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A conceptual model for migratory tundra caribou to explain and predict why shifts in spatial fidelity of breeding cows to their calving grounds are infrequent

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Abstract: Calving grounds of migratory tundra caribou (*Rangifer tarandus)* have two prominent characteristics. Firstly, the cows are gregarious, and secondly, the annual calving grounds spatially overlap in consecutive years (spatial fidelity). The location of consecutive annual calving grounds can gradually shift (either rotationally or un-directional) or more rarely, abruptly (non-overlapping). We propose a mechanism to interpret and predict changes in spatial fidelity. We propose that fidelity is linked to gregariousness with its advantages for individual fitness (positive density-dependence). Our argument is based on a curvilinear relationship between the density of cows on the calving ground (which we use to index gregariousness) and spatial fidelity. Extremely high or low densities are two different mechanisms which can lead to reduced spatial fidelity to annual calving grounds and reflect the caribou's adaptive use of its calving ranges.

Key words: calving grounds; gregariousness; spatial fidelity; mechanisms; *Rangifer tarandus*.

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Introduction

Bergerud *et al.* (2008) reminds us about caribou's (*Rangifer tarandus)* adaptable use of space. Our paper is to consider the adaptable use of calving grounds by migratory tundra caribou. The starting point is that calving grounds have two conspicuous characteristics. Firstly, the cows are highly gregarious and correspondingly, animal densities on the calving grounds can be high (e.g., Skoog, 1968; Bergerud *et al.,* 2008). As an example, density on the calving ground of the Bathurst herd in northern Canada in 1984 was 203 caribou/km^2 (photographic estimate) (Sutherland & Gunn, 1996).

The second characteristic is that there is a high degree of geographic overlap between annual calving grounds, as most information supports the return of breeding cows to the calving ground where they previously calved (for example, Skoog, 1968; Cameron *et al.,* 1986; Gunn & Miller, 1986; Schaefer et al., 2000; Bergerud *et al.,* 2008). For the Bathurst herd, Gunn *et al.* (2008) reported that the spatial overlap for the 24 calving distributions mapped during the 42 years of monitoring averaged 43% (± 3.8% SE). To emphasise that the cow's annual return to a calving ground is not just a return to a specific geographic place, in this paper we refer to spatial fidelity as the tendency of the cows to return to the general area that they previously used rather than a specific site.

Information on the geographic locations of calving grounds has increased since the 1960s and 1970s through the cumulative number of aerial surveys. As a result, changes in the geographic locations of area used for calving were documented, which led to questioning the concept of fidelity to these areas (e.g., Davis *et al.,* 1986; Valkenburg & Davis, 1986; Hinkes *et al.,* 2005). The amount of overlap between annual calving grounds varies and the annual differences in overlap of consecutive calving distributions can show a consistent direction (Gunn *et al.,* 2007, 2008). For example, Bergerud *et al.* (2008) describe directional shifts and their reversal for the Leaf and George River herds between 1973 and 1993 relative to changes in herd size. Without a strongly directional shift in most years, annual calving grounds tend to have a cumulative clumped distribution. For example, the Qamanirjuaq calving grounds between 1979 and 2004 mostly overlapped with no consistent directional shifts, which is a similar pattern to the Beverly herd for 1978-1994 (Gunn *et al.,* 2007). The Bathurst herd also had periods (1966-1984 and 1996-2007) when the annual calving grounds were relatively clumped. However, the herd also had a period of directional shift between 1984 and 1996 (Gunn *et al.,* 2008).

Although infrequent, directional shifts in spatial fidelity have resulted in one herd's calving ground overlapping neighbouring herd's calving grounds (which is different in degree from individual cows switching geographically discrete calving grounds). The two reported instances are from the Alaskan mountains, where the calving grounds of two large caribou herds shifted <25 km and engulfed the dispersed calving sites of two small herds (Davis *et al.,* 1986; Valkenburg *et al.,* 2003; Hinkes *et al.,* 2005).

The widespread use of telemetry is producing an increasing amount of information at both the herd and individual levels. The proportion of individual cows switching to neighbouring calving grounds vary between herds from the documented 0.5% over 9 years for the Mentasta and Nelchina herds in Alaska (Lieb *et al.,* 1994), to annual rates of 6.6% and 0.9% for the George River and Leaf River herds, respectively, between 1986 and 2003 (Boulet *et al.,* 2007). Proportions of cows switching to neighbouring calving grounds vary within a herd, which appears to be the case for the switching of individual cows between the Beverly and neighbouring Ahiak herd (this paper; Nagy *et al.*, 2011).

Our point is not, however, to simply catalogue historical variations in the use of calving grounds, but to search for underlying mechanisms to describe the adaptable use of space by barren-ground or migratory tundra caribou. As we learn more about the use of space relative to increasing and decreasing phases of population abundance (Bergerud *et al.,* 2008), we now have the opportunity to explore underlying mechanisms and concepts so we can have predictive insights into changes in calving ground use.

Davis *et al.* (1986) commented on the lack of a conceptual model of caribou socio-ecology to explain fidelity to calving grounds, among other aspects of caribou spatial dynamics. However, they offered no suggestions and there have been no concerted efforts to examine the relationship between the two characteristics of calving grounds (gregariousness and spatial fidelity) and how they relate to changes in spatial fidelity. In this paper, we propose a conceptual model based on a relationship between gregarious calving and spatial fidelity relative to the individual fitness of breeding caribou cows in raising a calf.

Proposed conceptual model

Our conceptual model is about the relationship between animal density on the calving grounds and the animal's fidelity to these areas. We consider density of breeding females on an annual calving ground to be an index of gregariousness. Density is usually measured through aerial transect surveys during calving. We define spatial fidelity as the distance between the centroids of the annual calving ground delineated at the peak of calving (based on definitions in Russell *et al.,* 2002) between any two consecutive years.

We propose a curvilinear relationship between density of caribou at calving and annual spatial fidelity to a herd's calving ground (Fig. 1). We propose that extremely high or low densities are two different mechanisms that trigger a change in spatial fidelity. We also propose that the underlying mechanism for the relationship depends on the advantages and disadvantages of gregarious behaviour to individual fitness of breeding females and their calves.

We used average density (numbers of caribou/km^2) of successive annual calving grounds as an index to gregariousness (based on estimated density measured during calving ground surveys). We are not using density-dependence in the sense of population dynamics – the relationship between density and rate of population increase (sensu Krebs, 2002). Individual fitness initially increases with density (positive density-dependence, also termed inverse density-dependence) (left hand side of Fig. 1). The decrease in individual fitness when conspecific density decreases is also known as an Allee effect (Stephens & Sutherland, 1999) and is often seen as a shortage of interactions among conspecifics at low density (Courchamp *et al.,* 1999).

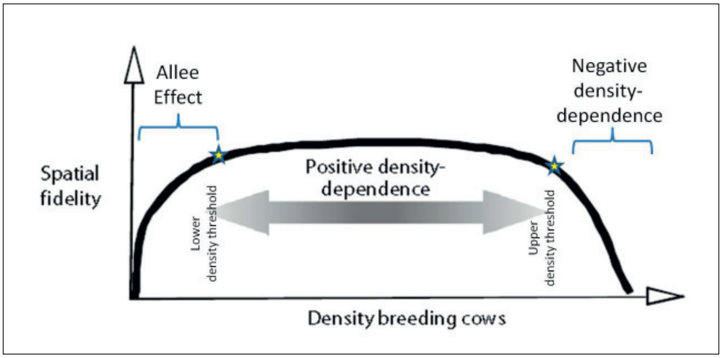

Fig. 1. Proposed curvilinear relationship between spatial fidelity and density of caribou on the calving ground.

Individual fitness increases with conspecific density through several mechanisms. Conventionally for caribou, predator-swamping is considered to be an advantage of gregarious calving (Bergerud *et al.,* 2008). McLellen *et al.* (2010) describe a relationship between population density, group size and predation rates for mountain caribou. Increased foraging is likely through reduced vigilance (Ims, 1990; Roberts, 1996; Childress & Lung, 2003; Mooring *et al.,* 2004) and through information from conspecifics' foraging. The cues that conspecifics learn from their neighbours about reproductive success, predators, and resources is termed 'public information' (Danchin *et al.,* 1998; Doligez *et al.,* 2003; 2004; Donahue, 2006; Boulinier *et al.,* 2008).

The Bathurst and Beverly herds are two herds where information on both the location of calving grounds and numbers of caribou has been monitored since the 1970s. For breeding cows on the calving grounds of at least the Bathurst and Beverly herds, as herd size increased, densities on the calving grounds also increased (Sutherland & Gunn, 1996; Gunn & Sutherland, 1997). Our conceptual model proposes that at some threshold, positive density-dependence shifts to negative density-dependence (right hand side of Fig. 1). We specify these two herds as we did not find a relationship between the size of the calving ground and population size in other herds (unpubl. data). By comparison for the George River herd in northern Quebec and Labrador, the calving grounds have changed in area relative to the number of breeding cows (Bergerud *et al.,* 2008; J. Taillon, pers. comm., 2010).

The simultaneous presence of positive and negative density-dependence was demonstrated for nest site fidelity and fledging success in a gregariously nesting sea bird colony (Kim *et al.,* 2009). For migratory tundra caribou, we suggest positive and negative density-dependence effects on individual fitness are expressed along a continuum of density values. At some threshold, negative density-dependence predominates and individual cows change their behaviour. Negative density-dependence is usually thought of as competition for forage but may also include increased risk of parasitism. For example, gregariousness was a risk factor for parasitism in red deer (*Cervus elaphus*; Vicente *et al.,* 2006). The risk of parasitism may increase as density (gregariousness) on the calving grounds increases. The peri-parturient rise in gastro-intestinal nematode egg output caused Folstad *et al.* (1991) to predict that calving grounds "…might develop into transmission foci for parasites, where females and their susceptible calves would experience intense parasitic transmission." As caribou density increases, so does the density of fecal pellets and the risk of exposure to parasites (Folstad *et al.,* 1991).

This conceptual curvilinear relationship between density (gregariousness) and spatial fidelity on the calving ground approximates a 'flattened inverse U' with a steep portion at extremely high or low densities (Fig. 1). From this conceptual model, we suggest that fidelity to a traditional calving ground will be reduced at extremely high or low densities.

At extremely high densities, positive density-dependence shifts to negative. One possible mechanism for this could be forage competition, which causes cows to congregate in areas not recently used for calving (higher forage biomass and a lower risk of parasite exposure). The second possible mechanism for changes in spatial fidelity is when densities are so low that positive dependence breaks down—there are no longer gains to individual fitness as there are too few individuals. For example, we predict that calf survival would decrease, which was the case in 2007 as calf-cow ratios on the Beverly traditional calving ground were low (Johnson *et al.,* in press). Consequently, cows will shift to neighbouring calving grounds to maintain conspecific attraction, especially if cows have overlapped on the winter range or during pre-calving migration.

The locations of the Bathurst and Beverly herd's calving grounds have been mapped since the 1970s. For the Beverly herd, calving overlapped within a traditional calving ground for all 15 years between 1978 and 2002 when calving distribution was mapped during aerial surveys (Gunn *et al.,* 2007). Peak herd size was in 1994 when densities on the calving ground were visually estimated at 13.5 caribou/km^2.

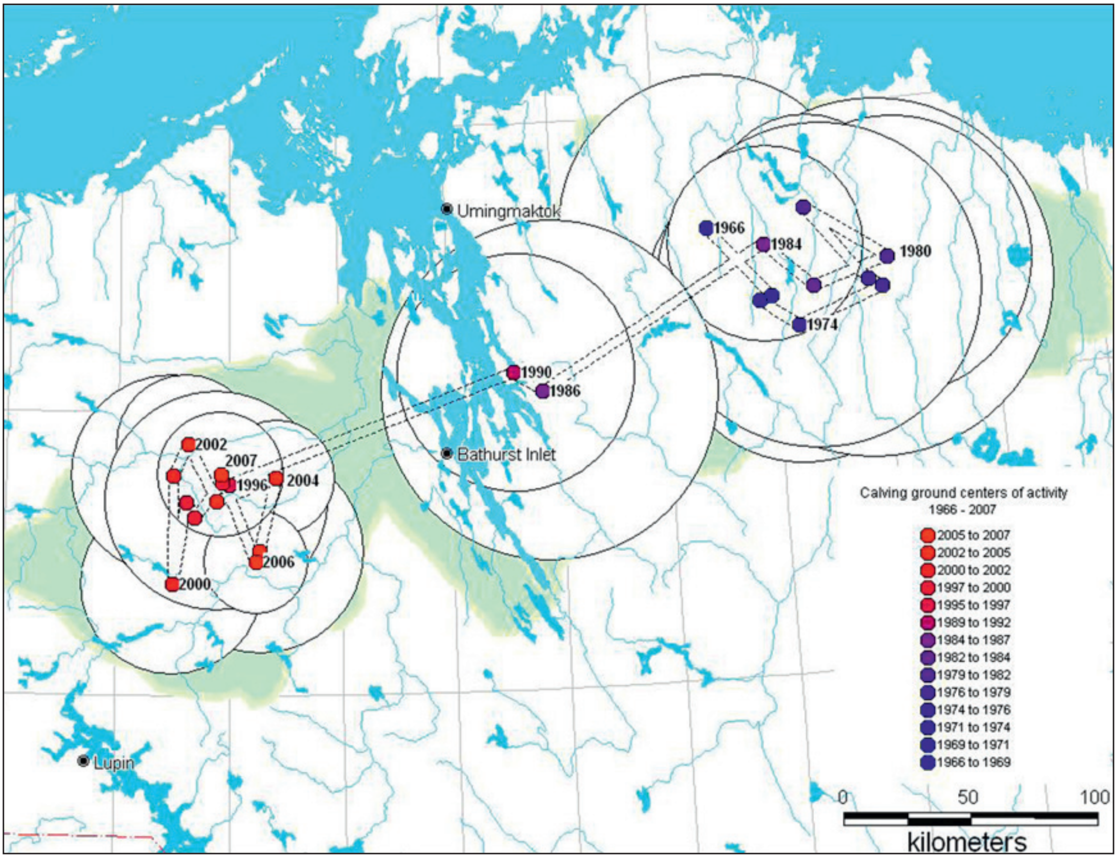

Fig. 2. Centroids of annual calving grounds at the peak of calving for the Bathurst herd, 1966 to 2007. The centroids are embedded in circles that are equivalent to the area of the annual calving ground; larger circles denote larger annual calving grounds (see Gunn *et al.,* 2008 for further explanation).

Subsequent monitoring was infrequent, but systematic strip transect surveys of the Beverly calving ground resulted in visually estimated densities of 4.0 and 0.4 caribou/km^2 in 2002 and 2007, respectively (Johnson *et al.,* in press).

Satellite collaring of cows in the Beverly herd did not start until 2006 (except one cow collared in 2001 which calved 4 of 5 years on the traditional Beverly calving grounds, with one non-breeding year). Since 2007, of the nine cows collared on the Beverly herd's winter or summer range with >1 year of calving on the Beverly calving ground, three remained on the Beverly calving ground for 2 years (Government of Northwest Territories, unpubl. data). Six cows moved to the neighbouring calving ground of the Ahiak herd about 250 km away (BABA, BAA, BA, BA0, B0A, B0A; B = Beverly calving ground, A = Ahiak calving ground, 0 = non-breeder). We suggest that the extreme low density in 2006-09 correlated with a reduced fidelity as cows maintained conspecific attraction by moving to a neighbouring calving ground.

The distribution of calving was not annually mapped until the use of satellite telemetry for some herds, including the Bathurst herd, starting in the mid-1990s. Gunn *et al.* (2008) estimated a centroid for each annual Bathurst calving ground between 1966 and 2007 based on aerial surveys or distribution of satellite-collared cows at the peak of calving (Fig. 2). There were the two periods (1966-1984; 1996-2007) when the centroids were clustered in the eastern and western parts of the calving range, linked by a period of directional shift between 1986 and 1996. The shifts between the consecutive 24 annual calving grounds averaged 17 km over 42 years (1966-2007) but were highly variable (3-120 km) (Table 1). The average yearly shift rate was 13 km (± 2.4 SE) for the 1966-1984 cluster of 10 centroids based on aerial surveys and when caribou densities were increasing, but had yet to reach a threshold density value that could trigger a change in calving ground fidelity.

Table 1. Size, distance between centroids, and direction of shift for successive peak calving grounds, determined by satellite collars and peak calving grounds for the Bathurst herd, NU (grey shading denotes consecutive years).

Shift dates	Peak calving ground area (sq km)	Distance between centroids (km)	Azimuth (°)
1966	8778		
1966-1970	6157	37	136
1970-1971	4275	5	245
1971-1974	6909	18	121
1974-1977	7180	36	64
1977-1978	11205	6	296
1978-1979	3113	37	318
1979-1980	6774	38	120
1980-1982	9429	31	249
1982-1984	3519	26	309
1984-1986	15096	104	236
1986-1990	5905	14	301
1990-1996	611	120	248
1996-1997	3472	3	291
1997-1998	1993	18	218
1998-1999	3950	7	330
1999-2000	3876	32	189
2000-2001	4731	43	1
2001-2002	3088	13	25
2002-2003	5758	25	153
2003-2004	1237	25	69
2004-2005	4932	26	193
2005-2006	1308	4	202
2006-2007	3785	37	338

The greater distances were between 1984 and 1996, based on only three aerial surveys over 13 years. The average yearly shift rate of the calving ground centroid was 21 km (± 4.0 SE) for the 1996-2007 cluster of 11 centroids when the densities of caribou on the calving ground were declining but had not reached the extreme low value to trigger an Allee Effect (see Table 8 in Gunn *et al.,* 2008 for details).

In between the two periods of overlap was a discontinuity as the 1984 and 1986 calving grounds did not overlap and were separated by 104 km. The 1986 and 1990 calving grounds overlapped, then the 1990 to 1996 calving grounds were also non-overlapping and their centroids were separated by 120 km. This shift resulted in a movement of the Bathurst calving ground from the east side to the west side of Bathurst Inlet; the distance between the centroids for the 1966-1984 grouping and the 1996-2007 grouping was 250 km (Fig. 2). The location of the annual calving ground overlapped between 1966 and 1984, when at the peak of calving, average density for the high density stratum was 203 caribou/km^2 (photographic estimate). Between 1986 and 2009, also based on photographic estimates, average densities declined from 111 to 7 caribou/km^2 (Nishi *et al.,* in press).

Discussion

We have proposed a mechanism leading to predictive insights about the spatial fidelity of migratory tundra caribou cows to their calving grounds. The mechanism is based on the two characteristics of migratory tundra caribou calving which are gregariousness and spatial fidelity. At extremely high or low levels of gregariousness (indexed by density), in response to negative or positive effects of density-dependence, spatial fidelity to the previous cumulative calving grounds will decline.

Typically, negative or positive effects of density are considered to be on rate of population growth. However, we identify the effects as behavioural – that the presence of conspecifics is both a positive and negative influence and likely acts along a continuum. To recognize these effects, we have to be aware of scale (individual to population) and variability (again individual, but also environmental). We also have to be aware of the dangers from the "tyranny of the dichotomous mind" (Dawkins, 2004), this being our tendency to emphasize distinct boundaries rather than continuums. Caution is needed in extrapolating from the shifts of individual cows to neighbouring calving grounds (based on satellite or conventional telemetry). It is uncertain how individual variation in calving behaviour becomes a shift in calving distribution relative to individual variability, as the expressions of individual variation may be the same behaviours that lead to shifts in distribution.

We have offered examples of changes in fidelity to annual calving grounds in two herds, each with close to 40 years of mapped annual calving grounds, with only two recorded examples of displacement to a currently unused area (Bathurst) or the Beverly cows partial shift to a neighbouring herd (Ahiak). For the Beverly herd, we suggest that extreme low densities correlate with a partial shift to a neighbouring calving ground as cows maintain conspecific attraction. For the Bathurst herd, peak high densities coincided with a shift to a calving area which was unoccupied and had not been used since decades earlier (Sutherland & Gunn, 1996). Then the degree of overlap in successive calving grounds was significantly greater during the decline in the number of breeding females (Gunn *et al.,* 2008).

We recognize that information about the reasons for changes in calving fidelity is incomplete. We lack information on whether the risk of parasitism and/or forage availability had changed on the Bathurst calving grounds in the early 1980s. We also do not have an understanding of how environmental variability plays into the relationship between calving fidelity and gregariousness—for example, Bathurst calving in 1986 occurred during a later snow melt (Sutherland & Gunn, 1996). Any relationship between calving ground fidelity and gregariousness will be complicated as the cows will be integrating current year's conditions with the previous year's performance on the calving ground (*sensu* colonial sea-birds which predicate nest site decisions on their previous fledging success and that of their neighbours; Danchin *et al.,* 1998).

The proposed curvilinear relationship between fidelity and density (gregariousness) accommodates the periodic changes in abundance typical of migratory tundra herds. The model also predicts that the greater the amplitude in densities, the more likely directional shifts will occur (negative density-dependence). For example, the George and Leaf River herds have high amplitude changes in herd size and shifts in calving distribution up to 400 km (Bergerud *et al.,* 2008; Couturier *et al.,* 2009). Between 1986 and 2003, the George River herd peaked in size at about 776 000 (±104 000) in 1993 before decreasing (Crete & Huot 1993, Manseau *et al*., 1996, Couturier *et al*., 2009) while the Leaf River herd probably peaked in 2001 and then started to decline (Couturier *et al*., 2009). When both the George River and Leaf River herds were increasing in size, their calving grounds directionally shifted north of the tree line. Then, as the herd began to decline, the size of calving ground of the George River herd increased and it started to shift south back toward the tree line. Bergerud *et al.* (2008:447) attributed the shift north to the cows reducing predation risk by spacing themselves away from wolves (*Canis lupus*), and the shift south to over-grazing. We note that the George River herd is atypical of all North American migratory tundra caribou herds, as the tundra portion of its annual range is only 11% (A. Gunn, unpubl. presentation 2008 CARMANET.ca). This may accentuate any relationship between density and rate of directional shifting in the calving ground.

At first sight, some movements of individual cows to another calving ground might seem counter to the concept that at high densities cows would not be expected to move to another high density calving ground. For example, rates of switching were annually variable between the George River and Leaf River herds. Boulet *et al.* (2007) recorded that 14 of 149 satellite-collared cows switched calving grounds (1986-2003) with herd-specific annual rates of switching calving grounds being 6.6% and 0.9% of the George River and Leaf River collared cows, respectively. Six of 13 cows (one cow had only two calving locations) reversed and returned to their natal calving ground. Two cows spent an equal number of years on either calving ground (6 and 8 years). The two calving grounds remained geographically separate by several 100 km. The George River herd had peaked when most of the cows switched to the Leaf River herd which was still increasing. However, without more information (densities on the calving ground, individual condition and parasite loads, habitat conditions) we are left with uncertainty.

We suggest directional shifts are more likely in mountainous terrain where herds may display either dispersed or gregarious calving behaviour. In the Alaskan mountains, there are two examples of herds with increasing population sizes that shifted their calving grounds. The new calving ground overlapped the calving area of a smaller and neighbouring herd (Davis *et al.,* 1986; Valkenburg *et al.,* 2003; Hinkes *et al.,* 2005). Although information on caribou densities on the calving grounds is not available, it is reasonable to assume that they were high for the larger herd. Between 1979 and 1987, the calving grounds of the smaller Yanert herd (500-1000 caribou) and the larger Delta herd (4000-8000 caribou) were only 10 – 50 km apart after the Delta herd's calving ground had shifted. In the second example, the smaller Kilbuck herd's (ca. 4000) traditional calving ground was 25 km away from the larger Mulchatna's (ca. 200 000) calving ground in 1994 (Hinkes *et al.,* 2005). The smaller mountain herds (Yanert and Kilbuck) had different calving strategies (scattered rather than gregarious) than the larger herds.

We acknowledge that other reasons, including weather and industrial development, can influence both individual cows (Carroll *et al.,* 2005) and calving ground locations (Cameron *et al.,* 2005). A variation in spatial fidelity, which is not the focus of this paper, is the effect of unusual weather during pre-calving migration. For example, late snow melt can mean extensive snowcover and cows calve before reaching the calving ground (e.g., Griffith *et al.,* 2002). Bergerud *et al.* (2008) remark that migrating cows halt before reaching the calving ground when snow cover is 100%. In coastal Alaska, Carroll *et al.* (2005) reported that during spring migration in May 2004, a combination of the Trans Alaska Pipeline, the Dalton Highway and the flooding Savaganirktok River delayed the Teshekpuk herd's pre-calving migration. Two of five collared cows calved before they reached the Teshekpuk herd's usual calving ground while the other three collared cows and many uncollared cows calved on the Central Arctic herd's calving ground. Attention must be paid to environmental conditions when interpreting unusual caribou movements, including apparent switching between calving grounds.

Further testing of the curvilinear relationship between gregariousness and spatial fidelity to calving grounds and how positive density-dependence shifts to negative density-dependence is necessary. Only a few herds have estimates of density of breeding cows on calving grounds, but many herds are monitored through satellite telemetry. We are investigating using nearest-neighbour distances between satellite-collared cows to estimate calving dispersion (the pattern of relative density, an index to gregariousness).

Our initial results for the Beverly and Bathurst herds are that the relationship between gregariousness and spatial fidelity is over a tenfold range in densities. Thus, we suggest fidelity to traditional calving grounds remains a robust hypothesis. We also suggest that changes in fidelity can be expected at either extremely low or high densities, which are relatively infrequent. Distinguishing between the two mechanisms for shifts in fidelity is key to caribou management and is indexed by whether the cows shift to an area with no or few cows, or an area with high densities. Instances when densities are so low that cows shift to maintain the advantages of gregariousness for calf survival are exceptional.

Understanding whether changes in spatial fidelity are predictable relates to designing calving ground protection as well as designating herds based on fidelity to calving grounds. Calls to protect the calving grounds of migratory tundra caribou are long-standing and frequent. For example, Inuit concerns prompted court action leading to the Department of Indian Affairs and Northern Development (Government of Canada) implementing Caribou Protection Measures to protect the calving and post-calving caribou of the Beverly and Qamanirjuaq herds in 1978 (BQCMB, 2004). Management of land use activities has not been extended to other herds in northern Canada, in part because of a perception about the mobility of calving grounds which argued against using land-based protection for calving grounds (Weihs & Usher, 2001).

We need to further test the conceptual relationship between fidelity and gregariousness and whether predictive thresholds are measurable for fidelity across a broad range of migratory tundra caribou calving grounds. We also expect that we need to re-examine the definition of "a herd's calving ground". Is the herd's calving ground the cumulative area used over time? What amount of data and years of survey are needed to adequately describe the extent of a herd's calving ground? Additionally, there is considerable diversity within migratory tundra caribou and their calving grounds – both ecological and in the amount of data available. We propose working within the CARMA network (http://www.carmanetwork.com/display/public/home) to collaborate using data from circumpolar herds to test and develop predictive relationships between spatial fidelity and gregarious behaviour for calving.

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