Causes and Consequences of Broad-Scale Changes in the Distribution of Migratory Caribou (*Rangifer tarandus*) of Southern Hudson Bay

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ABSTRACT. Understanding the factors driving changes in species distributions is fundamental to conservation, but for wide-ranging species this is often complicated by the need for broad-scale observations across space and time. In the last three decades, the location of summer concentrations of migratory caribou (*Rangifer tarandus*) in southern Hudson Bay (SHB), Canada, has shifted south and east as much as 500 km. We used long-term data (1987–2011) to test two hypotheses that could explain the distribution shift: forage depletion and anthropogenic disturbance. Over time and space, we compared the body size of live-captured adult female caribou, dietary quality from fecal nitrogen in July, the location of VHF- and GPS-collared female caribou in July, distribution of all-terrain vehicle (ATV) tracks and caribou tracks in August, and the proximity of collared caribou to sections of the coast with higher ATV activity in spring and summer. The forage depletion hypothesis was supported by greater body size and dietary quality in caribou of the eastern portion of SHB than in western SHB animals in 2009–11. The anthropogenic disturbance hypothesis was supported by the negative correlation of the distributions of ATV tracks and caribou tracks on the coast in 2010 and the fact that caribou avoided areas with ATV activity by 10–14 km. In 1987, collared caribou were observed largely along the coast in western SHB in mid-July, while in 2009–11, they were inland in western SHB and along the coast in eastern SHB. While these locations demonstrate a substantial change in summer distribution over three decades, we were unable to differentiate between forage depletion and anthropogenic disturbance as a single causal factor of the distribution shift.

Key words: anthropogenic disturbance; body size; diet; distribution; fecal nitrogen; forage; migratory caribou; Hudson Bay; *Rangifer tarandus*; range shift

RÉSUMÉ. La compréhension des facteurs qui influencent les changements caractérisant les distributions des espèces est fondamentale aux efforts de conservation, mais pour les espèces dont l'aire de distribution est étendue, ce principe est souvent compliqué par la nécessité de faire des observations à grande échelle, dans le temps et dans l'espace. Au cours des trois dernières décennies, l'emplacement des concentrations estivales du caribou migrateur (*Rangifer tarandus*) dans le sud de la baie d'Hudson (SBH), au Canada, s'est déplacé vers le sud et vers l'est dans une mesure de 500 km. Nous nous sommes appuyés sur des données de longue haleine (1987–2011) pour mettre à l'épreuve deux hypothèses susceptibles d'expliquer ce changement en matière de distribution, soit l'appauvrissement du fourrage et la perturbation anthropique. Au fil du temps et de l'espace, nous avons comparé la taille du corps des caribous femelles adultes capturées vivantes, la qualité de leur alimentation à partir de l'azote fécal en juillet, l'emplacement des femelles portant un collier de type VHF ou GPS en juillet, la répartition des traces de véhicules tout terrain (VTT) et des pistes de caribou en août de même que la proximité des caribous portant un collier aux tronçons de la côte où la présence de VTT est plus grande au printemps et à l'été. L'hypothèse de l'appauvrissement du fourrage a été étayée par la plus grande taille du corps et la qualité de l'alimentation du caribou de la zone est du SBH comparativement à celles du caribou de l'ouest du SBH entre 2009 et 2011. Pour sa part, l'hypothèse perturbation anthropique a été appuyée par la corrélation négative caractérisant la répartition des pistes de VTT et des traces de caribou sur la côte en 2010 et par le fait que les caribous sont restés à l'écart des zones fréquentées par les VTT dans une mesure de 10 à 14 km. En 1987, des caribous portant un collier ont été observés en grand nombre le long de la côte ouest du SBH à la mi-juillet, tandis que de 2009 à 2011, ils ont été repérés à l'intérieur des terres dans l'ouest du SBH et le long de la côte est du SBH. Bien que ces emplacements indiquent un important changement en matière de distribution estivale au cours de trois décennies, nous n'avons pas été en mesure de faire une distinction entre l'appauvrissement du fourrage et la perturbation anthropique en tant que facteur causal unique du changement de distribution.

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INTRODUCTION

Understanding the factors governing the distribution of species is increasingly relevant in the face of accelerating habitat degradation, heightened human disturbance, and climate change, the major drivers of species loss, endangerment, and range retraction (Wilcove et al., 1998; Laliberte and Ripple, 2004; Venter et al., 2006). Caribou (*Rangifer tarandus*, also known as reindeer) is a highly mobile, circumpolar ungulate that exemplifies both the value and the challenges of understanding distributional changes. Migratory females typically move in late spring and summer to the tundra, where insect harassment and predation risk are lower and forage is richer; these adaptations enhance reproductive success (Garner and Reynolds, 1986; Bergerud et al., 1990; Bergerud, 1996; Hinkes et al., 2005). Many herds demonstrate fidelity to calving and summering areas (Gunn and Miller, 1986; Schaefer et al., 2000), but the boundaries of these areas may gradually shift from year to year and change substantially over the long term (Gunn et al., 2012; Taillon et al., 2012). Caribou may disappear from whole segments of their range (Bergerud et al., 2008). At present, many caribou populations are declining (Vors and Boyce, 2009), but their large and often inaccessible ranges make it challenging to understand the drivers of these distributional changes.

The literature stresses two reasons for long-term changes in the location of migratory caribou summering areas. First, density-dependent relationships, such as increases in population density and resulting changes in forage resources and other factors such as parasitism or disease, may cause distribution shifts (Haber and Walters, 1980; Bergerud et al., 2008; Gunn et al., 2012). Caribou may shift ranges in response to reductions in forage quantity (Messier et al., 1988; Couturier et al., 1990) or quality (Klein, 1970; Gordon and Illius, 1989; Wolfe, 2000). A decline in the quality of the summer range can result in delayed arrival, reduced calf survival, and earlier departure from summering areas (Crête and Huot, 1993; Mahoney and Schaefer, 2002b; Couturier et al., 2009). Over decades, body size and population size can also reflect density-dependent fluctuations in available forage biomass (Crête and Huot, 1993; Mahoney and Schaefer, 2002b; Couturier et al., 2010; Mahoney et al., 2011).

Second, anthropogenic disturbance can alter migration routes, behaviour, and distribution (Nellemann et al., 2003; Dahle et al., 2008; Stankowich, 2008). Avoidance behaviour, even in response to disturbance occurring several kilometres away, has been related to jet noise (Harrington and Veitch, 1992), roads and industrial developments (Nellemann and Cameron, 1998; Dyer et al., 2001; Mahoney and

Schaefer, 2002a; Cameron et al., 2005; Joly et al., 2006), snow machines (Mahoney et al., 2001; Seip et al., 2007), and other recreational activity (Nellemann et al., 2000, 2010). In areas affected by multiple human activities, extirpation can result (Schaefer, 2003; Vors et al., 2007). Understanding changes in distribution often requires observations over decades and thousands of square kilometres, and these data are rare.

We used three decades of data collected by the Ontario Ministry of Natural Resources to examine the factors underlying spatial shifts in southern Hudson Bay (SHB) caribou. We tested the hypotheses that forage depletion or human disturbance caused the distribution changes. To assess these hypotheses, we divided the study area into three sub-areas (East, Centre, and West; Fig. 1) that corresponded to three major migration patterns (Newton, 2012) and divided the study duration into two periods, early (pre-2000) and late (post-2000). We examined several lines of evidence (body size, diet quality, location of caribou, and distributions of all-terrain vehicle and caribou tracks) across space, over time, or, when possible, both (Table 1).

MATERIALS AND METHODS

Study Area

The study area in SHB (approximately 300 000 km²) extends from the Nelson River, Manitoba, to Cape Henrietta Maria, Ontario, and south, including much of the Hudson Plains Ecozone and northern portions of the Boreal Shield Ecozone (Fig. 1). In Canada, ecozones represent broad ecological and physiographic regions that are further divided into ecoregions on the basis of biophysical and physiographic differences (Environment Canada and Agriculture and Agri-Food Canada, 2012). A 3–25 km wide band of treeless coastal mudflats, tidal marshes, beach ridges, tundra and open fens characterizes the coastal region; hereafter, we refer to this maritime tundra habitat in the Coastal Hudson Bay Lowland as the coast (Fig. 1). The coastal fens are interspersed with small, freshwater bodies and elevated beach ridges (Riley, 2003). Beach ridges progress southward from sand and gravel, to tundra heath, to treed communities dominated by white and black spruce (*Picea glauca* and *P. mariana*) and tamarack (*Larix laricina*, Rowe, 1972). Away from the coast, open boreal woodlands of black spruce and tamarack are gradually replaced by closed stands of black spruce in the Boreal Shield Ecozone (Rowe, 1972). Interspersed throughout are extensive peat plateaus and palsas intergrading into open and treed bogs, fens, and conifer swamps. In the centrally
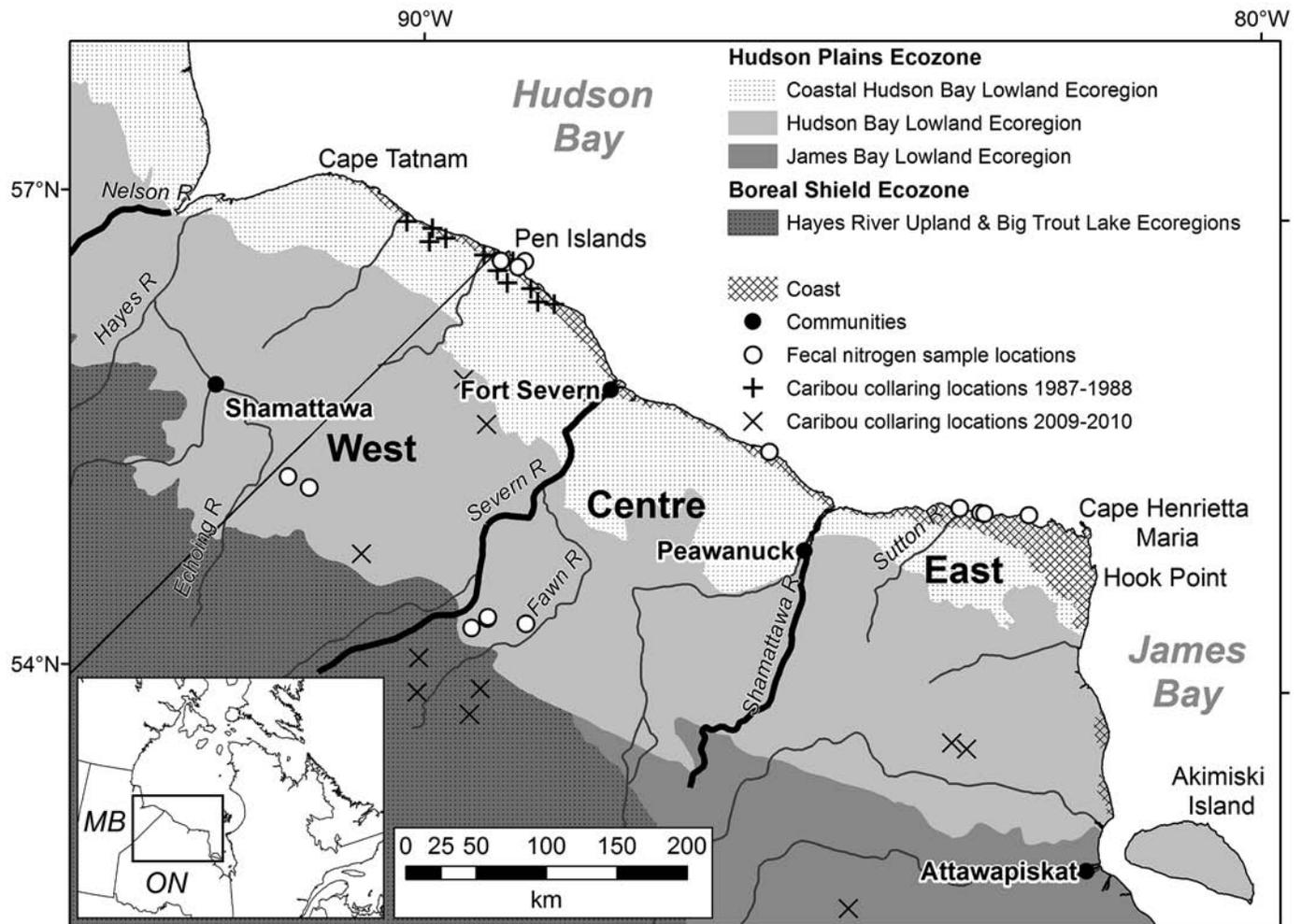
FIG. 1. The southern Hudson Bay study area, encompassing 95% of the area used annually by migratory SHB caribou in northern Ontario and northeastern Manitoba, Canada, in 1987–90 and 2009–11. Also shown are ecozones, ecoregions (Environment Canada and Agriculture and Agri-Food Canada, 2012), coast, fecal sampling locations, and caribou collaring locations. Three sub-areas—West, Centre, and East—are located between rivers represented by thicker lines. "Coast" refers to the area north of the southern boundary of tundra heath of Far North Land Cover Version 1.2, 2005–11 and the exposed land cover class (NRC, 2009).

located community of Peawanuck (Fig. 1), January low temperatures averaged −28.1°C and July highs averaged 20.6°C, 1995–2010 (EC, 2012).

Human disturbance in SHB is minimal, but has likely increased over time coincident with increased mobility, construction and use of winter roads, and population growth (OMNR, 1985; Abraham et al., 2011). In Fort Severn and Peawanuck, numbers of residents increased by ~ 150% from 1981 to 2006 (Statistics Canada, 2011), and harvesting practices have changed (Berkes et al., 1995; Tsuji and Nieboer, 1999). Over the decades, First Nations hunters have shifted their mode of transportation in the snow-free season. During the 1980s, they traveled primarily by freighter canoe (K.F. Abraham, unpubl. data). The rise of ATV sales in Canada reached a high volume only after the early to mid-1980s (Motorcycle and Moped Industry Council of Canada, unpubl. data). In the early period, ATV traffic in the West and Centre was very rare, but it increased in frequency and extent thereafter, to the point that these vehicles are now the most common form of transportation for

summer hunting activities (K.F. Abraham, J.E. Thompson, and M.E. Obbard, unpubl. data).

SHB Caribou: Status, History, and Distribution

Migratory (forest-tundra) SHB caribou (*Rangifer tarandus caribou*) bridge a gap between two kinds of caribou: genetically, these animals correspond with woodland (also known as sedentary or boreal) caribou, but in behaviour, they correspond with migratory tundra caribou to the north (McQuade-Smith, 2009; COSEWIC, 2011; Klütsch et al., 2012). The two caribou ecotypes in Ontario are considered to belong to separate designatable units by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC, 2011). In Ontario, SHB caribou migrate north to the Coastal Hudson Bay Lowland and exhibit large post-calving aggregations, while sedentary, forest-dwelling woodland caribou do not migrate long distances and calve alone (COSEWIC, 2011; Berglund et al., 2014). Migrating north just before calving season effectively allows female caribou

TABLE 1. Hypotheses, predictions, and data relating to the redistribution of southern Hudson Bay (SHB) caribou during the early and late periods.

Hypothesis: Forage depletion in the traditional summering area in the coastal West caused the redistribution of caribou in SHB	
Predictions	**Supporting data, area and dates**

Caribou during the late period in the West will have smaller body size compared to the early period in the West and the late period in the Centre and East	Hind foot length of collared female caribou
	    Early period: West (1987–88)
	        Hind foot length of VHF-collared caribou
	    Late period, West (2010), Centre & East (2009)
	        Hind foot length of GPS-collared caribou

During the late period, the nutritional status of caribou in the West will be lower than in the Centre and East	Percent nitrogen (proxy for forage quality) of scats collected during caribou abundance surveys *Late period: West, Centre & East (2011)*

Caribou in the late period in the West will migrate away from the coast earlier than those in the early period did; caribou in the late period in areas with higher quality forage will remain on the coast longer, as early period caribou did in the West	Location of collared female caribou in mid-July
	    Early period: West (1989)
	        Percent of VHF-collared caribou in the Coastal Hudson Bay Lowland Ecoregion on July 12 compared to elsewhere in sub-area
	    Late period: West (2010–11), Centre & East (2009–11)
	        Percent of GPS-collared caribou in the Coastal Hudson Bay Lowland Ecoregion on 9–15 July compared to elsewhere in sub-area

Hypothesis: Increased anthropogenic disturbance in the West caused the redistribution of caribou in SHB	
Predictions	**Supporting data, area and dates**
Higher densities of ATV tracks along shoreline of SHB will be correlated with lower densities of caribou tracks	Abundance and distribution of ATV tracks and caribou tracks along shoreline and 1 km from shoreline *Late period: West, Centre & East (2010)*

Collared caribou in areas of higher human disturbance on the coast will exhibit reduced use of these areas compared to caribou in coastal areas with less human disturbance	Minimum distance to shore of collared female caribou, April–August
	    Early period: West (1988–89)
	        Locations of VHF-collared caribou
	    Late period: West (2010–11), Centre & East (2009–11)
	        Locations of GPS-collared caribou

to avoid higher densities of their major predator, the wolf (*Canis lupus*), during spring and summer; wolves typically den farther inland and remain close to the den for several months (Heard and Williams, 1992; Bergerud, 1996; Bergerud et al., 2008). Migratory SHB caribou are not considered a species at risk in Ontario.

From the 1700s until the mid-1940s, caribou migrated from wintering areas in the Hudson Bay Lowland Ecoregion and Boreal Shield Ecozone to summering areas as far east as Cape Henrietta Maria and Akimiski Island (Lytwyn, 2002; Magoun et al., 2005). The Ontario Ministry of Natural Resources began monitoring the population of migratory caribou regularly in 1979 through summer coastal aerial surveys, from the Hayes River east to Cape Henrietta Maria and south to Hook Point (Magoun et al., 2005; Abraham et al., 2012). The first aerial survey found 2300 caribou in the West, but no animals in the Centre or East sub-areas (Magoun et al., 2005). A VHF-telemetry study collared migratory female caribou in the West and located them approximately once a month from September 1987 to March 1990. Twenty females were collared from 28 September to 5 October 1987, and four were collared from 7 to 14 June 1988 (Thompson and Abraham, 1994; Abraham and Thompson, 1998). During that time, these caribou summered on the coast and Coastal Hudson Bay Lowland in the West, and moved south to the Hudson Bay Lowland Ecoregion and

Boreal Shield Ecozone in the West in winter (Fig. 2; Thompson and Abraham, 1994; Abraham and Thompson, 1998).

Aerial surveys revealed that the distribution of caribou during summer changed markedly from 1986 to 2011 (Magoun et al., 2005; see Fig. 3). From 1998 to 2003, few caribou were seen on the coast in the West during aerial surveys; more frequent observations of caribou there in 2004–11 (Fig. 3) were likely the result of increased survey effort. During 2009–10, 43 migratory SHB animals were GPS-collared across the study area (Fig. 1; Berglund et al., 2014). From 2009 to 2011, collared caribou in all three sub-areas used the Coastal Hudson Bay Lowland in the summer and moved south to the Hudson Bay Lowland and Boreal Shield Ecozone and James Bay Lowland in the winter (Fig. 2; Newton, 2012). In 2011, an aerial survey tracking the locations of GPS-collared animals found large aggregations of caribou in the West and Centre inland in the Hudson Bay Lowland Ecoregion (Fig. 3; Berglund et al., 2014). In total, 16 638 caribou were observed that year across the study area (Berglund et al., 2014). The only large aggregations at the coast were seen in the East.

Forage Depletion Hypothesis

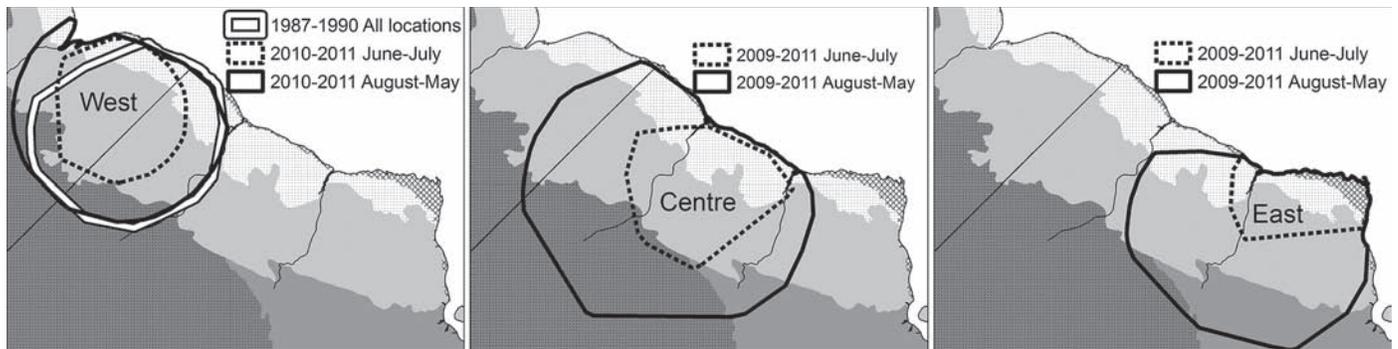**Body Size**: During collaring in 1987–88 and 2009–10, capture personnel measured hind foot length of all

FIG. 2. Minimum convex polygons (90% MCPs) of collared female caribou locations for three sub-areas, West, Centre, and East, based on caribou locations in 1987–90 and 2009–11. Shading, from lightest to darkest, indicates the Coastal Hudson Bay Lowland Ecoregion, the Hudson Bay Lowland Ecoregion, the James Bay Lowland Ecoregion, and the Boreal Shield Ecozone.
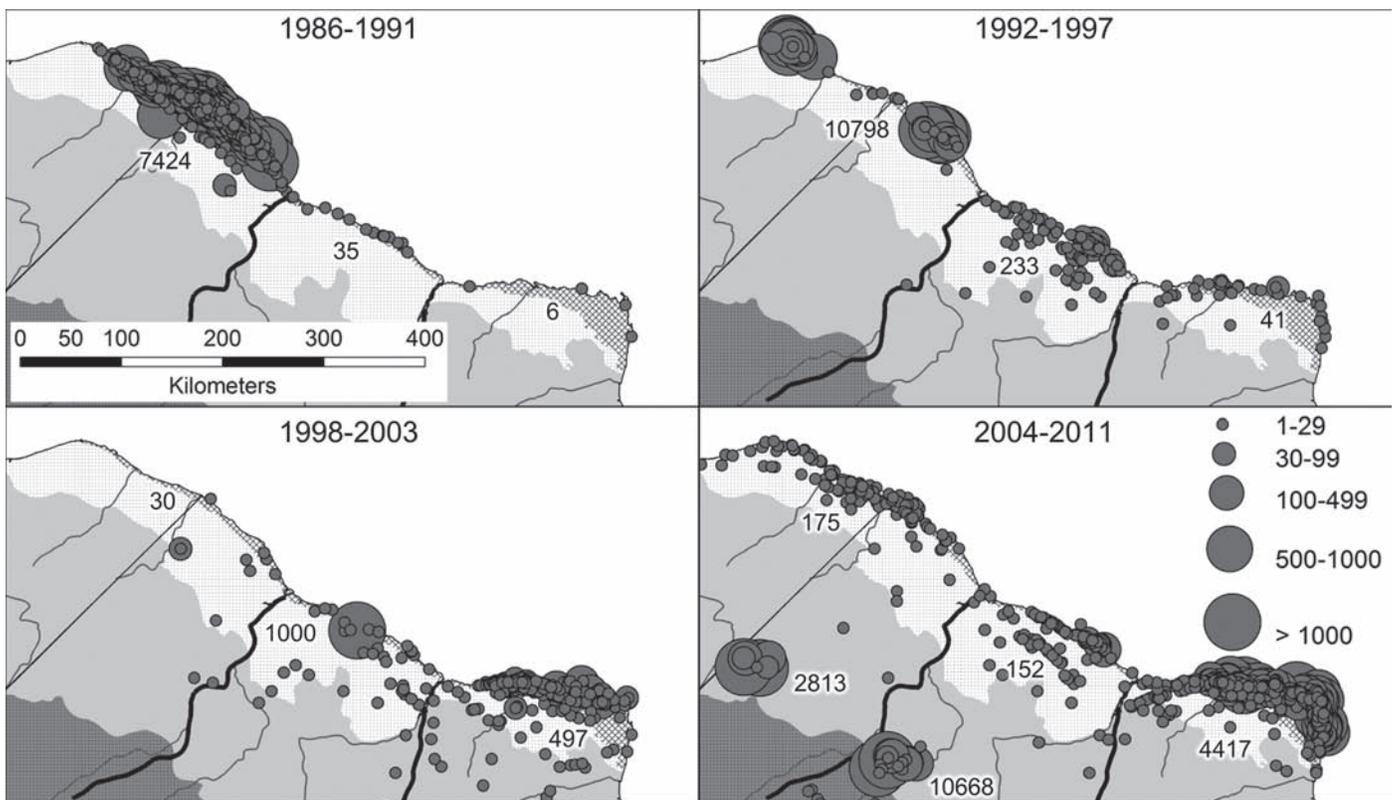

FIG. 3. Summer distribution of caribou across southern Hudson Bay in May–August of 1986–2011, from photographic and incidental aerial surveys (updated from Magoun et al., 2005:118 and Berglund et al., 2014:76–81). Circle size is proportional to the number of caribou observed in a group (see legend). Numbers on map indicate peak caribou abundance during the period indicated on each panel, given for each sub-area (and for the inland survey in 2011 in the West and Centre; Newton, 2012).

VHF- and GPS-collared female caribou, from the point of the hock to the tip of the hoof (Thompson and Abraham, 1994; Berglund et al., 2014). We measured adult females more than two years old; *Rangifer* body size is asymptotic after three years of age (Gerhart et al., 1997; Knott et al., 2005). We hypothesized that those in the West in the early period and in the Centre and East in the late period would have larger body sizes than those in the West in the late period (Table 1). We used a one-way ANOVA and post-hoc comparisons with $\alpha = 0.05$ (STATISTICA 7, StatSoft, 2004, Tulsa, Oklahoma) to determine whether significant differences in body size existed through time and across space.

Dietary Quality: Fecal nitrogen has been used as an accurate proxy for dietary nitrogen in more than 150 studies worldwide (Leslie et al., 2008) and is a valid indicator of forage quality (Leslie and Starky, 1985, 1987), including that of caribou forage (Bergerud, 1996; Barten et al., 2001). We expected that in the late period, dietary nitrogen for caribou in the Centre and East would be lower than in the West (Table 1). We collected fresh (damp to wet) fecal samples from each sub-area from 12 to 27 July 2011 (Fig. 1), during the period of the year that is the most energetically taxing for female caribou (Sadleir, 1984; Clutton-Brock et al., 1989). Samples represented all locations where caribou

were located during aerial surveys (Berglund et al., 2014). Eight samples collected at the coast in the Centre were dry; however, nitrogen content remains stable for weeks even when exposed to the elements and most insects (Leslie et al., 2008). Fecal nitrogen values for caribou do not differ between sexes given similar habitat (Bergerud, 1996), caribou have a varied diet (Bergerud, 1977), and we did not collect samples over multiple years or seasons, so we avoided biases resulting from monotypic diets and inappropriate timing of collection (Leslie et al., 2008). Samples (complete pellet groups) were placed into separate plastic bags and kept frozen until further analysis.

The entire sample was air-dried at room temperature for four days, ground with a coffee grinder (thoroughly cleaned between samples) to pass through a 1 mm sieve, and dried at 60°–63°C for 24 h. We determined nitrogen content using 250–300 mg of the sample with the Dumas combustion method, which is comparable to the Kjeldahl procedure (Etheridge et al., 1998), and an Elementar Vario-Max CN analyzer (Ontario Forest Research Institute, Sault Ste Marie, Ontario). To ensure precision, a blank was run after each sample; 10% of samples were run in duplicate to ensure consistent results were obtained (within 10% range), and 15 standard reference samples were run alongside caribou samples. Differences in percent fecal nitrogen among locations were examined using ANOVA, followed by post-hoc Tukey's HSD means tests.

Location of Caribou Mid-July: In mid to late summer, collared female SHB caribou exhibited large-scale movements away from the Coastal Hudson Bay Lowland in both the early and late periods (Newton, 2012). We hypothesized that if forage on the coast were limited in the late period, females would migrate inland sooner in the fall than they had done in the early period (Table 1). We inspected locations of female caribou on 12 July 1989 (Thompson and Abraham, 1994) and 9–15 July 2009–11 to determine whether fewer caribou remained on the coast mid-July (and therefore migrated earlier) in the late period than in the early period. Because of the coarse spatial and temporal resolution of telemetry data from 1987–90 (Thompson and Abraham, 1994), especially the lack of summer observations of VHF-collared caribou, it was not feasible to make more detailed comparisons of caribou movements over time.

Anthropogenic Disturbance Hypothesis

Distribution of ATV Tracks and Caribou Tracks: We quantified the distribution of ATV tracks and caribou tracks along the coast on 1–2 August 2010. We flew transect lines covering the entire northern shore of Ontario in a Eurocopter A-star 350 helicopter at 0 km and 1 km from shore at 150–170 km/h and 75–90 m above ground level, following the same route as aerial surveys for coastal population abundance surveys (Abraham and Thompson, 1998; Magoun et al., 2005; Berglund et al., 2014). Because caribou and ATVs may travel in single file, it was not possible

to determine how many animals or vehicles were associated with each track; we assumed, nevertheless, that the number of caribou or ATVs was correlated with the number of tracks. At 0 km from shore, the majority of observed tracks were in sand or mud and therefore closely reflected recent caribou and ATV presence in 2010. At 1 km from shore, tracks were observed both as recent depressions in mud and sand and as trails worn into vegetation; thus, observations at this distance represented the distribution of caribou and ATVs in 2010 as well as historical movements. An observer recorded the number of ATV and caribou tracks within each 8 km interval along the flight line. Tracks were followed visually to minimize double counts of the same tracks within an interval. Before flying, we anticipated difficulty in obtaining precise counts of tracks at each interval. Based on our observations of the number of caribou and ATV tracks during previous surveys along the coast, we chose to collect data in four unequal categories (caribou: 0, 1–10, 11–30, > 30; ATV: 0, 1–3, 4–10, > 10). We analyzed the relationship between caribou and ATV tracks using ordinal regression and a logit link function with the package rms (Harrell, 2014) using the function lrm in R (R version 3.1.2). Ordinal regression is a modification of binary logistic regression that accounts for the ordinal nature of the data. We checked for spatial autocorrelation using variograms with package gstat (Pebesma, 2004), ensured that variables were not collinear using a threshold of less than 10 for variance inflation factors (VIF), and assessed model fit using area under the ROC curve (AUC, Hosmer et al., 2013). Transect and sub-area were included as covariates. We analyzed transects separately, but we did not weight trails on the basis of condition (apparently fresh or worn) because we could not determine the age or frequency of use of those trails.

Minimum Distance to Shore of Collared Caribou: Because ATV disturbance differed spatially and temporally, we mapped all locations of VHF- and GPS-collared caribou between April and August to quantify how close female caribou came to shore where most ATV activity occurred (West and Centre in late period) compared to areas with less ATV activity (West in early period, East in late period). We used the "near" tool in ArcGIS version 10.1 (ESRI, 2010) to quantify the minimum distance to shore of each individual and compared these distances over time in the West and among sub-areas in the late period using a Kruskal-Wallis ANOVA followed by non-parametric post hoc comparisons. In all cases, we report means ± 1 SE, or medians and ranges, when data were not normally distributed.

RESULTS

Body Size

Hind foot length varied significantly among groups across time and space (Fig. 4; $F_{3, 62}$ = 12.33, $p < 0.001$).
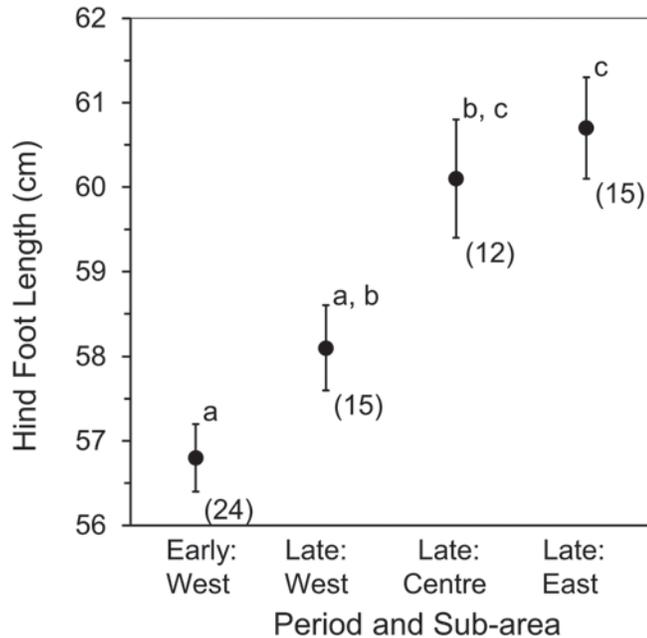
FIG. 4. Mean (± 1 SE) hind foot length of female migratory caribou in southern Hudson Bay, in the early and late periods, based on data from caribou collared in 1987–88 and 2009–10. Values followed by the same superscript (a, b, c) did not differ significantly based on Tukey's HSD tests. Sample sizes are given in parentheses.

Hind foot length was not significantly different in the West through time, but it increased in the late period along a west-east gradient (West: 58.1 ± 0.5 cm; Centre: 60.1 ± 0.7 cm; East: 60.7 ± 0.6 cm). Eastern caribou were significantly larger than early and late period Western caribou (Tukey's HSD; early period, $p < 0.001$; late period, $p = 0.011$). Central animals in the late period were significantly larger than Western animals in the early period ($p < 0.001$).

Dietary Quality

There were significant differences in fecal nitrogen across the study area in the late period ($F_{3, 76} = 19.1$, $p < 0.001$; Fig. 5); caribou in the West and Centre that moved inland to the Hudson Bay Lowland in July had lower fecal nitrogen than coastal groups in the Centre and East (Tukey's HSD test, $p < 0.008$ for all comparisons). Fecal nitrogen was similar across sub-areas inland in the Hudson Bay Lowland (West: 2.86 ± 0.11%, Centre: 2.74 ± 0.07%, Tukey's HSD test, $p = 0.84$) and across sub-areas at the coast (Centre: 3.48 ± 0.12%, East: 3.46 ± 0.08%, Tukey's HSD test, $p = 0.10$). No samples were collected during the early period, and insufficient sample size in the coastal West precluded comparison with other late period areas.

Location of Caribou in Mid-July

In the early period, 94% of Western female VHF-collared caribou were found in the Coastal Hudson Bay Lowland Ecoregion on 12 July 1989 (Table 2). In the late period, GPS-collared female caribou in each sub-area migrated
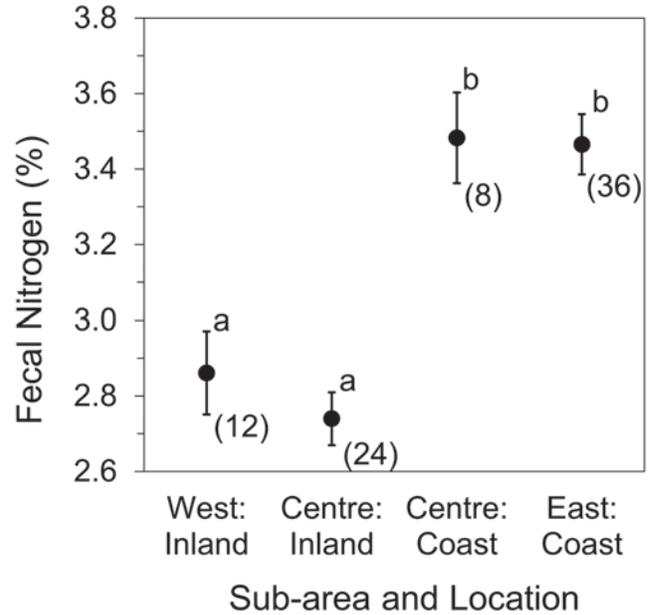

FIG. 5. Mean (± 1 SE) percent fecal nitrogen for caribou in southern Hudson Bay in July 2011. Values followed by the same superscript (a, b) did not differ significantly in Tukey's HSD tests. Sample sizes are given in parentheses.

TABLE 2. Percentage of female caribou in the Coastal Hudson Bay Lowland Ecoregion during the early period (12 July 1989, VHF-collared caribou) and the late period (9–15 July 2009–11, GPS-collared caribou) compared to total number of collared caribou (N, in parentheses) located in July in each sub-area, West, Centre, and East. Dashes indicate that no collared caribou were present in the sub-area.

Year	West	Centre	East
1989	94% (17)	–	–
2009	–	25% (8)	56% (16)
2010	0% (14)	10% (10)	78% (9)
2011	0% (11)	0% (11)	70% (10)

to the Coastal Hudson Bay Lowland Ecoregion during the calving season (Newton, 2012), but by mid-July, all caribou in the West had migrated south to the Hudson Bay Lowland Ecoregion. In the late period in the Centre, only 0%–25% of caribou remained on the Coastal Hudson Bay Lowland in mid-July, whereas the remainder (75%–100%, depending on the year) migrated south. In contrast, more than half of caribou in the East remained on the Coastal Hudson Bay Lowland in the late period (Table 2).

Distribution of ATV Tracks and Caribou Tracks

Ordinal regression of caribou tracks compared with ATV tracks revealed significant negative correlations where there were more than 10 ATV tracks ($n = 125$, $p = 0.001$). Covariates in the model were not collinear (VIF < 2.6 for all variables). Evaluation of the variogram indicated that the sub-area covariate was adequate to control for autocorrelation among sample points. The AUC assessment of model
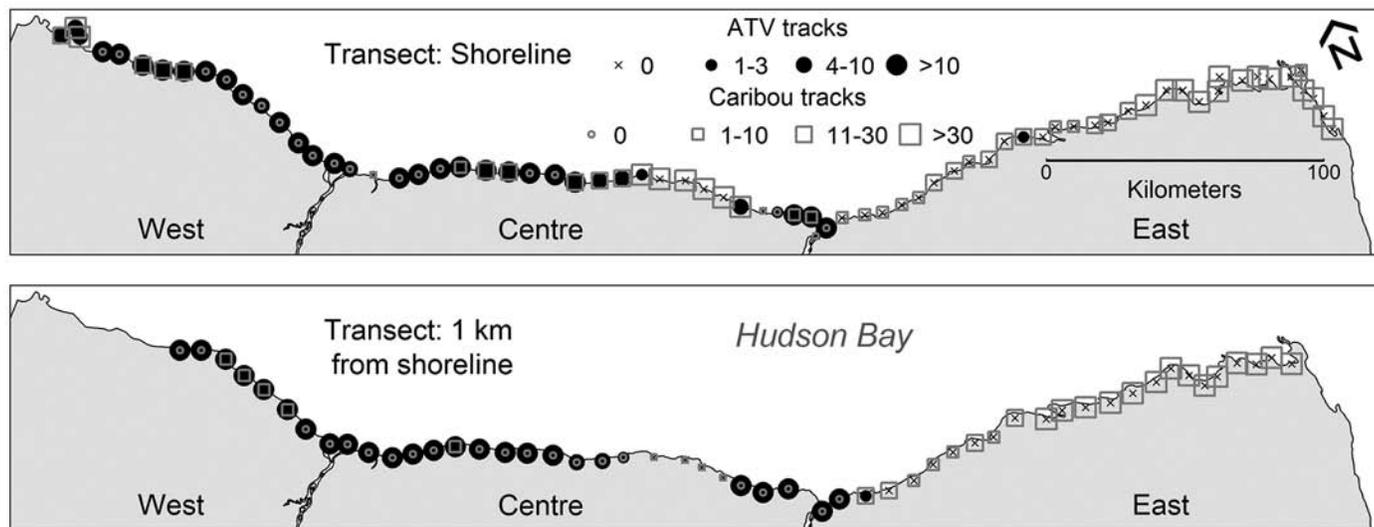
FIG. 6. Counts of caribou tracks and ATV tracks on two transects, (top) along the shoreline and (bottom) 1 km from the shoreline of southern Hudson Bay, in August 2010. Symbol size is proportional to the number of observations in each category (see legend).

fit demonstrated an acceptable discrimination ability (AUC = 0.77, Hosmer et al., 2013). Sub-areas in the East had significantly more caribou tracks than the Centre ($p = 0.036$), and the distributions of caribou tracks in the West and Centre were comparable ($p = 0.119$). We never observed many (more than 30) caribou tracks where more than 10 ATV tracks were located, and 30+ caribou tracks alongside one or more ATV tracks were found in only four of 125 observations (Fig. 6). We observed many more ATV tracks in the West and Centre than in the East.

Minimum Distance to Shore of Collared Caribou

The minimum distances to shore of collared female caribou in the spring and summer were significantly different through time and across sub-areas (Fig. 7, $H_{3, 97} = 39.2$, $p < 0.001$). Western caribou in the early period and Eastern caribou in the late period—those least affected by anthropogenic disturbance—had lower minimum distances to shore than caribou in areas with higher disturbance, i.e., Western and Central caribou in the late period (non-parametric post hoc comparisons, $p < 0.004$ for all comparisons). Notably, for Western caribou in the early period, some VHF-collared animals were 0 km from shore, and the median minimum distance was 1.8 km from shore. In contrast, in the late period no collared individual in the West traveled closer to the shore than 5.1 km, and the median distance to shore was 9.7 km. Central caribou, located between two major communities (Fort Severn and Peawanuck), remained a median distance of 14.1 km from shore in the late period.

DISCUSSION

Migratory caribou in SHB displayed pronounced local changes in summer distribution over three decades (Fig. 3, Magoun et al., 2005; Abraham et al., 2012; Newton, 2012;

Berglund et al., 2014). These changes corresponded to variations in dietary quality, body size (Figs. 4, 5), and anthropogenic disturbance (Figs. 6, 7). We suggest that caribou in SHB altered their distribution both eastward, to avoid ATV disturbance and seek better forage, and inland away from ATV activity on the coast. The latter movement may have contributed to decreased dietary quality, indicated by the lower percentage of fecal nitrogen of inland caribou. This conclusion is further supported by the findings of Newton et al. (2014); phytomass in the coastal West declined with increasing population size of caribou and has not yet recovered. Our observations show support for both hypotheses, demonstrating that neither factor explaining the change in caribou distribution can be discounted. However, we acknowledge that not all comparisons across space and time were possible because of limitations of the historical dataset.

Skeletal size in ungulates is unaffected by ephemeral, seasonal changes in resource availability, but it is a particularly useful gauge of forage resources during development (Huot, 1988; Crête and Huot, 1993; Gerhart et al., 1997; Knott et al., 2005; Mahoney et al., 2011). In SHB, we found no significant differences in body size through time in the West. In the late period, however, hind foot length exhibited a geographic cline, with larger adult females in the East (Fig. 4). Caribou living at lower densities in the East may have experienced more favourable foraging conditions during their development than their counterparts in the West. The abundance of caribou in SHB has increased over time (Magoun et al., 2005; Berglund et al., 2014); taken together, these data support the hypothesis that density-dependent food limitation could have driven caribou in the West to seek out alternative summering areas in the late period. For migratory caribou, summer food may be limiting, as shown by both spatial and temporal comparisons. In Newfoundland, for example, declines in body size of males and females over time were correlated with population
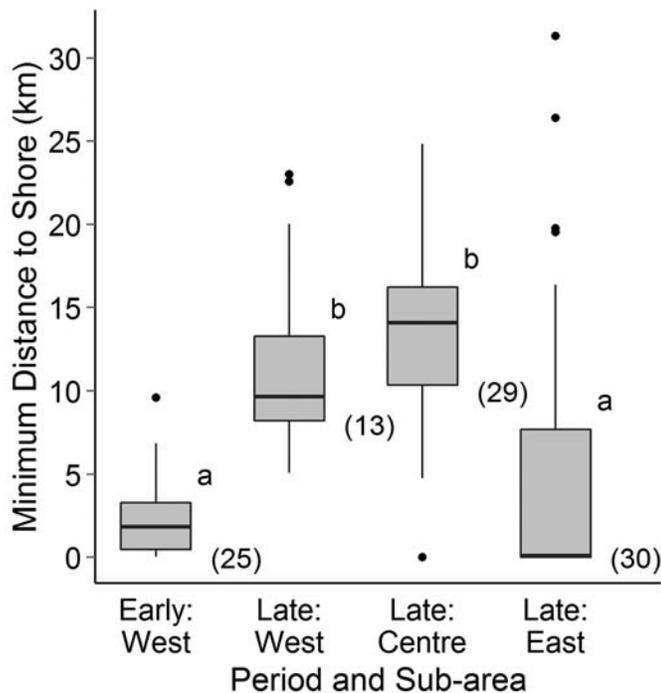
FIG. 7. Box plots of minimum distance to shore (km) of migratory female caribou in southern Hudson Bay in April–August, during the early and late periods, based on telemetry data from 1988–89 and 2009–11. Each box represents the interquartile range, the horizontal bar is the median, black dots indicate outliers, and vertical bars indicate the range (excluding outliers). Values followed by the same superscript (a, b) did not differ significantly in non-parametric post-hoc comparisons. Sample sizes are given in parentheses.

size at time of birth; decreases in stature were attributable to heightened, density-dependent competition for forage (Mahoney and Schaefer, 2002b; Mahoney et al., 2011). In Québec-Labrador, females in the George River herd were smaller than those in the adjacent Leaf River herd, a difference ascribed to insufficient and lower-quality forage (Crête and Huot, 1993). Over time, diminished stature in both herds has reflected their numeric growth (Couturier et al., 2010).

For mammals, post-partum dietary quality may be crucial, as the most severe energetic and fitness demands on the female occur during lactation (Sadleir, 1984; Clutton-Brock et al., 1989). In July, fecal samples on the coast displayed a higher percentage of nitrogen than inland samples (Fig. 5), indicating that coastal diets were more nutritious. This difference may be attributable, in part, to vegetation; coastal habitats typically contain a higher proportion of emerging herbaceous plants compared to areas south of the tree line (Riley, 2011). Furthermore, predation risk and insect harassment can also decrease feeding efficiency in ungulates (Hunter and Skinner, 1998; Barten et al., 2001; Laundré et al., 2001; Hebblewhite et al., 2008), including caribou (Hagemoen and Reimers, 2002; Bergerud et al., 2008; Witter et al., 2012). We surmise that decreased intraspecific competition, relief from biting insects, and lower wolf density on the coast, as reported for other coastal caribou summering areas (Garner and Reynolds, 1986; Heard et al., 1996), may have collectively enhanced

the nutritional status of female caribou near the SHB coast. If coastal diets are more nutritious, summering inland, as the majority of Western and Central caribou did in the late period (Table 2), may have deleterious effects on caribou body condition, survival, and reproduction in the future.

Changes in food resources can also be detected via shifts in migration timing (Crête and Huot, 1993; Mahoney and Schaefer, 2002b; Bergerud et al., 2008; Schaefer and Mahoney, 2013). For example, the Buchans caribou herd showed markedly later spring migration and earlier fall migration in response to summer forage limitation, a trend that reversed itself following a population peak (Schaefer and Mahoney, 2013). Migratory SHB caribou demonstrated altered migration timing, as indicated by the shift in July location of female caribou in the late period compared to the early period (Table 2), a shift consistent with the hypothesis of forage depletion. Nevertheless, we are unable to tease apart our two hypotheses with this evidence. Aerial coastal surveys reveal that caribou in the coastal Centre have never attained the mid-July coastal abundance once observed in the West or during the late period in the East (Magoun et al., 2005; Abraham et al., 2012; Berglund et al., 2014); the earlier fall migration inland in the West and Centre during the late period may be related to anthropogenic disturbance in those areas, as revealed by our track surveys in 2010. During the same period, many caribou in the East, exposed to less anthropogenic disturbance and apparently experiencing higher quality forage (as evidenced by larger body size), remained on the coast in mid-July.

Shifts in calving grounds for migratory *Rangifer* occur for a variety of reasons (Bergerud, 1996; Gunn et al., 2012; Taillon et al., 2012); however, shifts in summering areas related to density dependence appear more likely when tundra represents a small portion of a herd's annual range (Gunn et al., 2012). Caribou in SHB are the most southerly migratory population in continental North America (Hummel and Ray, 2008) and their habitat north of the tree line is only ~5% of their annual range, the smallest proportion for any such herd (Gunn et al., 2012). Our long-term observations are consistent with this idea.

Apart from food, the other major factor influencing caribou distribution is disturbance. In winter, caribou in northern Ontario avoid settlements (Poley et al., 2014) and caribou in British Columbia may abandon portions of their range following regular snow machine activity (Seip et al., 2007). During summer, females with calves may be particularly sensitive to human activity (Cameron et al., 2005; Schaefer and Mahoney, 2007). In the late period, we found a significant, negative relationship between the distributions of caribou tracks and ATV tracks (Fig. 6). Moreover, collared caribou in the early period in the West and late period in the East (those less affected by disturbance) were less than 2 km from shore, which is consistent with the hypothesis that caribou distribution reflects patterns of human disturbance. In contrast, caribou avoided areas frequented by ATVs by 9.7–14.1 km (Fig. 7), near the upper limit of what has been previously described as the response by caribou

and reindeer to disturbance (Vistnes and Nellemann, 2001, 2007; Mahoney and Schaefer, 2002a; Cameron et al., 2005; Joly et al., 2006; Schaefer and Mahoney, 2007; Vors et al., 2007; Weir et al., 2007; Nellemann et al., 2010; Polfus et al., 2011; Boulanger et al., 2012; DeCesare et al., 2012). Indeed, the magnitude of the effect of roads and human activity may easily be underestimated because caribou avoid a zone of influence that includes the immediate area of disturbance and also a substantial buffer area beyond it (Nellemann and Cameron, 1998; Vistnes and Nellemann, 2001; Joly et al., 2006). While we do not have a measure of anthropogenic disturbance over time, the growing human population, increased use of ATVs, and increased human access to remote areas (OMNR, 1985; Abraham et al., 2011; Statistics Canada, 2011) suggest heightened disturbance in SHB, especially in the West and Centre, where motorized travel is facilitated by raised beach ridges and winter roads between the communities of Peawanuck and Fort Severn in Ontario and Shamattawa in Manitoba.

Management Implications

It remains uncertain what level of disturbance migratory caribou can tolerate. In our study area, for example, disturbance from mineral exploration and exploitation, and also from increased ATV and snow machine use, has been increasing rapidly in caribou wintering range and near James Bay. For caribou and other ungulates, energy expended through increased vigilance and movement can compromise fitness (Frid and Dill, 2002; Cameron et al., 2005), and avoidance of human activity can lead to loss of valuable habitat (Cameron et al., 2005; Johnson et al., 2005; Stankowich, 2008; Polfus et al., 2011; Rogala et al., 2011). Therefore, demographic thresholds such as recruitment might be linked to range disturbance, key knowledge that can be gleaned from vital rates and habitat condition across multiple populations (e.g., EC, 2011).

Our findings highlight the importance of considering multiple limiting factors that could induce range shifts. Changes in body size, dietary quality, and the mid-July location of females were consistent with the hypothesis of forage depletion in the West; locations of collared female caribou and ATV and caribou track distributions revealed that anthropogenic disturbance could also be affecting summer distribution of caribou. The southward shift of summering areas for SHB caribou may come at the cost of decreased forage quality in July, fitting with our observations that fecal nitrogen levels were lower inland (Fig. 5). Eastern caribou may have escaped the effects of density dependence, as they exhibited increased body size and remained on the coast, where mid-summer forage is likely most nutritious.

Our study underscores that to conserve caribou, management must consider resource needs and life-history patterns at broad scales, as they do for other wide-ranging mammals (Woodroffe and Ginsberg, 1998). Migratory SHB caribou occupied a vast landscape, displayed marked changes in distribution during summer, and responded to human disturbance at a level well beyond conventional notions of edge effects (Laurance, 2000). To achieve success, conservation of migratory caribou must be undertaken at commensurate spatial and temporal scales to encompass, for example, the long-term shifts in calving and wintering areas (Taillon et al., 2012), as well as dramatic numerical changes (Bergerud et al., 2008). Even delineating population bounds for highly mobile animals demands considerable effort (Bethke et al., 1996). Thus, caribou pose a challenge. Long-term monitoring over wide spaces, incorporating not only population parameters, but multiple putative drivers of change, including vegetation, human and natural disturbance, climate change, predators, and parasites, is imperative if we are to understand and conserve this highly mobile and vulnerable animal.

REFERENCES

Abraham, K.F., and Thompson, J.E. 1998. Defining the Pen Islands caribou herd of southern Hudson Bay. Rangifer Special Issue 10:33–40.
http://dx.doi.org/10.7557/2.18.5.1439

Abraham, K.F., McKinnon, L.M., Jumean, Z., Tully, S.M., Walton, L.R., and Stewart, H.M. 2011. Hudson Plains Ecozone+ status and trends assessment. Canadian biodiversity: Ecosystem status and trends 2010. Technical Ecozone+ Report. Ottawa: Canadian Councils of Resource Ministers. 445 p.

Abraham, K.F., Pond, B.A., Tully, S.M., Trim, V., Hedman, D., Chenier, C., and Racey, G.D. 2012. Recent changes in summer distribution and numbers of migratory caribou on the southern Hudson Bay coast. Rangifer Special Issue 20:269–276.
http://dx.doi.org/10.7557/2.32.2.2275

Barten, N.L., Bowyer, R.T., and Jenkins, K.J. 2001. Habitat use by female caribou: Tradeoffs associated with parturition. Journal of Wildlife Management 65(1):77–92.
http://dx.doi.org/10.2307/3803279

Bergerud, A.T. 1977. Diets for caribou. In: Recheigl, M., Jr., ed. CRC Handbook Series in nutrition and food. Section G: Diets, culture, media, and food supplements. Cleveland, Ohio: CRC Press. 243–266.

———. 1996. Evolving perspectives on caribou population dynamics, have we got it right yet? Rangifer Special Issue 9:95–115.
http://dx.doi.org/10.7557/2.16.4.1225

Bergerud, A.T., Ferguson, R., and Butler, H.E. 1990. Spring migration and dispersion of woodland caribou at calving. Animal Behaviour 39(2):360–368.
http://dx.doi.org/10.1016/S0003-3472(05)80882-6

Bergerud, A.T., Luttich, S.N., and Camps, L. 2008. The return of caribou to Ungava. Montreal: McGill-Queen's University Press.

Berglund, N.E., Racey, G.D., Abraham, K.F., Brown, G.S., Pond, B.A., and Walton, L.R. 2014. Woodland caribou (*Rangifer tarandus caribou*) in the Far North of Ontario: Background information in support of land use planning. Biodiversity and Monitoring Technical Report 147. Thunder Bay, Ontario: Ontario Ministry of Natural Resources. 160 p.

Berkes, F., Hughes, A., George, P.J., Preston, R.J., Cummins, B.D., and Turner, J. 1995. The persistence of Aboriginal land use: Fish and wildlife harvest areas in the Hudson and James Bay Lowland, Ontario. Arctic 48(1):81–93.
http://dx.doi.org/10.14430/arctic1227

Bethke, R., Taylor, M., Amstrup, S., and Messier, F. 1996. Population delineation of polar bears using satellite collar data. Ecological Applications 6(1):311–317.
http://dx.doi.org/10.2307/2269574

Boulanger, J., Poole, K.G., Gunn, A., and Wierzchowski, J. 2012. Estimating the zone of influence of industrial developments on wildlife: A migratory caribou *Rangifer tarandus groenlandicus* and diamond mine case study. Wildlife Biology 18(2):164–179.
http://dx.doi.org/10.2981/11-045

Cameron, R.D., Smith, W.T., White, R.G., and Griffith, B. 2005. Central Arctic caribou and petroleum development: Distributional, nutritional, and reproductive implications. Arctic 58(1):1–9.
http://dx.doi.org/10.14430/arctic382

Clutton-Brock, T.H., Albon, S.D., and Guinness, F.E. 1989. Fitness costs of gestation and lactation in wild mammals. Nature 337:260–262.
http://dx.doi.org/10.1038/337260a0

COSEWIC (Committee on the Status of Endangered Wildlife in Canada). 2011. Designatable units for caribou (*Rangifer tarandus*) in Canada. Ottawa: COSEWIC. 88 p.

Couturier, S., Brunelle, J., Vandal, D., and St-Martin, G. 1990. Changes in the population dynamics of the George River caribou herd, 1976–87. Arctic 43(1):9–20.
http://dx.doi.org/10.14430/arctic1586

Couturier, S., Côté, S.D., Otto, R.D., Weladji, R.B., and Huot, J. 2009. Variation in calf body mass in migratory caribou: The role of habitat, climate, and movements. Journal of Mammalogy 90(2):442–452.
http://dx.doi.org/10.1644/07-MAMM-A-279.1

Couturier, S., Otto, R.D., Côté, S.D., Luther, G., and Mahoney, S.P. 2010. Body size variations in caribou ecotypes and relationships with demography. Journal of Wildlife Management 74(3):395–404.
http://dx.doi.org/10.2193/2008-384

Crête, M., and Huot, J. 1993. Regulation of a large herd of migratory caribou: Summer nutrition affects calf growth and body reserves of dams. Canadian Journal of Zoology 71(11):2291–2296.
http://dx.doi.org/10.1139/z93-321

Dahle, B., Reimers, E., and Colman, J.E. 2008. Reindeer (*Rangifer tarandus*) avoidance of a highway as revealed by lichen measurements. European Journal of Wildlife Research 54(1):27–35.
http://dx.doi.org/10.1007/s10344-007-0103-5

DeCesare, N.J., Hebblewhite, M., Schmiegelow, F., Hervieux, D., McDermid, G.J., Neufeld, L., Bradley, M., et al. 2012. Transcending scale dependence in identifying habitat with resource selection functions. Ecological Applications 22(4):1068–1083.
http://dx.doi.org/10.1890/11-1610.1

Dyer, S.J., O'Neill, J.P., Wasel, S.M., and Boutin, S. 2001. Avoidance of industrial development by woodland caribou. Journal of Wildlife Management 65(3):531–542.
http://dx.doi.org/10.2307/3803106

EC (Environment Canada). 2011. Scientific assessment to inform the identification of critical habitat for woodland caribou (*Rangifer tarandus caribou*), boreal population, in Canada: 2011 update. Ottawa: EC. 102 p. + appendices.

———. 2012. National climate data and information archive: 2010.
http://climate.weatheroffice.gc.ca

Environment Canada and Agriculture and Agri-Food Canada 2012. National ecological framework for Canada.
http://sis.agr.gc.ca/cansis/nsdb/ecostrat/index.html

ESRI (Environmental Systems Research Institute). 2010. ArcGIS version 10.1. Redlands, California: ESRI.

Etheridge, R.D., Pesti, G.M., and Foster, E.H. 1998. A comparison of nitrogen values obtained utilizing the Kjeldahl nitrogen and Dumas combustion methodologies (Leco CNS 2000) on samples typical of an animal nutrition analytical laboratory. Animal Feed Science and Technology 73(1-2):21–28.
http://dx.doi.org/10.1016/S0377-8401(98)00136-9

Frid, A., and Dill, L.M. 2002. Human-caused disturbance stimuli as a form of predation risk. Conservation Ecology 6(1): 11.
http://www.consecol.org/vol6/iss1/art11/

Garner, G.W., and Reynolds, P.E. 1986. Baseline study of the fish, wildlife and their habitats. Final Report, Arctic National Wildlife Refuge Coastal Plain Resource Assessment, Vol. I. Anchorage, Alaska: U.S. Fish and Wildlife Service. 392 p.

Gerhart, K.L., Russell, D.E., Van DeWetering, D., White, R.G., and Cameron, R.D. 1997. Pregnancy of adult caribou (*Rangifer tarandus*): Evidence for lactational infertility. Journal of Zoology 242(1):17–30.
http://dx.doi.org/10.1111/j.1469-7998.1997.tb02926.x

Gordon, I.J., and Illius, A.W. 1989. Resource partitioning by ungulates on the Isle of Rhum. Oecologia 79(3):383–389.
http://dx.doi.org/10.1007/BF00384318

Gunn, A., and Miller, F.L. 1986. Traditional behaviour and fidelity to caribou calving grounds by barren-ground caribou. Rangifer Special Issue 1:151–158.
http://dx.doi.org/10.7557/2.6.2.640

Gunn, A., Poole, K.G., and Nishi, J.S. 2012. 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. Rangifer Special Issue 20:259–267.
http://dx.doi.org/10.7557/2.32.2.2274

Haber, G.C., and Walters, C.J. 1980. Dynamics of the Alaska-Yukon caribou herds and management implications. In: Reimers, E., Gaare, E., and Skjenneberg, S., eds. Proceedings of the 2nd International Reindeer/Caribou Symposium, Røros, Norway, 1979. Trondheim: Direktoratet for Vilt og Ferskvannsfisk. 645–600 and annex.

Hagemoen, R.I.M., and Reimers, E. 2002. Reindeer summer activity pattern in relation to weather and insect harassment. Journal of Animal Ecology 71(5):883–892.
http://dx.doi.org/10.1046/j.1365-2656.2002.00654.x

Harrell, F.E., Jr. 2014. rms: Regression modeling strategies. R package version 4.2-1.

Harrington, F.H., and Veitch, A.M. 1992. Calving success of woodland caribou exposed to low-level jet fighter overflights. Arctic 45(3):213–218.
http://dx.doi.org/10.14430/arctic1395

Heard, D.C., and Williams, T.M. 1992. Distribution of wolf dens on migratory caribou ranges in the Northwest Territories, Canada. Canadian Journal of Zoology 70(8):1504–1510.
http://dx.doi.org/10.1139/z92-207

Heard, D.C., Williams, M.T., and Melton, D.A. 1996. The relationship between food intake and predation risk in migratory caribou and implications to caribou and wolf population dynamics. Rangifer Special Issue 9:37–44.
http://dx.doi.org/10.7557/2.16.4.1219

Hebblewhite, M., Merrill, E., and McDermid, G. 2008. A multi-scale test of the forage maturation hypothesis in a partially migratory ungulate population. Ecological Monographs 78(2):141–166.
http://dx.doi.org/10.1890/06-1708.1

Hinkes, M.T., Collins, G.H., Van Daele, L.J., Kovach, S.D., Aderman, A.R., Woolington, J.D., and Seavoy, R.J. 2005. Influence of population growth on caribou herd identity, calving ground fidelity, and behavior. Journal of Wildlife Management 69(3):1147–1162.
http://dx.doi.org/10.2193/0022-541X(2005)069[1147:IOPGOC]2.0.CO;2

Hosmer, D.W., Jr., Lemeshow, S., and Sturdivant, R.X. 2013. Applied logistic regression, 3rd ed. Hoboken, New Jersey: John Wiley & Sons, Inc.
http://dx.doi.org/10.1002/9781118548387

Hummel, M., and Ray, J.C. 2008. Caribou and the North: A shared future. Toronto: Dundurn Press.

Hunter, L.T.B., and Skinner, J.D. 1998. Vigilance behaviour in African ungulates: The role of predation pressure. Behaviour 135(2):195–211.
http://dx.doi.org/10.1163/156853998793066320

Huot, J. 1988. Review of methods for evaluating the physical condition of wild ungulates in northern environments. Nordicana Series No. 50. Québec: Centre d'études nordiques, Université Laval.

Johnson, C.J., Boyce, M.S., Case, R.L., Cluff, H.D., Gau, R.J., Gunn, A., and Mulders, R. 2005. Cumulative effects of human developments on Arctic wildlife. Wildlife Monographs 160. 36 p.

Joly, K., Nellemann, C., and Vistnes, I. 2006. A reevaluation of caribou distribution near an oilfield road on Alaska's North Slope. Wildlife Society Bulletin 34(3):866–869.
http://dx.doi.org/10.2193/0091-7648(2006)34[866:AROCDN]2.0.CO;2

Klein, D.R. 1970. Tundra ranges north of the boreal forest. Journal of Range Management 23(1):8–14.
http://dx.doi.org/10.2307/3896000

Klütsch, C.F.C., Manseau, M., and Wilson, P.J. 2012. Phylogeographical analysis of mtDNA data indicates post-glacial expansion from multiple glacial refugia in woodland caribou (*Rangifer tarandus caribou*). PLoS ONE 7(12): e52661.
http://dx.doi.org/10.1371/journal.pone.0052661

Knott, K.K., Barboza, P.S., and Bowyer, R.T. 2005. Growth in Arctic ungulates: Postnatal development and organ maturation in *Rangifer tarandus* and *Ovibos moschatus*. Journal of Mammalogy 86(1):121–130.
http://www.jstor.org/stable/4094295

Laliberte, A.S., and Ripple, W.J. 2004. Range contractions of North American carnivores and ungulates. Bioscience 54(2):123–138.
http://dx.doi.org/10.1641/0006-3568(2004)054[0123:RCONAC]2.0.CO;2

Laundré, J.W., Hernández, L., and Altendorf, K.B. 2001. Wolves, elk, and bison: Reestablishing the "landscape of fear" in Yellowstone National Park, U.S.A. Canadian Journal of Zoology 79(8):1401–1409.
http://dx.doi.org/10.1139/z01-094

Laurance, W.F. 2000. Do edge effects occur over large spatial scales? Trends in Ecology & Evolution 15(4):134–135.
http://dx.doi.org/10.1016/S0169-5347(00)01838-3

Leslie, D.M., Jr., and Starkey, E.E. 1985. Fecal indices to dietary quality of cervids in old growth forests. Journal of Wildlife Management 49(1):142–146.
http://dx.doi.org/10.2307/3801860

———. 1987. Fecal indices to dietary quality: A reply. Journal of Wildlife Management 51(2):321–325.
http://dx.doi.org/10.2307/3801009

Leslie, D.M., Jr., Bowyer, R.T., and Jenks, J.A. 2008. Facts from feces: Nitrogen still measures up as a nutritional index for mammalian herbivores. Journal of Wildlife Management 72(6):1420–1433.
http://dx.doi.org/10.2193/2007-404

Lytwyn, V.P. 2002. Muskekowuck Athinuwick: Original people of the great swampy land. Winnipeg: University of Manitoba Press.

Magoun, A.J., Abraham, K.F., Thompson, J.E., Ray, J.C., Gauthier, M.E., Brown, G.S., Woolmer, G., Chenier, C.J., and Dawson, F.N. 2005. Distribution and relative abundance of caribou in the Hudson Plains Ecozone of Ontario. Rangifer Special Issue 16:105–121.
http://dx.doi.org/10.7557/2.25.4.1776

Mahoney, S.P., and Schaefer, J.A. 2002a. Hydroelectric development and the disruption of migration in caribou. Biological Conservation 107(2):147–153.
http://dx.doi.org/10.1016/S0006-3207(02)00052-6

———. 2002b. Long-term changes in demography and migration of Newfoundland caribou. Journal of Mammalogy 83(4):957–963.
http://www.jstor.org/stable/1383501

Mahoney, S.P., Mawhinney, K., McCarthy, C., Anions, D., and Taylor, S. 2001. Caribou reactions to provocation by snowmachines in Newfoundland. Rangifer 21(1):35–43.
http://dx.doi.org/10.7557/2.21.1.1526

Mahoney, S.P., Weir, J.N., Luther, G., Schaefer, J.A., and Morrison, S.F. 2011. Morphological change in Newfoundland caribou: Effects of abundance and climate. Rangifer 31(1):21–34.
http://dx.doi.org/10.7557/2.31.1.1917

McQuade-Smith, K. 2009. Investigating the genetic component to geographical variation in behavior and metabolism in temperate mammals. MSc thesis, Trent University, Peterborough, Ontario.

Messier, F., Huot, J., Le Henaff, D., and Luttich, S.N. 1988. Demography of the George River caribou herd: Evidence of population regulation by forage exploitation and range expansion. Arctic 41(4):279–287.
http://dx.doi.org/10.14430/arctic1733

Nellemann, C., and Cameron, R.D. 1998. Cumulative impacts of an evolving oil-field complex on the distribution of calving caribou. Canadian Journal of Zoology 76(8):1425–1430.
http://dx.doi.org/10.1139/z98-078

Nellemann, C., Jordhøy, P., Støen, O.-G., and Strand, O. 2000. Cumulative impacts of tourist resorts on wild reindeer (Rangifer tarandus tarandus) during winter. Arctic 53(1):9–17.
http://dx.doi.org/10.14430/arctic829

Nellemann, C., Vistnes, I., Jordhøy, P., Strand, O., and Newton, A. 2003. Progressive impact of piecemeal infrastructure development on wild reindeer. Biological Conservation 113(2):307–317.
http://dx.doi.org/10.1016/S0006-3207(03)00048-X

Nellemann, C., Vistnes, I., Jordhøy, P., Støen, O.-G., Kaltenborn, B.P., Hanssen, F., and Helgesen, R. 2010. Effects of recreational cabins, trails and their removal for restoration of reindeer winter ranges. Restoration Ecology 18(6):873–881.
http://dx.doi.org/10.1111/j.1526-100X.2009.00517.x

Newton, E.J. 2012. Factors affecting changes in the distribution and abundance of migratory caribou (Rangifer tarandus) in the Hudson Bay Lowlands. MSc thesis, Trent University, Peterborough, Ontario.

Newton, E.J., Pond, B.A., Brown, G.S., Abraham, K.F., and Schaefer, J.A. 2014. Remote sensing reveals long-term effects of caribou on tundra vegetation. Polar Biology 37(5):715–725.
http://dx.doi.org/10.1007/s00300-014-1472-3

NRC (Natural Resources Canada). 2009. Land cover, circa 2000.
http://geogratis.gc.ca/

OMNR (Ontario Ministry of Natural Resources). 1985. Moosonee District: Background information. Publication 3120-1. Moosonee: OMNR. 167 p.

Pebesma, E.J. 2004. Multivariable geostatistics in S: The gstat package. Computers & Geosciences 30(7):683–691.
http://dx.doi.org/10.1016/j.cageo.2004.03.012

Poley, L.G., Pond, B.A., Schaefer, J.A., Brown, G.S., Ray, J.C., and Johnson, D.S. 2014. Occupancy patterns of large mammals in the Far North of Ontario under imperfect detection and spatial autocorrelation. Journal of Biogeography 41(1):122–132.
http://dx.doi.org/10.1111/jbi.12200

Polfus, J.L., Hebblewhite, M., and Heinemeyer, K. 2011. Identifying indirect habitat loss and avoidance of human infrastructure by northern mountain woodland caribou. Biological Conservation 144(11):2637–2646.
http://dx.doi.org/10.1016/j.biocon.2011.07.023

Riley, J.L. 2003. Flora of the Hudson Bay Lowland and its postglacial origins. Ottawa: National Research Council of Canada.

———. 2011. Wetlands of the Ontario Hudson Bay Lowland: A regional overview. Toronto: Nature Conservancy of Canada. 156 p.

Rogala, J.K., Hebblewhite, M., Whittington, J., White, C.A., Coleshill, J., and Musiani, M. 2011. Human activity differentially redistributes large mammals in the Canadian Rockies national parks. Ecology and Society 16(3): 16.
http://dx.doi.org/10.5751/ES-04251-160316

Rowe, J.S. 1972. Forest regions of Canada. Publication No. 1300. Ottawa: Canadian Forestry Service Department of the Environment.

Sadleir, R.M.F.S. 1984. Ecological consequences of lactation. Acta Zoologica Fennica 171:179–182.

Schaefer, J.A. 2003. Long-term range recession and the persistence of caribou in the taiga. Conservation Biology 17(5):1435–1439.
http://dx.doi.org/10.1046/j.1523-1739.2003.02288.x

Schaefer, J.A., and Mahoney, S.P. 2007. Effects of progressive clearcut logging on Newfoundland caribou. Journal of Wildlife Management 71(6):1753–1757.
http://dx.doi.org/10.2193/2005-479

———. 2013. Spatial dynamics of the rise and fall of caribou (Rangifer tarandus) in Newfoundland. Canadian Journal of Zoology 91(11):767–774.
http://dx.doi.org/10.1139/cjz-2013-0132

Schaefer, J.A., Bergman, C.M., and Luttich, S.N. 2000. Site fidelity of female caribou at multiple spatial scales. Landscape Ecology 15(8):731–739.
http://dx.doi.org/10.1023/A:1008160408257

Seip, D.R., Johnson, C.J., and Watts, G.S. 2007. Displacement of mountain caribou from winter habitat by snowmobiles. Journal of Wildlife Management 71(5):1539–1544.
http://dx.doi.org/10.2193/2006-387

Stankowich, T. 2008. Ungulate flight responses to human disturbance: A review and meta-analysis. Biological Conservation 141(9):2159–2173.
http://dx.doi.org/10.1016/j.biocon.2008.06.026

Statistics Canada. 2011. Peawanuck, Ontario (Code 3560091) and Kenora, Ontario (Code 3560) (table). Census Profile: 2011 Census of population. Ottawa: Statistics Canada.
http://www12.statcan.gc.ca/census-recensement/2011/dp-pd/prof/index.cfm?Lang=E

Taillon, J., Festa-Bianchet, M., and Côté, S.D. 2012. Shifting targets in the tundra: Protection of migratory caribou calving grounds must account for spatial changes over time. Biological Conservation 147(1):163–173.
http://dx.doi.org/10.1016/j.biocon.2011.12.027

Thompson, J.E., and Abraham, K.F. 1994. Range, seasonal distribution and population dynamics of the Pen Islands caribou herd of southern Hudson Bay: Final Technical Report. Moosonee, Ontario: OMNR. 94 p.

Tsuji, L.J.S., and Nieboer, E. 1999. A question of sustainability in Cree harvesting practices: The seasons, technological and cultural changes in the western James Bay region of northern Ontario, Canada. Canadian Journal of Native Studies 19(1):169–192.

Venter, O., Brodeur, N.N., Nemiroff, L., Belland, B., Dolinsek, I.J., and Grant, J.W.A. 2006. Threats to endangered species in Canada. Bioscience 56(11):903–910.
http://dx.doi.org/10.1641/0006-3568(2006)56[903:TTESIC]2.0.CO;2

Vistnes, I., and Nellemann, C. 2001. Avoidance of cabins, roads, and power lines by reindeer during calving. Journal of Wildlife Management 65(4):915–925.
http://dx.doi.org/10.2307/3803040

———. 2007. Impacts of human activity on reindeer and caribou: The matter of spatial and temporal scales. Rangifer Report 12:47–56.
http://dx.doi.org/10.7557/2.27.3.269

Vors, L.S., and Boyce, M.S. 2009. Global declines of caribou and reindeer. Global Change Biology 15(11):2626–2633.
http://dx.doi.org/10.1111/j.1365-2486.2009.01974.x

Vors, L.S., Schaefer, J.A., Pond, B.A., Rodgers, A.R., and Patterson, B.R. 2007. Woodland caribou extirpation and anthropogenic landscape disturbance in Ontario. Journal of Wildlife Management 71(4):1249–1256.
http://dx.doi.org/10.2193/2006-263

Weir, J.N., Mahoney, S.P., McLaren, B., and Ferguson, S.H. 2007. Effects of mine development on woodland caribou *Rangifer tarandus* distribution. Wildlife Biology 13(1):66–74.
http://dx.doi.org/10.2981/0909-6396(2007)13[66:EOMDOW]2.0.CO;2

Wilcove, D.S., Rothstein, D., Dubow, J., Phillips, A., and Losos, E. 1998. Quantifying threats to imperiled species in the United States. Bioscience 48(8):607–615.
http://dx.doi.org/10.2307/1313420

Witter, L.A., Johnson, C.J., Croft, B., Gunn, A., and Gillingham, M.P. 2012. Behavioural trade-offs in response to external stimuli: Time allocation of an Arctic ungulate during varying intensities of harassment by parasitic flies. Journal of Animal Ecology 81(1):284–295.
http://dx.doi.org/10.1111/j.1365-2656.2011.01905.x

Wolfe, S.A. 2000. Habitat selection by calving caribou of the Central Arctic herd, 1980–95. MS thesis, University of Alaska Fairbanks, Fairbanks, Alaska.

Woodroffe, R., and Ginsberg, J.R. 1998. Edge effects and the extinction of populations inside protected areas. Science 280(5372):2126–2128.
http://dx.doi.org/10.1126/science.280.5372.2126