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Shifting targets in the tundra: Protection of migratory caribou calving grounds must account for spatial changes over time

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ABSTRACT

Industrial development, expansion of human populations and climate change increasingly affect habitats of migratory species. Effective protection of critical habitats is urgently required because several large migratory species have declined over the last decades. Protection of critical habitats, such as the calving grounds of migratory ungulates, may however require consideration of temporal shifts in spatial location. We assessed changes in the location of calving grounds used by migratory caribou over 35 years by the Rivière-George (RG) herd and 15 years by the Rivière-aux-Feuilles (RAF) herd, in Northern Québec and Labrador, Canada. We also evaluated the proportion of annual calving ground within protected Wildlife Habitats established to protect caribou calving grounds. The annual size and location of calving grounds changed substantially over time: calving ground size remained relatively stable for the RAF but it declined over 85% for the RG. Calving grounds moved 300 km northward in the Ungava peninsula for the RAF and shifted over 230 km back and forth to the Labrador coast for the RG. Despite recent modifications, legally designated Wildlife Habitats in Québec protected less than 20% of the RG and RAF calving grounds. Protection of calving grounds of migratory caribou must consider the dynamic use of space by adult females. We present recommendations on the use of available monitoring data to better protect calving grounds of migratory caribou and critical habitats of large migratory species.

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1. Introduction

Protected areas (PAs), where human activities are limited, are the primary land-management strategy used to protect sensitive areas from industrial development and expanding human populations (IUCN, 2010). The number of PAs has increased to more than 120,000 worldwide in 2008 (UNEP-WCMC, 2010). Approximately 12% of the Earth's land surface is currently protected (IUCN, 2010). Although the number and size of PAs have increased, there is a need to widen their geographical scope (UNEP-WCMC, 2010) and we still know little about their effectiveness (Hockings et al., 2006).

Protected areas usually have fixed legislated boundaries that provide protection, but also certainty to developers outside the areas (Hockings et al., 2006). Criteria for selecting PAs include basic elements such as size, shape and connectivity (Hockings et al., 2006; CMS, 2011). Unless they are very large, protected areas that are fixed in space may not capture the variability in spatial and

temporal habitat use of animals (Thirgood et al., 2004), and the dynamism of ecological processes (Pressey et al., 2007). Static areas, thus, may not adequately protect species that show wide dispersal patterns, undertake extensive migrations or use very large seasonal ranges, such as most migratory large vertebrates (Thirgood et al., 2004; Bleisch et al., 2008; Craigie et al., 2010; Singh and Milner-Gulland, 2011). Inadequate knowledge of range use and seasonal movements of animals, especially spatial shifts of seasonal ranges, results in PAs that do not actually protect seasonal or annual ranges (caribou, *Rangifer tarandus*, Gunn et al., 2008; Mongolian gazelle, *Procapra gutturosa*, Mueller et al., 2008; Saiga antelope, *Saiga tatarica*, Singh et al., 2010). Connectivity between PAs seems therefore essential to maintain viable populations and migratory pathways. The establishment of networks of protected areas, rather than independent PAs is one of the primary conservation strategies developed by international conservation groups (IUCN, 2010; UNEP-WCMC, 2010; CMS, 2011). Moreover, studies on migratory ungulates suggest that PAs should include areas used in the past and predicted to be used in the future (Bleisch et al., 2008; Conroy et al., 2011; Singh and Milner-Gulland, 2011). Effective PAs for migratory mammals are urgently required because several large migratory species have declined in recent years because of changes in climate and human land use (Harris et al., 2009).

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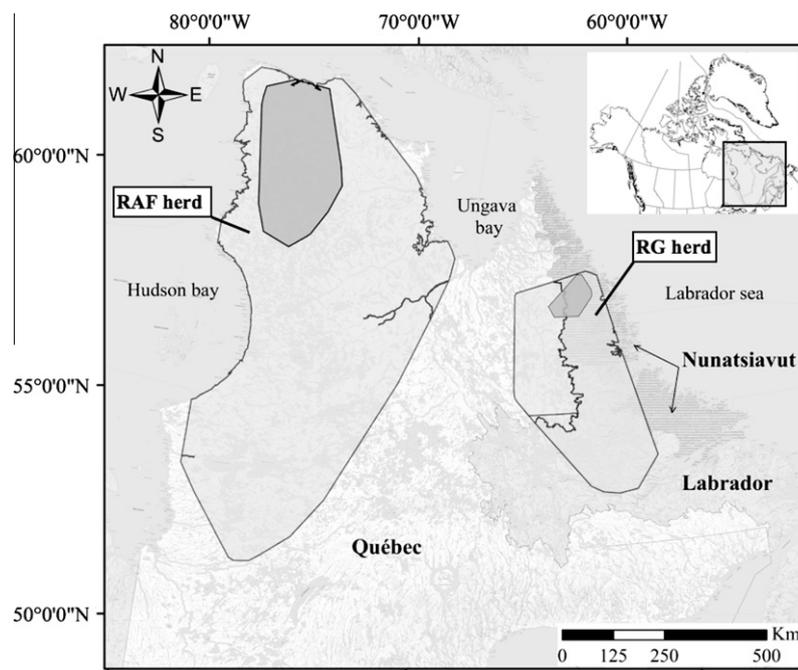


Fig. 1. Annual ranges and calving grounds of the Rivière-George (RG) and Rivière-aux-Feuilles (RAF) migratory caribou herds, Northern Québec and Labrador, Canada, estimated from telemetry locations of adult females in 2010. Darker polygons represent calving grounds within the annual ranges, delineated by black contour lines.

Wild migratory caribou and reindeer are a keystone species structuring northern ecosystems, with high cultural value for Aboriginal peoples (Hummel and Ray, 2008). Over the last decades, however, most herds have declined (Vors and Boyce, 2009; Festa-Bianchet et al., 2011). Increasingly, industrial development such as hydrocarbon exploitation, hydro-electric and mining activities (Wolfe et al., 2000; Vistnes and Nellemann, 2001; Haskell et al., 2006; Reimers et al., 2007) occurs near calving grounds, where parturient females and newborn calves are particularly sensitive to human activities (Nellemann and Cameron, 1998; Wolfe et al., 2000). Females return annually to traditional calving grounds (Gunn and Miller, 1986; Bergerud et al., 2008), defined as the area used by parturient caribou from calf birth through to when calves begin to consume vegetation (Russell et al., 2002). Fidelity to calving grounds may confer benefits such as familiarity with resources and topography, early access to new vegetation growth and predator avoidance (Bergerud et al., 2008; Gunn et al., 2008).

Currently, no calving ground of migratory caribou in North America is under permanent protection, although small portions of the annual ranges of a few herds are protected (Hummel and Ray, 2008). Some stakeholders have suggested that long-term legislated protection of calving grounds should be a priority (Hummel and Ray, 2008; Festa-Bianchet et al., 2011). Recent evidences, however, suggest that caribou calving grounds are not spatially fixed over the long term (Russell et al., 2002; Bergerud et al., 2008; Gunn et al., 2008), therefore their protection cannot assume spatial stability.

The two large herds of migratory caribou in Northern Québec and Labrador: the Rivière-George herd (RG) and the Rivière-aux-Feuilles herd (RAF) (Fig. 1, Boulet et al., 2007), have shown wide and asynchronous changes in abundance during the last decades (Couturier et al., 2010). In the late 1990s, the Québec Provincial Government designated the calving grounds of both herds as Wildlife Habitat, legally prohibiting activities that could be detrimental to caribou habitat within the defined area (Québec Government, 2011a, see Section 2 for details). Wildlife Habitats were first mapped based on calving ground aerial surveys in 1991 and 1993. Their boundaries were updated in 2004 based on satellite

locations of caribou females. Currently, there is no standardized method to evaluate the annual performance of Wildlife Habitats at protecting calving grounds of both herds.

We assess changes in the location of calving grounds based on 15 years of aerial surveys (1973–1988) and 20 years of satellite telemetry locations (1990–2010). We sought to (1) analyze variations in the location and size of calving grounds; (2) document the density of adult females and changes in overlap of calving grounds over time; (3) evaluate the proportion of annual calving grounds within protected Wildlife Habitat, and (4) suggest improvements in the protection of calving grounds.

2. Methods

2.1. Study area and populations

The Rivière-George herd (RG) and the Rivière-aux-Feuilles herd (RAF) are not genetically different (Boulet et al., 2007), but have shown, over the last few decades, large fluctuations in demographic parameters (Couturier et al., 2010). The RG herd increased from about 5000 individuals in the 1950s (Banfield et al., 1958) to more than 775,000 in 1993 (Couturier et al., 1996), then declined to approximately 385,000 in 2001 (Couturier et al., 2004) and 74,000 in 2010 (Québec Government aerial count). The RAF herd increased from 56,000 in 1975 (Le Hénaff, 1976) to 1,193,000 in 2001 (Couturier et al., 2004), and was estimated at 430,000 in 2011 (Québec Government aerial count).

2.2. Range use

In early spring, females migrate 250–650 km to calving grounds, typically used from late May to early July. Females of the RG herd aggregate on the high tundra plateaus on the east side of the Québec-Labrador Peninsula (57°N, 65°W) while females of the RAF herd calve in the Ungava Peninsula (61°N, 74°W) (Fig. 1). Over 93% of females return to their traditional calving ground each year (Boulet et al., 2007). There is no overlap in the calving grounds

of the two herds (Couturier et al., 2004). Seasonal ranges of the RG and RAF herds have been monitored since 1990 using mainly satellite radio-collars (Couturier et al., 2004).

2.3. Legal status of calving grounds

In the late 1990s, calving grounds of both herds were identified and protected as Wildlife Habitat by the Québec Provincial Government. Under this legislation, a migratory caribou calving ground is legally defined as an area north of the 52nd parallel and used by at least five adult female caribou per km² between 15 May and 1 July (Québec Government, 2011a). The Wildlife Habitat (or legally defined calving ground) of each herd was first delineated based on aerial surveys conducted in 1993 for the RG herd (13,850 km²), and in 1991 for the RAF herd (13,850 km²), and these delineations were used until 2003. The location of the Wildlife Habitat was updated in 2004 for both herds, using satellite locations of females from 1999 to 2003 (RG = 13,410 km² and RAF = 19,830 km²; Québec Government, 2004). Within the defined Wildlife Habitats, activities that may affect caribou habitat are prohibited from 15 May to 31 July (Québec Government, 2011a). Access to and activities within the period of protection of Wildlife Habitats may, however, be allowed if permits are issued by the Québec Government. These Wildlife Habitats are protected under the Regulation respecting Wildlife Habitats (R.R.Q., c C-61.1, r 18) and the chapter IV.1 of the Conservation and Development of Wildlife Act (R.S.Q., c. C-61.1) (Québec Government, 2011a). Although the RG herd moves seasonally through three jurisdictions (Québec, Labrador and the Inuit Land-Claim area of Nunatsiavut; Couturier et al., 2010) (Fig. 1), there is no current legal protection of calving grounds in either Labrador or Nunatsiavut.

2.4. Calving grounds delimitation

To describe the location and geographical extent of calving grounds, we used results from previous aerial surveys and recent satellite telemetry (see Table 1). From previous reports, we compiled spatial delineation and size of calving grounds from aerial surveys conducted near peak calving (the interval when approximately 50% of females calve) from 1974 to 1988 for the RG herd and in 1975 for the RAF herd (Table 1). Aerial surveys using the strip census method, with transects separated by 8–15 km, were flown at an altitude of 100–150 m and at 180–200 km/h. Observations of females with calves were directly transferred on topography maps (1:250,000) and boundaries of calving grounds were delineated to include all observations.

We extracted maps of calving grounds from government reports and transferred them to ArcMap (ArcGIS 9.2, ESRI) using as a reference the 1:250,000 digital hydrology database of the Québec Government (map sources: Folinsbee et al., 1974; Juniper, 1974; Le Hénaff, 1976, 1979a, 1979b; Luttich, 1978; Goudreault et al., 1985; Messier and Huot, 1985; Gagnon and Barrette, 1986; Crête et al., 1987; Vandal and Couturier, 1988; Crête et al., 1989; Vandal et al., 1989; Bergerud et al., 2008).

We used the locations of 150 females of the RG herd and 105 females of the RAF herd fitted with satellite collars (ARGOS, Largo, MD) to locate calving grounds from 1990 to 2010 (Table 1). Most females were captured on the calving grounds at sites separated by several kilometers (range for 2007–2009 (mean (SE)): RG: 21 (3) km; RAF: 83 (12) km), therefore we consider individuals to be independent and representative of the area used by the entire herd. All captures used a net-gun fired from a helicopter and physical restraint, a standard procedure for ungulates (Bookhout, 1996). Anesthetics were never used during captures, which followed guidelines from the Canadian Council on Animal Care. The average duration of individual monitoring was 2.5 years but some animals

were followed for up to 10 years. We used a filtering tool in Excel (Microsoft, Redmond, VA) to select the most accurate location (location accuracy: ≤ 150 –1000 m; see CLS, 2011 for details) per transmission period (one location/animal approximately every 3–5 days) and excluded locations generating travel rates > 50 km/day (see Austin et al., 2003 for a similar algorithm). We calculated daily movement rates (km/day) from the distance moved and time between successive locations for each individual (Couturier et al., 2010).

Using satellite locations, annual calving grounds were identified by the spatial aggregation of parturient females and by the obvious decline in movements, from more than 20 km/day during spring migration to less than 5 km/day during calving. For each year and herd, we examined successive locations, movement direction and patterns of use of calving grounds of individual females to identify (1) the decline in individual movement from migration to calving (from 20 km/day to 5 km/day within a few locations), (2) the period of use of the calving ground (≤ 5 km/day; few consecutive locations), and (3) the sharp increase in movement as females migrated to the summer range (from 5 km/day to ≥ 15 km/day within a few locations). Spatial aggregations were identified from visual examination of successive locations and movements direction. Similar techniques have been used to identify calving areas in other studies (moose, *Alces alces*, Testa et al., 2000; elk, *Cervus canadensis*, Vore and Schmidt, 2001; caribou, Gunn et al., 2008). We excluded females, mostly non-parturient, that did not reach the calving grounds.

From 1991 to 2010, we delineated annual calving grounds with 100% minimum convex polygons (MCP) using all locations of females monitored during calving that fulfilled the criteria of movement direction and patterns of use of calving grounds (Hawth Tool Extension, ArcMap, ArcGIS 9.2). Annual polygon size was independent of the number of females with radio-collars (RG: $F_{1,17} = 0.02$, $p = 0.90$; RAF: $F_{1,14} = 0.40$, $p = 0.54$) which ranged from 7 to 30 (mean (SE), RG: 16 (1); RAF: 14 (1)) and of the numbers of satellite locations used to calculate annual MCP (RG: $F_{1,17} = 0.19$, $p = 0.67$; RAF: $F_{1,14} = 0.94$, $p = 0.35$) which ranged from 50 to 336 (mean (SE), RG: 149 (10); RAF: 107 (21)).

We compared the spatial delineation of calving grounds using aerial surveys and satellite telemetry locations for 1993, when an aerial survey was conducted over the calving ground of the RG herd (Couturier et al., 1996). The survey estimated a calving ground of 21,048 km² (Couturier et al., 1996). The estimate from satellite-collared females covered 23,852 km² and overlapped 92.4% of the estimate from the aerial survey. In addition, almost all females and newborn calves observed during opportunistic aerial transects in 2007, 2008 and 2009 ($n = 100$ –700 observation points over an area of 3000–4000 km² (RG) and 13,000–1900 km² (RAF)), were within the calving grounds defined based on females with radio-collars (2007: RG: 88%, RAF: 100%; 2008: RG: 94%, RAF: 86% and 2009: RG: 100%, RAF: 100%).

2.5. Density estimates on calving grounds

Legally-defined calving grounds in Québec include areas used by at least 5 females/km². To determine whether annual calving grounds fit that definition, we extracted density estimates of adult females on annual calving grounds from government reports. When a density estimate was not available, we calculated densities with the same procedure used by the Québec government: multiplying herd size estimated from aerial counts by the proportion of adult females in autumn, estimated from the sex–age classification of several thousands caribou during migration (Couturier et al., 2004). This calculation assumes that, in a given year, all females observed in autumn were in the calving ground the previous June. We obtained density estimates for 13 years for the RG (1973, 1974,

1975, 1976, 1980, 1982, 1984, 1986, 1987, 1988, 1993, 2001 and 2010), and 3 years for the RAF (1986, 1987 and 2001).

2.6. Statistical analysis

We used linear regression to evaluate temporal changes in size of annual calving grounds and changes in the density of adult females on RG calving grounds over years and with population size (REG procedure, SAS Institute 9.2). We did not consider years when females calved during migration and did not reach the calving grounds (RG: 2002; RAF: 2004 and 2005).

We estimated the centroid of each annual polygon (Hawth Tool Extension, ArcMap, ArcGIS 9.2) and calculated the Euclidean distance between consecutive annual centroids to evaluate their year-to-year displacement. To evaluate the displacement of consecutive centroids over time, we used a linear regression of the location of the centroid at year ($n + 1$) on its position at year (n) (REG procedure, SAS Institute 9.2). We also calculated the percent overlap between pairs of consecutive annual polygons and estimated an overlap index based on Gunn et al. (2008):

$$\text{Overlap Index} = (2(\text{area_overlap})100)/(\text{area_polygon1} + \text{area_polygon2})$$

For the RAF herd, we used linear regression to test for changes in overlap over time (REG procedure, SAS Institute 9.2). For the RG, we also contrasted three periods with different demographic trends and calving ground sizes using student t -test (SAS Institute 9.2): (1) 1974–1987 (increasing population and calving ground size), (2) 1991–2000 (population decline, large calving grounds), and (3) 2006–2010 (small population, small calving grounds). Demographic parameters (Crête et al., 1996), dendroecological (Boudreau et al., 2003) and lichen abundance analyses (Boudreau and Payette, 2004), suggested that RG peaked in 1989 and then decreased. Following Couturier et al. (2009), we considered herd size to be “high” when it included over 500,000 individuals, and “low” under this level. Finally, we calculated the percentage of each annual calving ground included in the legally designated Wildlife Habitat.

All data met assumptions of normality and homogeneity of variance. Results are presented as means (SE). A level of $\alpha = 0.05$ was used to determine significance.

3. Results

3.1. Changes in size of calving grounds

The calving ground of the RG herd expanded from 1974 to 1988 (quadratic regression: $R_2 = 0.90$, $F_{1,15} = 57.7$, $p < 0.0001$; Fig. 2) coinciding with an increase in population size, then declined by over 85%, from 42,800 (7500) km² in the early 1990s to 5930 (730) km² in 2006–2010 (linear regression: $R^2 = 0.65$, $F_{1,17} = 31.0$, $p < 0.0001$; Fig. 2). When discovered in 1975, the RAF calving ground covered 19,740 km² (Le Hénaff, 1976). Between 1995 and 2010, it remained relatively stable at about 44,000 (5000) km², with an increasing trend ($R^2 = 0.24$, $F_{1,14} = 4.35$, $p = 0.06$, Fig. 2) matching the population expansion from the late 1990s to the early 2000s (Fig. 2).

3.2. Changes in spatial locations

The location of calving grounds changed over time for both herds. From 1974 to 1991, the RG calving ground moved westward in the Québec-Labrador Peninsula (Fig. 3). Centroids of the RG calving ground were clustered from 1974 to 1982, then shifted West by 156 (14) km from 1984 to 1991 (Fig. 3). From 1991 to the early

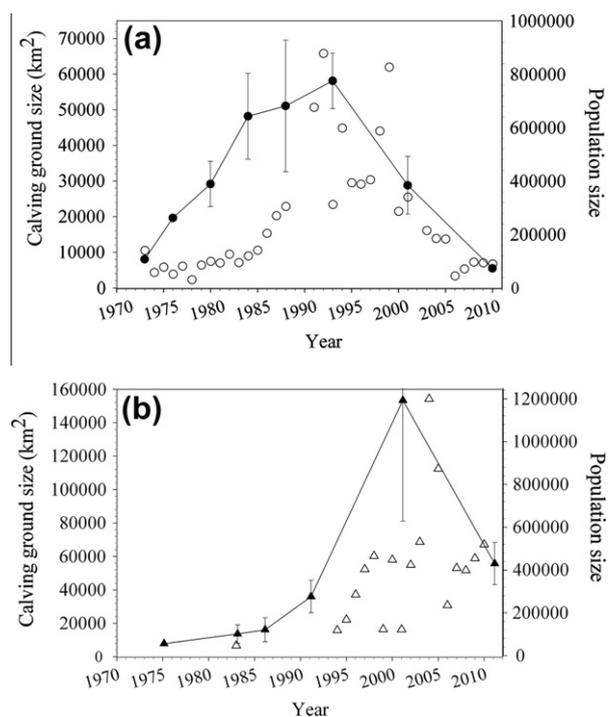


Fig. 2. Calving ground size (empty symbols) and population size (filled symbols and plain line) of (a) Rivière-George and (b) Rivière-aux-Feuilles migratory caribou herds from 1973 to 2010, Canada. Population size was estimated from aerial counts (mean \pm 90% conf. interval). High values (RG: 2002; RAF: 2004 and 2005) represent years when females calved during migration.

2000s the RG calving ground centroids were clustered, then moved eastward towards the Labrador coast by 227 (14) km in recent years (2006–2010; Fig. 3). From 2006 to 2010, the centroids remained clustered near 63°11N, 57°37W (Fig. 3). Since its discovery in 1975 (58°25'N; 73°25'W), the RAF calving ground moved about 300 km northward in the Ungava peninsula (average location of recent centroids: 60°44'N; 74°18'W). From 1995 to 2010, centroids of RAF herd moved yearly by 83 (13) km in the Ungava peninsula, with no obvious directionality ($F_{1,13} = 0.001$, $p = 0.97$; Fig. 4). There was no significant changes in the latitude of calving grounds over the past 20 years for the RG ($F_{1,18} = 0.34$, $p = 0.57$) and the past 15 years for the RAF ($F_{1,16} = 2.05$, $p = 0.17$; Fig. 4).

3.3. Overlap of consecutive annual calving grounds

The overlap between RG annual calving grounds was high for 1974–1980 (40 (10)%), 1991–1999 (49 (2)%) and 2005–2010 (59 (3)%) (Table 2 and Fig. 3). The overlap was high between 1974–1980 and 2005–2010 (40 (5)%), and both periods had low overlap with 1991–1999 (respectively, 8 (1)% and 6 (1)%) (Table 2 and Fig. 3). Overall, the overlap of the RG annual calving grounds averaged 30 (1)% (Table 2 and Fig. 3). There was no temporal change in the overlap of the RAF calving grounds among years ($F_{1,13} = 0.86$, $p = 0.36$) and overall, it averaged 48 (2)% (Fig. 4).

3.4. Density of adult females

Yearly adult female densities on calving grounds of RG herd were mostly over 5/km² (17.8 (3.5); min = 4.8; max = 46.5, $n = 13$), were independent of population size ($F_{1,12} = 0.39$; $p = 0.55$) and showed no obvious temporal trend ($F_{1,12} = 0.20$; $p = 0.68$). Estimates for RAF herd were available only in 1986, 1987 and 2001 (respectively: 8, 14 and 19 females/km²).

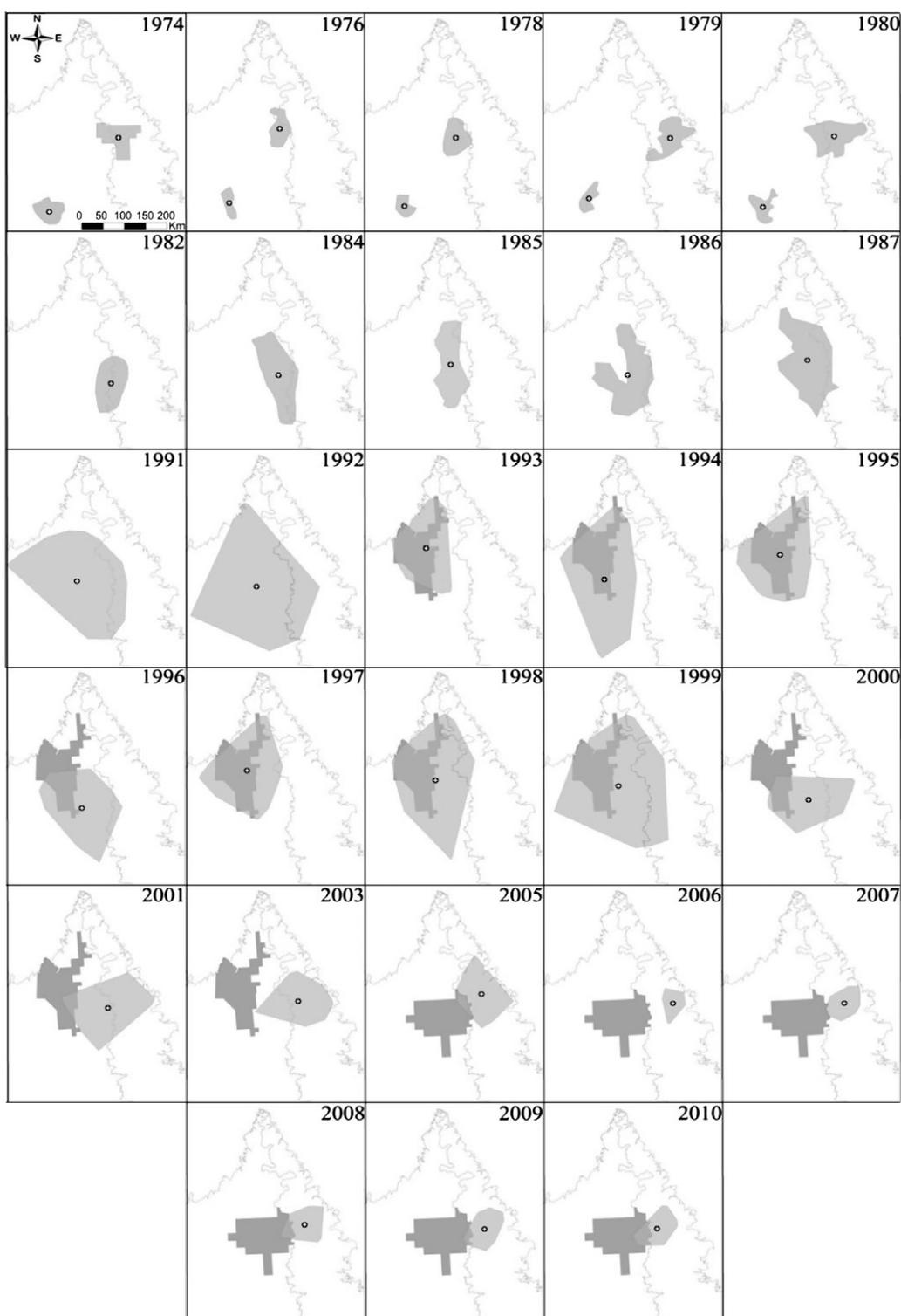


Fig. 3. Calving ground locations from 1974 to 2010 for migratory caribou of the Rivière-George herd, Canada. The darker polygons indicate the legal Wildlife Habitat, first defined in 1993 and updated in 2004. No calving ground locations were available in 2002 and 2004 for the RG. The centroid of annual calving grounds is shown by a black circle filled with a white cross.

3.5. Overlap with Wildlife Habitat

From 1993 to 2003, an average of 27 (5)% (range: 0–52%) of the RG annual calving grounds was inside the designated Wildlife Habitat. After the re-definition of the Wildlife Habitat in 2004, the percentage

of overlap with RG calving grounds declined to 10 (4)% (range: 0–26%) from 2004 to 2010 (Fig. 5). Overlap between RAF annual calving grounds and Wildlife Habitat was low both before and after the re-definition of the Wildlife Habitat in 2004 (1995–2003: 11 (4)%, range: 0–36%; 2004–2010: 23 (3)%, range: 13–31%) (Fig. 5).

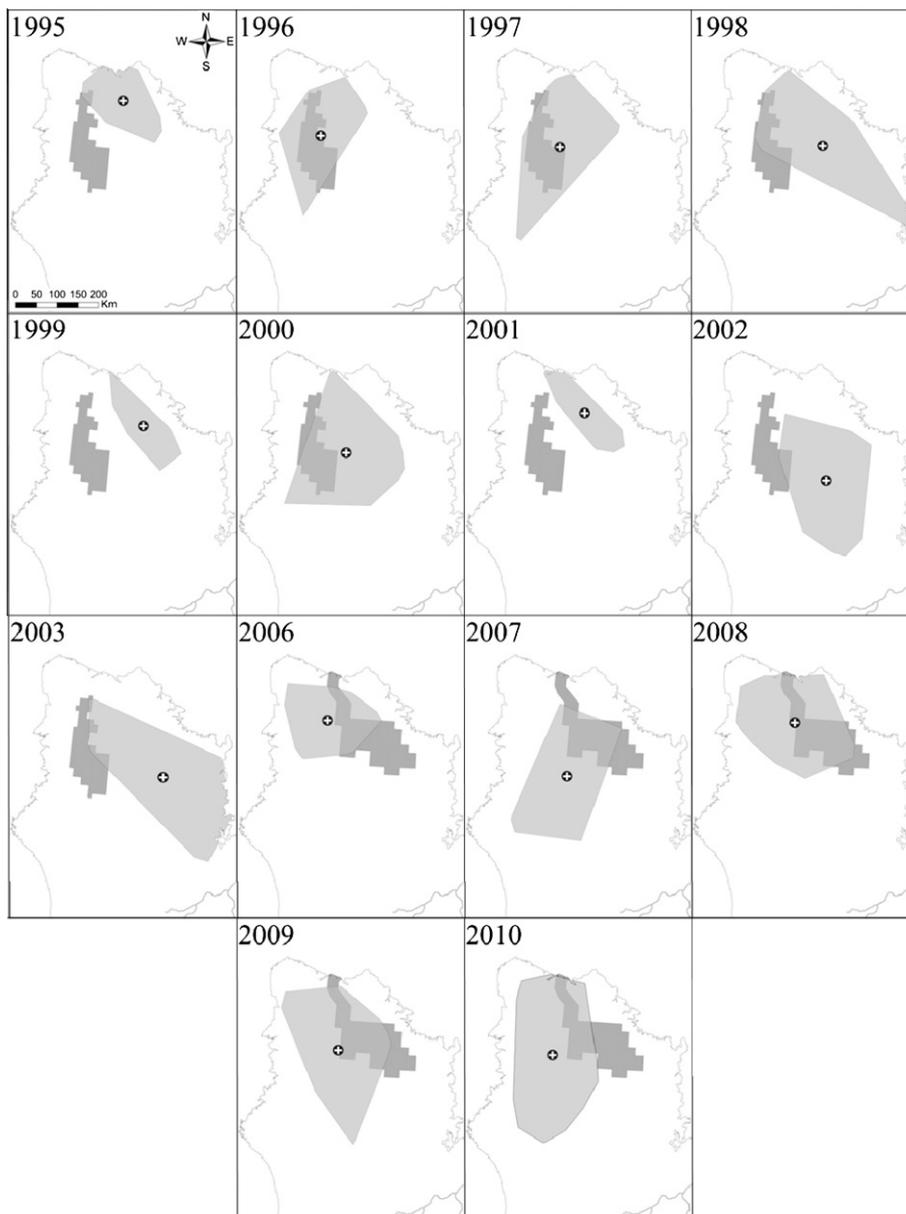


Fig. 4. Calving ground locations from 1995 to 2010 for migratory caribou of the Rivière-aux-Feuilles herd, Canada. The dark polygons represent the legal Wildlife Habitat, first defined in 1991 and updated in 2004. No calving ground locations were available in 2004 and 2005. The centroid of annual calving grounds is represented with a black circle filled with a white cross.

Table 1
Data sources for the delineation of annual calving grounds and the estimation of adult female density for the Rivière-George and the Rivière-aux-Feuilles migratory caribou herds, 1974–2010, Northern Québec and Labrador, Canada.

Herd	Calving ground extent and location		Density estimates	
	Data source	Years	Data source	Years
George	Aerial surveys from literature	1974–1988	Aerial surveys from literature	1973–1988
	Telemetry locations	1991–2010	Aerial counts and population classification	1993, 2001, and 2010
Feuilles	Aerial surveys from literature	1975	Aerial surveys from literature	1986, 1987
	Telemetry locations	1994–2010	Population counts and proportion of females in fall	2001

4. Discussion

There is an urgent need to evaluate the efficiency of legal protection of critical ranges for migratory animals throughout the

world (Bolger et al., 2008). Over the last few decades, most herds of migratory caribou have declined (Vors and Boyce, 2009), and stakeholders in Canada prioritize the protection of migratory caribou calving grounds, the vast majority of which do not currently

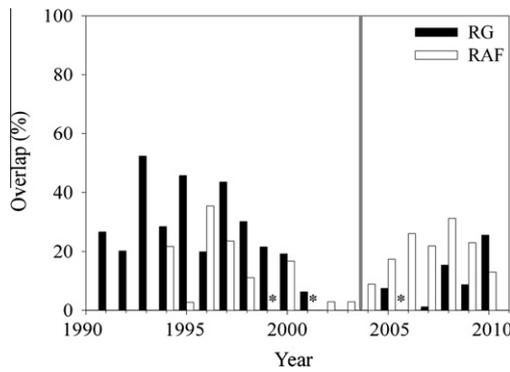


Fig. 5. Percentage of overlap between annual calving grounds of the Rivière-George (RG) and Rivière-aux-Feuilles (RAF) migratory caribou herds, and Wildlife Habitats protecting caribou habitat in Northern Québec, Canada. The gray line separates the years before and after Wildlife Habitats were updated. No calving ground estimates were available in 2002 and 2004 for the RG. Asterisks indicate years when there was no overlap between the annual calving ground and Wildlife Habitat.

enjoy any legal protection (Festa-Bianchet et al., 2011). We found that the size and location of calving grounds of two migratory herds changed substantially over time, suggesting that they cannot be adequately protected by setting aside areas based on only one or a few years of locations of parturient females. Despite a recent re-definition and expansion, legally designated Wildlife Habitats in Québec on average protected less than 20% of the RG and RAF calving grounds. Clearly, protection of calving grounds must consider the dynamic use of space by adult females. Here, we first discuss the evidence for temporal shifts in geographical locations of calving grounds, and then present recommendations on the use of monitoring data to better protect critical habitats of large migratory species.

Combining data from earlier aerial surveys and recent telemetry monitoring, we identified major changes in the size of the Rivière-George (RG) calving grounds since the 1970s (Figs. 2a and 3). Changes in size of the calving ground were related to variations in population size (Fig. 2a). Migratory caribou expand their annual range in response to increased population size (Fancy et al., 1989; Couturier et al., 2010). Messier et al. (1988) suggested that range expansion in the RG herd may have delayed its response to food limitation by giving access to additional forage. Range expansion could, however, increase energy expenditure through longer movements (Fancy and White, 1986), while new habitats may encompass higher proportions of less favorable foraging or environmental conditions (Messier et al., 1988). Interestingly, the RAF calving ground did not change in size between 1994 and 2010 while the population increased (Figs. 2b and 4), possibly because it already covered most suitable habitats in the northern Ungava Peninsula and could not expand, being limited by open water to the West, East and North (Fig. 1) and to the South by the tree line. In summer, the taiga is suboptimal habitat for migratory caribou, partly because of high predation risk (Bergerud et al., 2008). Because food limitation becomes apparent when new ranges can no longer be colonized (Messier et al., 1988), we suspect that over the last few years the RAF calving grounds, and adjacent summer ranges, experienced high grazing pressure and possible range degradation.

The location of calving grounds changed substantially over time for both herds (Figs. 2 and 3). Similar shifts for migratory caribou of the Bathurst herd were attributed to a warming trend coinciding with earlier vegetation green-up and trade-offs between access to new food resources and predation risk (Gunn et al., 2008). In saiga antelope, shifts of calving sites during the last decade are thought to be largely driven by environmental factors but also by

Table 2 Matrix of annual overlap (%) of calving grounds for the Rivière-George migratory caribou herd from 1974 to 2010, Northern Québec and Labrador, Canada.

	1974	1976	1978	1979	1980	1982	1984	1985	1986	1987	1991	1992	1993	1994	1995	1996	1997	1998	1999	2000	2001	2003	2005	2006	2007	2008	2009		
1974																													
1976	29																												
1978	34																												
1979	40	17																											
1980	88	41	36	62																									
1982	25	1	10	14	27																								
1984	18	26	58	7	28	64																							
1985	7	27	44	0	11	23	82																						
1986	14	22	38	4	23	39	76	69																					
1987	20	28	38	3	27	37	81	73	73																				
1991	15	13	17	4	18	28	46	38	52	61																			
1992	13	11	13	8	16	22	37	30	42	57	78																		
1993	0	1	9	0	1	0	22	21	37	40	45	45																	
1994	1	6	11	3	3	1	24	20	33	39	62	61	61																
1995	0	3	9	0	1	0	22	24	37	40	71	72	84	77															
1996	10	11	24	4	15	30	65	49	71	64	72	61	37	59	47														
1997	2	8	12	0	3	0	22	28	42	55	59	52	81	71	95	43													
1998	7	14	18	0	10	7	32	40	46	55	71	67	66	75	77	65	74												
1999	15	10	14	6	18	24	36	32	42	53	79	78	52	67	65	59	62	80											
2000	43	18	32	21	47	30	59	47	58	63	54	46	30	38	36	67	34	47	49										
2001	37	21	31	32	50	28	60	46	42	60	45	38	23	25	24	48	25	38	45	69									
2003	51	29	35	46	66	15	30	21	22	34	23	20	6	8	7	18	10	19	28	44	70								
2005	49	16	11	46	59	10	3	3	5	16	13	12	0	0	0	4	1	11	22	28	57	79							
2006	24	0	0	67	38	0	0	0	0	0	0	1	0	0	0	0	0	0	1	10	23	34	39						
2007	61	0	9	59	62	9	0	0	1	4	6	5	0	0	0	1	0	0	8	25	34	50	55	62					
2008	70	9	16	57	75	18	11	0	9	14	11	0	0	0	0	7	0	4	13	35	42	62	60	52	78				
2009	67	0	6	69	70	28	11	0	8	9	10	11	0	0	0	7	0	0	12	35	39	53	51	56	74	77			
2010	72	7	21	47	77	33	24	6	17	19	14	12	0	0	0	12	0	4	15	41	42	52	48	35	66	77	76		

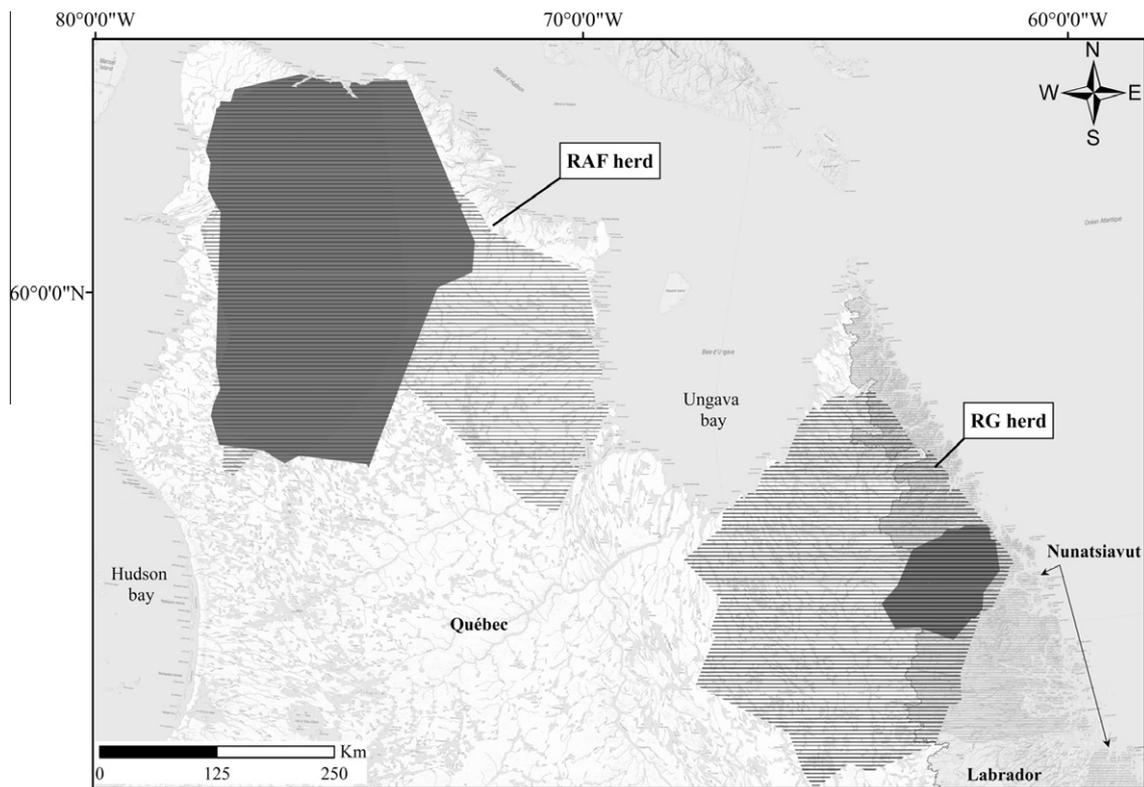


Fig. 6. Locations of the proposed traditional calving grounds (stippled) and annual calving grounds (dark gray) of the Rivière-George (RG) and Rivière-aux-Feuilles (RAF) migratory caribou herds, Northern Québec-Labrador, Canada. Traditional calving grounds represent the cumulative area used for calving by each herd. Annual calving grounds include the 5 past years of use of calving grounds (2006–2010).

increased human disturbance (Singh et al., 2010). In Northern Québec, shifts in calving grounds could be related to changes in population size that can induce range degradation, or to habitat preference. Sharma et al. (2009) suggested that, according to a Canadian General Circulation Model climate change scenario, seasonal ranges of the RAF and RG herds should change substantially over the next 50 years. The RG herd may become restricted to the northeastern Québec-Labrador Peninsula in the winter, spring, and summer, while the RAF herd may expand its distribution relative to its current range. These projections of potential changes in size and location of calving grounds (Sharma et al., 2009) imply that fixed areas are unlikely to provide long-term protection to the calving grounds of migratory caribou. A better understanding of the factors driving selection of calving grounds appears crucial. Remote sensing tools can determine the importance of local weather, large-scale climatic variation, topography and vegetation availability on calving ground selection (Mueller et al. 2008; Singh et al., 2010; Singh and Milner-Gulland, 2011). That information could clarify the processes driving spatio-temporal dynamics in calving grounds and improve future management under climate changes and expanding industrial development in northern regions.

The conservation of migratory species is challenging, because their large annual ranges (Shuter et al., 2011) would require large protected areas (Thirgood et al., 2004). The protection of static areas with legislated boundaries is often an efficient and cost-effective strategy to conserve specific habitats (Shuter et al., 2011). Fixed protected areas have been relatively successful for migratory species that consistently use the same areas over time, preventing habitat loss and human disturbance (Shuter et al., 2011). For caribou, however, only 10–27% of annual calving grounds were protected by Wildlife Habitats (Fig. 4). Wildlife Habitats cover very large areas, and the Québec government has made

efforts to redefine their locations to cope with temporal changes in calving ground locations. Nevertheless, current Wildlife Habitats perform poorly at protecting calving grounds that are large and dynamic over time. Despite large changes in population and calving ground size, density of adult females on calving grounds remained higher than 5/km², coherent with the legal definition of calving ground used by the Québec government. High densities are believed to dilute predation risk (Hamilton, 1971) and enhance predator detection (Nocera et al., 2008). Dilution and saturation effects on predation by bears and wolves have been suggested for migratory caribou at calving (Hinkes et al., 2005).

We recommend using ongoing monitoring to better protect calving grounds of migratory caribou. Clearly, the identification of annual calving grounds is necessary for effective management of calving ranges (Gunn et al., 2008) and can be identified from aerial surveys and/or telemetry-monitoring programs. Managers should set a priority over delineating annual calving grounds, while stakeholders including biologists, managers, hunters and Aboriginal Peoples should acknowledge past and predicted changes in the size and geographical location of calving grounds. Because the fidelity of caribou females to calving grounds is sensitive to both spatial and temporal scales of measurement (Schaefer et al., 2000), we recommend using the two definitions suggested by the Beverly and Qamanirjuaq Caribou Management Board (2004): *Traditional Calving Grounds* include the known cumulative area used for calving by a particular herd and are critical to capture their dynamic temporal and spatial use by adult females. They would include approximately 89,000 km² for the RG and 130,000 km² for the RAF (Fig. 6). The entire Traditional Calving Ground should be granted a basic level of protection, such as the prohibition of any structure that would prevent caribou from migrating or would permanently destroy their habitat. Greater

protection, including seasonal prohibition of most industrial activities, should be extended to the *Annual Calving Area* defined as the area used by calving caribou in any given year. Because important shifts in the location of calving grounds usually occur over several years (Figs. 3 and 4), an acceptable compromise between maximum protection and the delays imposed by legislative processes may be to extend the protection to areas used as annual calving grounds over a period of 3–5 years (Fig. 6). The boundaries of these areas could then be reviewed every 3–5 years depending on changes in the location of calving grounds and population demography, compared with actual locations of parturient caribou, and modified as required.

There is almost no legal protection of caribou calving grounds in Canada outside Québec (Hummel and Ray, 2008). The legal protection of calving range in Québec is limited to the period of use by caribou, 15 May to 31 July. Outside that period, there is no legal constraint on human activities that can potentially affect caribou habitat. Currently, several human activities occur year-round within (outside the period of protection) and in the vicinity of Wildlife Habitats: traditional aboriginal hunting and other activities, ecotourism, outfitting, mining exploration and exploitation (Québec Government, 2009), research and surveying for the development of new parks and protected areas (Québec Government, 2011b). We suggest that constraints on human activities within the Wildlife Habitat should be permanent, to prevent degradation of calving range. Migratory caribou generally avoid industrial sites, roads, pipelines and buildings (Griffith et al., 2002; Reimers et al., 2007; Vistnes and Nellemann, 2008), and move away from vehicles and aircraft (Wolfe et al., 2000). Human disturbance from industrial activities results in displacement of concentrated calving areas, reducing the use of high-quality foraging areas (Wolfe et al., 2000; Vistnes and Nellemann, 2001; Haskell et al., 2006; Reimers et al., 2007). Griffith et al. (2002) predicted a reduction in calf survival if disturbance from oil development displaced calving areas of the Porcupine caribou herd. In saiga antelope, Singh et al. (2010) showed that human disturbance can affect calving site selection, overriding environmental factors. We therefore suggest year-round protection of calving grounds from habitat modifications that could prevent caribou from accessing and using calving grounds, and complete protection of calving caribou from human disturbance.

Protection of migratory populations often involves international or inter-jurisdictional agreements (Shuter et al., 2011). Co-management boards have identified an urgent need to jointly manage migratory caribou herds in western Canada and Alaska (BQCMB, 2004; CARMA, 2011). The protection of calving grounds initiated by the Québec government should therefore be matched by similar initiatives by the Newfoundland-Labrador and Nunatsiavut governments, particularly for the RG herd that ranges over all three jurisdictions during calving. Concerted efforts of decision makers are critical as the designation of Wildlife Habitat or any other legislated land protections necessitate substantial time, resources and legislative activity. Considering the large areas covered by calving grounds of most migratory caribou herds in North America and the natural resources potentially present on these ranges, concerted efforts will be required to successfully protect calving grounds of migratory caribou.

The protection of calving grounds should be regularly updated to confront possible novel threats (Wilson et al., 2007) and ongoing environmental change (Sharma et al., 2009; Wiens and Bachelet, 2010; Conroy et al., 2011; Singh et al., 2010). As suggested for many migratory species, the conservation of caribou must focus on reducing human disturbance and preventing range destruction (Bolger et al., 2008; Gunn et al., 2008; Singh and Milner-Gulland, 2011). This is particularly relevant considering current plans for major developments in the north of Québec, including new

infrastructures, industrial exploration and exploitation, and the creation of new national parks (Plan Nord: Québec Government, 2009).

Effective conservation is hindered by our limited understanding of animal movement patterns in all parts of their seasonal distributions and of the drivers of migration (Singh et al., 2010). Other seasonal ranges of migratory caribou may be highly sensitive to disturbances, such as migratory routes (Shuter et al., 2011) and winter ranges near human infrastructure (Russell et al., 2002). Habitat degradation and fragmentation caused by human development and activities are known to disturb migratory patterns of ungulates (Harris et al., 2009). Similarly to calving grounds, winter ranges have a limited and relatively well-defined geographical extent, often with high densities of animals, but are not targeted by legislated protection. Future studies should focus on identifying the key components of migratory routes and winter ranges used by migratory caribou.

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