Single-island home range use by four female Peary caribou, Bathurst Island, Canadian High Arctic, 1993-94

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Abstract: Spatial and temporal use of seasonal, and collectively, annual ranges by four female Peary caribou (*Rangifer tarandus pearyi*) was investigated using satellite telemetry. Knowledge of how caribou use space allows a better understanding of their demands on those ranges and enhances evaluation of associated environmental stressors. The study took place during an environmentally favorable caribou-year with high reproduction and calf survival and low (none detected) 1+ yr-old mortality, 1 August 1993 to 31 July 1994, Bathurst Island, south-central Queen Elizabeth Islands, Canadian High Arctic. All four females exhibited a pattern of single-island seasonal, and collectively, annual range use. Estimates of the maximum area encompassed by each individual during the course of the annual-cycle varied from 1735 to 2844 km^2 (mean±SE=2284±250 km^2). Although, there was 46% spatial overlap among individual ranges, temporal isolation resulted in the four individuals maintaining seasonal ranges distinctly separate from each other. This collective area encompassed 4970 km^2 and equaled about 31% and 18% of Bathurst Island and the Bathurst Island complex, respectively. Individual wintering areas formed a relatively small portion of each individual's annual range (mean±SE=71±17 km^2): 24 km^2, 158 days of occupation, <1% of the annual area; 70 km^2, 187 days, 4%; 95 km^2, 200 days, 4%; and 94 km^2, 172 days, 6%. Seasonal movements were greatest during pre-rut and pre-calving.

Key words: displacement vs. travel, distributions, *Rangifer tarandus pearyi*, movements, satellite telemetry locations.

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Introduction

Collection of detailed information on seasonal and annual movements and distributions of Peary caribou (*Rangifer tarandus pearyi*) has been limited by the high costs to carry out studies that require considerable aerial support. Year-round monitoring has been prevented, even with the use of conventional Very High Frequency (VHF) radio telemetry, by winter unavailability of suitable survey aircraft; stormy weather, fog, and white-outs; along with the long 'Polar night' from November into February.

The Peary caribou was listed by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) as 'Threatened' in 1979 (Gunn et al., 1981) and then as 'Endangered' in 1991 (Miller, 1990b). In 1989, the Canadian Wildlife Service selected the south-central Queen Elizabeth Islands, centered on Bathurst Island (Fig. 1), to continue ecological studies of the relationship between Peary caribou and their environment, particularly the stresses of unfavorable winter and spring snow and ice conditions. The area is important because the Inuit of Resolute Bay (74°41'N, 94°50'W) on Cornwallis Island have resumed hunting caribou on Bathurst Island in the 1990s (Fig. 1). The caribou on Bathurst and its satellite islands are the most accessible to those hunters. Also, based on past performance this population of Peary caribou appears to have, during climatically favorable periods, the potential to support the desired level of annual harvest.

For the reasons listed above, satellite telemetry permits a much fuller investigation of the spatial and temporal aspects of seasonal and year-round range

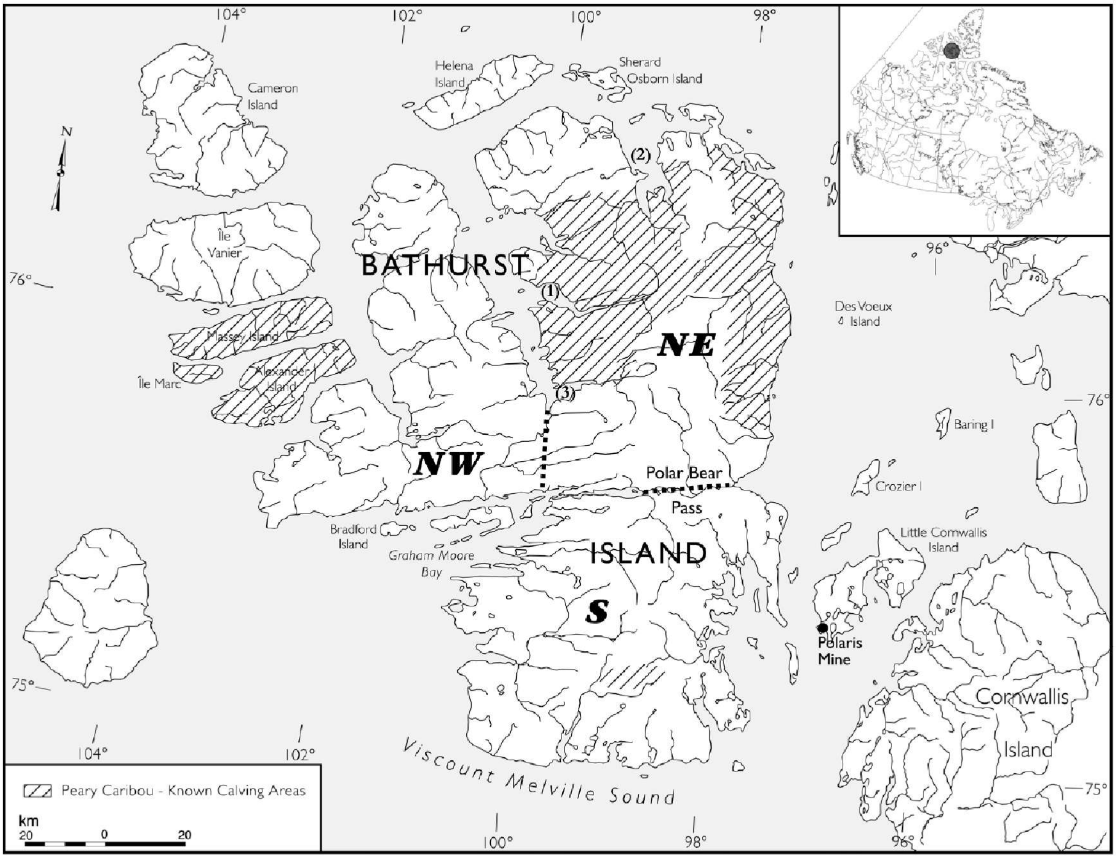

Fig. 1. Bathurst Island complex, south-central Queen Elizabeth Islands, Canadian High Arctic: Bathurst Island divided into 3 survey strata, northwest (NW), northeast (NE), and southern (S); and all known calving areas within the Bathurst Island complex shown (from Miller, 2002): (1) Stewart Bay area; (2) Young Inlet area; and (3) Dundee Bight area on Bathurst Island, plus Alexander and Massey islands to the west of Bathurst Island.

use than previously possible, even with VHF radio telemetry. The use of satellite telemetry neck-collars on Peary caribou was initiated in July 1993. The following is an analysis of seasonal, and collectively, annual range use by four female Peary caribou equipped with telemetry neck-collars on Bathurst Island, Canadian High Arctic, between 1 August 1993 and 31 July 1994. The findings are based on satellite location-data points obtained from Service Argos Inc. The sample size of animals is minute but the previous total lack of such detailed information for Peary caribou warrants documentation of these findings. This is particularly true because of the Peary caribou's 'Endangered' status and because these findings considerably advance our understanding of the ecology of Peary caribou. This work is a first step in gaining insight into how Peary caribou use seasonal range on a relatively large island (Bathurst Island, 16 042 km^2) during an environmentally favorable annual-cycle.

Material and methods

Study area and animals

Our study area is the 'Bathurst Island complex' - a grouping of 30 south-central Queen Elizabeth Islands in the Canadian High Arctic (Miller, 1998). The entire Bathurst Island complex is about 28 000 km^2. The islands are mostly low-lying and mainly below 150 m above mean sea level (amsl) in elevation, with typical high arctic tundra vegetation. The general climate, geology, topography, and vegetation have been described (see Miller, 1998 for references).

Bathurst Island itself was divided into three strata: Northeast (NE), 6630 km^2; Northwest (NW), 4068 km^2; and South (S), 5344 km^2 (Fig. 1). The major area of interest in this study is NE Bathurst Island. Although Bathurst Island is mainly low-lying, the terrain is broken and many sites lie between 150 and 300 m amsl, with a maximum elevation of 412 m amsl on northern NW Bathurst Island. The configuration of the island results in a proportionately long coastline with numerous drainages feeding freshwater into the sea. Many of these drainages along the west coast of NE Bathurst Island have steep embankments, rising to intermediate elevations >150 m amsl. The rough right-angle orientation of these drainages to the prevailing northerly winds and the rapidly increasing hours of daily sun during late winter promote the earlier removal of snow on those sites both by wind action and sublimation. The resulting mosaic of patches of snow-free ground and shallow snow-covered areas provide the most favorable late winter and spring ranges for Peary caribou.

Prior to our study, the Peary caribou on Bathurst Island suffered a 68% single-year major decline in winter and spring 1973-74 (Miller et al., 1977a; Miller, 1998; Miller & Gunn, this proceedings). Then, from some time after summer 1974, the caribou population on Bathurst Island and within the entire Bathurst Island complex experienced an overall continual period of growth to summer 1994, averaging about 13% • yr^{-1} (Miller, 1998; Miller & Gunn, this proceedings). By summer 1993 the inter-island population of Peary caribou within the Bathurst Island complex appeared to be of a healthy size, well represented by the various sex and age classes, and highly productive (Miller, 1995b). This favorable condition continued throughout autumn, winter, spring, and summer 1993-94: we counted 2400 Peary caribou by low-level helicopter survey and estimated about 2700 caribou within the Bathurst Island complex (Miller, 1995b). Nearly 95% (2273) of those caribou were seen on Bathurst Island and 79% (1790) of them were on NE Bathurst Island. Among the 12 survey search zones established on Bathurst Island, caribou were over-represented relative to the available landmass in each zone only on the interior of NE Bathurst Island (Miller, 1995b).

The potential for increasing abundance was high based on the population's sex and age composition within the Bathurst Island complex (Miller, 1995b). The sex ratio for the 1256 1-yr-old or older caribou (1+ yr-old) counted among those 1790 caribou on NE Bathurst Island was 39 males : 61 females (or 64 males : 100 females). Calves represented 30% of all caribou counted on NE Bathurst Island (the supposed theoretical maximum realized rate of annual increase, Bergerud, 1978). Nearly all (97%) of the breeding cows still had a calf at heel, and there was, on average, one bull for every three breeding cows.

Procedures

Peary caribou were captured using an aerial net-gun (Barrett et al., 1982). A Bell 206L (Jet Long Ranger) turbo-helicopter on high skid gear was used as the pursuit aircraft. Each telemetry neck-collar housed a satellite Platform Transmitter Terminal (PTT) package and a conventional VHF radio package (Telonics, Electronics Consultants, 932 E. Impala Avenue, Mesa, Arizona, U.S.A.). Details of the capture equipment and the telemetry packages; capture, handling, and release procedures; and results of the capture efforts are reported in Miller (1995b; 1997).

Location-data points were received monthly from Service Argos Inc., Landover, Maryland, U.S.A. Only location-data points with a Service Argos Quality Class (QC) rating of QC-1, -2, or -3 were used to determine a single location-data point for each duty-day. For the purpose of mapping the seasonal caribou movements, the location-data point with the highest QC rating (3, <150 m; 2, <350 m; and 1, <1000 m) was selected on each duty-day. When more than one location-data point of the same QC rating occurred on the same duty-day, they were averaged to obtain a single composite location-data point. Location-data points of QC-0 (>1000 m) were examined but were found unreliable.

The duty-cycle for the PTTs varied among four seasons: first a 5-day interval from 22 July 1993 until 30 September 1993 (12 h on, 108 h off); followed by a 2-day interval from 30 September to 15 November 1993 (12 h on, 36 h off); next a 5-day interval from 15 November 1993 until 14 May 1994; and then a 2-day interval from 14 May to 23 July 1994. The duty-cycle was then automatically reset to a new four-season cycle. Thus, between 1 August 1993 and 31 July 1994, the PTTs could potentially provide location-data points on 108 days.

To estimate the maximum area encompassed by each individual caribou during the course of their annual-cycle we connected the perimeter points of their satellite location data. We separated each individual's range use into temporal periods based on the known annual life-history cycle of caribou (e.g., Bergerud, 1978). Consecutive location-data points within these temporal periods were either linear directional movements or multi-directional traverses within a confined area. We grouped these consecutive location-data points by their respective style into temporal periods by visual inspection. We designated those discernible periods as either an 'Area Period' or 'Movement Period' (see Table 2). We then described each individual's annual use with schematic illustrations that clarify their spatial and temporal aspects (see Figs. 2-5). A Movement Period can best be described as an extended duration of range use along a continual path of travel, as opposed to an Area Period which has breadth and has all observations confined to a more specific section of range.

Table 1. Approximation of annual size of areas encompassed by perimeter locations and associated relevant land statistics for four female Peary caribou, Bathurst Island, Canadian High Arctic: based on connection of satellite perimeter location-data points obtained during an environmentally favorable year, 1 August 1993 to 31 July 1994.

Animal I.D.[a]	Maximum latitudinal axis (km)	Maximum longitudinal axis (km)	Size of annual home range (km^2)	% of total area of Bathurst Island occupied[b]	% of total area of Bathurst Island complex[b]
93-02F	81	57	2844	17.7	10.3
93-03F	59	57	1735	10.8	6.3
93-04F	47	58	2017	12.6	7.3
93-05F	89	47	2542	15.8	9.2
(Mean±SE)	(69±9.7)	(55±2.6)	(2284±250)	(14.2±1.6)	(8.3±0.9)

[a] Satellite-collared animal I.D., F equals female.

[b] Bathurst Island equals 16 042 km^2 and Bathurst Island complex equals 27 592 km^2.

We make a distinction among 'movement', 'travel', and 'displacement': movement or travel is the actual path traveled by a caribou and is the asymptotic limit of discrete location-data points as the time interval between them becomes shorter. This actual path is always unknown with satellite location-data - only continuous location data would provide this. The distance the animal actually moves or travels can at best only be approximated by the displacement between consecutive points. The terms 'movement' and 'travel' are thus misleading in their application to actual 'rates of movement', 'movement distance', 'rates of travel', and 'travel distance'. Whereas, 'displacement' is directly measurable using these data and best defines the actual point to point measurement and its ecological limitations should be clear. Thus, we use displacement as our unit of measure and we define 'displacement' as the difference between the initial position and any later position, measured as a horizontal plane vector. For example, two observations at a 5-day interval yields a 100 km south to north displacement during migration. However, the animal may have traveled 50 km NW from its origin, then 100 km due east, and finally 90 km again NW. Thus, it actually traveled 240 km to realize a 100-km displacement. Therefore, any measure of movement or travel distance and or rates, in this example, would be 58 percent in error. In addition, we still would not know whether that movement, travel, or displacement was accomplished in 3 or 4 days rather than 5 days, as determined by the 5-day sampling interval.

We examined variation in short-term rates of displacement by seven time interval classes (0.01-0.2, 0.2-0.4, 0.4-0.6, 0.6-0.8, 0.8-1.0, 1.0-2.0, and 2.0-8.0 h) location data. We restricted our analyses to only those rates of travel that were physically possible for a caribou to sustain (set at <16 km • h^{-1}). The majority (62%) of the spurious values that we omitted came from the lowest time interval class, 0.01-0.2 h. More importantly, the frequency of occurrence of spurious values was many times greater in this shortest time interval class than in other classes.

Results

Satellite location data

Adequate sets of location-data points in QC-1, -2, and -3 were obtained for four females during the study year (Tables 1-3, Figs. 1-7, females 93-02, 93-03, 93-04, 93-05). The limited number and fragmentary distribution of location-data points obtained in QC-1, -2, and -3 for the fifth PTT-collared animal (female, 93-01) did not allow any analysis or production of a map of her seasonal range and movements or her annual distribution. However, the limited QC-1 to QC-3 location-data points obtained from her suggested that she too had remained on NE Bathurst Island throughout the study period.

Range use

Other than by coastlines, neither the size nor the configuration of the area encompassed by each female appeared to be influenced by the size or configuration of NE Bathurst Island. None of the four females used any of the remaining 11 072 km^2 on Bathurst Island during the August 1993 to July 1994 study period: 1783 km^2 on the NE; 3945 km^2 on the NW; and 5344 km^2 on the S. All location-data points indicate that the females captured on NE Bathurst Island in late July 1993 remained there through July 1994 (Figs. 2-5). Estimates of the areas

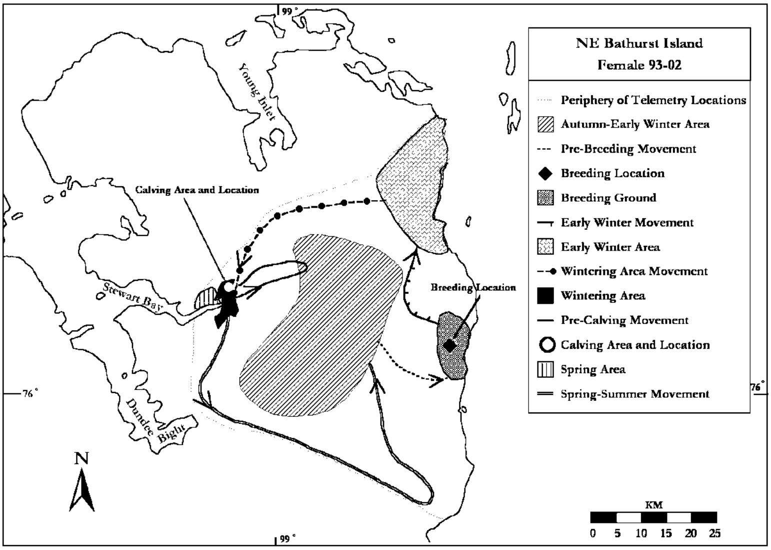

Fig. 2. Schema of seasonal range occupation and major directional movements of female Peary caribou 93-02 during the annual-cycle of the study period, Bathurst Island, Canadian High Arctic, 1 August 1993 to 31 July 1994: extrapolated from satellite location-data points.

encompassed by each individual averaged 2284 ± 250 km^2 SE and varied from 1735 to 2844 km^2 (Table 1).

The collective land area encompassed by these four females was 4970 km^2: essentially all (98%) of it was on NE Bathurst Island and represents 73% of the NE Stratum (Figs. 1-5). Less than 3% (123 km^2) of the collective area extended into NW Bathurst Island (Figs. 1, 4). Female 93-04 was the only one of the four that occupied it. Thus, the four females collectively ranged over only 18% of the entire Bathurst Island complex and only 31% of Bathurst Island.

All individuals occupied the smallest ranges during most of the winter on a monthly and seasonal basis (Table 2; Figs. 2-5). Female 93-02 confined herself to only 24 km^2, female 93-04 to 70 km^2, female 93-05 to 94 km^2, and female 93-03 to 95 km^2.

Shifts in monthly ranges were relatively large in September, October, and November during Pre-Breeding, Breeding, and Early-Winter periods

Table 2. Discernible periods recognized for four PTT-collared female Peary caribou, Bathurst Island, Canadian High Arctic, 1 August 1993 to 31 July 1994.

Discernible periods in a caribou-year	Female 93-02	Female 93-03	Female 93-04	Female 93-05
Autumn Movement		1 Aug-26 Aug		
Autumn-Early Winter Area	1 Aug-10 Oct	26 Aug-14 Oct	1 Aug-2 Oct	1 Aug-25 Sep
Pre-Breeding Movement	10 Oct-16 Oct	14 Oct-18 Oct	2 Oct-14 Oct	25 Sep-16 Oct
Breeding Location	18 Oct	18 Oct	18 Oct	18 Oct
Breeding Ground	16 Oct-20 Oct	18 Oct-24 Oct	14 Oct-18 Oct	16 Oct-20 Oct
Early Winter Movement	20 Oct-25 Oct			
Early Winter Area	25 Oct-20 Nov			
Wintering Area Movement	20 Nov-15 Dec	24 Oct-26 Oct	18 Oct-30 Oct	20 Oct-25 Nov
Wintering Area	15 Dec-22 May	26 Oct-14 May	30 Oct-4 May	25 Nov-16 May
Pre-Calving Area		14 May-28 May	18 May-1 Jun	
Pre-Calving Movement	22 May-1 Jun	28 May-1 Jun	4 May-18 May	16 May-30 May
Calving Location	3 Jun	4 Jun	3 Jun	3 Jun
Calving Area	1 Jun-5 Jun	1 Jun-5 Jun	1 Jun-9 Jun	
Calving-Spring Area				30 May-17 Jun
Spring Movement		5 Jun-13 Jun		17 Jun-19 Jun
Spring Area	5 Jun-19 Jun			
Late Spring-Early Summer Area				19 Jun-3 Jul
Spring-Summer Movement	19 Jun-13 Jul		9 Jun-23 Jul	
Summer Movement				3 Jul-17 Jul
Summer Area	13 Jul-31 Jul			17 Jul-31 Jul

(Table 2; Figs. 2-5). Subsequently, shifts in range size of similar magnitudes then occurred during the Pre-Calving Period in May at the end of late winter and in the beginning of June, just before spring calving (Figs. 2-5). At the time, accessibility to an adequate quantity of forage was assured by the widespread relative abundance of summertime forage throughout the region. However, the relatively large size of each caribou's summer range most likely resulted from its tracking of the plant phenology in order to maximize and prolong its intake of the highest quality forage as new stands became available on different parts of its range (e.g., Miller, 1995b; 1998).

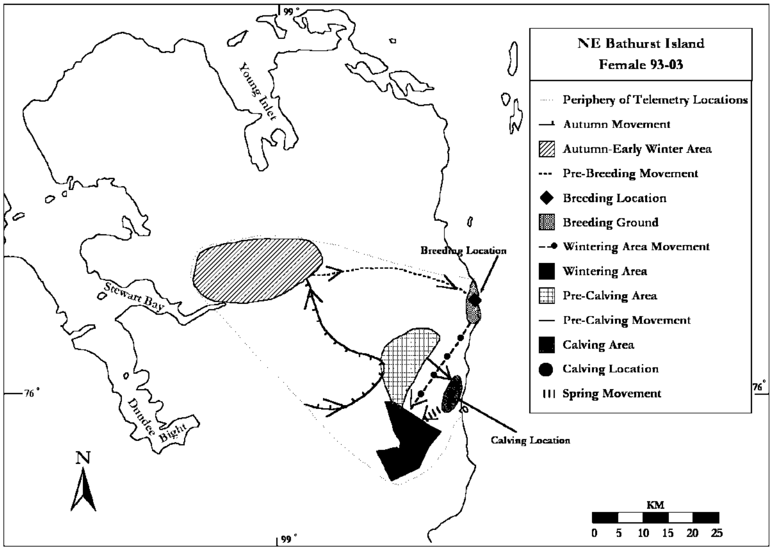

Fig. 3. Schema of seasonal range occupation and major directional movements of female Peary caribou 93-03 during the annual-cycle of the study period, Bathurst Island, Canadian High Arctic, 1 August 1993 to 31 July 1994: extrapolated from satellite location-data points.

Individual Ranges

We were able to collectively discern 20 periods among the four PTT-collared female Peary caribou during the annual-cycle of the study period (Table 2; Figs. 2-5). However, each individual female exhibited only 11 to 14 of those detectable breaks in their respective pattern of range use (Table 2). Only eight of the discernible divisions were shared by all four females (Table 2).

Only one female (93-02) made a detectable Autumn Movement, which lasted 26 days. Time spent by all four females on their respective Autumn-Early Winter Area varied from 49 to 71 days (mean±SD=59.8±9.4 days). Then, Pre-Breeding Movement lasted for 4 to 21 days (mean±SD=10.8±7.6 days) before each female arrived on her respective Breeding Ground, where they spent only 4 to 6 days (mean±SD=4.5±1.0 days). Only one female (93-02) made a 5-day Early Winter Movement from the Breeding Ground to an Early Winter Area, where she spent 26 days, before making her Wintering Area Movement. The other three females each made a Wintering Area Movement directly from their respective Breeding Ground to their respective Wintering Area. Wintering Area Movement varied from only 2 days to 36 days (mean±SD=18.8±14.8 days). Each female then spent nearly half or slightly

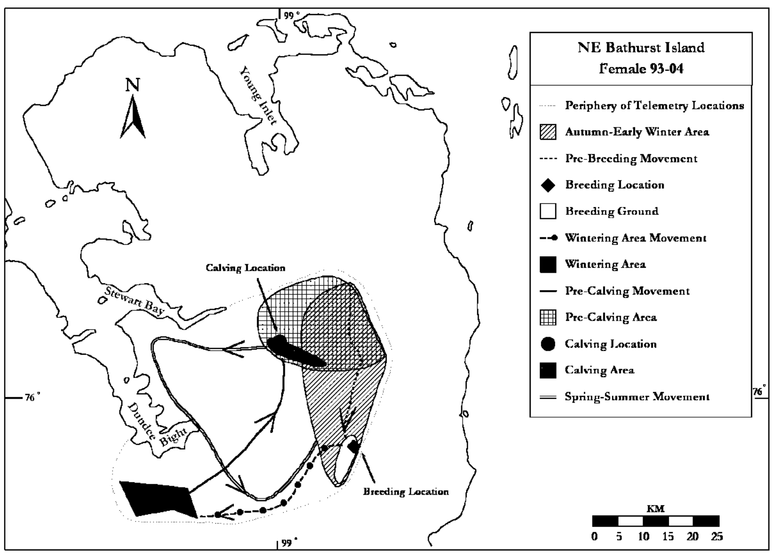

Fig. 4. Schema of seasonal range occupation and major directional movements of female Peary caribou 93-04 during the annual-cycle of the study period, Bathurst Island, Canadian High Arctic, 1 August 1993 to 31 July 1994: extrapolated from satellite location-data points.

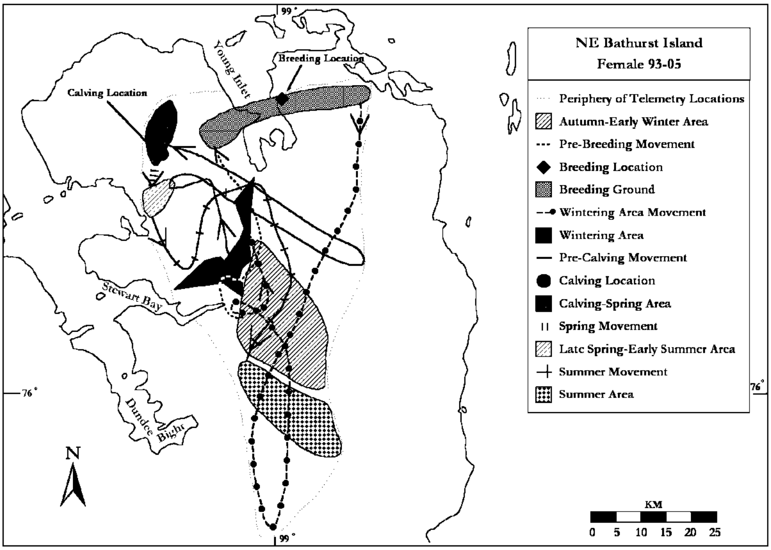

Fig. 5. Schema of seasonal range occupation and major directional movements of female Peary caribou 93-05 during the annual-cycle of the study period, Bathurst Island, Canadian High Arctic, 1 August 1993 to 31 July 1994: extrapolated from satellite location-data points.

more than half of the annual-cycle on her respective Wintering Area (mean±SD=179.3±18.2 days): duration, 158-200 days (Figs. 2-5). Two of the females (93-03, 93-04) occupied a Pre-Calving Area for 14 and 13 days, respectively, before making their Pre-Calving Movement. The Pre-Calving Movement varied from 4 to 14 days (mean±SD=10.3±4.8 days) among the four females. Three of the females (93-02, 93-03, 93-04) then spent 5, 4, and 8 days, respectively, on their Calving Area. The fourth female (93-05), however, occupied a Calving-Spring Area, where she spent 18 days (4 days before calving and 14 days post-calving). A detectable Spring Movement was made by only two females (93-04, 93-05), 8 and 2 days, respectively. Only one Spring Area was recorded, 93-02, 14 days (no satisfactory location-data points were obtained for 93-03 between 13 June and 29 July 1994 but the 29 July location placed her in the same general area as her 13 July location). One female (93-05) held a Late Spring-Summer Area for 14 days. Two of the four females (93-02, 93-04) made an extensive Spring-Summer Movement of 24 and 44 days duration, respectively. One female (93-05) made a Summer Movement that lasted 14 days. Lastly, two females (93-02, 93-05) occupied a Summer Area for 18 and 14 days, respectively (the number of satellite location-data points were not satisfactory enough to evaluate the Summer Area for 93-03). Female 93-04 remained in a movement phase from 9 June until at least 23 July 1994, but whether she settled on an area during the last week of July or kept moving is unknown.

Table 3. Measures of variation in long-term rates of displacement for four female Peary caribou, Bathurst Island, Canadian High Arctic, 1 August 1993 to 31 July 1994: presented by individual female and by movement period.

Animal I.D.	Movement period	Duration of movement period (days)	Displacement distance (km)	Minimum distance traveled (km)	Ratio: displacement vs. Minimum distance	Displacement as % of minimum distance
93-02	Wintering Area	25	45.6	59.6	1:1.3	76.5
	Pre-Calving	10	4.0	34.0	1:8.5	11.8
	Spring-Summer	24	34.8	120.4	1:3.5	28.2
93-03	Autumn	26	28.2	54.8	1:1.9	51.4
93-04	Pre-Breeding	12	35.2	38.0	1:1.1	92.6
	Wintering Area	12	34.8	38.3	1:1.1	90.9
	Pre-Calving	14	33.1	38.2	1:1.2	86.6
	Spring-Summer	44	22.4	90.4	1:4.0	24.8
93-05	Pre-Breeding	21	31.7	50.3	1:1.6	63.0
	Wintering Area	36	36.0	171.2	1:4.8	21.0
	Pre-Calving	14	29.2	133.1	1:4.6	21.9
	Summer	14	40.5	87.7	1:2.2	46.2

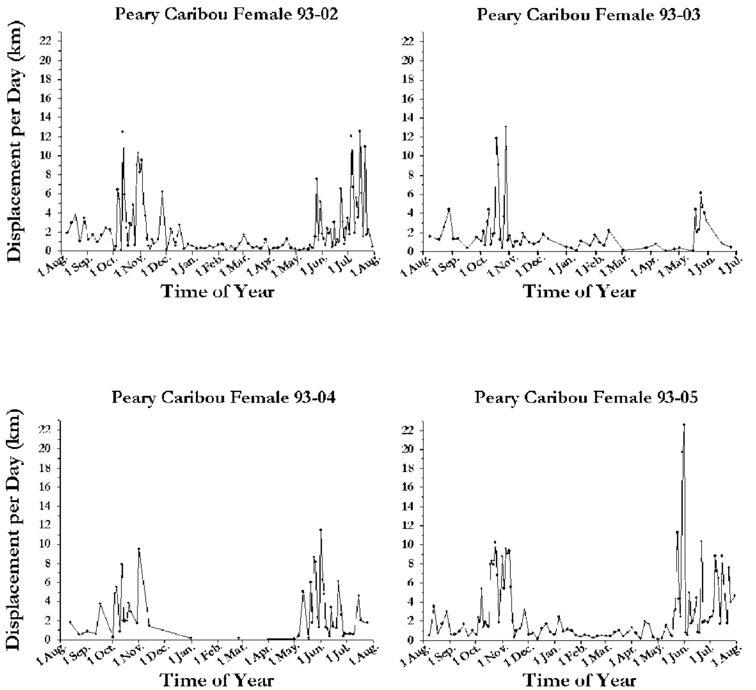

Fig. 6. Average daily displacements (km) for four PTT-collared female Peary caribou, Bathurst Island, Canadian High Arctic, 1 August 1993 to 31 July 1994: extrapolated from satellite location-data points.

Potential social affinities

Spatial overlap only among the four caribou was 46% of their overall range (Figs. 2-5). This is an ecologically limited statistic as it does not account for the all-important temporal overlap that occurred, which was much less. Although spatial overlap of individual ranges during the annual-cycle of the study period was appreciable, no evidence of any social affinities between or among any of the four females was obtained. Close association of the females was restricted temporally (Figs. 2-5). The temporal potential for socialization among all four females occurred only in August. Thus, although two to four females occurred on the same general section of range at the same time, all distances separating them at those times did not support close association between or among any of them (Table 3). Analysis of separation distances for 357 paired same-date observations did not indicate that any of the four females belonged to the same persistent social grouping or even to the same temporary social aggregation during any period of the 1993-94 annual-cycle.

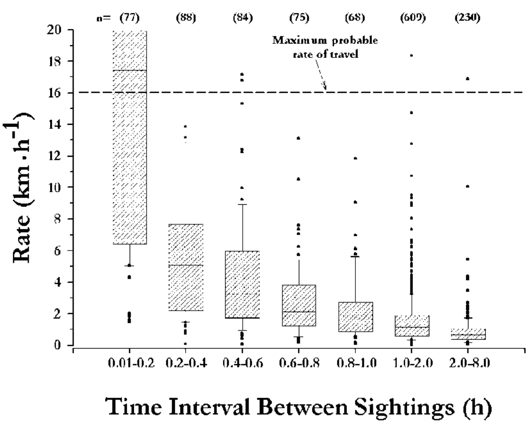

Fig. 7. Standard Box Plot (10th, 25th, 50th, 75th and 90th percentiles, and outliers) illustrating variation in short-term rates of displacement by time interval classes for four female Peary caribou, Bathurst Island, Canadian High Arctic, 1 August 1993 to 31 July 1994.

Displacement vs. minimum distance traveled

The distances moved by Peary caribou in this study, their associated rates of displacement and the assumed rates of travel were not outstanding for caribou (Table 3; Fig. 6). About 52% of the consecutively paired samples obtained in the 0.01-0.2 h time interval were not used because their application would have yielded rates of displacement or travel that are physically impossible for caribou to sustain over hours (Fig. 7). The remaining usable samples in the 0.01-0.2 h class still produced the highest average rate of displacement. From this class the average rate of displacement fell by 52% between 0.2-1.0 h and declined a further 64% between 1.0-8.0 h. For the 48-h and the 120-h class, the average rate of displacement fell another 15% and then plummeted nearly 94% more at 240 to 1056 h (Table 3).

About half of the rates of displacement obtained during the ultra-short 0.01-0.2 h time interval appear to be markedly inflated by the influence of the compressed time interval and the possible maximum error associated with location-data points. At maximum possible error, based on information provided by Service Argos Inc., this error varied between 2000 m for QC-1 to QC-1 comparisons and 700 m for QC-2 to QC-2 comparisons.

Displacement distances, the direct line displacement from the beginning point to the end point, for large time-scale movements (Table 3: 240-1056 h; n=12) averaged 59% less than the summed distance the animals displaced along consecutive sample points to the same end. Based on the summation of points in this shorter time scale, on average, the caribou traveled at least 2.4 times as far as going directly from start point to end point. This represents a significant error in using the start point to end point distance over even several hours let alone over several days or more to obtain distance traveled or a rate of travel. Among the 12 Movement periods this ratio varied between 1:8.5 and 1:1.1. That is, the displacement equaled only about 12% to nearly 93% of the measured minimum distances traveled during each Movement Period (Table 3).

Productivity

The winter and spring of 1993-94 (and 1992-93) were highly favorable for caribou survival and the production and rearing of young. All five females captured on NE Bathurst Island had calves at heel in late July 1993 and in August 1993 2-3 weeks after capture and release. Visual observations obtained during VHF radio-tracking flights and other aerial search efforts between April and August 1994 indicated that all five 1993 calves survived to be yearlings and that all five cows again produced viable neonates on the known calving areas on NE Bathurst Island in the first week of June 1994 (Figs. 1-5). All of those calves and yearlings were still alive in August 1994.

All 5 females most likely calved about 3 June 1994, each of them had a newborn (1 or 2 d-old) calf at heel on 4 June when all five females were located visually during VHF radio-tracking helicopter searches. Female 93-01 calved on the west side of the major drainage running north-south from Young Inlet south to Stewart Bay. Female 93-05 calved at about the same latitude as female 93-01 but several kilometers to the west (93-05's offspring appeared no more than a day, and possibly only hours old, when seen on 4 June 1994). Female 93-02 calved near the head of Stewart Bay on the north side of the river flowing into the head of the bay (Stewart River). Female 93-04 calved several kilometers SE of the head of Stewart Bay and north of Dundee Bight. The fifth cow, 93-03, calved several kilometers inland from the east coast on NE Bathurst Island at about 76°N latitude.

Peak rutting activities apparently took place between 14 and 22 October 1993. The most likely date of breeding for all five PTT-collared females appears to be 18 October 1993, determined by back dating from 3 June 1994 for an assumed average 228-day gestation period (Bergerud, 1978). All five females participated in the rut on NE Bathurst Island (Figs. 2-5).

Discussion

Range use

All of the existing information indicates that Peary caribou on Bathurst Island favor northern Bathurst Island and particularly NE Bathurst Island (e.g., Tener, 1963; Miller et al., 1977a; Ferguson, 1987; Miller, 1987; 1989; 1995b; 1998). This study is, however, the first to document year-round use of NE Bathurst Island by individual Peary caribou. The findings indicate that caribou on Bathurst Island obtained their daily maintenance requirements on relatively small ranges, especially during wintertime. Use of larger sections of range during summer and autumn apparently simply reflect the widespread relative abundance and availability of forage and the foraging strategies employed at those times of the year (e.g., Miller, 1995b; 1998; Thomas et al., 1999).

An alternative in range-use patterns by Peary caribou involving multi-island seasonal ranges and collectively as annual range was exhibited by an additional female and a male Peary caribou during this study period (Miller, 2002). The female used five islands (Fig. 1: Vanier, Cameron, Alexander, Massey, and Marc), moving from one island to the next on 11 separate occasions throughout the year. The male used six islands (Fig. 1: Bathurst, Vanier, Cameron, Alexander, Massey, and Marc), moving from one island to the next on 16 separate occasions. As for the four female caribou on Bathurst Island in our study, their seasonal home ranges were the largest in summer and smallest in winter and their seasonal movements (displacements) greatest during pre-rut and pre-calving periods. The collective multi-island home range area of each of these two caribou was smaller in size than that of the four female Peary caribou that remained year-round on NE Bathurst Island: female, 1221 km^2; and male, 1607 km^2 vs. between 1735 to 2844 km^2 for the four females.

Gunn & Fournier (2000) satellite tracked four female caribou on NW Victoria Island from 1987 to 1989. Their findings were similar to ours: the animals occupied the smallest monthly home ranges in winter and the largest in summer and monthly movements (displacements) were greatest during pre-calving and pre-rut periods. They also found on a multi-year basis that the four individuals maintained similar annual home ranges from year to year on NW Victoria Island and did not move to other areas of the island.

Individual ranges

None of the PTT-collared females made any use of S Bathurst Island and only one made a slight excursion to NW Bathurst Island over the 'artificial boundary' between the survey strata of NE and NW Bathurst Island during the study period. It is most likely that the actual range used by each female for annual forage requirements on NE Bathurst Island is only a relatively minor proportion of the area that we encompassed by connecting the perimeter satellite location-data points for each caribou. Much of the area encompassed by each caribou might never have been used by them and what was used may be linked more directly to intra- and inter-specific interactions and variations in individual learned behavior rather than the forage supply *per se*. Even the relative unavailability of forage in winter and spring caused by snow and ice conditions did not appear to have been a major determinant in the favorable year of 1993-94.

We have no direct measure of the amount of range that was used to meet each animal's annual food budget. We can, however, estimate the theoretical minimum range necessary to meet a Peary caribou's annual forage requirements at a given rate of foraging that is sustainable by the vegetation being used. That is, we can assume from Miller (1998) that 730 kg dry matter (DM) of forage • caribou^{-1} • yr^{-1} is a reasonable estimate of the annual forage requirements of the small-bodied Peary caribou, based on findings from White & Trudell (1980a; 1980b), White et al. (1981), and R. G. White (pers. comm., 1998). For the sake of discussion, we will arbitrarily assume that Peary caribou within the Bathurst Island complex obtained an extremely low value, on average, of 0.1 g DM forage • m^{-2}. When we make this assumption, we find that one of those caribou could still realize its annual food requirements from as little as 7.3 km^2. This represents only an exceptionally minor proportion (0.3-0.4%) of the area encompassed by each of the four females on Bathurst Island in 1993-94 (Table 1).

This assumed rate of forage utilization would represent only 1% of an assumed standing crop of 10 g DM forage • m^{-2}. Most importantly, it represents only 0.3% of the average plant biomass estimated by Thomas et al. (1999) on adjacent eastern Melville Island in summer 1974, immediately after the major winter and spring die-offs of nearly half of all the caribou (and muskoxen, *Ovibos moschatus*) throughout the western Queen Elizabeth Islands (Miller et al., 1977a: ca. 99 000 km^2).

Detailed documentation of the relatively extensive displacements that were made in early winter, late winter, spring, and summer (Figs. 2-5) could be of great importance in evaluating range-use patterns. If those displacements had occurred in an environmentally stressful year, they would have been interpreted as responses to relative forage unavailability brought on by severe snow and ice conditions, or even an absolute forage shortage. However, summer 1993 to summer 1994 was a highly favorable period for the caribou under consideration, with high reproduction and survival of calves in 1993 and 1994, high recruitment from 1992 to 1993 and 1993 to 1994, and such low annual mortality among 1+ yr-old caribou that it went undetected during considerable search effort in each year (Miller, 1995b; 1997; 1998). The winter range was open with relatively little restriction of the forage supply. Therefore, there is no reason to believe that displacements were weather or food motivated in 1993-94. We should not, however, lose track of the fact that such displacements in unfavorable years could possibly be in response to widespread relative forage unavailability. If they were, however, they should be longer in duration and possibly with no return to origin. Perhaps, most importantly, extensive displacements should be associated with a detectable higher seasonal mortality, no mortality at all was detected during this study.

That all of the caribou maintained their smallest monthly ranges during wintertime (Figs. 2-5) warrants special consideration. As the forage supply is both absolutely and relatively more abundant and widely available during the remainder of the year, it seems reasonable that Peary caribou could live year-round on similar-sized areas. This supposition is strongly supported by subsequent satellite location data obtained from female 93-03 in 1994-96 (unpubl. data). In late December 1994, female 93-03 and at least her 1994 offspring moved off southeastern Bathurst Island and traveled eastward across the sea ice to Baring Island—a small, flat island only 21 km^2 in size and about 50 km east from Bathurst Island. They then remained on Baring Island for 13 months until late January 1996, possibly along with three bulls and a subadult male. We observed the three bulls and subadult male in association with female 93-03 and her yearling in July 1995. Even if the males remained on Baring Island for only 6 months (Jun-Nov 1995), the collective animal-months of range use would have totaled >4 yr or the equivalent, on average, of 5 km^2 • animal^{-1} • yr^{-1}. Each animal most likely would have ranged over the entire island during their stay there. When vegetation on Baring Island was visually inspected and sampled in summer 1998, no evidence of range overuse was detected (A. Gunn & G. Henry, 2001, pers. comm.). Therefore, we must conclude that when necessary, it is possible for Peary caribou to live year-round for at least 1 year on about 10 $km^2 \bullet animal^{-1} \bullet yr^{-1}$ at a mean density of about 10 caribou • 100 $km^2 \bullet yr^{-1}$ or possibly, even as little as on about 5 $km^2 \bullet animal^{-1} \bullet yr^{-1}$ at a mean density of about 20 caribou • 100 $km^2 \bullet yr^{-1}$. It is interesting to note, although not directly comparable and perhaps solely by coincidence, that a 5 km^2 annual home range is a value reported for Svalbard reindeer (R. t. platyrhynchus) by Tyler (1987).

At first thought, the reader may think that severe reduction in the size of range used during winter is a common phenomenon among North American cervids. However, this wintertime restriction in the use of range by Peary caribou is not directly comparable to areas where deer use 'wintering yards.' Those deer concentrate when experiencing prolonged deep snow cover on relatively small areas within the animal's total winter range. Spatial restriction on tundra range where snow depth seldom interferes with travel per se is, seemingly, contrary to what would be expected for seriously food-stressed caribou. This appears especially true as Peary caribou live in a region of relatively low plant biomass. The most important distinction between deer yards and restricted winter range for Peary caribou is that deer in wintering yards have a 3-dimensional forage supply while Peary caribou have essentially only a 2-dimensional forage supply. That is, deer in wintering yards survive by feeding on vegetation that is available above the snow cover (3rd dimension). Peary caribou on high arctic tundra range must find low-growing forage plants during severe snow and ice periods on snow-free or shallow snow-covered sites (not ice-covered) in order to survive the prolonged rigors of a severe winter and spring.

The winter and spring of 1993-94 were highly favorable to caribou survival and to the subsequent production and early survival and rearing of calves in spring and summer 1994. Therefore, the small monthly home range sizes during winter 1993-94 may reflect the favorable environmental setting of that winter. Visual inspections were made of snow and ice conditions on sites throughout the Bathurst Island complex during late winter (Apr-May) and spring (Jun). Ice was absent until mid to late June in 1994. Much of the snowpack remained powdery with a 'sugar' base throughout the winter and until the melt began in spring. Some sites had hard packed crusts, but the caribou broke through the crusts with their hooves and the soft snow below was easily moved away to expose the vegetation. Wind action usually significantly packs the snow over large areas, if not range-wide, often to 'hardpan' by that time in most years. It is reasonable to argue that the restricted use of range in winter 1993-94, although probably only a reflection of the favorable conditions of that winter, could also be beneficial during periods of extreme forage unavailability brought on by snow and ice covers. Widespread inaccessibility of forage could promote restricted range use by caribou, as once a relatively favorable foraging area was found, it would be more beneficial to remain in that general area (e.g., 100 km^2 or more) where some forage was accessible on an ongoing basis rather than to keep moving to new areas in search of a possible, but unknown, accessible forage supply. Another consideration is that we were seeing movement patterns that actually were forged during less favorable years.

Evaluating the use of range on any one island, particularly during periods of extreme forage unavailability is complicated by the fact that there can be, in reality, free-movement between and among Arctic Islands for at least 9-10 months of each year. To further obscure the matter, Peary caribou on some Queen Elizabeth Islands can move nearly year-round (e.g., Miller 1995a). Annually occurring seasonal inter-island movements (migrations) have been documented for caribou on the Queen Elizabeth Islands and on the more southerly Arctic Islands (e.g., Miller et al., 1977a; 1977b; 1982; Miller & Gunn, 1978; 1980; Miller, 1990a). Thus, environmentally forced inter-island movements by some Peary caribou during prolonged periods of widespread or nearly range-wide, extreme relative forage unavailability should be expected (especially by Peary caribou living on relatively small islands). The benefits of the trade-offs for Peary caribou between remaining on familiar range vs. responding to extreme food stress by en masse long-distance emigrations beyond previously known traditional ranges are speculated about but in reality, such events have not been proven. Thus, the supposition for them, in the absence of any direct evidence that they have ever taken place, remains purely speculative and highly debatable. However, 'range shifts' during periods of food stress by some Peary caribou within their population's long time overall traditional range are known but for the most part, the magnitude and frequency of such events remains speculative. The value to the caribou making any of these displacements would be directly proportional to the intensity, duration and expanse of the environmental stressors which were in place at the time. Many Peary caribou are "reluctant to quit" traditional range and seek relief on unfamiliar ground during periods of extreme environmental stress—many of them dying on their then current home range instead (e.g., Miller et al., 1977a; Miller, 1998; Gunn & Dragon, 2002). However, some do respond by egress but most often, their subsequent fate is unknown (e.g., Miller, 1990a; 1998; Gunn & Dragon, 2002). Also, it is not known whether such environmentally-forced movements result in emigration and establishment of new ranges, or the surviving animals simply return to their previous range when conditions once again become favorable. Thus, the temporal scale of the data-set becomes the all-important factor in such evaluations (i.e., multi-year studies).

Displacement vs. minimum distance traveled

Values obtained from calculation of rates of minimum distances traveled for each consecutive duty-day from the beginning to the end of each of the 12 Movement periods are seriously misleading (Table 3). The minimum distance traveled differs considerably, on average, from the displacement distance by 45.0±43.8 km standard deviation.

Calculated rates for minimum distances traveled were unrealistically low, ranging from 0.09-0.40 km • h^{-1} and averaging 0.16±0.03 km • h^{-1}. It appears that from an ecological standpoint, the use of rates of travel obtained from >2 h time intervals (or, on occasion, even > 1 h) will cause a serious negative distortion of the resultant estimates of minimal distance traveled and associated rates of travel. The mean rate of travel of only 0.16 km • h^{-1} is grossly undervalued and represents <5% of the 3.6 km • h^{-1} mean value obtained for animals in the 0.2-1.0 h time interval. Based on the average rate of 3.6 km • h^{-1}, it appears that these caribou spent on average, only 5% (range 2.4-11.0%) of their respective Movement periods involved in travel - we believe this is obviously a misleading statistic that has no ecological foundation in fact.

The use of satellite location-data points for estimating actual distance traveled is dependent on the time interval between successive locations. This condition is especially confounded by not knowing the number of intervening rest or foraging periods between each bout of movement or travel. Such distance estimates are fraught with realized and probable error and thus, should be considered suspect without some form of independent validation (see Table 3: travel vs. displacement; and example in Methods). Ideally, such validation would take the form of direct timed visual observation and measurement of the exact path taken by the animal (cf. Miller et al., 1982). When possible, Global Positioning System (GPS) satellite telemetry could be employed in association with visual observations to obtain continual location data.

We know that caribou on arctic island ranges travel at 3-4 km • h^{-1} while foraging (Miller et al., 1982) and likely considerably faster when making changes in seasonal ranges or range shifts (e.g., Pruitt, 1960). We derived from Russell et al. (1993:15) that the average number of active hours in a day is about 14.8 h (based on yearly mean 'active/lying cycle' of 4.7 h with a mean 2.9 h active period). Therefore, we examined the apparent gross discrepancy in minimal distances traveled on their respective Wintering Area and the rates of travel for those movements for the two females (93-02 and 93-05) with complete usable records at 5-day intervals during 158 and 172 days of occupation on their Wintering Area, 24-km^2 (Fig. 2: 93-02) and 94-km^2 (Fig. 5: 93-05). Based on the sequential duty-day locations, female 93-02 supposedly moved only 78.4 km (average rate 0.02 km • h^{-1}) and female 93-05 134.5 km (average rate 0.03 km • h^{-1}) in these periods. When we apply the mean rate of 3.5 km • h^{-1} from Miller et al. (1982), at 8 h • d^{-1}, each female would have traveled 28 km • d^{-1} (i.e., movements during 54% of the daily active time derived from Russell et al. (1993), times 3.5 km • 8 h^{-1}). Therefore, 93-02 should have traveled a minimum distance of 4428 km during her 158 days on her Wintering Area and female 93-05 should have traveled a minimum distance of 4816 km during her 172 days on her Wintering Area. It appears from this exercise that our satellite location data can account for only <2 to <3% of 93-02's and 93-05's travel distances during their respective stays on their Wintering Area.

On a 365-day basis, at the average daily rate of travel of 3.5 km • h^{-1} for 8 h • d^{-1} for 365 days, we obtain a minimum distance traveled of 10 220 km. In contrast, the sum total sequential travel distance measured during the entire annual-cycle for female 93-02 was 678.7 km and for female 93-05 was 821.8 km. Thus, the satellite location-data points only account for 7 and 8%, respectively, of the distances likely traveled by those two female caribou throughout the annual-cycle of the study period. Even when the measured distances traveled are inflated from the 8 h the PTT was on to cover each 24-h period during 365 days, we can still account for only 45-54% of the distance that would be traveled by each of those females at a mean rate of 3.5 km • h^{-1} on each day of the year.

Productivity

The high productivity indicates that caribou on Bathurst Island and throughout the Bathurst Island complex were not being stressed by the limitations of the absolute forage supply or the relative unavailability of forage during the study period (Miller, 1995b, 1998; Gunn & Dragon, 2002; Miller & Gunn, this proceedings). Although the environmental conditions were highly favorable in winter and spring 1993-94, the cows all returned to previously known calving areas in June 1994. This most likely reflects the fidelity of caribou cows to their calving grounds (e.g., Gunn & Miller, 1986). Many sites on the calving areas on Bathurst Island (Figs. 1-5) have characteristics that result in at least some shallow snow and most importantly snow-free patches of ground at least just before, during, and immediately after calving. In a year with a severe winter and spring, these calving areas allow higher levels of survival among cows and higher initial production of viable neonates as well as subsequent better survival among those calves. Thus, although use of these calving areas is not necessary in all years—the collective overall calving area identified in Fig. 1 is particularly critical in the relatively few but more unfavorable years. In the few most extreme worst years, when major die-offs occur, use of even these calving area sites fail to make an appreciable difference—and major losses to near total or total calf crop failure occurs (Miller et al., 1977a; Miller, 1998; Gunn & Dragon, 2002).

Maintenance of fidelity (traditions) to calving areas most likely demands annual or near annual repetitive use by at least a core of individuals, even in the favorable years. Therefore, these calving areas (Fig. 1) should be protected at all times to foster the persistence of Peary caribou within the Bathurst Island complex, south-central Queen Elizabeth Islands, Canada.

Conclusions

Although our findings represent only a minute look into how Peary caribou use space over time, on a relative basis they represent a meaningful advance in our knowledge base. The findings in this study together with those in the sister study (Miller, 2002) indicate that different range-use patterns exhibited by Peary caribou incorporate feasible combinations of alternatives available to them.

The area encompassed by each satellite-collared caribou between 1 August 1993 and 31 July 1994 overestimates the annual minimum range required to sustain a caribou. Those values do, however, clearly show us that each animal remained within only a relatively minor portion of the range that was available to it on Bathurst Island and, of particular importance, did not even use all of the range on NE Bathurst Island. Subsequent to our study, female 93-03 lived for 13 consecutive months on only 21 km^2 (Miller, 1997, 1998, unpubl. data: Baring Island) but our satellite data indicated a home-range of 1735 km^2 in 1993-94. Thus, she was capable of living for 13 months on the equivalent of only 1% of the area we estimated in 1993-94 or over 82 times greater than the amount of annual range actually required.

The four individuals maintained seasonal ranges distinctly separate from each other: spatial separation was maintained for much of the year and temporal separation virtually year-round. The differences in range use (spatial and temporal templates) likely reflect variation in the individual's learned use of range compared to other caribou within the island complex, with overall limitations imposed by relative unavailability or absolute availability of forage.

Evaluation of the impact of environmental stressors on Peary caribou on an island basis can be seriously complicated and confounded because those caribou can make inter-island movements during winter and spring when environmental pressures are strongest. However, our findings indicate that Peary caribou can winter on relatively small areas, much smaller than previously thought by people investigating or otherwise interested in Peary caribou on the Queen Elizabeth Islands.

The use of the term 'movement' or 'travel' in evaluating supposed rate or distance measurements obtained from satellite telemetry is both confounding and at best of questionable ecological value. Although defining such a measurement as a 'displacement' is still limiting, the successive between-point values are most accurately described as displacements and the attendant limitations should become obvious to the reader. The magnitude of error associated with supposed measure of movement or travel is governed mainly by the time interval between obtaining successive location-data points. Together with longer time intervals, the actual pattern of movement or travel will also make a major contribution to the resulting error. Future workers should pay due heed to the potential for error when using such measurements in making biological and ecological evaluations.

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