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Subpopulation structure of caribou (*Rangifer tarandus* L.) in arctic and subarctic Canada

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Abstract. Effective management and conservation of species, subspecies, or ecotypes require an understanding of how populations are structured in space. We used satellite-tracking locations and hierarchical and fuzzy clustering to quantify subpopulations within the behaviorally different barren-ground caribou (*Rangifer tarandus groenlandicus*), Dolphin and Union island caribou (*R. t. groenlandicus* × *pearyi*), and boreal (*R. t. caribou*) caribou ecotypes in the Northwest Territories and Nunavut, Canada. Using a novel approach, we verified that the previously recognized Cape Bathurst, Bluenose-West, Bluenose-East, Bathurst, Beverly, Qamanirjuaq, and Lorillard barren-ground subpopulations were robust and that the Queen Maude Gulf and Wager Bay barren-ground subpopulations were organized as individuals. Dolphin and Union island and boreal caribou formed one and two distinct subpopulation, respectively, and were organized as individuals. Robust subpopulations were structured by strong annual spatial affiliation among females; subpopulations organized as individuals were structured by migratory connectivity, barriers to movement, and/or habitat discontinuity. One barren-ground subpopulation used two calving grounds, and one calving ground was used by two barren-ground subpopulations, indicating that these caribou cannot be reliably assigned to subpopulations solely by calving-ground use. They should be classified by annual spatial affiliation among females. Annual-range size and path lengths varied significantly among ecotypes, including mountain woodland caribou (*R. t. caribou*), and reflected behavioral differences. An east–west cline in annual-range sizes and path lengths among migratory barren-ground subpopulations likely reflected differences in subpopulation size and habitat conditions and further supported the subpopulation structure identified.

Key words: arctic; calving grounds; caribou; clustering; fuzzy clustering; hierarchical linkage; home range; path length; Rangifer tarandus; *space use; subarctic; subpopulation.*

INTRODUCTION

Management, conservation, and biodiversity of species, subspecies, or ecotypes can only be addressed effectively if we understand how populations are structured in space. Andrewartha and Birch (1984) concluded that "natural populations" consist of many interbreeding "local populations," and that dispersal among them is almost certain. Little or no dispersal is expected among natural populations because they are isolated by barriers to movement. Wells and Richmond (1995) recommended that when groups of individuals are "spatially, genetically, or demographically" separated from each other the term population should be used, and when they are not, one should use the terms "group, subpopulation, or local population." Berryman (2002), attempting to clarify the terminology, defined a population as "a group of individuals of the same species that live together in an area of sufficient size to permit normal dispersal and/or migration behavior and in which numerical changes are largely determined by birth and death rates." Schaefer (2006), however, argued that Berryman's (2002) definition included vague and ambiguous terms like "together," "sufficient," "normal," and "largely" that are open to interpretation. Further,

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Harwood (2009) argued that "we cannot assign an individual to the population unless we have defined the population and we cannot define the population until we have assigned all of the individuals." Without an unambiguous definition, "we can only sample an area, and our sample cannot be assumed to be representative of more than this" (Harwood 2009).

A number of techniques have been used to identify subpopulations of animals for research and management, including comparing the spatial distribution of individuals with that of a random distribution (Amarasekare 1994), hierarchical and/or fuzzy classification of movement data (Bethke et al. 1996, Schaefer et al. 2001, Klaver et al. 2008), movement and mtDNA data (Calambokidis et al. 2001), DNA data (Barr et al. 2008), and carbon and nitrogen stable isotopes (Witteveen et al. 2009). However, Harwood (2009) argued that populations are composed of a number of individuals whose membership in a population is determined by a "relevant degree of interaction" or connectivity to the rest of the population. Thus he argues that populations are defined by the "relationship between individuals" and not by "an externally imposed classification."

Social relationships determine the degree of interaction or connectivity expected among individuals within a species, subspecies, or ecotype. As a result, behaviors such as spatial tenure (e.g., territories or overlapping home ranges), degree of sociality (e.g., solitary or gregarious), and movement ecology (e.g., migratory or nonmigratory) determine, in part, how populations are structured. It is reasonable to hypothesize that populations of solitary or gregarious and migratory or nonmigratory species may be structured differently. It is also reasonable to assume that populations are structured by area fidelity, habitat discontinuity, resource distribution in continuous habitats, and barriers to movement.

The objective of our study was to quantify the subpopulation structure of four behaviorally different ecotypes of caribou, including migratory and tundra-wintering barren-ground (*Rangifer tarandus groenlandicus*), Dolphin and Union island (*R. t. groenlandicus* × *pearyi*), and boreal (*R. t. caribou*) caribou in northern Canada using satellite telemetry data. Although we had insufficient location data to assess the subpopulation structure of the mountain woodland ecotype (*R. t. caribou*), we included information about their use of annual ranges for comparison. Migratory barren-ground caribou are usually found in large groups, and females collectively migrate annually between winter ranges near or below tree line and calving grounds on the tundra (Banfield 1954). Tundra-wintering barren-ground caribou remain above tree line year round (Calef and Heard 1981), but little is known about their ecology. Seasonal movements and activities are synchronized among female barren-ground caribou (Maier and White 1998). Dolphin and Union island caribou also remain above tree line throughout the year. They collectively migrate over the sea ice between calving to autumn ranges on Victoria Island, where they are geographically isolated from barren-ground caribou, and their winter ranges on mainland Nunavut (NU). Boreal caribou are sedentary and remain largely within the boreal forest throughout the year. Females are solitary (i.e., cows, cow–calf pairs) during precalving to late summer, and form mixed-sex groups of 3–8 or more caribou the rest of the year (Stuart-Smith et al. 1997, Metsaranta and Mallory 2007). Activities of female boreal caribou are coordinated in time but not in space, and are thus more independent of conspecifics than female barren-ground caribou. Mountain woodland caribou occur in small groups most of the year and migrate annually to calving grounds in the mountains. Barren-ground caribou females have been assigned to subpopulations based on the belief that they aggregate on and maintain fidelity to specific calving grounds (Skoog 1968, Miller 1982). In contrast, boreal and Dolphin and Union island caribou disperse to calve (Bergerud et al. 2008).

We hypothesized that subpopulations of caribou within these ecotypes are largely structured by the degree of spatial affiliation that exists among individuals, migratory connectivity, habitat discontinuity, and/or barriers to movement, and that these structures and behaviors could be quantified using hierarchical and fuzzy clustering. Because there are nine barren-ground caribou calving grounds in the Northwest Territories (NT) and Nunavut (Fig. 1), we hypothesized that there should be nine subpopulations that are organized around the annual movements of females that used them. Because association during calving represents only a brief period in an annual cycle, we extended the definition of subpopulation to a more inclusive perspective that includes individuals that are spatially affiliated throughout most or all of the year. Female Dolphin and Union island caribou are most strongly affiliated during spring and fall migrations, so we hypothesized that there should be one subpopulation that is organized as individuals and is structured by migratory connectivity and barriers to movement. Because boreal caribou are dispersed over the landscape and are weakly affiliated during much of the year, we hypothesized that there should be one subpopulation organized as individuals, and, if subpopulations exist, they are primarily structured by habitat discontinuity. Because the behaviors of ecotypes and the distribution of resources within their subpopulation ranges vary, we hypothesized that this variation should be manifested in two ecologically important factors: annual home range size and path length.

METHODS

Satellite-tracking studies undertaken in the Northwest Territories and Nunavut have varied over time with study objectives (Appendix A). Caribou were captured and handled according to standard operating procedures of the

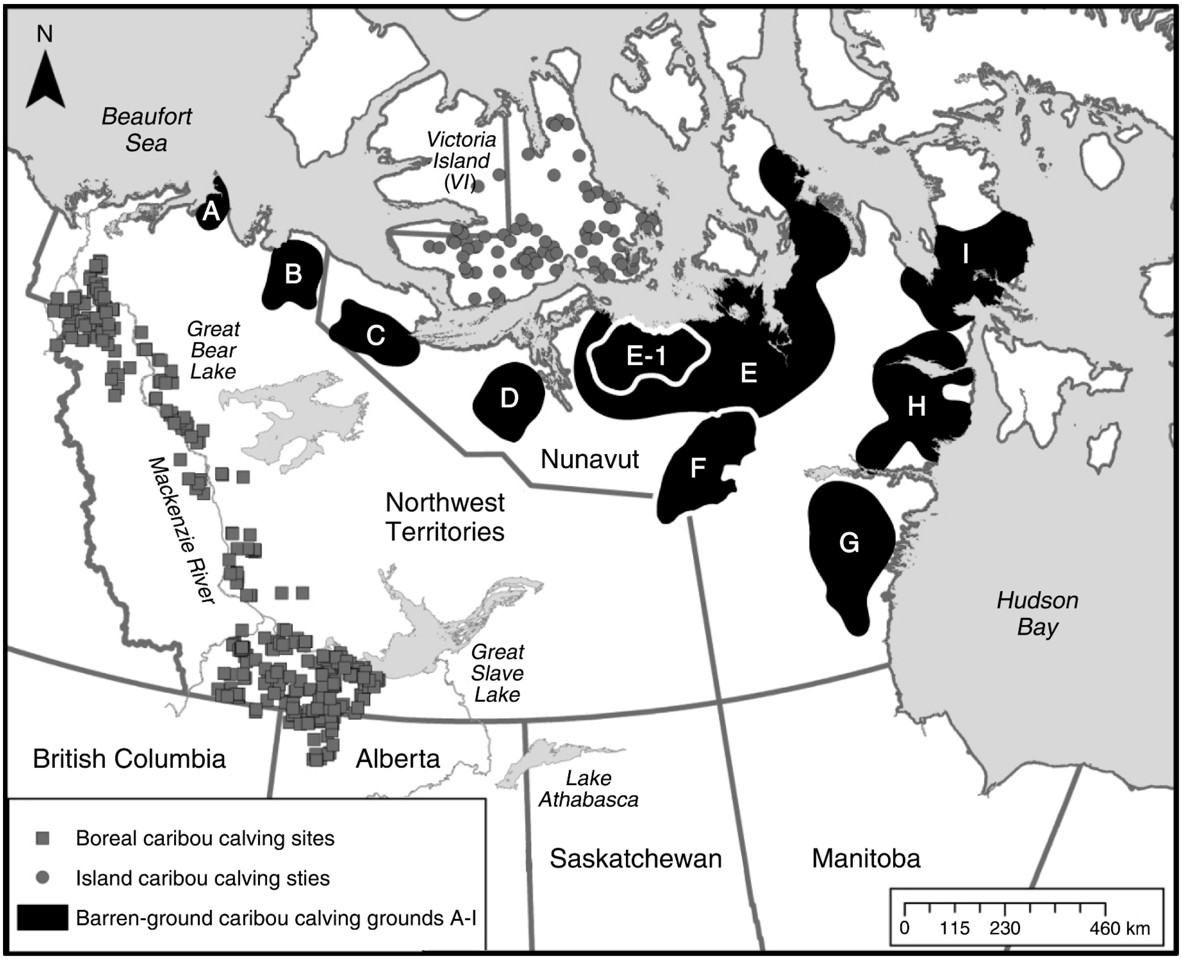

Fig. 1. Barren-ground, Dolphin and Union island, and boreal caribou calving grounds or calving sites in the Northwest Territories, Nunavut, and northern Alberta (J .A. Nagy, *unpublished data*). See *Methods* and Table 3 for the individual calving grounds.

Northwest Territories Wildlife Care Committee or Nunavut Wildlife Live-capture Protocols (Campbell 2002) following methods in compliance with the Canadian Council on Animal Care. Animals were equipped with either ARGOS Doppler shift (DS) or Global Positioning System (GPS) satellite collars (Telonics, Mesa, Arizona, USA and Service Argos, Landover, Maryland, USA). DS and GPS collars provided locations on 1–10 day and 0.33–1 day intervals, respectively, although most DS collars provided locations on 1–5 day intervals. Locations were recorded as longitude and latitude coordinates and projected to the NAD 1983 projection datum of the North America Lambert Conformal Conic coordinate system. We convert longitude and latitude data to *x*, *y* coordinates using Hawth's Tools (Beyer 2007). All geographic information system (GIS) analyses used ArcMap 9.3 (Environmental Systems Research Institute, Redlands, California, USA).

We used sums-of-squares agglomerative hierarchical linkage (Ward's [Bethke et al. 1996]) and fuzzy *c*-means clustering methods (Schaefer et al. 2001) to identify and validate caribou subpopulations (Kos and Psenicka 2000). We conducted hierarchical clustering using PC-ORD 5 (MjM Software Design, Gleneden Beach, Oregon, USA) and STATA 9 (STATCORP, College Station, Texas, USA), with the number of distinct subpopulations indicated by a sharp rise in the values of the post-hierarchical clustering Duda-Hart pseudo test (Rabe-Hesketh and Everett 2007). We conducted fuzzy *c*-means clustering using the program FUZME 2.0 (Minasny and McBratney 2002), with the diagonal distance transformation option to standardize measurements to equal variance and prevent *y*-coordinates from dominating *x*-coordinates (McBratney and Moore 1985, Klaver et al. 2008). We specified fuzzy exponents (*m*) in increments of 0.1 from 1.5 to 3.0 (Odeh et al. 1992*b,*) and 2–15 potential subpopulations for barren-ground caribou and 2–99 potential subpopulations for boreal and Dolphin and Union island caribou. A maximum of 99 potential subpopulations can be specified in FUZME 2.0. The fuzzy performance index (FPI) and normalized classification entropy (NCE) validity functions were

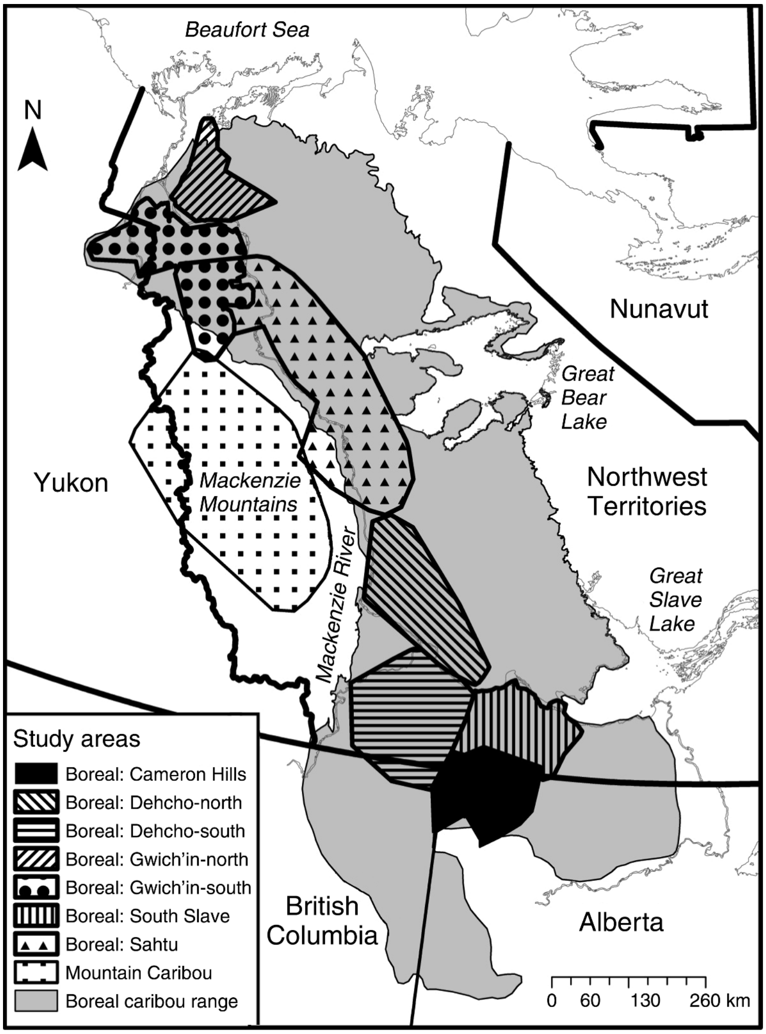

FIG. 2. Location of the boreal and mountain (Mackenzie Mountains) caribou study areas in the Northwest Territories and northern Alberta, Canada.

used to identify the optimal number of subpopulations (Odeh et al. 1992*a*).

Fuzzy clustering is sensitive to data configuration (Ohashi 1984). Our data spanned ~2400 km east–west, with the north–south span increasing from ~500 km in the west to 1600 km in the east. Fuzzy cluster analyses of all caribou data combined were affected by the predominantly east–west orientation of the data. For example, with each incremental increase in m from 2.0 to 3.0, more Dolphin and Union island caribou were assigned to adjacent barren-ground caribou subpopulations. We resolved configuration issues by analyzing data for (1) migratory barren-ground caribou using calving grounds A, B, C, D, E-1, and F (west-central); (2) migratory barren-ground caribou using calving grounds C, D, E-1, and F, and Dolphin and Union island caribou (central); (3) migratory and tundra-wintering barren-ground caribou using calving grounds E including area E-1, F, G, H, and I (east-central; Fig. 1); and (4) boreal caribou separately (Fig. 2). Females using calving grounds E-1 and F provided continuity between the classifications of western and eastern migratory barren-ground caribou.

For cluster analyses, we subsampled the data to a 5-day interval because interlocation intervals varied among studies, and included individuals with four or more locations per month and full years of data in our analyses to reduce sampling bias. We used matrices of median monthly interval x, y coordinates for west-central, central, and boreal caribou (24 variables), and 14-day interval x, y coordinates for east-central caribou (52 variables [Bethke et al. 1996]). We used the median location to account for data asymmetries (Sokal and Rohlf 1995). We used higher-resolution x, y coordinate data for the east-central area to increase the probability of separating migratory and tundra-wintering caribou subpopulations.

We used stepwise analyses (1) to identify distinct well-organized (distinct) subpopulations (Triantafilis et al. 2001), and (2) to determine if they were robust or organized as individuals. For distinct subpopulations (step one), the Duda-Hart pseudo *t* test and the validity functions had to indicate the same number of subpopulations (Schaefer et al. 2001), $\geq$90% of individuals had to be assigned to the same subpopulations by hierarchical and fuzzy ($m = 2.0$) clustering, and $\geq$90% of the individual had to be consistently assigned to the same subpopulation by fuzzy clustering for most values of m. We determined assignment consistency by comparing each individual's subpopulation assignment at $m = 2.0$ (moderate level of fuzziness) with those at $m = 1.5$–1.9 (less fuzzy) and m = 2.1–3.0 (more fuzzy).

To determine if distinct subpopulations were robust or organized as individuals (step two), we conducted fuzzy clustering on the data for individuals that were assigned to each subpopulation for $m = 2.0$ in step one. We only used fuzzy clustering because hierarchical clustering will generate group structures even when none exist (Pillar 1999). For robust subpopulations, the fuzzy clustering validity functions had to be $\geq$0.90 for most $m \geq 2.0$, indicating that there were no significant substructures in the data and females were strongly spatial affiliated. For distinct subpopulations that were not robust, the validity functions either indicated that (1) there were significant substructures in the data, or (2) females were organized as individuals. If significant substructures were indicated and sample sizes were adequate, we repeated step two until analyses indicated subpopulations were robust or were organized as individuals. Subpopulations were organized as individuals if the validity functions approached 0 when the specified number of potential subpopulations equaled n. Individuals in these subpopulations were spatially independent of each other and were primarily structured by migratory connectivity, habitat discontinuity, and/or barriers to movement.

Utilization distributions

We used the GIS program Home Range Tool (HRT [Rodgers et al. 2007]) to generate fixed-kernel utilization distributions (50, 60, 70, 80, 90, and 95% UD) for each barren-ground, island, and boreal caribou. We used the reference bandwidth, a raster cell size of 1000 m, and minimized the extent of each UD. We calculated mean 90% UD for barren-ground caribou that were assigned to each subpopulation by hierarchical and fuzzy clustering (excluding females that used multiple calving grounds) and island caribou. We considered the mean 90% UD as the core range of barren-ground and island caribou subpopulations, but where appropriate, we clipped them to the coastline to exclude marine areas that were not used. We mapped boreal caribou subpopulation core ranges by merging all individual 90% UD. Each caribou contributed equally to the delineation of subpopulation core ranges.

Home range size and migratory path length

We generated annual (calculated from the date of capture) minimum convex polygons (MCPs) and paths (straight-line distances between sequential locations) for each caribou using Hawth's Tools (Beyer 2007). To ensure an unbiased sample, we included data for GPS- and DS-collared individuals with $\geq$329 locations each year (90% of possible locations for one-day interlocation interval collars) and $\geq$66 locations each year (90% of possible locations for a five-day interlocation interval collar), respectively. We measured MCP areas and path lengths, standardized these to 365 days (areas or length divided by number of days tracked × 365), and normalized them using a $\log_{10}$ transformation. We used ANOVA and Tukey's honestly significant difference (hsd) pairwise comparisons (SPSS 11.5, Chicago, Illinois, USA [Maier and White 1998]) to determine if MCP areas and path lengths varied significantly among ecotypes, study areas (boreal caribou), and subpopulations (migratory and tundra-wintering barren-ground caribou). We analyzed DS and GPS collar data separately, because MCP areas and path lengths are influenced by sample size (Borger et al. 2006).

RESULTS

We obtained full years of data for 360 barren-ground, 140 boreal, 10 mountain woodland, and 25 island caribou (Tables 1 and 2 and Appendix B). We excluded 11 barren-ground caribou from analyses: seven because they remained on late winter ranges during the calving period, three had insufficient data, and one because its activity areas were located between but overlapped the distribution of the Beverly and Qamanirjuaq barren-ground subpopulations. Cluster analyses produced unusable results when this animal was included. For barren-ground caribou with $\geq$1.95 years of data, 91.4% (180/197), 8.1% (16/197), and 0.5% (1/197) used one, two, and three calving grounds, respectively. A tundra-wintering barren-ground caribou used three calving grounds.

Migratory barren-ground caribou formed six distinct and robust subpopulations including the Cape Bathurst, Bluenose-West, Bluenose-East, Bathurst, Beverly, and Qamanirjuaq (Table 3). Tundra-wintering barren-ground caribou formed three distinct subpopulations: the Lorillard was robust, and the Queen Maude Gulf and Wager Bay were organized as individuals (Table 3). Dolphin and Union island caribou formed one distinct subpopulation that was organized as individuals. Boreal caribou formed two distinct subpopulations that were organized as individuals.

Two factors influenced analyses of east-central caribou data: (1) ranges of migratory and tundra-wintering caribou overlapped in this area, and (2) the Beverly subpopulation was changing use of calving grounds. By using a two-step analytical approach we separated individuals belonging to these ecotypes. Step one indicated three distinct subpopulations dominated

Table 1. Numbers of female caribou tracked with satellite collars for full years and included in hierarchical and fuzzy cluster analyses, by matrix interval, ecotype, subpopulation, and calendar years tracked, in the Northwest Territories, Nunavut, and northern Alberta, Canada (1993–2009).

Caribou ecotype and subpopulation†	Number of caribou tracked by calendar year‡																Total
	93	94	95	96	97	98	99	00	01	02	03	04	05	06	07	08	
A) Matrix interval: 12-month (*x*, *y*) coordinates (24 variables)																	
Migratory barren-ground																	
Cape Bathurst				5	5	4	6	5	1	8	8	4	6	14	21	23	39
Bluenose-West				2	4	5	11	9	4	5	4	2	8	13	20	25	44
Bluenose-East				3	5	9	8	7	2		3	3	17	20	22	28	51
Bathurst				7	7	18	15	14	13	7	11	13	17	16	22	18	52
Beverly			1	4	3	3		1	4	8	5	3	7	19	24	42	62
Total			1	21	24	39	40	36	24	28	31	25	55	82	109	136	248
Boreal										2	10	15	49	62	73	85	140
Dolphin and Union island							16	16	14	11	14	9	1				25
B) Matrix interval: 26 two-week (*x*, *y*) coordinates (52 variables)																	
Migratory and tundra-wintering barren-ground																	
Beverly			2	3	3	2			4	5	3	2	7	18	25	42	53
Quanmanirjuaq	4	5	7	5	9	8	8	8	8	7	6	13	10	22	22	29	61
Queen Maude Gulf				2	2	2			1	2	4	3	3	3	3	9	15
Lorillard						2	9	12	11	13	13	13	9	6	1		21
Wager Bay								4	4	3	8	7	4	2			11
Total	4	5	9	10	14	14	17	24	28	30	34	38	33	51	51	80	161

† Assignment of caribou to subpopulations was based on hierarchical and fuzzy classification (fuzzy exponent $m = 2$).

‡ Years when individuals were tracked for all or a portion of a calendar year (93 = 1993, . . . , 08 = 2008).

by Qamanirjuaq, Beverly, and tundra-wintering caribou (Table 3). Step two indicated the Qamanirjuaq-dominated subpopulation was robust (Table 3). For the Beverly-dominated subpopulation, the validity functions for $m = 1.8–2.2$ (moderate level of fuzziness) indicated three distinct subpopulations dominated by (1) females that used calving ground F but included some that used E-1 or both (Beverly A), (2) females that used calving ground E-1 but included some that used F or both (Beverly B), and (3) females that only used calving ground E including area E-1 (Queen Maude Gulf A; Table 3). Validity functions for the pooled Beverly A

Table 2. Numbers of full years that female caribou were tracked using satellite collars and included in hierarchical and fuzzy cluster analyses, by matrix interval, ecotype, and subpopulation, in the Northwest Territories, Nunavut, and northern Alberta, Canada (1993–2009).

Caribou ecotype and subpopulation†	Number of years caribou tracked							Total
	1	2	3	4	5	6	7	
A) Matrix interval: 12-month (*x*, *y*) coordinates (24 variables)								
Migratory barren-ground								
Cape Bathurst	13	11	8	6	1			39
Bluenose-West	22	11	6	4		1		44
Bluenose-East	25	9	8	9				51
Bathurst	12	17	11	8	4			52
Beverly	32	16	9	4	1			62
Total	104	64	42	31	6	1		248
Boreal	58	57	21	4				140
Dolphin and Union island	9	5	6	5				25
B) Matrix interval: 26 two-week (*x*, *y*) coordinates (52 variables)								
Migratory and tundra-wintering barren-ground								
Beverly	26	13	9	4	1			53
Qamanirjuaq	22	12	21	5		1		61
Queen Maude Gulf	8	5	1	1				15
Lorillard	3	6	5	1	3	2	1	21
Wager Bay	4	3	3	1				11
Total	63	39	39	12	4	3	1	161

† Assignment of caribou to subpopulations was based on hierarchical and fuzzy classification (fuzzy exponent $m = 2$).

TABLE 3. Results of hierarchical and fuzzy cluster analyses used to identify distinct and robust subpopulations of barren-ground, Dolphin and Union island, and boreal caribou in the Northwest Territories, Nunavut, and northern Alberta, Canada.

	Tests for distinct subpopulations†				
	Concordant classification			Assignment consistency (fuzzy clustering)	
Areas and subpopulations (subpopulation calving ground)	No. subpopulations	Range of m when no. subpopulations concordant	No. caribou assigned to same classes by both cluster methods	No. caribou classified consistently	Range of m
1) West-central area	5	1.9–2.9	244/248 (98.4%)	247/248 (99.5%)	$1.8 \le m \le 2.9$
Cape Bathurst (A)					
Bluenose-West (B)					
Bluenose-East (C)					
Bathurst (D)					
Beverly (E, F)					
2) Central area§	4	1.5–3.0	188/191 (98.4%)	190/191 (99.5%)	$1.5 \le m \le 3.0$
Dolphin and Union island					
3) East-central area	3	1.5–3.0	158/161 (98.0%)	160/161 (99.4%)	$1.5 \le m \le 3.0$
Qamanirjuaq (G)					
Beverly (E and F)	3	1.8–2.2	52/64 (82.4%)	61/64 (95.3%)	$1.2 \le m \le 2.2$
Beverly A					
Beverly B					
Beverly A and B					
QMG A (E)¶					
Tundra-wintering	3	$2.0 \le m \le 2.4$	33/36 (91.7%)	33/36 (92%)	$1.5 \le m \le 3.0$
QMG B (E)					
Lorillard (H)					
Wager Bay (I)					
QMG A and B (E)					
4) Boreal	2	1.5–3.0	140/140 (100%)	131/140 (93.6%)	$1.5 \le m \le 3.0$
Northern					
Southern					

† For subpopulations to be distinct, the post-hierarchical clustering Duda-Hart pseudo t test and both fuzzy clustering validity functions had to indicate the same number of subpopulations (Appendices C and D), ≥90% of individuals had to be assigned to the same subpopulations by hierarchical and fuzzy ($m = 2$) clustering (concordant classification; Appendix E); and ≥90% of individuals had to be consistently assigned to the same subpopulation by fuzzy clustering for most values of m (assignment consistency). Assignment consistency was determined by comparing each individual's subpopulation assignment at $m = 2.0$ (moderate level of fuzziness) with those at $m = 1.5$–1.9 and $m = 2.1$–3.0.

‡ For a subpopulation to be robust, the fuzzy clustering validity functions (fuzzy performance index and normalized classification entropy) had to be ≥0.90 for most $m \ge 2.0$, indicating that females were strongly spatially affiliated.

§ The central area also included the Bluenose-east, Bathurst, and Beverly subpopulations; results of tests for robustness are given under the west-central area.

¶ QMG is Queen Maude Gulf.

and B data indicated that these females formed one of the most robust subpopulations of migratory barren-ground caribou we examined (Table 3). The Queen Maude Gulf A females were organized as individuals (Table 3). For the tundra-wintering caribou-dominated subpopulation, validity functions for $m = 2.0$–2.4 (moderate level of fuzziness) indicated three distinct subpopulations dominated by females that used calving ground H (Lorillard), I (Wager Bay), or E (Queen Maude Gulf B), respectively (Table 3). The Lorillard subpopulation was robust (Table 3). Although Queen Maude Gulf A ($n = 11$) and B ($n = 4$) females may belong to different subpopulations, we pooled them to increase n to test for robustness. The pooled Queen Maude Gulf A and B ($n = 15$) and Wager Bay ($n = 11$) females were organized as individuals (Table 3).

All barren-ground caribou subpopulations were dominated by females that used one calving ground, except the Beverly (Table 3). The Beverly subpopulation included females that used calving ground F or E-1 or changed use from F to E-1 (Fig. 1). The Queen Maude Gulf subpopulation used calving ground E including area E-1. Therefore, we documented the use of two calving grounds by one barren-ground subpopulation and use of one calving ground by two barren-ground subpopulations.

Utilization distributions

Each subpopulation of barren-ground, island, and boreal caribou used distinct core ranges (Fig. 3). The mean area of overlap among core ranges of the robust migratory Cape Bathurst, Bluenose-West, Bluenose-East, and Bathurst barren-ground caribou subpopula-

Table 3. Extended.

Test for robust subpopulations (range of *m* when validity functions were $\geq$0.90 or minimized at individuals)‡	Subpopulation robust	No. caribou and calving grounds used
$2.3 \leq m \leq 3.0$	yes	$n = 39$, A = 36, A and B = 1, B = 2
$2.0 \leq m \leq 3.0$	yes	$n = 44$, B = 42, C = 2
$1.9 \leq m \leq 3.0$	yes	$n = 51$, C = 49, B and C = 1, D = 1
$1.8 \leq m \leq 3.0$	yes	$n = 52$, D = 45, C and D = 2, D and E = 4, E = 1
$2.0 \leq m \leq 3.0$	yes	$n = 62$, E = 46, F = 9, F and E = 7
25 individuals for $1.5 \leq m \leq 3.0$	no	$n = 25$ dispersed calving
$1.7 \leq m \leq 3.0$	yes	$n = 61$ G = 61
		$n = 21$, E = 7, F = 9, F and E = 5
		$n = 32$, E = 29, F = 1, F and E = 2
$1.9 \leq m \leq 3.0$	yes	$n = 53$, E = 36, F = 10, F and E = 7
11 individuals for $1.5 \leq m \leq 3.0$	no	$n = 11$, E = 11
small *n*	n/a	$n = 4$, E = 3, I = 1
$2.0 \leq m \leq 3.0$	yes	$n = 21$, H = 18, H and I = 2 I = 1
11 individuals for $1.5 \leq m \leq 3.0$	no	$n = 11$, I = 8, H and I = 2, H = 1
15 individuals for $1.5 \leq m \leq 3.0$	no	$n = 15$, E = 14, I = 1
57 individuals for $1.5 \leq m \leq 3.0$	no	$n = 57$ dispersed calving
83 individuals for $1.5 \leq m \leq 3.0$	no	$n = 83$ dispersed calving

tions was 18% (range 5–27%). In comparison, the mean area of overlap among core ranges of Beverly females that used calving grounds F, E-1, or E-1 and F was 63% (range 56–72%) or about three times greater than for other robust migratory subpopulations (Fig. 4). These three ranges reflect the Beverly subpopulations change in calving-ground use.

Annual home range and path length

Mean annual-range areas (DS collars, ANOVA $F_{4,597} = 466.0$, $P < 0.001$) and path lengths (DS collars, ANOVA $F_{4,597} = 339.6$, $P < 0.001$) varied significantly among ecotypes (Tables 4 and 5).

Annual ranges used by boreal and migratory barren-ground caribou were significantly smaller and larger, respectively, than those for all other ecotypes (Tukey's hsd pairwise comparisons, $P < 0.05$). For boreal caribou, mean annual-range areas (GPS collars, ANOVA $F_{3,145} = 9.7$, $P < 0.001$) and path lengths (GPS collars, ANOVA $F_{3,145} = 4.8$, $P = 0.003$) varied significantly among study areas (Tables 4 and 5). We did not find a clear pattern for these differences. For migratory barren-ground caribou, mean annual-range areas (DS collars, ANOVA $F_{5,332} = 179.9$, $P < 0.001$) and path lengths (DS collars, ANOVA $F_{5,332} = 185.4$, $P < 0.001$) varied significantly among subpopulations (Tables 4 and 5). A significant west to east positive cline (Cape Bathurst < Bluenose-West < Bluenose-East < Bathurst < Beverly = Qamanirjuaq subpopulations) was evident in annual-range sizes and path lengths for these caribou (Tukey's hsd pairwise comparisons, $P < 0.05$). For tundra-wintering caribou, mean annual ranges (DS collars, ANOVA $F_{2,74} = 21.5$, $P < 0.001$) and path lengths (DS collars, ANOVA $F_{2,74} = 16.2$, $P < 0.001$) varied significantly among subpopulations (Table 4 and 5). The eastern-most Lorillard and Wager Bay subpopulations had significantly smaller annual ranges and shorter path lengths than the western-most Queen Maude Gulf subpopulation (Tukey's hsd pairwise comparisons, $P < 0.05$).

DISCUSSION

The concept of a population as a group of interbreeding individuals that have little or no contact with other similar groups is different from what really occurs (Caughley 1980). Theoretical and empirical evidence indicates that population types range from "classical closed populations to interacting systems of subpopula-

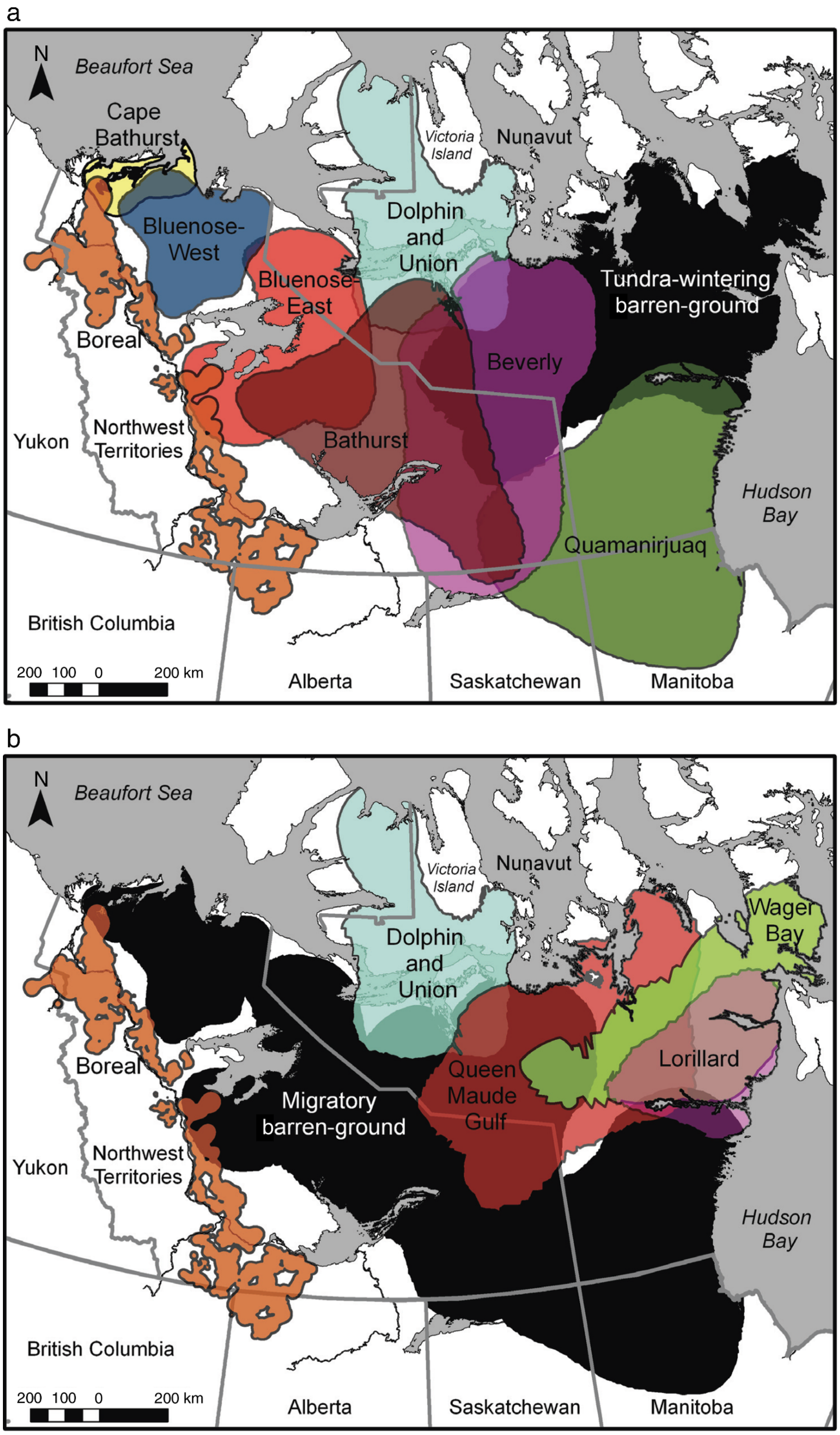

FIG. 3. Core ranges (mean 90% utilization distribution) used by (a) migratory Cape Bathurst, Bluenose-West, Bluenose-East, Bathurst, Beverly, Qamanirjuaq, tundra-wintering barren-ground, boreal, and Dolphin and Union island caribou, and by (b) tundra-wintering Queen Maude Gulf, Wager Bay, and Lorillard and migratory barren-ground, boreal, and Dolphin and Union island caribou subpopulations in the Northwest Territories and Nunavut, Canada (1993–2009). Portions of ranges extending into Yukon Territory, Alberta, Saskatchewan, and Manitoba, Canada, are shown.

tions" (Thomas and Kunin 1999). The population is a central concept for ecology (Berryman 2002), and its complexities must be taken into account for effective management (Schaefer 2006, Harwood 2009). Because population size and distribution will change over time (Harwood 2009), the temporal and spatial characteristics used to define them must be clear to avoid confusion and misunderstanding (Olexa and Gogan 2007).

Space use patterns and affiliations of individuals indicate how populations are structured (Wells and Richmond 1995), and our ability to document these patterns and affiliations has been enhanced by the availability of continuous high-resolution location data acquired through the use of satellite collars. Sufficient numbers of collars must be adequately distributed in the area of interest and tracked long enough at an appropriate resolution so that the resulting observations and conclusions drawn are biologically meaningful and not artifacts of sampling design (Klaver et al. 2008, Harwood 2009). At present, our ability to assess variations in space use patterns among individuals at finer temporal and spatial scales in large subpopulations, e.g., barren-ground caribou, is limited by the proportionately small number of animals that have been tracked annually.

Fuzzy classification has enhanced our ability to assign individuals to groups when their affiliations or the boundaries among groups are uncertain or vague (McBratney and Odeh 1997). Schaefer et al. (2001) and Klaver et al. (2008) used fuzzy clustering to define subpopulations of cervids. Using a novel approach, we used fuzzy clustering to identify distinct subpopulations in four behaviorally different caribou ecotypes and describe how they were structured. We verified that the migratory Cape Bathurst, Bluenose-West, Bluenose-East, Bathurst, Beverly, and Qamanirjuaq barren-ground caribou subpopulations, which were previously recognized using the calving-ground classification system (Banfield 1954, Thomas 1969, Parker 1972, Heard 1983, Nagy et al. 2005), were robust. Data for five of the migratory subpopulations were obtained over 14–17 years, indicating that subpopulation structure and area fidelity were maintained over time. In addition, we verified that the tundra-wintering Queen Maude Gulf, Lorillard, and Wager Bay subpopulations previously described by Calef and Heard (1981) and Heard et al. (1987) were distinct, but only the Lorillard subpopulation was robust. Because the movements of the Queen Maude Gulf and Wager Bay subpopulations were unconstrained by habitat discontinuity or barriers to movement, they may be behaviorally different from other barren-ground caribou, or sample sizes were inadequate to determine spatial affiliation. Additional satellite-tracking studies are required to understand the subpopulation structure of tundra-wintering caribou.

Females in five of the six robust migratory barren-ground caribou subpopulations used one calving ground and supported the concept of calving-ground fidelity. However, by 2010, Beverly females had largely abandoned their "traditional" calving ground in favor of one used by the Queen Maude Gulf subpopulation. This shift in use likely began in the mid 1990s. The distance between geographic centers of calving grounds used by Beverly females during 2006 to 2008 is ~245 km. The Bathurst subpopulation made a similar shift in calving-ground use between 1986 and 1996. The distance between geographic centers of calving grounds used by Bathurst females before 1987 and in 1996–2010 is ~250 km. Bathurst females also calved on a number of sites between these two areas over a 10-year transition period (Sutherland and Gunn 1996). In Alaska, Hinkes et al. (2005) documented three patterns of calving-ground use by barren-ground caribou, including subpopulations that maintained annual fidelity to the same calving ground, subpopulations that maintained fidelity to one calving ground for a period, alternated use between this and a new one for a period, and then only used the new one, and subpopulations in which, following the influx of one subpopulation into the winter range of a second, most but not all of the females from the second subpopulation began using the calving ground of the first. These examples indicate that shifts in calving-ground use over time may be common and should be

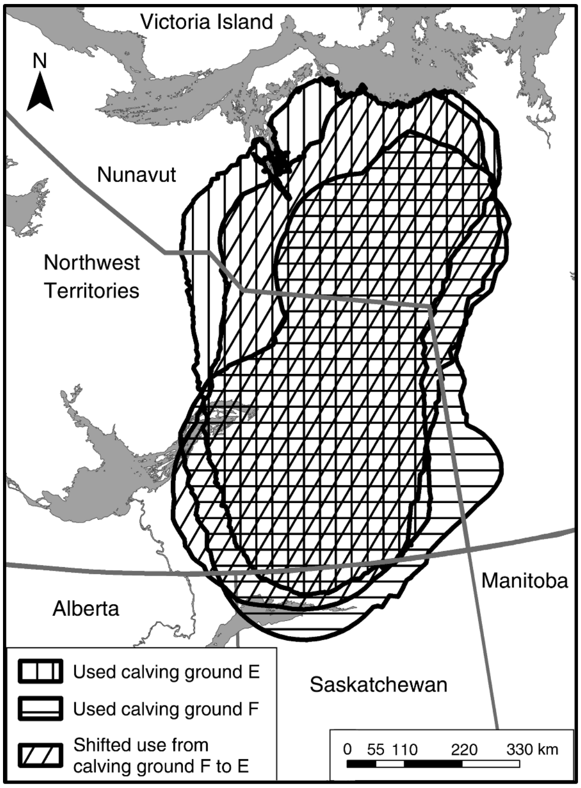

FIG. 4. Core ranges (90% utilization distribution) of migratory female barren-ground caribou that either used calving grounds E-1 or F or switched use from F to E-1 (Beverly subpopulation) in the Northwest Territories and Nunavut, Canada (1993–2009).

TABLE 4. Sizes of annual minimum convex polygons (MCPs) for boreal, mountain woodland, Dolphin and Union island, and barren-ground caribou tracked using satellite collars in the Northwest Territories, Nunavut, and northern Alberta (1993–2009).

	Annual MCPs for GPS satellite-collared caribou‡							Annual MCPs for DS satellite-collared caribou‡						
Ecotype, study area, or subpopolation†	Location interval	Caribou (n)	MCPs (n)	Mean area (km^2)	SD	Min. area (km^2)	Max. area (km^2)	Location interval (days)	Caribou (n)	MCPs (n)	Mean area (km^2)	SD	Min. area (km^2)	Max Area (km^2)
Ecotypes														
Boreal	8 h	85	149	2478	1512	249	7466	1–5	55	104	2122	1644	206	10 120
Mountain woodland								3	10	31	14 460	9513	7	31 674
Dolphin and Union island								1–20	25	52	36 844	16 409	10 502	83 025
Tundra-wintering barren-ground	1 d	6	6	93 902	33 596	65 636	158 066	1–10	28	66	43 245	29 780	3346	125 312
Migratory barren-ground	8 h	133	218	136 367	85 650	8487	357 389	1–10	154	343	107 574	60 002	1577	306 830
Boreal caribou study areas														
Gwich'in settlement	8 h	26	48	2951	1528	476	7211	1–5	12	22	3227	2044	561	10 120
Sahtu settlement	8 h	18	32	1878	1590	659	7466	1–5	1	4	924	208	738	1157
Cameron Hills/ South Slave	8 h	29	49	2787	1392	434	6217	1–5	16	23	2061	1473	837	8007
Dehcho	8 h	12	20	1549	832	249	3391	1–5	26	55	1792	1388	206	6229
Migratory barren-ground														
Cape Bathurst	8 h	18	33	21 642	8928	8487	64 947	1–10	17	41	19 137	7064	1577	36 959
Bluenose-West	8 h	19	33	47 859	11 654	21 456	68 267	1–10	22	50	60 504	19 563	21 407	105 696
Bluenose-East	8 h	15	19	112 125	24 977	64 721	161 884	1–10	31	61	98 429	42 056	26 837	185 192
Bathurst	8 h	1	1	113 153		113 153	113 153	1–10	38	92	123 220	41 086	47 470	254 009
Beverly	12 h	44	65	172 189	55 391	93 270	355 946	1	13	30	159 693	49 041	72 298	306 830
Qamanirjuaq	1 d	36	67	208 323	60 252	37 797	357 389	1–10	31	64	158 726	48 373	66 769	258 710
Tundra-winter barren-ground														
Lorillard								1–10	18	51	39 717	27 875	3346	123 812
Wager Bay								1–10	9	14	50 235	28 741	8497	97 502
Queen Maude Gulf	1 d	6	6	93 902	33 596	65 636	158 066	1–5	1	1	125 312		125 312	125 312
Total		224	373						272	596				

† Values for migratory and tundra-wintering barren-ground and island caribou are for subpopulations.
‡ Abbreviations are: GPS, Global Positioning System; DS, Doppler Shift.

anticipated to ensure that areas that are suitable for calving but are currently unused, are managed for potential future use. In addition, and contrary to Skoog (1968), barren-ground caribou cannot be reliably assigned to subpopulations based on calving-ground use alone.

We believe that definitions requiring barren-ground caribou subpopulations to consistently use the same "traditional" calving grounds promote a restricted view of the ecology of the species. Changes in calving-ground use over time by subpopulations would, by some definitions, require designation of new subpopulations rather than recognizing the relocation of existing ones. We believe that a more meaningful and robust method of classifying subpopulations of barren-ground caribou is one based on the annual spatial affiliation of females and not just on their calving distribution. Thus we recommend a change in the classification method to one based on our approach. Our definition is consistent with, but is less restrictive than Miller's (1982), in that it allows for (1) distinct subpopulations to have adjacent calving grounds; (2) one subpopulation to use two or more calving grounds over time; or (3) two or more subpopulations to use the same calving ground.

We documented an east–west cline in annual home range sizes and path lengths among migratory barren-ground caribou subpopulations, further supporting the subpopulation structure we identified. This variation may be related to differences in population size, habitat quality, proportions of subpopulation ranges that are above tree line, topography, weather patterns, and predator diversity and density. The more than doubling of annual migratory path lengths between western and eastern migratory subpopulations suggests that the energetic costs to caribou of disturbances that may alter their normal patterns of activity or range use should be considered when effects of petroleum and mineral exploration and development, vehicle traffic, and low-level aircraft overflights are assessed.

Dolphin and Union island caribou were organized as individuals. Because these caribou are migratory and are either geographically or temporally isolated from most other caribou during the year, they are likely structured by migratory connectivity and barriers to movement. These caribou are behaviorally similar to boreal and barren-ground caribou: they are organized as individuals but are structured in part by migratory connectivity.

Boreal caribou formed two subpopulations of females organized as individuals across ranges separated by large areas burned by wildfires in the central NT (Government of the Northwest Territories fire history data). This habitat discontinuity may be temporary if

TABLE 5. Annual-path lengths for caribou tracked using satellite collars in the Northwest Territories, Nunavut, and northern Alberta, Canada (1993–2009).

	Annual-path lengths for GPS satellite-collared caribou‡							Annual-path lengths for DS satellite-collared caribou‡						
Ecotype, study area, or subpopolation†	Location interval	Caribou (*n*)	Path lengths (*n*)	Mean length (km)	SD	Min. length (km)	Max. length (km)	Location interval (days)	Caribou (*n*)	Path lengths (*n*)	Mean length (km)	SD	Min. length (km)	Max. length (km)
Ecotypes														
Boreal	8 h	85	149	1204	245	644	2022	1–5	55	104	620	182	213	1228
Mountain woodland								3	10	31	1140	380	241	1747
Dolphin and Union island								1–20	25	52	1323	285	774	1800
Tundra-wintering barren-ground	1 d	6	6	2461	238	2111	2791	1–10	28	66	1678	427	653	2809
Migratory barren-ground	8 h	133	218	3119	707	1519	4847	1–10	154	343	2249	646	658	4006
Boreal caribou study areas														
Gwich'in Settlement Area	8 h	26	48	1263	278	735	2022	1–5	12	22	744	213	438	1228
Sahtu Settlement Area	8 h	18	32	1180	213	720	1667	1–5	1	4	500	62	422	571
Cameron Hills/South Slave	8 h	29	49	1229	216	684	1659	1–5	16	23	615	145	383	863
Dehcho	8 h	12	20	1038	211	644	1417	1–5	26	55	581	166	213	972
Migratory barren-ground														
Cape Bathurst	8 h	18	33	2041	193	1593	2461	1–10	17	41	1155	242	658	1702
Bluenose-West	8 h	19	33	2488	259	1858	3057	1–10	22	50	1751	276	1113	2284
Bluenose-East	8 h	15	19	3256	258	2757	3725	1–10	31	61	2132	363	1332	2755
Bathurst	8 h	1	1	2865		2865	2865	1–10	38	92	2492	346	1746	3592
Beverly	12 h	44	65	3592	457	2603	4847	1	13	30	2820	363	1889	3592
Qamanirjuaq	1 d	36	67	3466	494	1519	4721	1–10	31	64	2788	502	1849	4006
Tundra-winter barren-ground														
Lorillard								1–10	18	51	1730	411	653	2809
Wager Bay								1–10	9	14	1462	438	679	2489
Queen Maude Gulf	1 d	6	6	2461	238	2111	2791	1–5	1	1	2022		2022	2022
Total		224	373						272	596				

† Values for migratory and tundra-wintering barren-ground and island caribou are for subpopulations.

‡ Abbreviations are: GPS, Global Positioning System; DS, Doppler Shift.

natural habitat regeneration occurs. Our findings are consistent with the observations of Bergerud (1996) that boreal caribou tend to form a near-continuum across a region of favorable calving sites.

Mean annual home ranges for boreal caribou in our study areas were 6–14 times larger than the smallest and up to two times larger than the largest mean annual ranges reported in Alberta (Stuart-Smith et al. 1997) and Saskatchewan (Rettie and Messier 2001). Stuart-Smith et al. (1997) obtained caribou locations about every two weeks, while Rettie and Messier (2001) obtained locations every 2–4 days, and thus differences among home ranges in our areas may in part be a result of sampling frequency (Borger et al. 2006). In many parts of Alberta, forest management practices, agricultural expansion, and oil, gas, and mineral resource exploration and extraction activities have resulted in loss, alteration, and fragmentation of caribou habitat (McLoughlin et al. 2003). In Alberta, boreal caribou currently occupy remnant stands of boreal forest, and their movements may be further constrained by development impacts within these areas (Dyer et al. 2002), thus possibly leading to smaller annual home ranges. In the NT most of the boreal caribou range is comparatively pristine and continuous; thus their movements may not be constrained by human impacts, possibly leading to larger home ranges.

Harwood (2009) posed the question, that "given a group of individual organisms, dispersed over space and/or time, with a variation in their degree of connectivity to the other individuals, can we (1) subdivide these individuals into two or more subgroups, and/or (2) take a sample of these individuals that is representative of the whole group or subgroups?" We show that an externally imposed classification system, i.e., fuzzy clustering, can be used to assign individuals to distinct well-organized subpopulations. Demographic information such as population estimates, pregnancy and parturition rates, and causes and rates of mortality can be obtained by tracking individuals within these subpopulations. The factors structuring these subpopulations, i.e., strong spatial affiliation among its members or environmental conditions, will indicate whether these data are representative of robust subpopulations (e.g., migratory barren-ground caribou) or geographic areas (e.g., boreal caribou).

The only way to understand caribou population ecology without influencing their behavior is by incorporating satellite tracking in study designs. The deployment of satellite collars is initially invasive, but well-designed, long-

PLATE 1. Woodland caribou, early September, Mackenzie Mountains, Northwest Territories, Canada. Photo credit: J. A. Nagy.

term, high-resolution satellite-tracking studies (i.e., using GPS collars), in combination with rigorous analyses of the resulting data using statistical procedures like fuzzy clustering, provide an opportunity to obtain biological information critical for management decisions. Clearly, the benefit of improved technology is that we can define and track changes in population structure and other important ecological processes over time. This is particularly important when considering the potential impacts of natural and anthropogenic disturbances, including climate change, on caribou and their habitats and on the northern people that depend on them.

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APPENDIX A

History of satellite tracking studies undertaken in the Northwest Territories and Nunavut, Canada, 1993–2009 (*Ecological Archives* A021-105-A1).

APPENDIX B

Number of female caribou with full years of satellite tracking data, by ecotype, subpopulation, and years tracked, in the Northwest Territories, Nunavut, and northern Alberta, Canada, 1993–2009 (*Ecological Archives* A021-105-A2).

APPENDIX C

Values of the Duda-Hart *t* test statistic for Ward's hierarchical clustering of movement data for migratory and tundra-wintering barren-ground, Dolphin and Union island, and boreal caribou in the Northwest Territories, Nunavut, and northern Alberta, Canada (*Ecological Archives* A021-105-A3).

APPENDIX D

Values of the validity functions (i.e., fuzziness performance index and normalized classification entropy) for an appropriate number of subpopulations indicated by fuzzy clustering of movement data for migratory and tundra-wintering barren-ground, Dolphin and Union island, and boreal caribou in the Northwest Territories, Nunavut, and northern Alberta, Canada (*Ecological Archives* A021-105-A4).

APPENDIX E

Comparison of assignments by fuzzy (fuzzy *c*-means) and hierarchical (Ward's method) clustering of individual migratory and tundra-wintering barren-ground, Dolphin and Union island, and boreal caribou to subpopulations in the Northwest Territories, Nunavut, and northern Alberta, Canada (*Ecological Archives* A021-105-A5).