	11
1999-2000	76	114	62	13

Data Analyses

Range Expansion and Drift

Changes in total GRCH winter range size 1986-2000 were calculated using a minimum convex polygon (MCP) home range estimator. MCPs are one of the oldest and most common methods used to estimate home range size (Mohr, 1947). The area polygon is constructed by connecting the outer locations to form a convex polygon, and home range size is then calculated as the area of that polygon (White & Garrott, 1990: 148). MCP home ranges were calculated using Arcview™ GIS and the 'Animal Movement' program (Hooge & Eichenlaub, 1998). By dividing the 14-year period into 5 segments of 2 or 3 years each, changes in winter range size over time were calculated by constructing the cumulative MCP (an outer boundary encompassing all radio-collared animal locations for a given time period), and calculating the area for each time segment. Changes in area over time were plotted. Because the size of minimum area polygons increases with number of animal locations, and because they do not reflect intensity of use within the polygon, they often overestimate home ranges (Jennrich & Turner, 1969; White & Garrott, 1990). However, their simplicity, data inclusivity, and the ease with which they may be calculated make MCPs a popular method for home range estimation. Additionally, further precision obtained by the use of a more sophisticated technique is unnecessary given the coarse time and spatial scale of pooled changes in winter range size.

To evaluate long-term changes in winter range size occurring as a function of range expansion/contraction, or range drift, annual winter ranges for several intensities of use were calculated and mapped for each of the 14 years of the study using a nonparametric kernel density estimator (Worton, 1995). Kernel estimators allow one to assess use distribution (UD) by creating a probability density estimate based on location data (Seaman & Powell, 1996). Proportional usage of different portions of the home range can therefore be estimated. The core area of a given probability is the area enclosed by a contour within which locations are closer together than would be expected under the assumption of uniform use of the home range area (Worton, 1987). Calculation of a kernel-based home range estimate requires that a grid be superimposed on the location data. The probability that each cell lies within the home range can then be calculated (UD), and a smoothing parameter 'H' (Worton, 1989) estimated. Using least squares cross-validation (LSCV), the smoothing parameter that minimizes discrepancies between the estimated and true densities is selected (Worton, 1995). The bivariate normal density kernel with least squares cross-validation of the smoothing parameter has been shown through simulations to produce the most accurate home range estimates among several available nonparametric methods (Seaman & Powell 1996).

We calculated and plotted 50, 75, and 90 percent probability polygons using Arcview™ GIS and the 'Animal Movement' program (Hooge & Eichenlaub, 1998), which uses the Worton (1989) algorithm. Least squares cross validation was used to calculate an optimal smoothing parameter for each year. Grid size was set at 5 km^2 for all analyses. However, area values increase at higher levels of 'H', and, given that optimal 'H' values differed between years, the smoothing parameter was fixed in order that area estimates between years be comparable. The value of the fixed parameter was determined by taking the median value based on all LSCV calculated winters. Probability polygons for each winter season were then recalculated using the fixed smoothing parameter. Table 2 lists the values of the LSCV calculated 'H' and the fixed value used for the final area calculations.

Table 2. A comparison of cross-validated and model-forced smoothing parameters calculated for GRCH winter ranges 1986-2000, showing discrepancies between estimated and true densities. Parameters calculated using least squares cross validation (LSCV) are shown relative to the median value that was forced into all final models. For years with an LSCV-based smoothing parameter lower than the median value, probability polygons will overestimate true areas. Conversely, if LSCV values are larger than the (forced) median values, probability polygons will underestimate actual areas. Note that no pattern of consistent over/under estimation occurs. Accordingly, study results are not an artefact of the algorithms used to estimate winter range size in the George River caribou herd.

Winter season	LSCV based H	Forced H (Median value)	Estimate?
1986-1987	36.3	46.7	Over
1987-1988	57.6	46.7	Under
1988-1989	46.6	46.7	Good Fit
1989-1990	64.9	46.7	Under
1990-1991	80.7	46.7	Under
1991-1992	46.9	46.7	Good Fit
1992-1993	47.4	46.7	Good Fit
1993-1994	45.9	46.7	Good Fit
1994-1995	65.3	46.7	Under
1995-1996	25.3	46.7	Over
1996-1997	32.5	46.7	Over
1997-1998	40.9	46.7	Good Fit
1998-1999	42.9	46.7	Good Fit
1999-2000	87.7	46.7	Under

Over the course of the study period, the number of radio-collared caribou (and thus the number of locations) ranged from 4 to 19 (96-569 locations). To evaluate the possible influence of variation in sample size on the area calculations, we plotted the number of radio-collared caribou and the number of locations, respectively, with area estimates for each probability polygon, and visually assessed each for any linear trends.

Winter Range Fidelity

To evaluate inter-year fidelity in GR caribou to win-

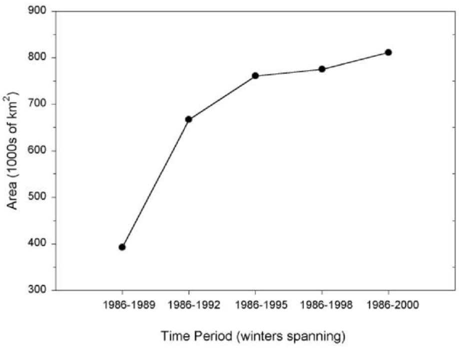


Fig. 2. Cumulative winter range size in the George River caribou herd 1986-2000, based on 100% MCP for each time period indicated (n = 4306).

tering areas, avoidance of sites used in subsequent winters was assessed at several spatial scales and degrees of use intensity. If winter forage is an important determinant of winter range use and site selection, then the probability of caribou occurring in an area one year should be negatively related to the probability of occurring in the same area the following year, particularly at higher use intensities. Based on this principle, we assessed avoidance to wintering areas used in preceding years at 5 spatial scales. In order to link use intensity to avoidance or fidelity behaviors, scales associated with mean values for 50, 75 and 90 per cent contours were chosen. These corresponded to a grid size of 320 km^2 (15 grid cells), 245 km^2 (24 grid cells) and 150 km^2 (60 grid cells), respectively. Additional scales were added at the landscape level, set at 500 km^2 (6 grid cells), and at the individual level, set at 100 km^2 (135 grid cells). A smaller scale was not selected to reduce the possibility that animals occur in multiple cells within the same year. In order to keep cell locations consistent among years, the same grid extent was used for all analyses, and pooling winter locations for the entire 14-year period set its boundaries. Radio-collared animal density was estimated using two methods: first by counting the number of radio-collared animals, and second by counting the number of locations observed by radio transmissions within each cell, for all 5 spatial scales. Spearman rank correla-

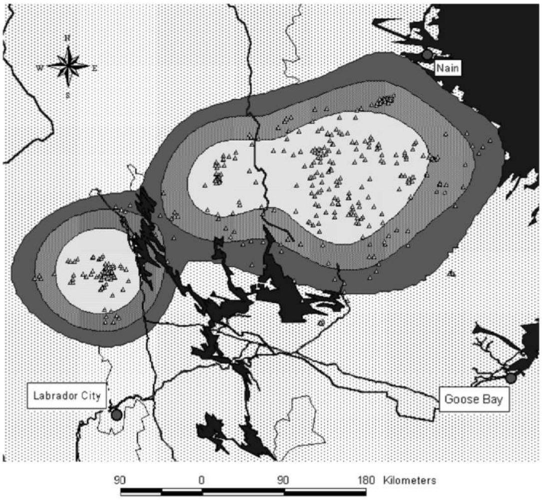


Fig. 3. An example of a kernel home range estimate for winter 1995-6, showing probability contours for 50, 75, 90 per cent use distributions. Observed animal locations are superimposed on the kernels.

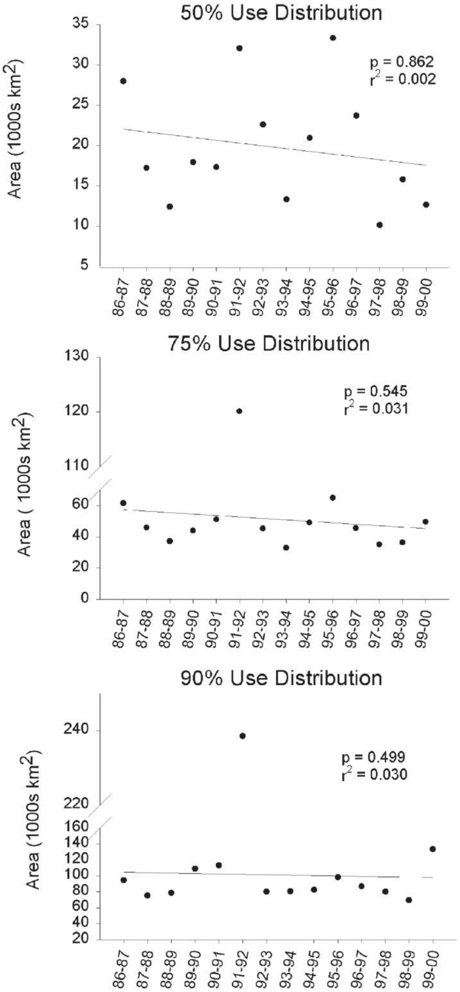


Fig. 4. The relationship between winter range size and year for George River caribou for three different use distributions for the period 1986-2000. No significant trends in winter range size over time exist.

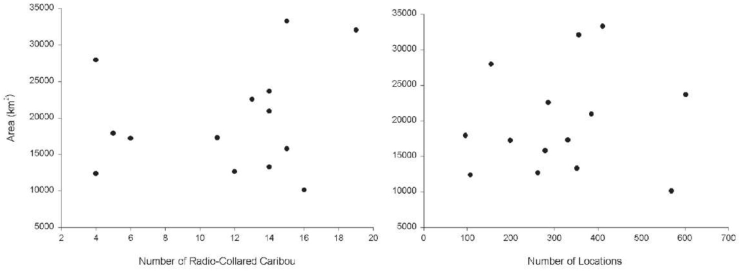
tions were used to compare cell densities (animals and locations) at time t versus time t-1, and a significant negative relationship among years was interpreted to indicate avoidance. Double 0's were disregarded. This analysis was repeated for each spatial scale.

Results

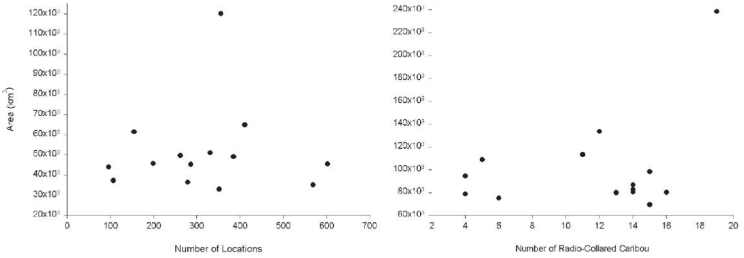
Range Expansion and Drift

The cumulative winter range of the George River caribou herd doubled in size during the period 1986-2000, from 392 796 km^2 (1986-1989) to 811, 138 km^2 (1998-2000) (Fig. 2). Much of this increase occurred prior to 1995; areas calculated based on the 100% MCPs show a marked expansion of winter range size of about 90% from 1986 to1995, and a gradual increase thereafter (Fig. 2). However, while the total (or cumulative) winter range of the GRCH increased, this expansion did not occur as a result of an increase in winter range size over time, but rather as a consequence of range drift. Fig. 3 shows an example of annual winter range size calculated using a kernel home range estimator for 50, 75 and 90 percent-use distributions. No significant relationship in annual winter range size over time was observed at any of the latter use intensities (P = 0.862, P = 0.545, P = 0.499, respectively) (Fig. 4). This result is unlikely to be the product of use of a fixed smoothing parameter, as the forced median value provided a good approximation of LSCV calculated values, and no pattern of consistent underestimation was observed (Table 2). In most cases, the forced median value was a good approximation of LSCV calculated values, and succeeded in minimizing discrepancies between estimated and true densities. Exceptions include the winters of 1990-1991 and 1999-2000, in which winter range size were underestimated, and the year 1995-1996, in which areas were overestimated through use of the fixed smoothing parameter (Table 2). Further, area estimates for all probability polygons did not vary with either the number of radio-collared caribou or the number of locations per year (Fig. 5), a feature indicating that changes in winter range size over time are not an artefact of variable sample size between years.

a) 50 % Use Distribution



b) 75% Use Distribution



c) 90% Use Distribution

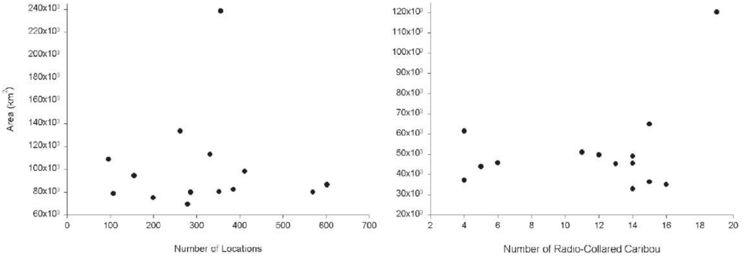


Fig. 5. Area estimates for 50 (a), 75 (b) and 90 (c) Probability Polygons as a function of the number of satellite-derived locations and radio-collared caribou, respectively. The absence of a positive linear relationship indicates that changes in winter range size over time cannot be ascribed to variable sample size between years.

Winter Range Fidelity and Avoidance

George River caribou exhibited avoidance of wintering areas at several spatial scales. Avoidance occurred across a use threshold, where the degree of use (or density) during the previous winter determined the level of avoidance during the subsequent winter (Table 3). At the landscape scale (500 km^2) and for the area associated with the 90% use distribution (320 km^2), caribou exhibited neither avoidance nor

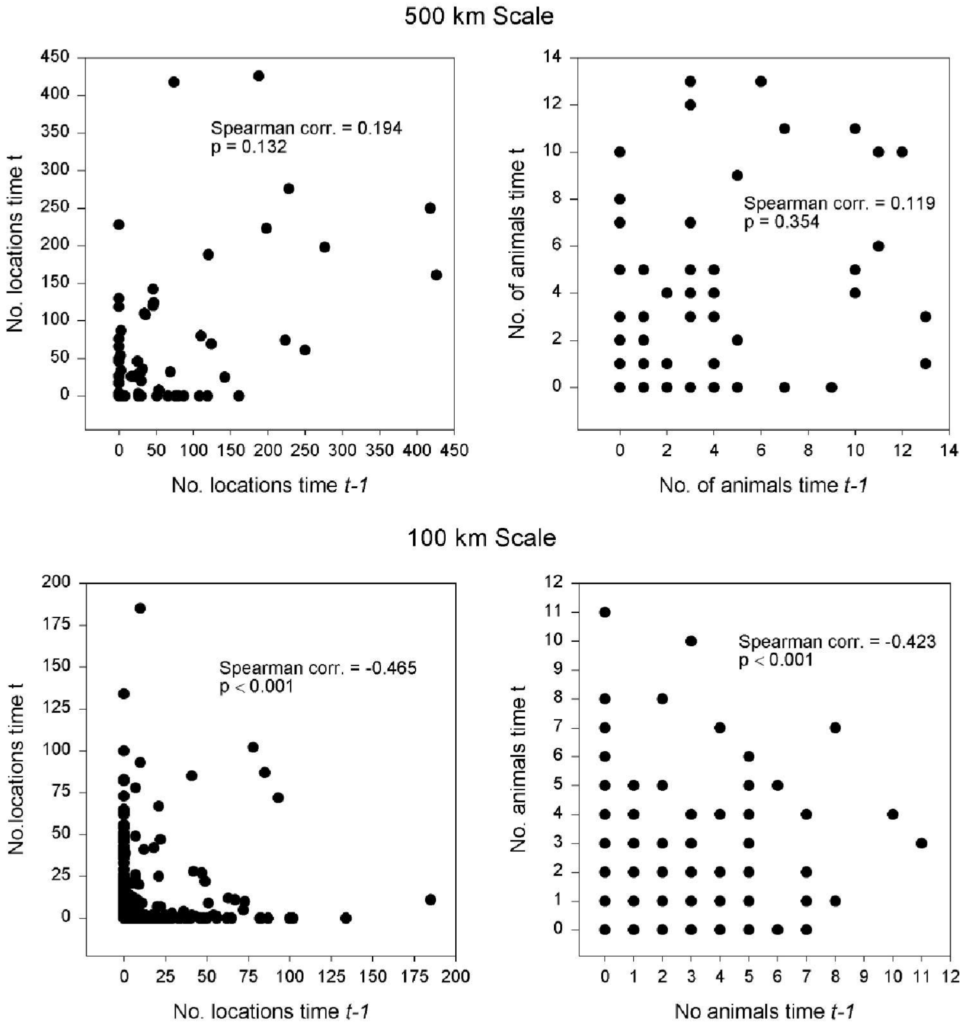


Fig. 6. An example of inter-year winter range use in the George River caribou at two levels of use intensity (500 km and 100 km spatial scales). Caribou density at time t is plotted as function of density at time t-1. At the landscape level, caribou do not avoid areas used during the previous year. At smaller scales (and thus greater levels of use intensity) however, caribou avoid areas used extensively the previous year.

fidelity (Table 3, Fig. 6). However, caribou significantly avoided areas used the previous winter at spatial scales below and including 245 km^2 (corresponding to a 75% use distribution) (Table 3). As the spatial scale decreased, the degree of avoidance increased. For example, at the 100-km^2 scale, location and radio-collared animal density explained 47% and 42% of the variation in the following winter, respectively ($P < 0.0001$). That is, there was an almost 50% probability that there would be little use in presently heavily used cells in the following winter at that spatial scale. The same patterns were observed in both indicators of use intensity, though trends were more pronounced in the location density estimator. The latter could be due to the fact that location density within grid cells incorporates time spent at the location: a high number of locations within an area are a product of both the number of animals in the cell and the duration of time spent within the cell. Given this characteristic, location density is probably a better indicator of use intensity.

The large winter range size observed over 1991-1992 at 75 and 90 per cent use (Fig. 4, outlier) distributions reflects range use by the GRCH during that winter: radio-collared animals were widely dispersed among 3 focal areas, two in close proximity just north of the Smallwood Reservoir, and a 3rd much further NW, near Ungava Bay. At higher use distributions (an hence lower animal densities), larger portions of location data are included within the probability polygon, thus dispersion of location data across the landscape will also result in larger area estimates (but accurate depictions of the distribution of radio-collared animals during that period).

Discussion

Ecotypic designations of Rangifer have been established on the basis of site fidelity, the propensity of animals to remain in or return to a particular place, during parturition (Bergerud, 1996). The George River caribou are migratory, traveling large distances over the Québec-Labrador peninsula, and aggregating on traditional calving grounds each June, thereby displaying one of the most consistent behaviors of migratory caribou (Gunn & Miller, 1986). Winter ranges however, are far less predictable. Schaefer et al. (2000), in a multi-scale study of site fidelity in the GRCH, found that individual caribou displayed no philopatry to wintering areas. They denote a distinct annual rhythm where average distances in inter-year locations during winter for individual animals was 400-450 km (Schaefer et al., 2000). Indeed, it is widely believed that one of the most predictable characteristics of caribou winter ranges is that they are unpredictable. Consequently, shifts in winter ranges are not well known. Ferguson & Messier (2000) documented mass winter emigration of caribou in Canada's high Arctic between 1984 and 1992, and proposed that the range shift occurred as a result of forage depletion caused by long-term overgrazing. Winter range drift allowed caribou to maintain access to adequate forage, and caribou that emigrated to ungrazed winter areas improved their body condition (Ferguson & Messier, 2000).

Range drift was associated with a density-dependent response to forage limitation in the GRCH. Forage depletion occurs rapidly in lichen-dominated subarctic and arctic woodlands given the low productivity of these regions. Further, the standing crop of terricolous lichens is the product of several decades of annual production (Arsenault et al., 1997). Studies on the influence of caribou winter grazing on the landscape have suggested that lichen removal exceeds annual production (Arsenault et al., 1997), and that consequently lichen may become progressively depleted through both consumption and trampling (Klein, 1987; Messier et al., 1988). By shifting winter ranges, George River caribou maximize their intake of winter forage, possibly compensating for the poor quality of their summer range (Manseau et al., 1996). Huot & Groudreault (1985) observed that female caribou shot in April 1984 were fatter than those shot in the fall of 1983. Poor physical condition of George River caribou in fall, an unusual occurrence for herbivores in northern ecosystems, was also documented by Couturier et al. (1990). During the period 1983-1987, winter survival of this herd generally increased or remained stable during the winter, yet declined during the summer (Hearn et al., 1990).

The relative importance of summer versus winter ranges to caribou population productivity and physical condition, however, is controversial. In a study of a southern Alaska Peninsula caribou herd, Post & Klein (1999) found that differences in forage availability and quality on winter ranges were of secondary importance in explaining differences in herd productivity. However, they qualified their interpretation by emphasizing the importance of a good quality summer range for this to be true. Additionally, winter ranges of poor quality were able to reduce the productivity of the herd, though to a lesser degree than summer ranges (Post & Klein 1999). Alternatively, Skoglund (1985; 1986) found that a decline in female body size, and a reduction in recruitment in populations of wild reindeer were attributable to winter food limitation, and that these effects were most apparent at high population densities. With respect to the GRCH, summer nutrition has been linked to poor physical condition and insufficient milk production in female caribou (Crête & Huot, 1993). The demographic consequences of suboptimal summer foraging were falling pregnancy rates and decreased survival (Crête et al., 1996). Collectively, these traits indicate that summer nutrition is an important component of population regulation in the GRCH (Messier et al., 1988, Hearn et al., 1990; Crête & Huot, 1993; Crête et al., 1996).

Nonetheless, this study shows that George River caribou shift winter range use between years, and that range drift is associated with use intensity (below a use threshold), where more use presumably results in added forage depletion, and leads to subsequent avoidance during the following winter. This study suggests that the relative importance of winter or summer ranges to population trends may be dynamic, and contingent on the quality of the summer range. If, as is the case for the GRCH, the summer grounds are overgrazed, then winter foraging (and hence winter ranges), may be used to compensate for the poor quality of the summer range. Winter foraging thus allows caribou to ameliorate their physical condition and suspend the effects of density-dependent summer forage limitation on herd productivity. In situations were the summer range contains abundant, nutritious forage, winter ranges may be of diminished importance to the productivity of caribou (as in Post & Klein, 1999). Regardless, the available evidence underscores the importance of forage limitation as a mechanism of population regulation in the GRCH, and suggests that caribou population trends should be considered in light of both summer and winter range resources. We propose the following hierarchical model to estimate the potential importance of summer and winter ranges to herd productivity. The model is contingent on the quality of the summer range: if it is good or adequate, winter range use is of secondary importance. If the summer range has deteriorated, winter ranges become increasingly important as a compensatory mechanism. If both summer and winter ranges are in poor condition, or if appropriate winter habitat is located prohibitively distant from the summer range, then the population is in imminent danger of collapse. A declining population trend (Couturier et al., 1990), an overgrazed summer range (Manseau et al., 1996), poor fall physical condition (Couturier et al., 1988; Huot, 1989), and the occurrence of winter range drift all suggest that currently, winter ranges are an important component of the population dynamics of the GRCH.

The population consequences of compensatory winter foraging by the GRCH may be dramatic fluctuations in population size caused by delayed density-dependent effects (Messier et al., 1988; Couturier et al., 1990). In shifting winter ranges once a use threshold is reached, caribou expand their cumulative range and may continually access areas with ample forage (Ferguson & Messier, 2000). In theory, this behavior would be successful in delaying the physical and demographic effects of overgrazing on the summer range as long as there was no shortage of areas with sufficient forage to access, or until the distance traveled to new wintering areas were to exceed the energetic benefits obtained from foraging within them. If the latter criteria were to occur, the population would have nowhere to go but down as the full effect of density-dependent forage limitation is experienced. Messier (1994) and Saether (1997) have suggested that a stable equilibrium between large herbivores and their food supply is unattainable in situations where delayed-density dependence is occurring through compensatory foraging, and in the absence of large numbers of predators. Accordingly, large, possibly cyclic fluctuations in population size have been observed in North American caribou herds, including the GRCH (summarized in Couturier et al., 1990).

In order to clarify the nature of interactions between habitat use in the George River caribou and linkages to population dynamics, further research is necessary. Most importantly, information on space use must be joined with associated demographic parameters such as survival and fecundity, and with seasonal and annual changes in physical condition. Also, behavioral research centered on activity budgets and degree of mobility should be combined with measures of use intensity to assess winter range quality. Finally, a model simulating the energetic costs associated with range drift should be developed. Collectively, the latter research projects would allow for the development of realistic models of the population dynamics of a northern ungulate highly adapted to life in a subarctic environment.

Acknowledgements

We thank numerous conservation officers and research staff of the Newfoundland and Labrador Wildlife Division who assisted in the field operations. J. Schaefer made helpful suggestions on the experimental design, and provided insightful feedback throughout the research process. D. Goulding designed and wrote the Arcview™ scripts used in the study. P. March assisted with database management. J. Fenske helped to produce the figures. S. Couturier and Q. van Ginhoven improved the manuscript through their constructive reviews. Financial support was provided by the provincial Department of Tourism, Culture, and Recreation (Inland Fish and Wildlife Division), and from the Department of National Defence.

References

Arseneault, D., Villeneuve, N., Boismenu, C., LeBlanc, Y, & Deshaye, J. 1997. Estimating lichen biomass and caribou grazing on the wintering grounds of northern Québec: an application of fire history and landsat data. – Journal of Applied Ecology 34: 65-78.

Bergerud, A. T. 1996. Evolving perspectives on caribou population dynaminсs, have we got it right yet? – Rangifer 9: 95-116.

Bergman, C. M. 1998. George River caribou monitoring in Labrador: knowledge as the basis for sustainable development. Department of Forest Resources and Agrifoods, Inland Fish and Wildlife Division. P.O. Box 3014, Stn. B, Goose Bay, Labrador, Canada.

Bergman, C. M., Schaefer, J. A., & Luttich, S. N. 2000. Caribou movement as a correlated random walk. – Oecologia 123: 364-374.

Couturier, S., Brunelle, J., & Lapointe, G. 1988. Decline of physical condition and decrease of recruitment in the George River caribou herd. Proc. Third North American Caribou Workshop. Alaska Dept. Fish and Game. Juneau. – Wildl. Tech. Bull. No. 8: 35-37.

Couturier, S., Brunelle, J., Vandal, D., & St-Martin, G. 1990. Changes in the population dynamics of the George

River caribou herd, 1976-87. – Arctic 43 (1): 9-20.

Couturier, S., Courtois, R., Crepeau, H., Rivest, L. P., & Luttich, S. 1996. Calving photocensus of the Riviere George Caribou Herd and comparison with an independent census. – Rangifer Special Issue No. 9: 283-296.

Crête, M. & Huot, J. 1993. Regulation of a large herd of migratory caribou: summer nutrition affects calf growth and body reserves of dams. – Canadian Journal of Zoology 71: 2291-2296.

Crête, M., Couturier, S., Hearn, B. J., & Chubbs, T. E. 1996. Relative contribution of decreased productivity and survival to recent changes in the demographic trend of the Riviere George Caribou Herd. – Rangifer Special Issue No. 9: 27-36.

Elton, C. 1942. Caribou herds and modern trade. – In: Elton, C (ed.). Voles, mice and lemmings: problems in population dynamics. Oxford University Press. London.

Ferguson, M. A. D. & Messier, F. 2000. Mass emigration of arctic tundra caribou from a traditional winter range: population dynamics and physical condition. – Journal of Wildlife Management 64 (1): 168-178.

Gunn, A. & Miller, F. L. 1986. Traditional behaviour and fidelity to caribou calving grounds by barren-ground caribou. – Rangifer Special Issue No.1: 151-158.

Hearn, B. J., Luttich, S. N, Crête, M., & Berger, M. B. 1990. Survival of radio-collared caribou (Rangifer tarandus caribou) from the George River herd, Nouveau-Québec - Labrador. – Canadian Journal of Zoology 68: 276-283.

Hooge, P. N. & Eichenlaub, W. M. 1998. Animal movement to extension, A review. ver. 1.1 documentation. Alaska Biological Science Center, Anchorage AK, U.S.A. http://www.absc.usgs.gov/glba/gistools.htm.

Huot, J. & Goudreault, F. 1985, Evaluation of several indices for predicting total body fat of caribou. – In: T.C. Meredith & A.M. Martell (eds.). Proceedings of the Second North American Caribou Workshop, Val Morin, Canada. McGill subarctic Research paper No. 40: 157-175. McGill Subarctic Research Station, Schefferville, Québec.

Huot, J. 1989. Body composition of the George River caribou (Rangifer tarandus caribou) in fall and late winter. – Canadian Journal of Zoology 67: 103-107.

Jennrich, R. I & Turner, F. B. 1969. Measurement of non-circular home range. – Journal of Theoretical Biology 22: 227-237.

Klein, D. R. 1987. Vegetation recovery patterns following overgrazing by reindeer on St. Mathew Island. – Journal of Range Management 40: 336-338.

Manseau, M, Huot, J., & Crête, M. 1996. Effects of summer grazing by caribou on composition and productivity of vegetation: community and landscape level. – Journal of Ecology 84: 503-513.

Messier, F., Huot, J., Henaff, L., & Luttich, S. 1988. Demography of the George River Caribou Herd: evidence of population regulation by forage exploitation and range expansion. – Arctic 41 (4): 279-287.

Messier, F. 1994. Ungulate population models with predation: a case study with the North American moose. – Journal of Ecology 75: 478-488.

Mohr, C. O. 1947. Table of equivalent populations of North American small mammals. – American Midland Naturalist 37: 223-249.

Post, E. & Klein, D. R. 1999. Caribou calf production and seasonal range quality during a population decline. – Journal of Wildlife Management 63 (1): 335-345.

Rodgers, A. R. 2001. Recent telemetry technology. – In: Millspaugh, J. J. & Martzluff, J. M. (eds.). Radio Tracking and Animal Populations. Academic Press. San Diego, CA.

Russell, J., Couturier, S., Sopuck, L. G., & Ovaska, K. 1996. Post-calving photo-census of the Riviere George caribou herd in July 1993. – Rangifer Special Issue No. 9: 319-330.

Saether, B. E. 1997. Environmental stochasticity and population dynamics of large herbivores: a search for mechanisms. – Trends in Ecology and Evolution 12: 143-149.

Schaefer, J. A., Bergman, C. M., & Luttich, S. N. 2000. Site fidelity of female caribou at multiple spatial scales. – Landscape Ecology 15: 731-739.

Seaman, D. E. & Powell, R. A. 1996. An evaluation of the accuracy of kernel density estimators for home range analysis. – Journal of Ecology 77: 2075-2085.

Skogland, T. 1985. The effects of density-dependent resource limitations on the demography of wild reindeer. – Journal of Animal Ecology 54: 359-374.

Skogland, T. 1986. Density dependent food limitation and maximal production in wild reindeer herds. – Journal of Wildlife Management 50 (2): 314-319.

Thomas, D. C. & Hervieux, D. P. 1986. The late winter diets of barren-ground caribou in North-Central Canada. – Rangifer Special Issue No. 1: 305-310.

White, G. C. & Garrott, R. A. 1990. Analysis of wildlife radio-tracking data. Academic Press. San Diego, CA.

Williams, I. M. & Heard, D. C. 1986. World status of wild Rangifer tarandus populations. Proceedings of the 4th International Reindeer/Caribou Symposium, Whitehorse, Canada, 1985. – Rangifer Special Issue No. 1: 19-28.

Worton, B. J. 1987. A review of models of home range for animal movement. – Ecological Modelling 388: 277-298.

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

Worton, B. J. 1995. Using Monte Carlo simulation to evaluate kernel-based home range estimators. – Journal of Wildlife Management 59: 794-800.