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Have geographical influences and changing abundance led to sub-population structure in the Ahiak caribou herd, Nunavut, Canada?

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Abstract: We examined the premise that changing abundance and environmental conditions influence the seasonal dispersion and distribution of migratory tundra caribou (*Rangifer tarandus groenlandicus*). The Ahiak herd's (north-central Nunavut, Canada) calving shifted from dispersed on islands to gregarious calving on the mainland coast. As abundance further increased, the calving ground elongated east and west such that we proposed a longitudinal climate gradient. As well, the calving ground's east and west ends are different distances from the tree-line, which dips south closer to Hudson Bay. We proposed that whether caribou winter on the tundra or within boreal forest and the different climate across the long calving ground could contribute to differential survival and productivity such that sub-population structure would result. At the scale of the individual cows (identified through satellite-collars), we did not find inter-annual spatial fidelity to either the western or eastern parts of the calving ground. At the population scale (aerial surveys of calving distribution), we also did not find discontinuities in calving distribution. The spatial association of individual cows during calving compared with their association during the rut was inconsistent among years, but overall, cows that calve together, rut together. At this time and with the available evidence, we could not infer sub-population structure from shifts in dispersion and distribution as influenced by geography and changes in abundance for the Ahiak herd.

Key words: Ahiak herd; calving; geography; *Rangifer tarandus groenlandicus;* rutting; spatial fidelity; sub-population; tree-line.

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Introduction

The general premise for this paper is that physical geography (landforms and climate) and abundance influence migratory tundra caribou's (*Rangifer tarandus groenlandicus*) seasonal and annual distribution (Bergerud *et al.,* 2008). Seasonal ranges contract or expand with changes in abundance within the constraints imposed by how physical geography influences distribution.

The Ahiak herd (previously named as the Queen Maud Gulf herd; Gunn *et al.,* 2000) seasonally ranges mostly in north central Nunavut, Canada (Fig. 1). We first describe how abundance and physical geography influence the herd's calving and winter distribution. Sec-

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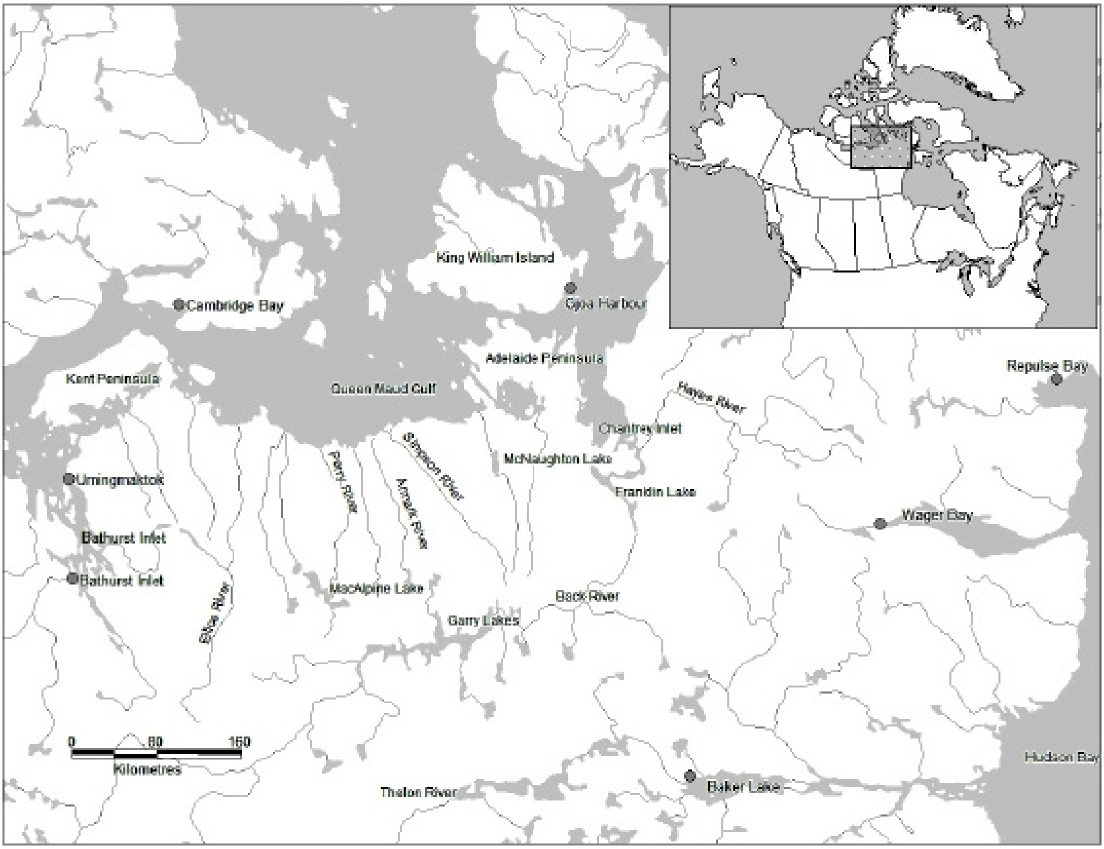

Fig. 1. Queen Maud Gulf and surrounding area, north central mainland, Nunavut.

ondly, we examined whether those influences contribute toward sub-population structure within the Ahiak herd. Wells & Richmond (1995) defined a subpopulation as *"an arbitrary spatially-delimited subset of individuals from within a population"*.

The geographical influences are firstly, the configuration of Queen Maud Gulf's coast line which stretches in a relatively straight east-west direction for 300 km and has 100s of islands and islets. Compared to other caribou calving grounds, the Ahiak herd's annual calving grounds (*sensu* Russell *et al.,* 2002) are unusually long and narrow (~340 km x ~75 km).

The second geographical influence is how the extent of the low-lying coastal plains of the northeast Nunavut mainland affects the position of the tree-line and in turn, caribou winter and pre-calving migration distribution. Within mainland Canada, from west to east toward Hudson Bay, the low elevation arctic coastal plain widens out and consequently the tree-line (Timoney *et al.,* 1992) dips south and widens (Fig. 2). The tree-line is more accurately described as a forest-tundra biome (Timoney *et al.,* 1992; Payette *et al.,* 2001) lying between the southern limit (<0.1% cover) of upland tundra and the northern limit (<0.1% cover) of trees >3-4 m tall. From Mackenzie Delta to north of Yellowknife, the forest-tundra biome is 60 -150 km wide compared to 230–340 km for the zone from the Dubawnt River to central

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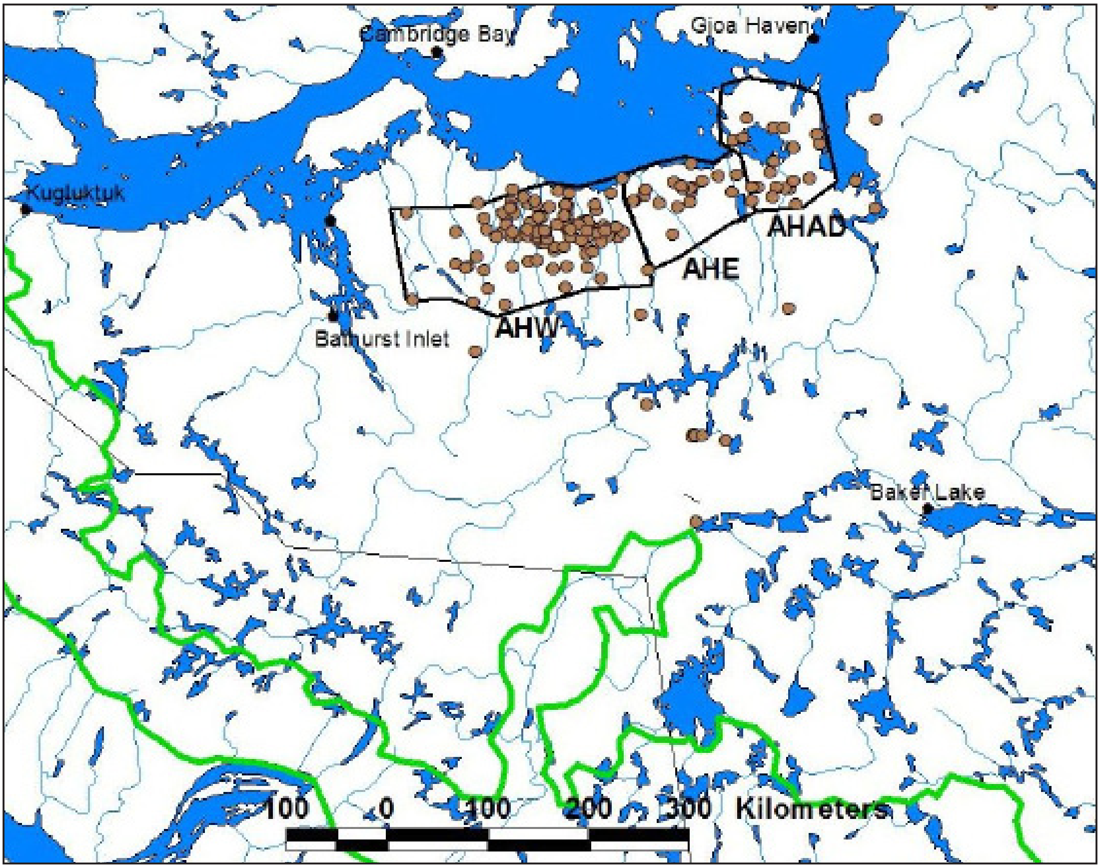

Fig. 2. Location of the Ahiak West (AHW), East (AHE), and Adelaide Peninsula (AHAD) blocks of the Ahiak calving grounds, assigned primarily based on aerial survey data 2006-09. Brown dots are June calving locations from collar data, 1995-2010. The tree-line and forest-tundra biome is shown within the green polygon (Timoney *et al.,* 1992; Payette *et al.,* 2001).

Manitoba-Keewatin (Timoney *et al.,* 1992). The southeast extension of the tundra west of Hudson Bay increases the likelihood for some Ahiak caribou to be wintering on the tundra.

In the paper's second part, we examine how the geographical influences (long straight coast line and position of the tree-line) could lead to sub-population structure. A longitudinal environmental gradient in the timing of snowmelt or plant green-up across the east-west length of the calving ground could influence early calf survival. If individual cows had fidelity between years to either the western or eastern calving ground and the environmental gradient is marked; sub-population structure could develop if the association of cows on the calving grounds is similar to the pattern of association during the rut. Additionally, if individual cows wintering on the tundra or within the forests are more likely to calve at the east or west end of the elongated coastal calving ground, then sub-population structure could develop or be accentuated in response to different environmental conditions during winter and pre-calving migration. Cows wintering within forest-tundra and lichen woodland communities of the boreal forest (Payette *et al.,* 2001), versus those wintering on the tundra, will face different ecological conditions during winter and pre-calving migration, which could affect their reproductive success and survival.

Sub-population structure development

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would depend on inter-annual fidelity by individual breeding females within the calving ground. While annual fidelity of individual cows to calving grounds is well documented, fidelity to specific sites has not been reported (for example, Fancy & Whitten, 1991). Our premise was that the length of the calving ground would be sufficient for cows to possibly exhibit annual fidelity to part of the calving ground.

Our objective is to review evidence for use patterns of the calving grounds at the individual scale (based on satellite-collared cows) and at the population-scale (using information from aerial surveys of calving distribution). Our hypothesis is that the Ahiak calving grounds are comprised of two or more calving sub-populations.

By focusing on a relatively detailed description of space use by the Ahiak herd, we aim to contribute to better understand the spatial dynamics of migratory caribou. The Ahiak herd is unusual in its long narrow calving ground and if it contributes to sub-population, the information will be useful to management. We need to be aware of similarities and differences between herds especially in the context of longer-term changes in space use as herds change in abundance.

Methods

We compiled information from government reports (Table 1) to derive descriptive statistics and spatial analyses for telemetry (1996-2008) and aerial survey data (2006-10) (Government of Northwest Territories, Department of Environment and Natural Resources). We also used 11 calving and rut locations from 2008-10 from a cooperative project for monitoring and baseline studies, Agnico-Eagle Mines Limited, AREVA Ltd and Government of Nunavut (M. Campbell, pers. comm.; Gebauer *et al.,* 2011). We tested four predictions that followed from our negative hypothesis:

1) Distribution of calving cows would be discontinuous across the calving ground and individual breeding females would show inter-annual fidelity to discrete areas within annual calving grounds observed in consecutive years.

2) Based on the sample of collared cows, 5% or less of the collared breeding females would switch calving locations in subsequent years between the western, central and eastern areas of an annual calving ground. (We selected 5% based on annual rates of switches of breeding females).

3) Based on aerial surveys of the Ahiak calving grounds, 2006-10, there would be an observable pattern of discontinuity along the east-west axis in the distribution of breeding females and newborn calves (measured at a grid scale interval of 10 km).

4) Cows that calved together on an annual calving ground (at the scale of the east or west halves of the calving ground), will not solely associate together during the subsequent fall rut. Thus, within a year, collared breeding females that calved within i) the western portion of the calving ground, or ii) the combined central and eastern portions would not be associated with other cows that calved within the same area of the coastal calving ground during the subsequent fall rut (temporal index is 20 October) at a rate greater than would be expected by chance (*i.e.*, >50% probability).

Distribution and abundance of caribou calving in the Queen Maud Gulf

To describe caribou calving along the coast of Queen Maud Gulf relative to changes in abundance, we compiled earlier accounts (Gavin, 1945; Appendix G in Gunn *et al.,* 2000), pre-calving surveys from 1983 and 1993 (Heard *et al.,* 1987; Buckland *et al.,* 2000), and systematic aerial calving ground surveys in 1986, 1996, and 2006-2010 which were strip transect surveys designed to map the distribution and estimate densities of caribou (Gunn *et al.,* 2000; D. Johnson, unpubl. data). We also include

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Table 1. Sources and type of data used in analysis.

Type	Source	No. cows	Publication or project leader[a]	Project objectives or rationale
1996-98 telemetry	WMIS[b]	4	Gunn et al., 2000	Herd identity of wintering caribou east of Bathurst Inlet
2001-02 telemetry	WMIS	9	Gunn & D'Hont, 2002	Bathurst herd project (overlaP on winter ranges)
2006-08 telemetry	WMIS	33	D. Johnson	Beverly distribution
2009-10 telemetry	WMIS	21	A. Kelly	Beverly distribution
2009-10 telemetry	NIRB Public Registry	7	M. Campbell; Gebauer et al., 2011	Monitoring for Meadowbank mine; baseline data for AREVA Ltd.
2006-08 calving surveys	WMIS		D. Johnson unpubl. data; Poole et al., 2013; A. Kelly	Assess distribution and trend in density breeding females

[a] Use of data does not imply agreement with the interpretations presented in this paper.

[b] Wildlife Management Information System, Government of Northwest Territories

information from wildlife baseline surveys for mining development (Calef & Hubert, 2002; Rescan, 2011).

The 2006-10 aerial systematic surveys used transects aligned north-south and on-transect sightings were recorded as sex age classes and allocated to 10 km segments to quantify both dispersion and distribution of caribou on the calving grounds (D. Johnson, unpubl. data; Poole *et al.,* 2013). To compare the 2006 to 2010 systematic calving distribution (D. Johnson, unpubl. data), we created 90% fixed kernel polygons on the un-weighted distribution of breeding females each year and examined overlap between sequential calving grounds; where percent overlap in polygons = (*Common area in year i and year i+1)/((∑ area year i and year i+1)/2*).

Climate gradients across the calving ground

Russell et al. (2013) used a retroactive spatial climate database to create climate descriptions for the seasonal ranges of circumpolar migratory tundra caribou. The database consisted of 22 "caribou-relevant" climate indicators that covered the period 1979-2011. The actual derivations of these 22 variables are presented in Russell et al. (2013). We used this database to compare climate in the three Ahiak calving ground blocks (see next section for a description of the blocks). We tested for differences in climate variables and decadal trends among the

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blocks using an Analysis of Variance and Duncan's-Waller multiple range tests (SAS, version 9.10). Seasons presented in the analysis were: calving (June), summer (July and August), autumn (September – November), winter (December – March) and spring (April – May).

Queen Maud Gulf calving and rut associations

To examine the relationship between calving and rut associations, we used both individual and population-scale information. The individual scale information was from 74 adult cows fitted with conventional satellite or GPS collars and we used those data to describe the dispersion of individuals and their association. The various projects fitting satellite collars on adult female caribou had different objectives and, with the exception of 2007, all caribou were collared on winter range (Gunn *et al.,* 2000; Gunn & D'Hont, 2002; Gunn *et al.,* 2013). In July 2007, the collaring was conducted on the post-calving range (Johnson & Fleck, 2009). We acquired the data from the Government of Northwest Territories through their Wildlife Management Information System (WMIS). We accessed the calving and rutting locations of caribou cows collared near Baker Lake in 2008 and 2009 from Gebauer et al. (2011; available on the Nunavut Impact Review Board's Public Registry; accessed December 2011). We compiled a database using collared cows with at least one calving location on Queen Maud Gulf coastal calving ground 1996-2010. We also included those cows with a history of calving on the traditional Beverly calving grounds (south of Garry Lakes) but which had shifted to the Queen Maud Gulf coastal calving ground (Nagy *et al.,* 2011; Gunn *et al.,* 2012). Calving date was based on examination of daily movement rates coupled with spatial movements in GIS, such that calving was determined from a rapid drop in daily movement rate (generally to <2 km/day) and localization, followed by a 5-10 day period of reduced movement (Fancy & Whitten, 1991). The rut and winter distributions were indexed from collar locations on 20 October and 1 February each year, respectively (Gunn *et al.,* 2000).

For the population-scale analyses, Poole & Nishi (unpubl. data) had divided the calving ground into three blocks based on a qualitative assessment of caribou density observed during systematic aerial surveys from 2006-10 (GNWT ENR WMIS): Ahiak West (AHW) – from the western boundary of calving as far east as the Armark River (roughly the eastern boundary of the high or medium density zones in the past); Ahiak East (AHE) – from Armark River east to just east of McNaughton Lake; and Ahiak Adelaide (AHAD) – Adelaide Peninsula to the western shore of Chantrey Inlet (Fig. 2). The east-west width of the blocks varied: AHW was 235 km wide; AWE 120 km and AHAD 85 km. We used these three blocks to compile descriptive statistics on the consecutive calving locations to describe inter-annual patterns of calving location fidelity for individual calving cows and distances to rut and winter locations. We tabulated the distances between consecutive annual calving locations to describe the frequency of distance classes between consecutive calving year i to year i + 1. For some analyses, we combined the blocks as two calving associations (see below).

To compare whether cows that calved together were also associated during the rut based on the locations of collared cows, we combined AHE with AHAD to increase sample sizes. This gave us two sets of calving locations which we termed calving associations, the western and central/eastern. First we described the dispersion of the collared cows during the rut relative to each other. For each year, we calculated for the two calving associations and the combined rut locations the mean (average X and Y coordinate) centroid and the mean distances (and standard deviations) from the centroids to the individual caribou locations; the distances be-

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Table 2. Density of caribou in 1986, 1996 and 2007-08 during aerial calving distribution surveys over the Ahiak calving grounds.

Year	Aerial coverage (%)	Survey area (km^2)	Density (caribou/km^2)	Reference
1986	23.2	7,320[a]	1.4	Gunn et al., 2000
1996	5.2	21,901[a]	3.9	Gunn et al., 2000
2006	4.5	25,379[b]	3.1	D. Johnson, unpubl. data
2007	4.6	23,929[b]	3.0	D. Johnson, unpubl. data
2008	6.7	23,696[b]	1.1	D. Johnson, unpubl. data

[a] Stratum area (Gunn *et al.,* 2000).

[b] Approximate size of the 2006, 2007 and 2008 calving areas at peak of calving (D. Johnson, unpubl. data)

tween centroids for the calving associations and combined rut locations were also calculated. Distances calculations were performed using in-house developed programs that use MapInfo Professional libraries (Pitney Bowes Software, Troy, NY).

Our second approach to compare whether cows that calved together were associated during the rut was to determine whether the overlap in the area used by the two rutting associations was due to chance or were in disagreement. To describe the area used, we calculated minimum convex polygons (MCP) buffered with one standard deviation for the rut locations based on the associations of individual cows during calving. Mapping was done in MapInfo Professional software. We compared the two rut MCPs to test if their differences are due to 'chance' or disagreement using the Kappa Index of Agreement (KIA) (http://www.spatialanalysisonline.com/output/). We used Idrisi GIS software (Clark Labs, Worcester, MA) to calculate the KIA for all pairings of the calving associations (by year) and combined rut locations and MCPs of the western and central/eastern calving associations. To judge the strength of the agreement, we used the classification by Landis & Kock (1977) (< 0 – poor; 0 to 0.2 – slight; 0.21 to 0.4 – fair; 0.41 to 0.6 – moderate; 0.61 to 0.8 – substantial; 0.81 to 1.0 – almost perfect).

For the spatial analysis of rut association, we removed three outliers as their rut distribution was highly distant (>400 km) from the other collared cows. We had no way of knowing the reproductive status, physical condition or health of these caribou which are possible reasons for the geographic isolation of single cows (or to the extent they were with other uncollared cows).

Results

Distribution and abundance of caribou calving in the Queen Maud Gulf

Caribou numbers were low in the Queen Maud Gulf coastal area and Adelaide Peninsula in the 1920s and increasing by the 1960s although population estimates were not obtained (Gavin, 1945; Banfield, 1950; Kelsall, 1968; Pelly, 2000; Gunn *et al.,* 2000). The rate of increase between the 1950s and 1980s was qualitative until the first systematic estimates in 1986 and 1996, which estimated that the herd increased 2-3 fold. The mean density of caribou on survey in 1996 was almost three times higher than in 1986 (Table 2), suggesting abundance had increased. Subsequently, during the period 1996–2007, the calving ground sur-

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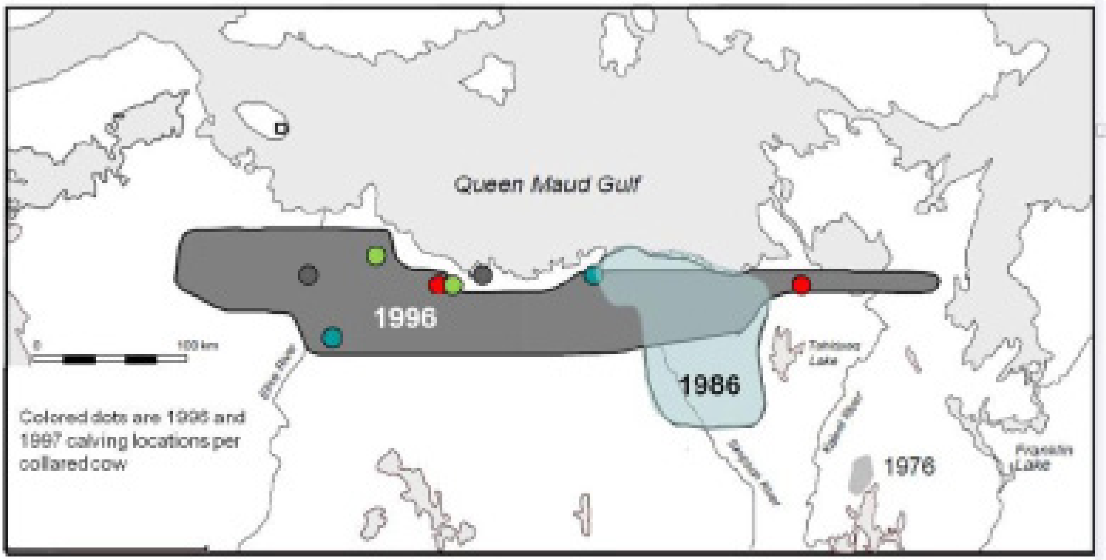

Fig. 3. The approximate extent of the Ahiak herd's calving distribution in June 1986 and 1996 (Gunn *et al.,* 2000), and 1996–97 calving locations from collared cows.

veys indicated no apparent trend in the density of caribou on the calving ground (Table 2). The lower densities in June 2008 may have reflected an unusual year as pregnancy rates were low and not all cows may have reached the calving ground or were later than the timing of the survey (D. Johnson, unpubl. data).

Gavin (1945) describes caribou calving dispersed on the numerous islands and islets along the shallow coast of Queen Maud Gulf. In June 1985 and 1986, cows and newborn calves were seen on the coastal islands (Gunn *et al.,* 2000; A. Gunn, unpubl. field notes). However, gregarious calving was observed on the adjacent mainland coast and during a systematic transect survey in June 1986, calving density was measured and distribution mapped with the western boundary of calving cows being the Simpson River (Gunn *et al.,* 2000).

By June 1995, the distribution of cows and calves extended to west of the Perry River and north of MacAlpine Lake (Gunn, 1996). The June 1995 survey overlapped a narrow survey area south of Kent Peninsula where baseline information on caribou distribution was collected from 1994 to 2002 for the Hope Bay mine project (Calef & Hubert, 2002). In June 1996, east-west systematic transects east of Bathurst Inlet mapped calving distribution east to the coast of Chantrey Inlet (Gunn *et al.,* 2000). The southern boundary of the calving ground was not delineated. Compared to 1986, the 1996 calving distribution had extended east and west of the 1986 distribution and was continuous across the width of the Queen Maud Gulf coastal area from Chantrey Inlet west to the Hope Bay area east of Bathurst Inlet (Gunn *et al.,* 1997; Gunn *et al.,* 2000) (Fig. 3).

Additionally, the basis for assuming that the 1986 calving ground had extended west was Inuit observations of pre-calving cows heading east of Bathurst Inlet (Gunn *et al.,* 2000). The capture sites east of Bathurst Inlet and movements of the collared caribou in April-June 1996 also supported an eastward pre-calving migration toward coastal Queen Maud Gulf. The calving locations for both 1996 and 1997 revealed use of the length of coastal calving grounds between the Ellice and Simpson rivers (Gunn *et al.,* 2000). Between 1996 and 2006,

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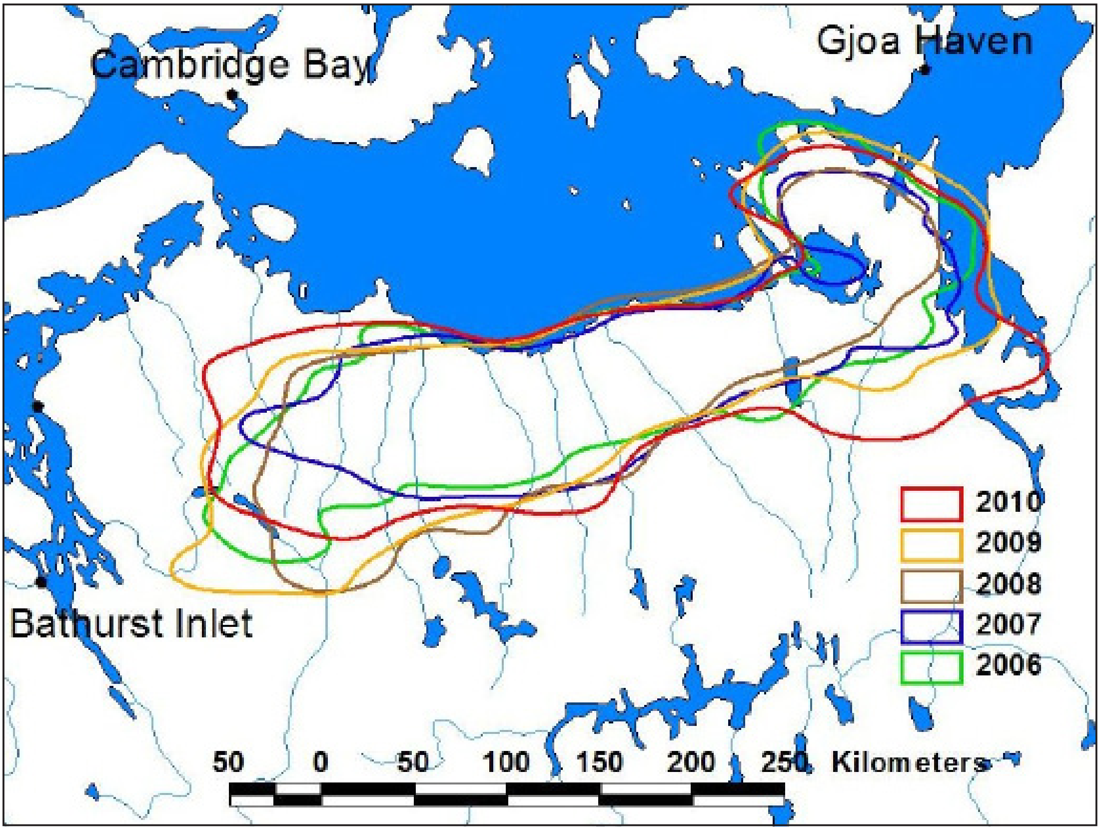

Fig. 4. Distribution of breeding females on the Ahiak calving grounds, 2006-10 (data source was D. Johnson, unpubl. data; Poole *et al.,* 2013).

the western boundary of calving distribution contracted from approximately the area just east of the Hope Bay-Spyder Lake corridor in 1996 to the vicinity of the Ellice River in 2006 (Gunn *et al.,* 2000; D. Johnson, unpubl. data). The comparison of the 2006-10 calving distributions along the Queen Maud Gulf showed an average 82% overlap (range 81–84%) during 2006-10, with changes among years primarily at eastern and western ends rather than changes in width (Fig. 4).

Climate gradients across the calving ground

There was a pattern in both winter and spring snow depth among blocks. In winter the AHE block had consistently highest snow 40.5 ± 2.1 (SE) cm and AHW consistently lowest snow depths (34.6 ± 2.0 cm). For the spring period leading up to calving the AHE block had significantly deeper snow than AHW (41.9 ± 2.7 cm versus 34.2 ± 2.2 cm, respectively) in every decade and higher than AHAD (35.3 ± 1.9 cm) in the 1990s. In the 2000s decade, this difference between AHE and AHW extended into the calving period (Table 3). Snow density in spring was consistently higher in AHE than AHW in all decades, significantly so in the 1980s and 1990s (0.272 ± 0.007 gm•cm-3 versus 0.254 ± 0.008 gm•cm-3, respectively).

If we consider decadal differences (Table 4),

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Table 3. Significant differences for decadal snow depth, daily precipitation and daily temperature (ANOVA and Duncan's-Waller multiple range tests) among blocks based on MERRA climate variables.

Decade	Variable	Season	*P*	F value	Block Differences
1980s	snow depth	spring	0.012	4.58	AHE > AHW
1980s	snow depth	winter	0.008	5.27	AHE > AHW
1980s	snow density	spring	0.06	2.90	AHE > AHW
1980s	mean daily temperature	winter	0.0002	9.50	AHAD > AHE, AHW
1980s	daily precipitation	winter	0.0025	6.62	AHE, AHAD > AHW
1990s	snow depth	spring	0.0003	5.51	AHE > AHAD > AHW
1990s	snow depth	winter	0.0004	9.13	AHE > AHAD > AHW
1990s	snow density	spring	0.06	2.90	AHE > AHW
1990s	mean daily temperature	winter	<0.0001	43.39	AHAD > AHE > AHW
1990s	daily precipitation	winter	<0.0001	12.60	AHE > AHAD > AHW
2000s	snow depth	calving	0.09	2.65	AHE > AHW
2000s	snow depth	spring	0.06	2.95	AHE > AHW
2000s	mean daily temperature	winter	0.0003	9.16	AHAD > AHE > AHW
2000s	daily precipitation	winter	0.01	4.50	AHE > AHW

spring snow depths were consistently higher in the 1990s while the 1980s had the lowest spring snow depths. Spring snow depths were significantly higher in the 1990s compared to the 2000s in AHAD (40.6 ± 2.6 cm versus 35.3 ± 1.9 cm, respectively) and AHE (45.9 ± 2.7 cm versus 38.1 ± 2.0 cm, respectively). For all three blocks, drought index was higher in the 1990s compared to the other 2 decades during the calving (4.6 ± 0.91 versus 2.5 ± 0.46, respectively) and summer (19.3 ± 5.5 versus 9.7 ± 2.4, respectively) seasons. We did find differences in summer precipitation in the AHW and AHE blocks. In the AHE the mean daily precipitation in summer was significantly higher in the 1980s compared to the 2000s (46.6 ± 6.4 cumulative mm. month versus 36.6 ± 3.6, respectively) while the AHW had significantly higher summer precipitation in the 1980s compared to both the 1990s and the 2000s (46.3 ± 6.5 versus 35.1 ± 4.6, respectively). Further during the calving period in AHW the 2000s were the wettest decade, significantly higher than the 1990s and the 1980s (46.6 ± 6.4 versus 36.6 ± 3.6, respectively). Although there was a decadal and spatial pattern in respect to growing degree days (GDD) to July 15th, the relatively high annual variation meant that differences between decades and among blocks were not significant. Comparing decades, the 1990s experienced the highest GDD, while the 2000s were the coolest. Among blocks the AHW was consistently warmer (higher GDD) in every decade while the AHE had the lowest GDD in all decades. Mean GDD to July 15th were 388 ± 94.5 (AHW), 356 ± 76.9 (AHAD) and 345 ± 80.2 (AHE).

Queen Maud Gulf calving and rut associations

Spatial distribution of calving locations

We tested our prediction that 5% or less of the collared breeding females would switch calving locations in subsequent years between the western, central and eastern areas of an annual calving ground. We used 74 individual cows and 157 collar-years for all cows with at least one calving location along the Queen Maud Gulf coastal (Ahiak) calving ground (2001-10). We

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Table 4. Significant differences for snow depth, daily precipitation and daily temperature (ANOVA and Duncan's-Waller multiple range tests) among decades based on MERRA climate variables.

Block	Variable	Season	*P*	F value	Decadal Differences
AHE	drought index	calving	0.008	5.84	1990s > 1980s, 2000s
AHE	drought index	summer	0.01	4.60	1990s > 1980s, 2000s
AHE	snow depth	spring	0.0009	5.01	1990s > 2000s
AHE	snow depth	winter	0.01	4.99	1990s > 1980s, 2000s
AHE	snow density	spring	0.09	2.45	1990s > 2000s, 1980s
AHE	snow density	winter	0.02	3.96	1990s, 2000s > 1980s
AHE	mean daily precipitation	summer	0.05	3.01	1980s > 1990s
AHE	mean daily precipitation	winter	0.01	4.84	1990s > 1980s, 2000s
AHAD	drought index	calving	0.02	4.54	1990s > 2000s
AHAD	drought index	summer	0.05	3.16	1990s > 2000s
AHAD	snow depth	spring	0.05	3.10	1990s > 2000s
AHAD	snow depth	winter	0.02	4.44	1990s > 2000s
AHAD	snow density	winter	0.03	3.72	1990s > 1980s
AHW	drought index	calving	0.02	4.28	1990s > 2000s
AHW	drought index	summer	0.0004	8.90	1990s > 2000s, 1980s
AHW	snow density	spring	0.01	4.40	2000s, 1990s > 1980s
AHW	snow density	winter	0.009	4.95	2000s > 1990s, 1980s
AHW	mean daily precipitation	calving	0.03	3.78	2000s > 1990s, 1980s
AHW	mean daily precipitation	summer	0.009	5.15	1980s > 2000s, 1990s

excluded six cows (8.1% - 6/74 cows; 5.7% - 6/105 collar-years) which calved on the Ahiak calving ground and switched to either the north east mainland (NEM) or Bathurst (BA) calving ground (1 cow AHW – BA – BA; one cow AHE – AHE – NEM – AHAD – AHE; two cows AHAD – NEM and one cow NEM – AHE). However, we included the eight cows whose initial known calving ground was the traditional Beverly ground and which subsequently calved on the Ahiak calving ground for at least 1 year. Agnico-Eagle Mines Limited and Government of Nunavut (M. Campbell, pers. comm.) deployed nine collars near Baker Lake, Nunavut in May 2008 and together with support from AREVA Ltd., deployed 21 collars on the tundra north of Baker Lake were in November 2009 (Gebauer *et al.,* 2011). Four collared cows calved on Adelaide Peninsula in 2008; two in 2009 and five in 2010 calved south of Adelaide Peninsula (Gebauer *et al.,* 2011). The other cows calved northeast of Chantrey Inlet within previously recorded calving distributions (Gunn & Fournier, 2000a; b).

We had only 1 year of calving locations for 18 cows on the Ahiak herd's calving ground and 15 of those (83%) calved within AHW. Of the 49 cows with 2 or more years of calving locations, 27 cows (55%) did not switch among the three blocks covering the length of the Ahiak calving ground and 24 (89%) of those cows calved in AHW. Conversely, 22 of 49 cows (45%) with more than 1 year's calving locations switched among blocks. Of these 22 cows that switched blocks, 13 of 14 (93%) cows with their initial calving location on the Ahiak calving ground calved 1 year in AHW then shifted to AHE or AHAD. Most shifts were west to east but two

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cows did shift from AHE or AHAD to AHW. Eight cows which initially calved on the traditional Beverly calving ground switched to the Ahiak calving ground: five of those cows with 2 or more years calving locations on the Ahiak calving ground switched among the blocks.

To test whether individual breeding females would show inter-annual fidelity to discrete areas within annual calving grounds observed in consecutive years, we examined the frequency of distance classes between consecutive calving year 1 to year 2; 72 paired calving locations. We restricted the period to 2006-10 as annual sample sizes were largest. Most (82%) were 25-150 km apart and the 10% tail end of the frequencies were separated by >150 km, which suggests use of the extent of the calving ground (Fig. 5).

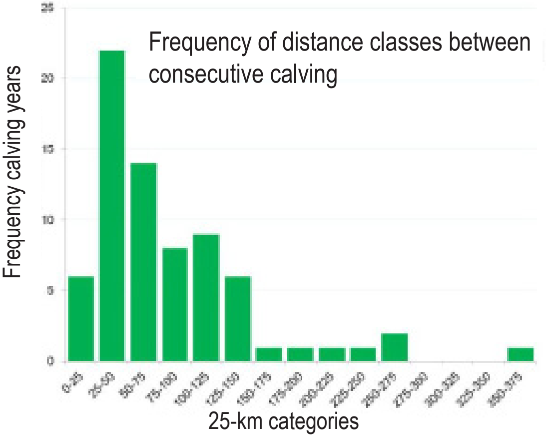

Fig. 5. Frequency classes based on distances between consecutive annual calving locations of satellite-collared breeding females, Ahiak herd, 1996–2010.

<u>Calving to rut distances</u>

The calving to rut distances varied but were not significantly different among AHW, AHE, and AHAD for 2006-10 (PROC GLM, F = 0.46, df = 2,120, $P = 0.63$; Table 5). The mean distances were 411 ± 14.6 km ($n = 91$) for the cows calving in AHW; 429 ± 28.2 km ($n = 18$) in AHE, and 379 ± 56.1 km ($n = 14$) for AHAD calving.

Table 5. Mean (standard errors) straight-line distances between calving and rut locations for collared cows that calved in either the Ahiak west (AHW), Ahiak east (AHE) and Ahiak Adelaide Peninsula (AHAD), blocks of the Queen Maud Gulf coastal calving area, 1996-2010.

	AHW			AHE			AHAD		
Year	$\overline{x}$ km	SE	n	$\overline{x}$ km	SE	n	$\overline{x}$ km	SE	n
1996	380	26.5	2	438		1			
1997	511	60.6	3						
2001	311	52.0	4						
2002	318	103.0	4	449	41.0	2			
2003	228		1				152		1
2004	644		1						
2005	265	88.7	5				412		1
2006	439	40.2	10	416	70.9	3			
2007	548	46.6	10	568	61.7	3	676		1
2008	359	23.7	19	310	58.0	3	153	41.3	4
2009	481	19.9	20	431		1	527	67.7	4
2010	339	11.1	12	412	56.6	5	541	0.1	2
Total	411	14.6	91	429	28.2	18	379	56.1	14

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Table 6. Mean distances (standard deviation) between individual rut locations and centroids for western and central/eastern calving association.

	Western calving association			Central/eastern calving association		
Year	$\bar{x}$ km	SE	*n*	$\bar{x}$ km	SE	*n*
2001	183	30.2	3	nda[a]	nda	
2002	200	44.1	4	nda	nda	
2005	138	38.4	4	nda	nda	
2006	137	28.6	10	177	37.2	4
2007	72	12.6	9	58	10.4	3
2008	100	20.0	20	141	38.2	6
2009	150	12.3	20	143	15.3	5
2010	64	10.4	12	138	21.7	10

[a] nda = no data available.

<u>Rut distribution relative to calving associations</u>

We predicted that cows that calved together on an annual calving ground (at the scale of the east or west halves of the calving ground), will not solely associate together during the subsequent fall rut. Thus, within a year, collared breeding females that calved within i) the western portion of the calving ground, or ii) the combined central/eastern portions would not be associated with other cows that calved within the same area of the coastal calving ground during the subsequent fall rut (temporal index is 20 October) at a rate greater than would be expected by chance (*i.e.*, >50% probability). Our results were that the degree of dispersion of the collared cows during the rut (20 October) as measured by the mean distance of individual locations relative to the centroid for the two calving associations did not differ annually between the two calving associations (western: $\bar{x}$ = 118 ± 8.8 SE; central/eastern: $\bar{x}$ = 136 ± 14.3; t = 1.98, df = 108, P = 0.29; Table 6; Fig. 6). In 2007 the dispersion was less than the other years (individual locations were more tightly clustered around the centroid) for both calving associations. In 2010, the individual locations were more clustered for cows from the western calving association).

The distribution of the rut varied between years based on the geographic location and respective position of the centroids of western and central/eastern calving associations to all rut locations (Fig. 6). The distribution suggested that the centroids of western calving associations during the rut are shifted to the southwest and central/eastern calving associations to the northeast (centres of activity ranging 117–276 km apart), except in 2007 when the cows from both the east and west calving associations had least dispersion (centroids ~32 km) and were furthest to the southwest (Fig. 6, Table 7). The straight-line distances between the centroids of the rut distribution based on the two calving associations varied among years (33 – 276 km). The greatest distance between the centroids was in 2008 (276 km) which was likely an atypical year as pregnancy rates were low during 2007-08 winter (D. Johnson, unpubl. data). The distance was least in 2007 (33 km) compared to 202 km (2006), 138 km (2009) and 117 km (2010).

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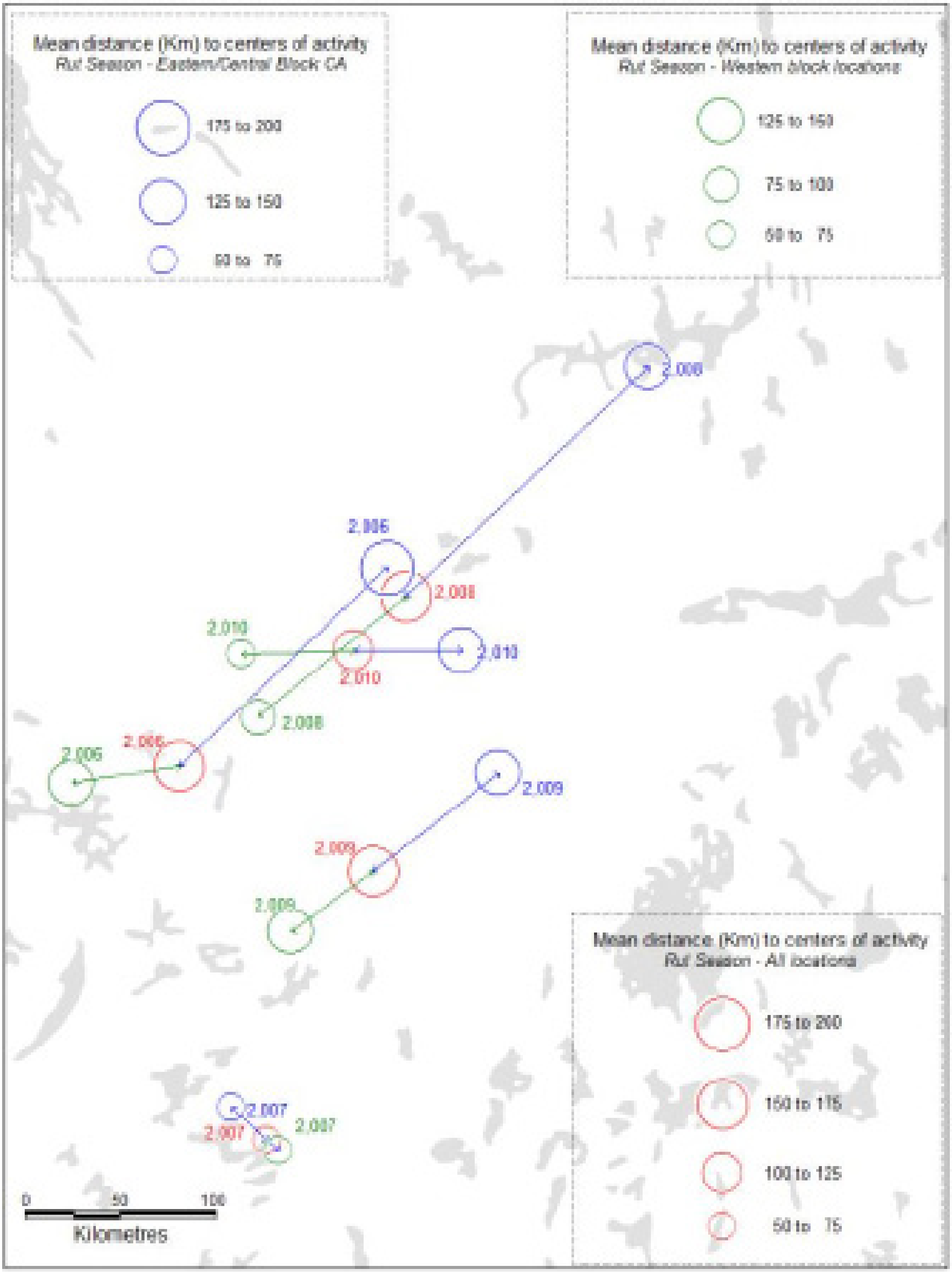

Fig. 6. Location and mean distance between centroids for rutting locations based on western, eastern/central and combined calving associations, 2006-10.

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Table 7. Kappa Index of Agreement calculated for Minimum Convex Polygons (MCP) buffered with 1 standard deviation of distances from centres of activity to constituent locations, western block calving areas, eastern and central block calving areas, and all calving areas (<0–poor; 0 to 0.2 –slight; 0.21 to 0.4 – fair; 0.41 to 0.6 – moderate; 0.61 to 0.8 – substantial; 0.81 to 1.0 – almost perfect).

	Kappa Index of Agreement		
Year	MCP of AHW calving as reference	MCP of AHE/AHAD calving as reference	Overall Kappa
2006	0.19	0.32	0.24
2007	0.22	0.97	0.36
2008	0.00	0.00	0.00
2009	0.31	0.74	0.43
2010	0.57	0.14	0.22

Between years, cows from the two calving associations overlapped to varying degrees during the rut (2006-10; Fig. 7, Table 7). In 2007 and 2009, the agreement between the two calving associations and rut overlap was high to moderate suggesting that cows which calved together were together (in closer association) during the rut. However, the agreement was slight in 2008 and fair in 2010 (Table 7).

Calving distribution relative to the tree-line

To describe the pre-calving migration distance travelled across tundra relative to tree-line, we measured the distance from calving locations to the closest point on both the northern and southern edges of forest-tundra biome (Timoney *et al.,* 1992; Payette *et al.,* 2001). The mean distances differed significantly among calving blocks (Table 8; PROC GLM, F > 43.0, df = 2,146, $P < 0.0001$; Duncan's multiple range test, $P < 0.05$). For both the distance to northern and southern edges of the forest-tundra biome (Table 8), caribou calving in the western part of the Ahiak calving ground (AHW) were closer than caribou from the eastern portion (AHE), which was closer than those calving locations on the Adelaide Peninsula (AHAD). Most distances to the northern edge of tree-line were to the tongue of the forest-tundra biome that follows the Thelon River north to Aberdeen Lake (Fig. 1). Caribou that calved on the Adelaide Peninsula would have travelled an average 31% greater distance if they had wintered within the boreal forest compared with caribou that calving in the AHW calving block.

Winter distribution relative to the tree-line

Caribou wintered mostly on the tundra and forest-tundra biome. In total, 57% of February locations were on tundra; 24 % in forest-tundra biome, and 18% of locations were in the boreal forest (south of forest-tundra biome). The percentages changed with the destination of pre-calving migration as 52%, 64% and 84% of the cows calving in AHW, AHE, and AHAD, respectively, wintered on the tundra. For caribou wintering in the boreal forest, 21%; 14% and 0% of the caribou returned to calve in AHW,

Table 8. Distance (km) from calving locations within 3 calving blocks on the Ahiak calving ground, 1997-2010, to the north (N) and south (S) of forest – tundra biome (Timoney *et al,*. 1992, Payette *et al.,* 2001).

		Dist. to N edge of tree-line		Dist. to S edge of tree-line	
Calving block	*n*	$\bar{x}$ km	SE	$\bar{x}$ km	SE
AHW	107	310	2.5	588	3.4
AHE	19	336	3.4	687	5.5
AHAD	23	366	7.9	761	7.0

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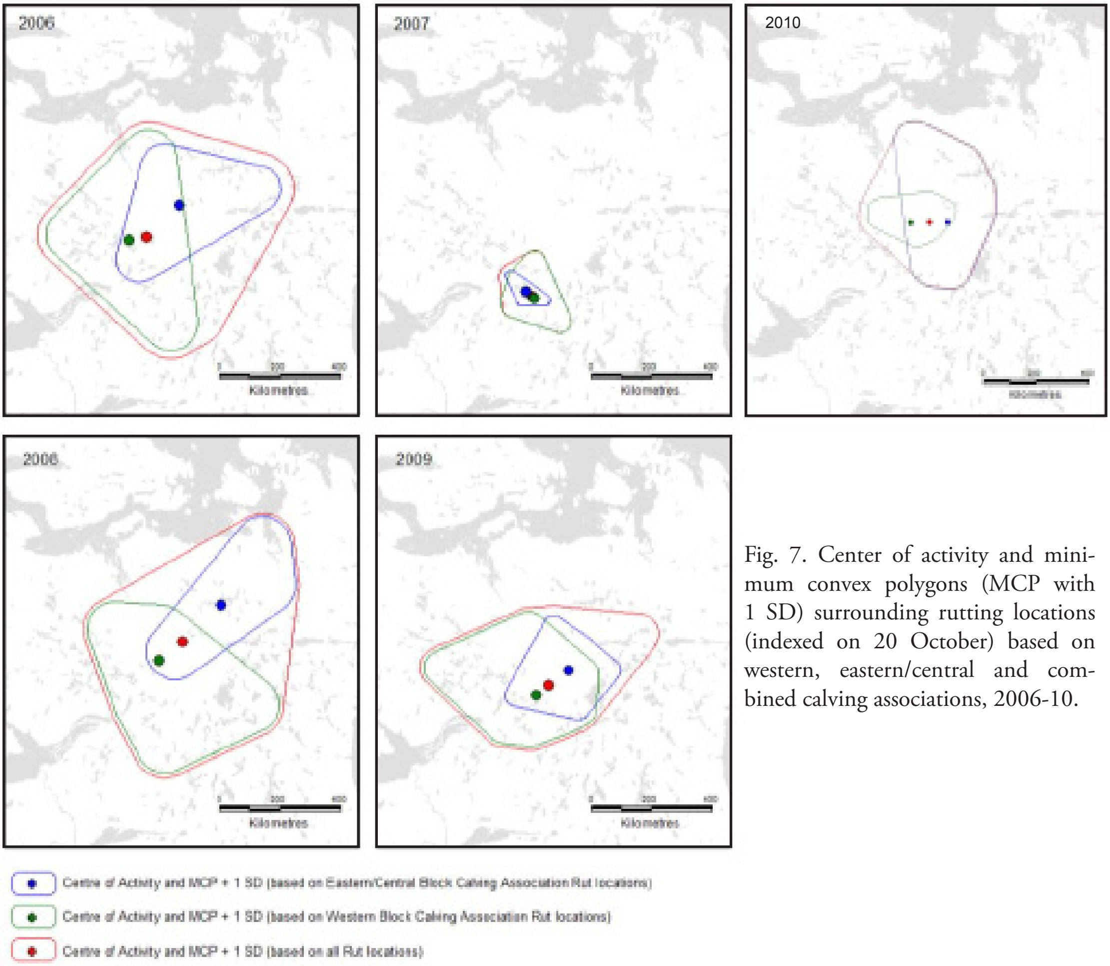

Fig. 7. Center of activity and minimum convex polygons (MCP with 1 SD) surrounding rutting locations (indexed on 20 October) based on western, eastern/central and combined calving associations, 2006-10.

AHE, and AHAD, respectively. The pre-calving migration straight-line distance (distance between winter location and calving) differed among calving blocks (PROC GLM, $F = 3.17$, df = 2.95, $P = 0.047$) and was similar (Duncan's multiple range test, $P < 0.05$) for AHW (525 ± 17.4 km; $n = 75$) and AHE (513 ± 60 km; $n = 14$), but significantly shorter for AHAD (397 ± 32.7 km; $n = 11$) (Table 9). Individual cows did not show high fidelity to wintering within tundra, tree-line, or taiga. Nearly three quarters (73%) of cows with ≥2 years of wintering locations switched among blocks ($n = 33$). Similarly, 68% ($n = 47$) sequential pairs of wintering areas switched between years.

Population-scale: Calving distribution based on 2006-10 calving ground surveys

To test our prediction that the distribution of calving cows would be discontinuous across the calving ground, we used the 2006-10 aerial systematic surveys with transects spaced at 10 or 20 km intervals (D. Johnson, unpubl. data; Poole *et al.*, 2013). We examined for a pattern of discontinuity along the east-west axis in the distribution of breeding females and newborn calves (measured at a grid scale interval of 10 km). The distribution data do not reveal any obvious spatial breaks in the distribution of cows and calves along the east-west axis of the coastal calving area. There were no north-south tran-

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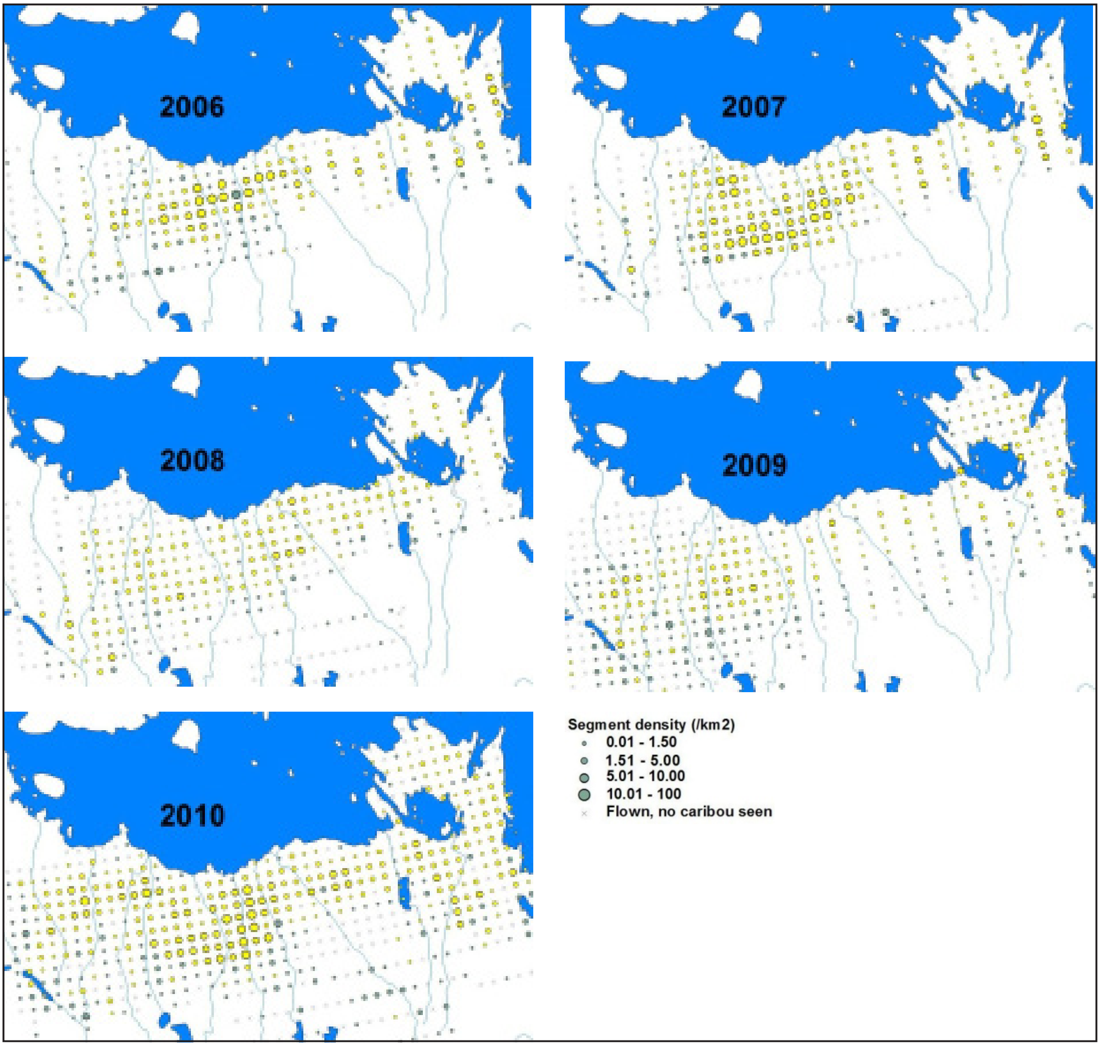

Fig. 8. Density of caribou observed by 10-km segment, Ahiak calving ground distribution surveys, 2006-10. Yellow circles denote density of 1+-year-old caribou where breeding females were present within a segment, regardless of the proportion of non-breeders. Grey circles are density of non-breeders where no breeders present within that segment. Crosses are segments flown but no caribou observed. Scale and graduated symbols constant among years.

sects with no breeding cows and/or calves, or only bulls and juveniles (Fig. 8).

Discussion

Changing abundance and geography (the long relatively straight coastline) influenced the dispersion and distribution of the Ahiak herd's calving. When abundance was low, caribou calved dispersed across the many islands along the Queen Maud Gulf coast. As abundance increased by the mid-1980s through mid-1990s, calving shifted to gregarious calving on a long narrow coastal calving ground. The main elongation of the calving ground was between 1986 and 1995 – a period when densities on the calving ground increased three-fold. The tree-line shifts south as width of the Hudson Bay coastal plain increases, and its orientation relative to

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Table 9. Mean (standard errors) for straight-line distances between calving and winter locations for the Ahiak west (AHW), east (AHE) and Adelaide Peninsula (AHAD), 1997-2010.

	AHW			AHE			AHAD		
Year	$\bar{x}$ km	SE	*n*	$\bar{x}$ km	SE	*n*	$\bar{x}$ km	SE	*n*
1997	324	42.1	3						
2001	609		1						
2002	767		1	509	151.7	2			
2003	519	164.5	2				492		1
2004	337		1				294		1
2005	812		1						
2006	514	73.4	2	424	290.9	2	618		1
2007	482	24.8	10	613	113.9	3	414		1
2008	639	29.1	13	550		1			
2009	433	25.7	22	280		1	338	32.0	5
2010	596	31.3	19	529	112.2	5	429	66.2	2

the elongated calving ground increased the likelihood that cows calving on the eastern part had wintered on the tundra. However, individual cows annually varied as to whether they wintered in the boreal forest or tundra.

We did not find support for our four predictions about the use patterns of the calving grounds at the individual scale (based on satellite-collared cows) and at the population-scale (using information from aerial surveys of calving distribution). Thus our hypothesis (the Ahiak calving grounds are comprised of two or more calving sub-populations) was not supported. We had projected that the climate gradients across the elongated calving ground and its location relative to whether cows were more likely to winter on the tundra or boreal forest would affect survival and productivity and lead to sub-population structure.

At the population scale, we found no evidence that the distribution of calving cows or non-breeders was discontinuous in any one year although there were variations in density. For example, Poole et al. (2013) applied an Inverse Distance Weighted (IDW) interpolation to map the spatial pattern of density clumping using 2007 (Fig. 9).

The areas of higher density of breeding cows were connected by areas with lower density of cows and calves which coincides with the area of deeper snow in winter and spring. This pattern of spatial variation in the high densities is similar to, for example the Central Arctic herd, which has two areas of higher calving densities linked by areas of lower density and the cows and calves mingle during the other seasons of the year (Arthur *et al.,* 2009).

At the individual scale of satellite-collared cows, while most collared cows used the western third of the calving ground, almost half the individual cows shifted their annual calving locations within the length of the calving ground. Satellite-collared cows annually varied in the degree to which they associated during the rut and there was no clear-cut pattern of cows calving in one half of the calving ground remaining as a consistent (inter-annual) association during the rut. The cows mainly wintered on

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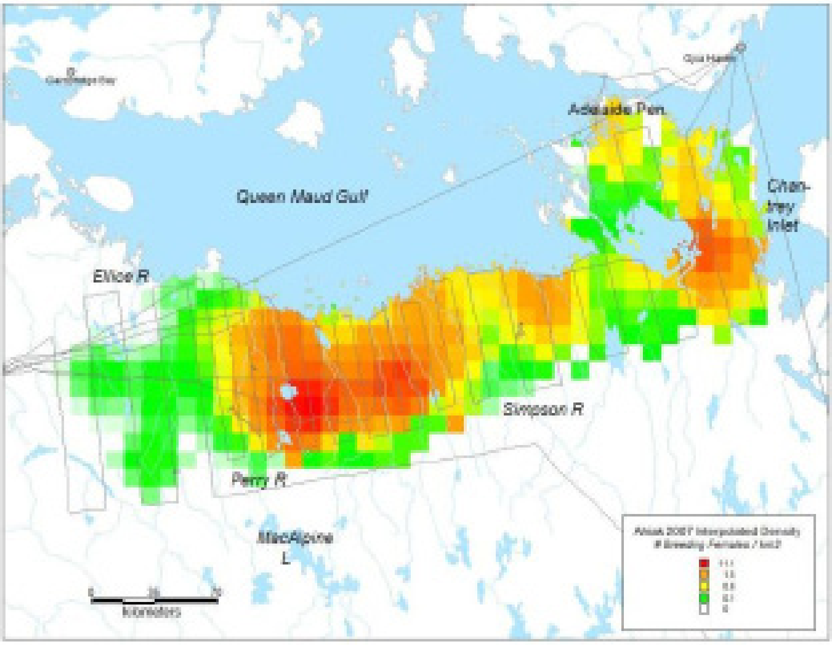

Fig.9. Distribution of breeding female caribou observed during the Ahiak survey flown in June 2007. Relative density conducted using Inverse Distance Weighting (IDW) mapping interpolation using a 10 x 10 km pixel, exponent of 2, and a 15 km search radius (Poole *et al.,* 2013: Fig. 23).

the tundra and within the forest-tundra biome, which partly reflects the geographical extent of the tundra. Individual cows varied among years as to whether they wintered in the forest-tundra biome or above tree-line on the tundra.

We used three methods to estimate calving relative to rut associations. The overlap of the individual rut locations have a stronger pattern of clustering of the calving associations during the rut than the distances between the centers of the rut distribution. This is because MCPs do not consider the dispersion of constituent caribou locations that lie within them (Nilsen *et al.,* 2008), while the mean distances that form the centroids are sensitive to the dispersion of the individual locations. The dispersion of individual locations likely has both process (biological) and measurement error (sample size). Inter-annual comparisons are limited because the membership of the calving associations varied among years (*i.e.*, the scale of calving spatial fidelity was not at the block scale). The overall results suggest that for 2006–10, cows that calve together also rut together. Low sample size and uncertainty about how the collared cows represent the seasonal distribution of all caribou at finer geographical scales are possible limitations of our conclusions.

The level of information available on the Ahiak herd over time varied, with the least amount of information for the earlier years. The frequency of aerial surveys of the coastal calving area to describe the calving distribution and abundance of breeding females was uneven over time. Similarly, the annual sample of collared cows occurred after the time when abundance was increasing (1986-96) and was low during 2001-06, which weakens inferences that can be drawn from the telemetry data. We also acknowledge that we have described the caribou dispersion and distribution over a 25 year period when abundance of the Ahiak and neighbouring herds changed.

Changing abundance in neighbouring herds may play a role in the likelihood of sub-population structure. An extreme decline in the neighbouring Beverly herd (J. Adamczewski, unpubl. data) may have caused a loss of gregarious calving on the traditional Beverly range, and subsequent movement of cows to the Ahiak herd although documentation of this

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through satellite-collared cows only started in 2007 (Gunn *et al.,* 2012). Alternatively, Nagy et al. (2011: Fig. 3, p. 234) proposed that the Queen Maud Gulf (*i.e.*, Ahiak) herd's long narrow calving ground could be the consequence of adjacent calving by two different sub-populations: the Beverly herd shifting from its traditional calving ground in the mid-1990s to the western part of Queen Maud Gulf and the caribou calving on the eastern Queen Maud Gulf coast in the 1980s. However, we could not infer sub-population structure for the coastal calving area based on the currently available evidence.

Another possibility for both a historical influence on the Ahiak calving ground and future sub-population structure is the caribou calving on Adelaide Peninsula. Until about the 1920s and 1930s, caribou migrated across Adelaide Peninsula in May and crossed to King William Island where they calved and summered before returning to Adelaide Peninsula in the fall (summarized in Appendix G of Gunn *et al.,* 2000). In June 1976, a few cow-calf pairs were counted south of Adelaide Peninsula (although the flight-lines did not extend further west; Fischer *et al.,* 1977). It is speculative whether the 1976 calving distribution shifted northwest (to the area mapped as calving in 1986), northeast of Chantrey Inlet, or disappeared. The 1976 calving area was surveyed in 1986 and no caribou were seen (Gunn & Fournier, 2000a). The possibility that calving shifted northeast of Chantrey Inlet is suggested from observations of calving caribou recorded in 1975, 1985, 1986, 1989 and 1991 (Gunn & Fournier, 2000a) and from seasonal movements of satellite collared cows in 1991-93 (Gunn & Fournier, 2000b). The four satellite-collared cows in 1991-93 showed that caribou wintering south of the Boothia Peninsula toward Baker Lake would calve northeast of Chantrey Inlet (and not Adelaide Peninsula) (Gunn & Fournier, 2000b).

The caribou which calved on Adelaide Peninsula mostly wintered on the tundra and reduced the length of their pre-calving migration by just over 100 km relative to the caribou which calved west of Adelaide Peninsula; caribou calving west of Adelaide Peninsula were more likely to winter within the closer forest and forest-tundra biome. We suggest that the shorter pre-calving migration distance for caribou that calved on Adelaide Peninsula may be from an energetic trade-off between the costs of foraging on the tundra, travel, and predation risk (Couturier *et al.,* 2010).

Currently, the high proportion of cows shifting calving locations along the length of the calving ground among years and the switching of cows wintering on the tundra or taiga/forest-tundra biome suggests a high degree of plasticity – the ability to change biology or behavior to respond to changes in the environment – in individual behaviour within a population (for example, Couturier *et al.,* 2010). However, variance in inter-annual selection of calving and wintering areas by individual adult females may be reduced if changing environmental conditions increase energetic costs and reduce fitness of cows and calves. While we could not infer population sub-structure for the Ahiak herd from the currently available evidence, it is not a future impossibility given the Ahiak herd's particular geographical attributes – the long narrow calving ground and the southeast tilt and width of the tree-line.

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ing programs of the Beverly and Ahiak herds. We also acknowledge Mitch Campbell (Government of Nunavut, Arviat, NU) who led the 2009-10 collaring of caribou near Baker Lake. We thank Marco Festa-Bianchet and an anonymous reviewer for their helpful comments.

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