

Mapping the distribution of a prey resource: neonate caribou in Newfoundland

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The recently diminished caribou (*Rangifer tarandus*) population in insular Newfoundland, Canada, has been severely limited by predation on newborn calves. These neonates are patchily distributed on the landscape; therefore, to adequately understand predator–prey interactions, the temporal and geographic extent of the distribution of caribou calves must be identified so that current areas with calves can be differentiated from areas without calves. We used telemetry locations of 309 caribou calves and 100 adult females from 4 herds, 2008–2010, to estimate the spatiotemporal distribution of caribou calves during the time when they were most vulnerable to predation, to evaluate the predictability of the calf resource among years, and to assess the degree of aggregation during calving. Patterns of calf distribution were predictable in time and space from year to year, with an average distributional overlap of 68% between years. The dispersion of female caribou during calving varied among herds from highly aggregated (8% and 20% of herd range) to more dispersed (50–70% of herd range). Postcalving (up to 9 weeks) distributions also varied among herds; the 2 more-dispersed herds remained sedentary, whereas both highly aggregated herds migrated away from their calving grounds at the end of June. The most-aggregated herd remained so as it migrated from its calving ground, whereas the less-aggregated herd spread out and moved in a variety of predictable directions. Dispersion and movement patterns varied with forest cover; herds with less forest cover in their range were more aggregated and migratory than herds with more forest cover.

Key words: calving, caribou, dispersion, distribution, mortality, predator, prey, *Rangifer*, resource, telemetry

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Quantifying the variation in the spatiotemporal distribution, dispersion, and predictability of resources on a landscape is important because divergent patterns are likely to influence the spatial organization and abundance of consumers differently (Wilmers et al. 2003; Eide et al. 2004; Yang et al. 2010). The response of consumers may vary depending upon their vagility and social structure (Wilmers et al. 2003), and differential effects may be especially pronounced when resources are pulsed (Ostfeld and Keesing 2000; Wilmers et al. 2003).

Generalist consumers that live communally and are wide-ranging may be able to more effectively exploit aggregated and ephemeral resource pulses than solitary, specialized, and sedentary foragers (Ostfeld and Keesing 2000; Wilmers et al. 2003).



Caribou (*Rangifer tarandus*) calves are highly vulnerable to predation during their 1st weeks of life (e.g., Whitten et al. 1992; Adams et al. 1995). Because of this susceptibility, parturient caribou have developed spacing strategies to alleviate losses (Bergerud 1988, 1996), thus influencing the spatial and temporal dispersion of calves as a prey resource. Sedentary caribou, which are typically found in forested environments, reduce their movements and spread out at calving time to remain inconspicuous (Bergerud 1988, 1996), giving birth in small wetlands (Fuller and Keith 1981; Brown et al. 1986) or on islands (Bergerud et al. 1990). Migratory caribou, which usually inhabit open environments (Bergerud 1988, 1996), limit their risk and exposure to predators by migrating above tree line, where they aggregate on calving grounds and give birth in synchrony (Dauphine and McClure 1974; Bergerud 1996). Migration onto calving grounds may provide additional relief from predation because calving grounds may be situated in areas of low predator density (Fancy and Whitten 1991; Seip 1991) and may offer increased foraging opportunities (Cameron et al. 1992). Both sedentary and migratory ecotypes typically display among-year fidelity to calving and postcalving areas (Gunn and Miller 1986; Fancy and Whitten 1991; Schaefer et al. 2000), which may reduce predation risk (Schaefer et al. 2000; Wittmer et al. 2006).

In Newfoundland, Canada, caribou calves are preyed upon heavily by black bears (*Ursus americanus*), coyotes (*Canis latrans*), Canada lynx (*Lynx canadensis*), and bald eagles (*Haliaeetus leucocephalus*) during the first 9 weeks after parturition (Mahoney and Weir 2009; Trindade et al. 2011; Peek et al. 2012). For 3 herds, annual rates of neonate survival were estimated to be $4\% \pm 5\%$ ($\bar{X} \pm 95\%$ confidence interval) from 2003 to 2007, with predation accounting for 65–89% of all mortalities (Trindade et al. 2011). It has been suggested that increased calf survival is needed to halt or reverse an island-wide population decline, and calf predation is believed to be the proximate limiting factor for the caribou population (Mahoney and Weir 2009; Trindade et al. 2011; Peek et al. 2012). Previous research in Newfoundland indicated that parturient caribou migrated to calving grounds in late March or early April where they gave birth at the end of May in a synchronized 2-week period (Bergerud 1974). During June these female–calf herds were more aggregated than at any other time of the year and remained on the calving grounds until July when they dispersed (Bergerud 1974). Coincident with the population decline in the last 15 years, the calving distributions of some herds in Newfoundland seem to have shifted (Mahoney and Weir 2009), and the Committee on the Status of Endangered Wildlife in Canada has reported that most caribou in Newfoundland have changed from an aggregated to a dispersed calving distribution (Committee on the Status of Endangered Wildlife in Canada 2011).

Our objectives were to identify the distribution of caribou calves from 4 herds in Newfoundland when they were most vulnerable to predation, and to investigate annual variation in the spatial and temporal predictability of the distribution of calves among herds. Because the dispersion and predictability

of prey resources can influence the spatial organization of carnivores (Eide et al. 2004), and because resource selection functions (Boyce et al. 2002; Manly et al. 2002) built without information about the geographic limits of a heterogeneous resource may overpredict the influence of that resource (e.g., Jepsen et al. 2002), determining the geographic extent and location of calving grounds and postcalving distributions will be useful for analyses of predator–prey interactions. We used caribou calf and adult female telemetry data from 3 study areas to identify the distribution of 0- to 9-week-old calves for 4 focal herds from 2008 to 2010, to determine whether herds were aggregated or dispersed during and after calving, to identify when herds migrated from calving grounds, and to evaluate the predictability of the distribution of calves among years. We hypothesized that herds would display high levels of fidelity to calving grounds and postcalving areas among years, regardless of their movement and dispersion patterns (Schaefer et al. 2000), and that within herds there would be little variation in the timing of migratory movements among years (Gunn and Miller 1986). We predicted that the movement and dispersion patterns of herds would vary with the amount of forest cover in each herd's range (Bergerud 1988, 1996). We expected herds living in open ranges to use spacing strategies associated with migratory caribou, and thus be highly aggregated during calving, whereas we anticipated herds living in forested ranges to use spacing strategies associated with sedentary caribou, and thus be more dispersed during calving.

MATERIALS AND METHODS

Study areas and caribou herds.—Our study areas (Fig. 1) encompassed part or all of the range of the La Poile, Middle Ridge, Northern Peninsula, and St. Anthony caribou herds in Newfoundland. The St. Anthony herd originated from a series of introductions of caribou from elsewhere in Newfoundland in 1976, 1977, and 1982 (Bergerud and Mercer 1989), whereas the other 3 herds were historic, indigenous herds. The study landscape was a mixture of bogs, heaths, barrens, and coniferous and mixed forests of balsam fir (*Abies balsamea*), black spruce (*Picea mariana*), tamarack (*Larix laricina*), mountain maple (*Acer spicatum*), birch (*Betula* spp.), and alder (*Alnus* spp.). The La Poile study area was 10,916 km², and included most of the range of the La Poile caribou herd. This herd declined from a peak of approximately 10,000 individuals in the mid-1990s to an estimated 4,000 individuals in 2010 (G. Luther, Department of Environment and Conservation, Government of Newfoundland and Labrador, pers. comm.). The Middle Ridge study area was 13,243 km², and encompassed the entire range of the Middle Ridge caribou herd. This herd decreased from an estimated peak of almost 16,000 individuals in the late 1990s to approximately 7,400 animals in 2010 and was estimated to be the largest herd in Newfoundland. Females from the Middle Ridge herd calved in 2 areas; the majority of calves were born in an area designated Middle Ridge North, but a few hundred caribou migrated south to give birth in an area called Middle Ridge South (Fifield et al.

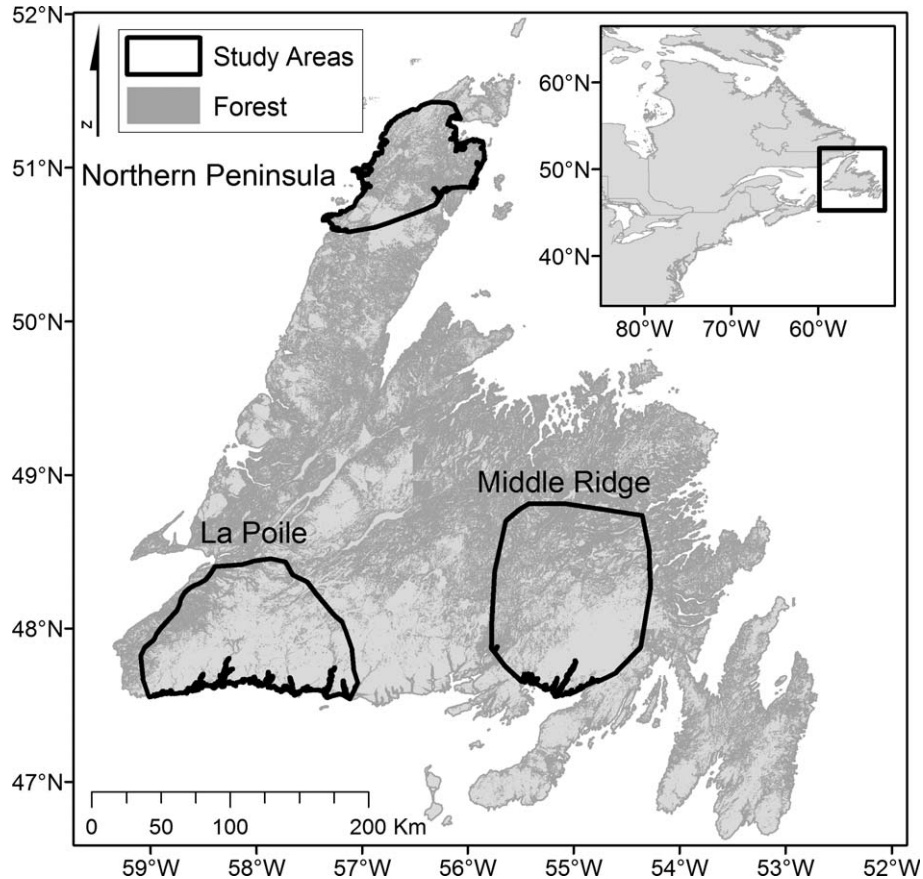


FIG. 1.—Research on caribou (*Rangifer tarandus*) was conducted in Newfoundland, Canada, from 2008 to 2010 in the La Poile, Middle Ridge, and Northern Peninsula study areas.

2013). The Northern Peninsula study area was 5,391 km², and contained the northern portion of the Northern Peninsula caribou herd range, and the entire range of the St. Anthony caribou herd. The Northern Peninsula herd declined from a peak of approximately 9,500 individuals in the early 2000s to an estimated 5,100 animals in 2010. The St. Anthony herd decreased from approximately 8,500 animals in the late 1990s to fewer than 2,300 individuals in 2010. The populations of caribou in our study areas represented approximately 50% of total numbers in Newfoundland.

Caribou calf capture and telemetry.—We captured caribou neonates estimated to be 1–5 days postpartum from late May to early June in the 3 study areas. We searched the study areas by helicopter in the last week of May, and captured calves by hand. We marked captured calves with uniquely numbered ear tags and collected morphological measurements from each calf. We determined the sex of each calf, and estimated its age by noting the degree of hoof wear and umbilicus condition (bloody, wet, dry, or absent). We outfitted calves with expandable, breakaway very-high-frequency radiocollars containing a motion-sensitive transmitter (Advanced Telemetry Systems, Isanti, Minnesota; Lotek Wireless Inc., New Market, Ontario, Canada; Sirtrack, Havelock North, New Zealand; Telemetry Solutions, Concord, California). Collars typically dropped off within 2 years. Transmitter pulse rate

doubled if stationary for > 4 h. Our capture and handling procedures conformed to guidelines established by the American Society of Mammalogists (Sikes et al. 2011).

We monitored caribou calves daily for the 1st week postcapture, 2–4 times per week for the next 5 weeks, once every 5–10 days from 6 weeks postcapture until the end of August, and then on a biweekly or monthly basis thereafter. Monitoring consisted of visual observations of collared calves from a helicopter or fixed-wing aircraft or listening checks conducted at altitude in a helicopter or fixed-wing aircraft to verify collar status (active mode versus mortality mode). The locations of capture sites, slipped collar retrievals, mortality sites, and visual observations of collared calves were estimated with a handheld global positioning system (GPS) unit (Garmin GPSMAP 76CSx; Garmin International, Olathe, Kansas). We considered these locations to be “confirmed locations” because of the high degree of accuracy associated with the GPS unit (typically < 10 m). Conversely, we characterized locations associated with listening checks collected at altitude in aircraft as “unconfirmed locations,” because of their unquantified degree of accuracy.

Adult caribou capture and telemetry.—Adult female caribou from the La Poile herd were captured during October, December, and January–March, 2004–2009, from the Northern Peninsula and St. Anthony herds during October

and February, 2007–2008, and from the Middle Ridge herd during April–May, 2009. Because the calving range of the Northern Peninsula herd extended beyond the borders of our study area, we restricted our analysis to collared females that were located within the study area at least once from 28 May to 31 July. The Newfoundland and Labrador Department of Environment and Conservation captured and immobilized caribou by aerial darting from a helicopter with a mixture of carfentanil (12 mg/kg) and xylazine (0.2 mg/kg) or a mixture of ketamine (2 mg/kg) and xylazine (6 mg/kg) administered intramuscularly with a CO₂-powered pistol (Palmer Cap-Chur Inc., Power Springs, Georgia). Individuals were measured and fitted with an Argos satellite collar (Telonics, Inc., Mesa, Arizona) or a GPS collar (Lotek Wireless Inc.) in La Poile, a GPS collar (Lotek Wireless Inc.) in Middle Ridge, or an Argos satellite collar (Lotek Wireless Inc.) in Northern Peninsula. GPS collars recorded a location every 2 h in La Poile, every 2 h in Middle Ridge from 21 May to 31 July, and every 5 h in Middle Ridge from 1 August to 20 May, and Argos collars acquired locations for 6 h every 4 days. Animal capture and handling procedures conformed to guidelines established by the American Society of Mammalogists (Sikes et al. 2011). To improve the precision of acquired GPS locations we screened successful fixes and removed 2-dimensional locations with dilution of precision > 5 (Lewis et al. 2007). We filtered Argos locations and retained fixes with an estimated accuracy of < 1,000 m (Argos class 1, 2, or 3) that were more than 30 min apart.

Distribution of caribou calves during calving.—To describe the distribution of caribou calves during their 1st weeks of life (but see below for postcalving distribution), we relied on a definition from the literature that characterized annual calving grounds as the area used from the peak of calving (when 50% of females in a herd have calved) until calves begin foraging at 3 weeks of age (Russell et al. 2002; Gunn et al. 2008). We used telemetry locations of adult female caribou and calves from 28 May (Bergerud 1975) until 18 June to delineate the location and geographic extent of the annual calving grounds in the 3 study areas from 2008 to 2010. We excluded calves in cow-calf pairs when both individuals were collared, and adult females that were migrating during this time period (identified by long-distance linear movements > 30 km from wintering grounds to calving aggregations) because we assumed they were traveling without calves (e.g., Fifield et al. 2013). Annually, this removed an average of 3% of collared adult females from each herd (range = 0–13%). To eliminate the discrepancy in the number of locations per individual in the data sets of the 3 collar types (very high frequency [calves], Argos [adult females], and GPS [adult females]), we randomly sampled 1 location/day from each adult female caribou data set, calculated the mean number of confirmed locations per calf in the annual very-high-frequency data sets of each herd from 28 May to 18 June, randomly sampled an equivalent number of locations per adult female from that herd's annual Argos and GPS daily data sets between 28 May and 18 June, and combined the calf locations and subsampled adult female

locations into 1 data set for each herd to use during analysis. We used calf telemetry data alone in Middle Ridge North in 2008 and in Middle Ridge South in 2008 and 2010 because we did not have any adult females collared in those areas in those years. We delineated estimates of the annual calving grounds using 95% fixed kernel density estimators (Worton 1989) with smoothing factors of $0.8 \times$ reference bandwidth (Worton 1995). We used the package *adehabitatHR* (Calenge 2006) in program R version 2.15.2 (R Development Core Team 2012) to generate kernels, and the packages *rgdal* (Keitt et al. 2013), *rgeos* (Bivand and Rundel 2012), *sp* (Bivand et al. 2008), and *spatstat* (Baddeley and Turner 2005) for other spatial operations. We trimmed kernels to the coastline wherever part of a kernel extended over the ocean. To assess fidelity and to identify potential shifts in the geographic distribution of calves between years we estimated the Euclidean distance between the centroids of annual calving grounds (Taillon et al. 2012) and the degree of overlap between pairs of annual calving grounds by calculating an overlap index (OI) derived from Gunn et al. (2008):

$$OI = (2 \times \text{area of overlap} \times 100) / (\text{area of calving ground 1} + \text{area of calving ground 2}).$$

Postcalving distributions of caribou calves.—From 2008 to 2010 more than 87% of all predation mortality on collared calves occurred by 31 July; therefore, we sought to describe the distribution of caribou calves not only during the calving season, but until 31 July as well. We examined the movement patterns of collared caribou to estimate when caribou migrated out of the calving grounds. To confirm our visual assessment in areas and years where we had collars on adult females we estimated the mean proportion of time that these individuals were located within the calving grounds from the peak of calving until migration began and from when migration began until 31 July, by dividing the number of Argos and GPS fixes located inside the calving grounds by the total number of fixes for each adult female. We delineated estimates of the postcalving distribution of calves by using 95% fixed kernel density estimators (Worton 1989) with smoothing factors of $0.8 \times$ reference bandwidth (Worton 1995). In La Poile we again removed the discrepancy in locations per adult female between the Argos and GPS collars using the sampling procedure described above to create a consolidated data set of subsampled locations that was used to delineate postcalving distributions. To assess fidelity and to identify potential shifts in the postcalving distribution of calves we estimated the Euclidean distance between the centroids of annual postcalving distributions (Taillon et al. 2012) and the degree of overlap between pairs of annual postcalving distributions using the overlap index described above (Gunn et al. 2008).

Patterns of dispersion.—We considered a caribou herd to be aggregated during the calving and postcalving periods if the area used by the herd during those periods was < 75% of the entire range of the herd (cf. Dingle 1996:34). We estimated the degree of aggregation in calving ground and postcalving areas (where applicable) for each herd by dividing the area of

TABLE 1.—Number and type of collars deployed on caribou (*Rangifer tarandus*) calves (very high frequency [VHF]) and adult female caribou (Argos and global positioning system [GPS]) in the La Poile (LP), Middle Ridge North (MRN), Middle Ridge South (MRS), Northern Peninsula (NP), and St. Anthony (SA) calving grounds from 2008 to 2010 in Newfoundland, Canada.

Year	Calving ground										
	LP			MRN		MRS		NP		SA	
	VHF	Argos	GPS	VHF	GPS	VHF	GPS	VHF	Argos	VHF	Argos
2008	31	18	9	24		17		13	27	20	21
2009	41	15	9	34	20	11	1	12	20	29	21
2010	27	8		18	14	16		13	13	13	20

multiyear calving ground and postcalving delineations by the area of a herd’s multiyear range delineation. We had few confirmed calf locations after July, so we used only locations of adult females to delineate range estimates, and we pooled data across years because of small sample sizes of adult females in some years. Multiyear calving ground and postcalving delineations were derived by merging annual herd delineations. We delineated multiyear estimates of each herd’s range using all locations of collared females from 2008 to 2010 (2009 to 2010 in Middle Ridge) with 99% fixed kernel density estimators (Worton 1989), using a smoothing factor of $0.8 \times$ reference bandwidth (Worton 1995). In La Poile, we removed the discrepancy in locations per adult female between the Argos and GPS collars using the sampling procedure described above. Subsampled data sets from La Poile were then combined into 1 data set that was used to delineate the herd range. Herd ranges were trimmed to the coastline wherever they extended over the ocean. We used National Topographic Series Geographical Information Systems coverage (Natural Resources Canada 2009) to estimate the percentage of forest cover in each herd’s range. We then assessed whether forest cover influenced patterns of dispersion during calving by using linear regression in program R to test for a relationship between the percentage of forest cover in a herd’s range and the degree of aggregation of that herd on the calving grounds.

RESULTS

Caribou capture and telemetry.—We radiocollared 319 caribou calves from 2008 to 2010 and the Newfoundland and Labrador Department of Environment and Conservation collared 146 female caribou from 2004 to 2009. Data sets from 30 La Poile, 22 Middle Ridge, 27 Northern Peninsula

(located within the study area), and 21 St. Anthony adult female caribou contained locations 28 May–31 July in at least 1 year from 2008 to 2010 and were used in our analysis (Table 1). Data screening to improve precision of GPS collars eliminated < 1% of successful fixes. Filtering of Argos locations eliminated 48% of successful fixes (the large decrease in successful fixes resulted because the collars often acquired > 5 fixes at 1 time).

Distribution of caribou calves during calving.—We excluded 10 calves in cow–calf pairs where both individuals were collared from Middle Ridge North in 2009, as well as all movements of 6 adult female caribou (1 La Poile in 2008, 2 La Poile in 2009, 1 La Poile in 2010, 1 Middle Ridge in 2009, and 1 Middle Ridge in 2010) during 28 May–18 June, and movement segments from 2 caribou (28 May–29 May, La Poile 2009; and 28 May–8 June, Middle Ridge 2009) before estimating annual calving ground kernels because these individuals were migrating from wintering grounds to the calving grounds during those time periods (Table 2). In 2009 we did not collect enough confirmed caribou calf locations in Middle Ridge South to generate a kernel (Seaman et al. 1999), so we used all calf locations (confirmed and unconfirmed) and locations of 1 adult female to generate the Middle Ridge South calving ground kernel in that year. We may have biased the location and size of our calving ground estimate in that year by using unconfirmed locations. There was no indication that the location of the calving grounds for any herds shifted appreciably from 2008 to 2010; the degree of overlap between annual delineations of calving grounds was high (\bar{X} = 65%, range = 44–84%) and centroids were clustered (\bar{X} = 4.0 km, range = 0.9–7.2 km) for all herds in all years (Fig. 2; Table 3).

Postcalving distributions of caribou calves.—During 28 May–31 July, an average of 86% of the Northern Peninsula and

TABLE 2.—Estimated size (km²) of annual delineations of calving grounds, with the number of telemetry locations and collared caribou (*Rangifer tarandus*) used to make delineations for the La Poile, Middle Ridge North, Middle Ridge South, Northern Peninsula, and St. Anthony calving grounds from 2008 to 2010 in Newfoundland, Canada.

Year	Calving ground														
	La Poile			Middle Ridge North			Middle Ridge South			Northern Peninsula			St. Anthony		
	Area	Fixes	<i>n</i>	Area	Fixes	<i>n</i>	Area	Fixes	<i>n</i>	Area	Fixes	<i>n</i>	Area	Fixes	<i>n</i>
2008	706	243	57	311	167	24	162	95	17	1,246	78	40	816	118	41
2009	778	187	63	955	79	43	297	40	12	1,638	93	32	1,579	146	50
2010	523	77	34	822	59	31	552	39	16	1,013	31	26	1,491	38	33

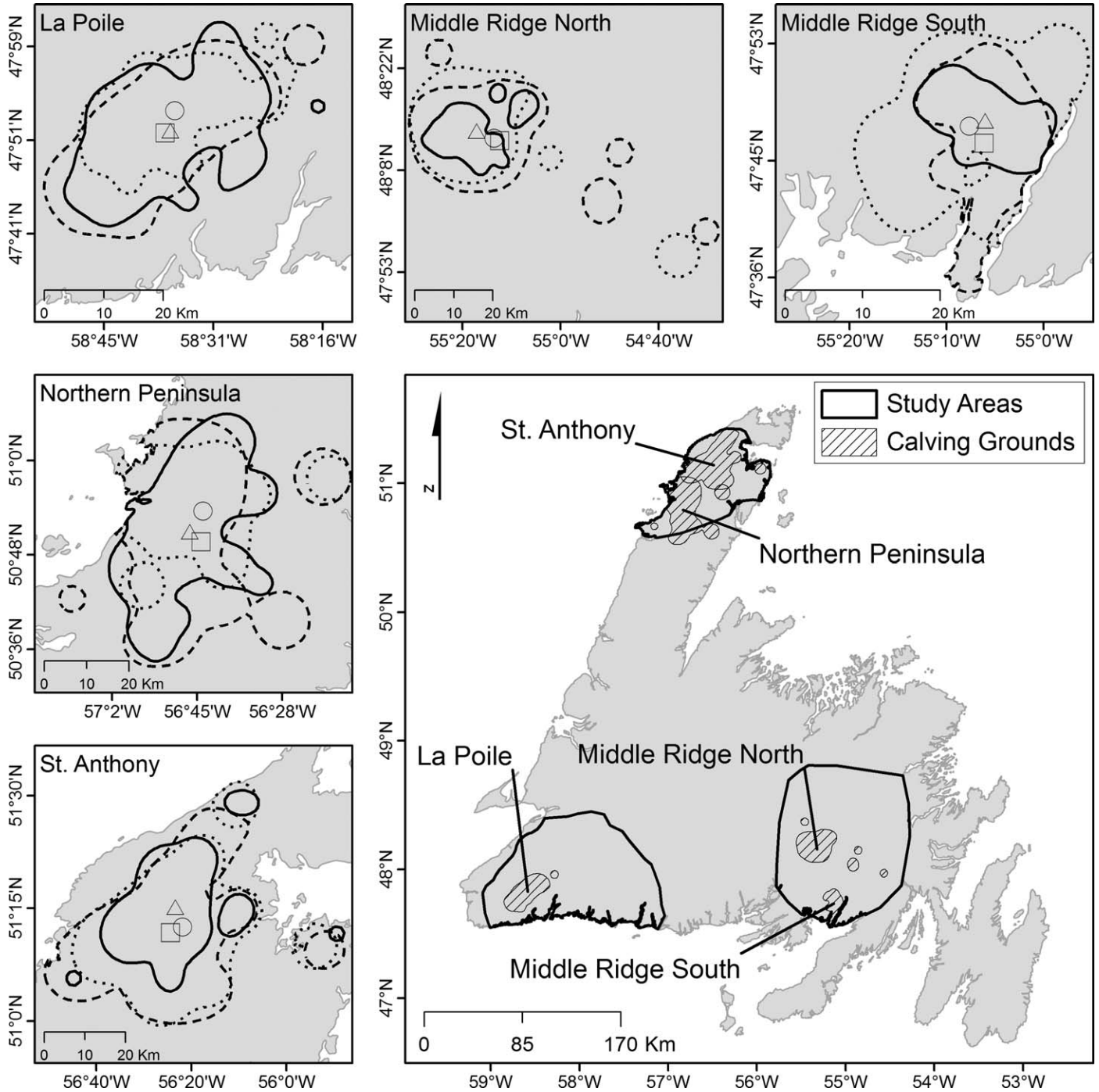


FIG. 2.—Calving ground locations for caribou (*Rangifer tarandus*) from the La Poile, Middle Ridge, Northern Peninsula, and St. Anthony herds in Newfoundland, Canada. Inset maps show annual delineations of calving grounds (2008 [—], 2009 [---], and 2010 [•••]) and centroids (2008 [Δ], 2009 [□], and 2010 [○]).

93% of the St. Anthony herds’ adult female caribou locations were within their herd’s delineation of annual calving grounds, indicating that most caribou remained within the calving grounds during this time period, and therefore, that these delineations described the distribution of the majority of caribou calves in the Northern Peninsula study area through the time of their greatest vulnerability to predators (Table 4). Some adult female caribou in these herds (4 Northern Peninsula in

2008, 1 Northern Peninsula in 2009, 3 St. Anthony in 2008, 1 St. Anthony in 2009, and 1 St. Anthony in 2010) made movements during this period into areas that were part of their herd’s annual delineations of calving grounds in other years, suggesting that a composite layer of annual delineations for each caribou herd may more accurately capture the distribution of adult females and their calves during this time. Indeed, when we combined the annual delineations of calving grounds from

TABLE 3.—Degree of overlap (%) and distance between centroids (km) in parentheses for annual caribou (*Rangifer tarandus*) calving grounds for the La Poile, Middle Ridge North, Middle Ridge South, Northern Peninsula, and St. Anthony calving grounds from 2008 to 2010 in Newfoundland, Canada.

Year	Calving ground									
	La Poile		Middle Ridge North		Middle Ridge South		Northern Peninsula		St. Anthony	
	2008	2009	2008	2009	2008	2009	2008	2009	2008	2009
2009	80 (0.9)		49 (4.8)		67 (2.9)		68 (3.5)		61 (6.3)	
2010	71 (3.4)	69 (4.0)	50 (6.3)	68 (1.5)	44 (2.2)	61 (2.9)	70 (5.8)	64 (7.2)	66 (5.2)	84 (3.2)

2008 to 2010 into a composite delineation for each herd, an average of 98% of telemetry locations for adult females in Northern Peninsula and 99% of telemetry locations for adult females in St. Anthony were within the composite delineations of calving grounds for their respective herds (Table 4). Although the calving grounds of the Northern Peninsula and St. Anthony herds were close together, they were separated by an east–west highway, and we did not document any instances of collared females or calves moving into the calving grounds or postcalving areas of the other herd from 2008 to 2010.

Caribou from the La Poile herd exited the calving grounds en masse at the end of June in each year from 2008 to 2010. From 28 May to 27 June, an average of 92% of all adult female caribou locations were within the annual delineations of calving grounds, indicating that these delineations described the distribution of the majority of caribou calves from the peak of calving until 27 June (Table 4). After 27 June, almost no caribou remained within the calving grounds (Table 4). Because La Poile caribou were continually moving east throughout the month of July we delineated 2 distributions of postcalving areas for the herd from 28 June to 14 July (time 1) and from 15 July to 31 July (time 2; Fig. 3). As they migrated east, the distribution of La Poile caribou was consistent from 2008 to 2010, as evidenced by the clustered centroids of the distributions and the high degree of overlap between pairs of postcalving distributions during the same time period (Table 5; Fig. 3).

Most female caribou remained inside the Middle Ridge North calving grounds until the end of June in each year from 2008 to 2010. From 28 May to 27 June (2009–2010) an average of 90% of all locations of adult females were within the annual delineations of calving grounds, indicating that these delineations represented the distribution of most caribou

calves from the peak of calving until 27 June (Table 4). Collared adult females that were within the primary distribution of the calving grounds from 28 May to 18 June 2009–2010 began exiting the calving grounds in the last week of June and the 1st week of July. Most caribou moved north-northeast–northeast out of the calving grounds (11 of 17 in 2009, and 7 of 12 in 2010), but animals also exited to the south (3 of 17 in 2009, and 3 of 12 in 2010) and north-northwest (2 of 17 in 2009, and 1 of 12 in 2010), or remained within the calving grounds throughout July (1 of 17 in 2009, and 1 of 12 in 2010). Caribou that calved in areas disjunct from the primary distribution remained in those same areas from 28 May to 31 July. Because caribou remained in the same areas until 31 July after exiting the calving grounds, we used 1 kernel in each year to describe the postcalving distribution of calves from 28 June to 31 July (Fig. 3). The postcalving distributions of caribou in Middle Ridge North were consistent from 2009 to 2010; the overlap was high (81%), and the centroids were close (3.9 km).

Because we lacked fine-resolution location data for adult females in Middle Ridge South (except for 1 animal in 2009), and because there were few confirmed locations of collared calves after 18 June, we were unable to identify precisely when caribou began leaving the Middle Ridge South calving ground or to generate a kernel describing their distribution after 18 June (Seaman et al. 1999). In 2008 and 2010, some (5 of 11) caribou calves exited the calving grounds and moved farther south after 18 June (although this area was included in the 2009 annual calving ground delineation). All of these caribou moved north into their annual calving ground delineation sometime in July. In July, a few (3 of 12) calves migrated north into the postcalving distributions of the Middle Ridge North cohort, while the rest remained within the calving ground delineations. A composite layer combining the annual

TABLE 4.—Mean percentage of time (%) adult female caribou (*Rangifer tarandus*) were located within annual delineations of the La Poile (LP), Middle Ridge North (MRN), Northern Peninsula (NP), and St. Anthony (SA) calving grounds from 28 May to 31 July, 2008–2010, in Newfoundland, Canada. Sample size (*n*) and standard errors (*SE*) also are presented.

Year	Calving ground																							
	> 27 June						< 28 June						28 May–31 July											
	LP			MRN			LP			MRN			NP			SA			NP ^a			SA ^a		
<i>n</i>	%	<i>SE</i>	<i>n</i>	%	<i>SE</i>	<i>n</i>	%	<i>SE</i>	<i>n</i>	%	<i>SE</i>	<i>n</i>	%	<i>SE</i>	<i>n</i>	%	<i>SE</i>	<i>n</i>	%	<i>SE</i>	<i>n</i>	%	<i>SE</i>	
2008	26	3	1				26	99	< 1				27	87	5	21	85	5	27	99	1	21	99	1
2009	22	10	1	19	28	6	22	97	1	19	93	3	20	98	1	21	98	1	20	99	1	21	99	1
2010	7	1	4	13	24	4	7	80	4	13	87	4	13	74	6	20	95	3	13	97	1	20	100	< 1

^a Combined 2008–2010 annual calving ground delineation.

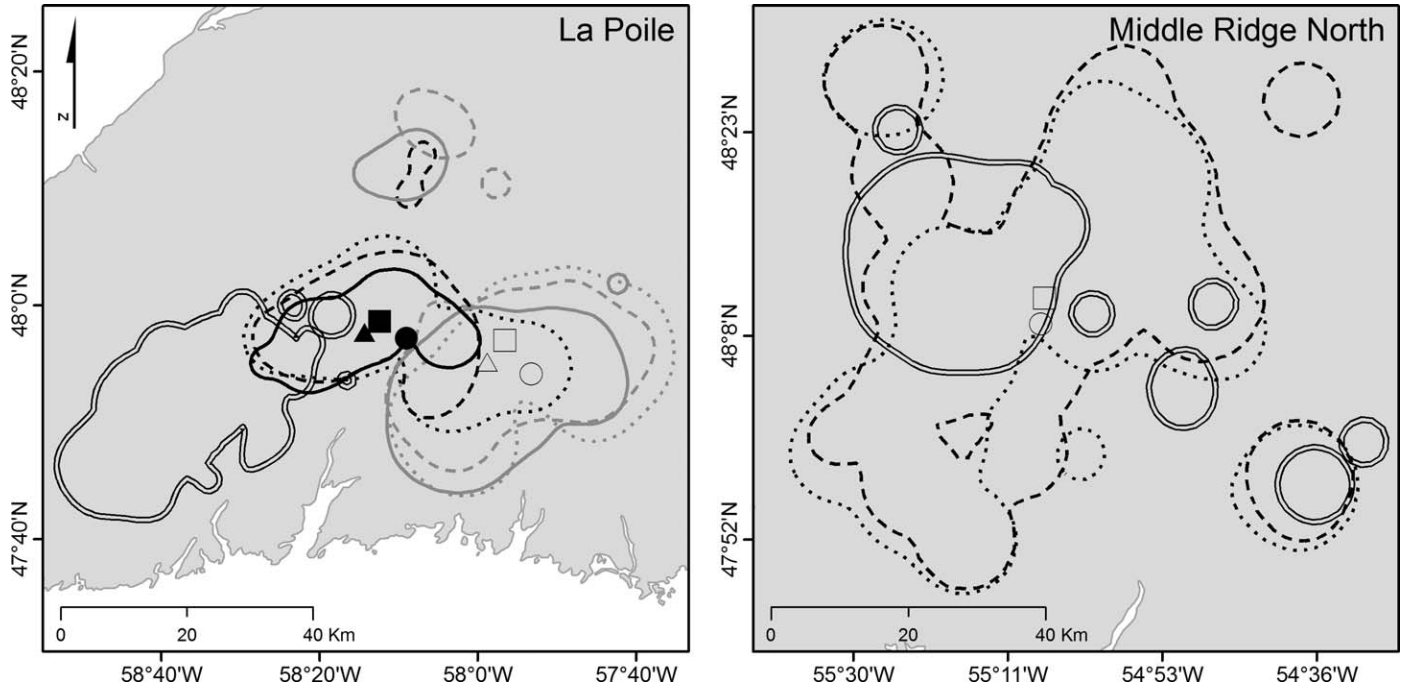


FIG. 3.—Postcalving distributions of caribou (*Rangifer tarandus*) calves from the La Poile and Middle Ridge herds in Newfoundland, Canada, from 28 June to 31 July. In each area a composite of annual delineations of calving grounds from 2008 to 2010 is shown for reference (⇒), with annual delineations of postcalving areas (2008 [—], 2009 [---], and 2010 [•••]) and centroids (2008 [Δ], 2009 [□], and 2010 [○]) in years with available data. In La Poile, time 1 (28 June–14 July) distributions are delineated in black and centroids are filled, whereas time 2 (15 July–31 July) distributions are delineated in gray and centroids are open.

delineations of calving grounds from 2008 to 2010 encompassed all calf locations in Middle Ridge South from 18 June to 31 July, 2008–2010 (except for the locations of calves that migrated north to the Middle Ridge North postcalving areas in July), indicating that this delineation described the distribution of calves remaining in the Middle Ridge South area after 18 June.

Patterns of dispersion.—We restricted our assessment of aggregation in Middle Ridge to Middle Ridge North because we only had 1 adult female collared in Middle Ridge South. All herds were aggregated during calving (La Poile = 8%, Middle Ridge = 20%, Northern Peninsula = 50%, and St. Anthony = 70%). Both southern herds were highly aggregated during calving, with their calving grounds comprising ≤ 20% of their range, whereas the northern herds were more dispersed, with their calving grounds comprising ≥ 50% of their range. The degree of aggregation on the calving grounds declined with increasing forest cover in a herd’s range (degree of aggregation = $1.393 \times (\text{percentage of forest cover}) - 19.417$, $F_{1,2} = 40.71$, $P = 0.024$, $R^2 = 0.953$; Fig. 4). Females from the La Poile herd remained highly aggregated throughout July, using an estimated 8% of their range from 28 June to 14 July, and 12% of their range from 15 July to 31 July. Middle Ridge females that calved in Middle Ridge North were less aggregated after leaving their calving ground, using an estimated 58% of their total range from 28 June to 31 July, which was almost 3 times the area used during calving.

DISCUSSION

As expected, and consistent with findings from previous research (Schaefer et al. 2000; Wittmer et al. 2006; Faille et al. 2010), we observed coarse-scale fidelity in the interannual spatial and temporal distribution of caribou calves in all 4 herds throughout June and July, irrespective of differences in movements and dispersion patterns among herds (Figs. 2 and 3; Tables 3–5). The predictability of this seasonal and ephemeral resource pulse may influence the dispersion and abundance of predators in our study areas. Generalist consumers (i.e., black bears, coyotes, and bald eagles) that can subsist on alternate resources at other times of the year often are able to respond to temporal resource pulses (Wilmers et al. 2003), and may exhibit a positive numerical response, either by increasing population growth or by moving into areas of pulsed resources (Ostfeld and Keesing 2000).

TABLE 5.—Degree of overlap (%) and distance between centroids (km) in parentheses for postcalving distributions of the La Poile caribou (*Rangifer tarandus*) herd in Newfoundland, Canada, during time 1 (28 June–14 July) and time 2 (15 July–31 July), 2008–2010.

Year (time)	2008 (1)	2009 (1)	2010 (1)	2008 (2)	2009 (2)
2009 (1)	74 (3.0)				
2010 (1)	59 (6.7)	75 (5.0)			
2008 (2)	9 (20.0)	23 (18.3)	41 (13.4)		
2009 (2)	12 (22.3)	10 (20.1)	43 (15.7)	74 (4.5)	
2010 (2)	5 (27.2)	5 (25.5)	36 (20.6)	74 (7.2)	77 (6.8)

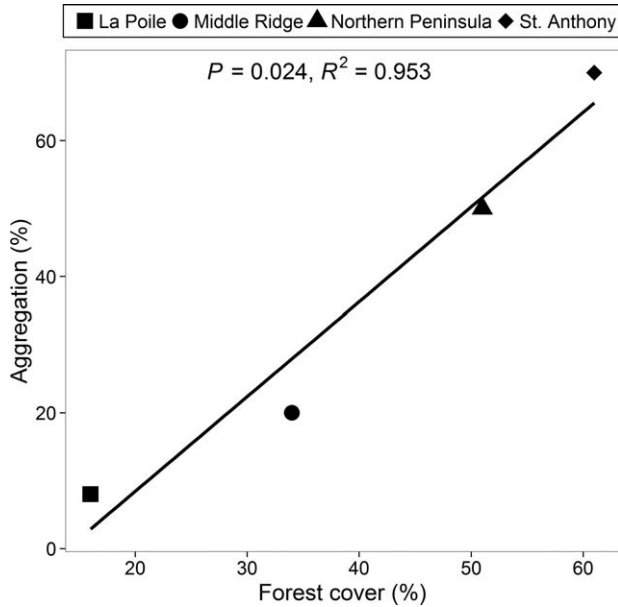


FIG 4.—Relationship between the degree of aggregation (%) on the calving grounds and the amount of forest cover (%) in the range of the La Poile, Middle Ridge, Northern Peninsula, and St. Anthony caribou (*Rangifer tarandus*) herds from 2008 to 2010 in Newfoundland, Canada. Note that estimates for Middle Ridge do not include females that calved in Middle Ridge South, because we did not have cows collared in that area.

Somewhat contrary to the Committee on the Status of Endangered Wildlife in Canada (2011), we found evidence of aggregated distributions during calving, although the degree of aggregation varied among herds. In our study herds the movement patterns of female caribou varied from mostly sedentary to highly mobile, and coincided with dispersion patterns and forest cover (Figs. 3 and 4). As predicted, herds with more forest cover in their range were less aggregated and more sedentary than herds with less forest cover. Animals from the La Poile and Middle Ridge herd occupied the least forested ranges, were highly aggregated during calving, and migrated away from their calving grounds in July, whereas caribou from the Northern Peninsula and St. Anthony herds occupied the most forested ranges, were more dispersed during calving, and remained in their calving grounds throughout June and July. In fact, although their annual range was more expansive than their calving range, most adult females from the Northern Peninsula and St. Anthony herds exhibited no migratory movements at any time during the year from 2008 to 2010. La Poile females inhabited the least forested range and were more aggregated during calving than females from the other herds (Fig. 4). Their movements were highly synchronized in space (Fig. 3) and time (Table 4) as they exited the calving grounds, and they migrated far from their calving ground (Fig. 3). In contrast, females from the Middle Ridge herd lived in a more forested region than La Poile females, and were not as aggregated during calving. Their movements were less coordinated in direction (Fig. 3; “Results”) and timing (Table 4) as they left

the calving grounds, and they spread out, but remained closer to their calving ground, upon exiting (Fig. 3).

Variation in dispersion and movement patterns among herds may have resulted from a combination of differences in the distribution and abundance of forage resources, current levels of predation risk, or, for the 3 indigenous herds, in historic levels of predation risk, all of which were likely to be influenced by the amount of available forest cover. Migratory behavior in caribou may have developed in response to wolves (*Canis lupus*—Bergerud 1988, 1996), which were historically present in Newfoundland, but were extirpated in the 1920s (Mahoney and Schaefer 2002). Migration is thought to be an evolutionary response to temporal and spatial variation in resources designed to increase foraging opportunities or decrease predation risk (Fryxell et al. 1988). Similarly, aggregated distributions of large herbivores may result because of the advantages they confer; aggregations may allow individuals to maximize energy intake (e.g., the “forage-maturation hypothesis”), dilute predation risk, and increase the probability of detecting a predator (Fryxell 1991). It is quite surprising that, within a relatively confined area (Newfoundland is 108,860 km²), we observed such divergent dispersion and movement patterns among caribou herds of similar genetic stock (Wilkerson 2010). Clearly, an opportunity awaits to investigate the trade-offs between foraging and predation risk that are likely responsible for patterns in the spatiotemporal dispersion of caribou in Newfoundland.

Regardless of the mechanisms, differences in movement and dispersion patterns of calves could result in dissimilar predator–caribou interactions among the 3 study areas. In the Northern Peninsula, predators could prey on calves from both herds throughout their period of peak vulnerability, and nonresident consumers would have more time to recruit (Wilmers et al. 2003) from surrounding areas because the distribution of calves remains unchanged during that period. In La Poile, and to a lesser extent, Middle Ridge, calf predators would have to move with the herds; otherwise, most individuals preying on calves in June likely are different than the individuals preying on calves in July (depending on the size and configuration of predators’ home ranges during that time). Similarly, nonresident consumers would have a smaller spatiotemporal window in which to respond to the pulsed resource of calves from these herds, which may disproportionately favor recruitment of more vagile and social predator species in these areas (e.g., Wilmers et al. 2003). Of the primary calf predators in our study areas, bald eagles are likely to have the largest foraging radii, and are the most social, often roosting communally, where information about food resources may be shared (Buehler 2000; Wilmers et al. 2003). Conversely, nonresident female lynx (Vashon et al. 2008), territorial coyote pairs (Gese et al. 1988; Nilsen et al. 2005), and female black bears (Garshelis et al. 1983; Benson and Chamberlain 2007) may be less likely to recruit to these herds because of their social structure (Sandell 1989) and smaller foraging radii. We might expect male bears (Garshelis et al. 1983; Benson and Chamberlain 2007) and lynx (Vashon et al.

2008), transient coyotes (Gese et al. 1988), and dispersing subadult coyotes, bears (Bowman et al. 2002), and lynx (Schwartz et al. 2002) to have intermediate recruitment abilities.

Studies that have examined the connection between predators and the distribution of neonatal ungulates have used resource selection functions to model the relative probability of occurrence of ungulate calves using landscape attributes as surrogates for prey resource availability (Bastille-Rousseau et al. 2011; Latham et al. 2011). In ecosystems where ungulate neonates are aggregated and patchily distributed at the landscape scale, however, areas with young calves must be identified and differentiated from areas with few or no calves; otherwise resource selection functions assessing predator–prey interactions may produce spurious results if the suite of habitat characteristics associated with concentrations of calves can be found elsewhere on the landscape (e.g., Jepsen et al. 2002). Although we identified a large amount of variation in the degree of dispersion, all focal herds exhibited some level of aggregation during and after calving (Fig. 4; “Results”); consequently, resource selection functions evaluating the influence of young calves on the predator guild within our study areas would need to be geographically and temporally constrained by our distribution estimates to avoid the possibility of overpredicting the potential significance of caribou calves as a prey resource.

When certain areas in space and time play a critical role in the survival and recruitment of a species of conservation concern, the ability to identify these areas is essential for population management. Caribou in Newfoundland seem to be limited by calf predation that occurs primarily from birth to 9 weeks of age; if these numerical and predation trends are not quickly reversed, the population may be considered for Threatened or Endangered listing at the federal and provincial levels (Mahoney and Weir 2009). Our estimates of the distribution of caribou calves from 0 to 9 weeks of age coincided with the areas where most caribou calves from 4 of the 5 largest herds in Newfoundland were killed by predators, and therefore, where management interventions, such as predator reduction, could be focused. The scale of such interventions would likely need to be much larger than our distribution estimates, however, to account for the extensive movements of predators (e.g., Mosnier et al. 2008). Overlap between the distribution of predators and prey is a fundamental requirement of the predation process (Lima and Dill 1990); thus, the data presented here can be incorporated into further research, perhaps with GPS collars on predators, to identify the spatial scale over which predator–calf interactions operate.

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