

Conservation of caribou (*Rangifer tarandus*) in Canada: an uncertain future¹

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Abstract: Caribou (*Rangifer tarandus* (L., 1758)) play a central role in the ecology and culture of much of Canada, where they were once the most abundant cervid. Most populations are currently declining, and some face extirpation. In southern Canada, caribou range has retreated considerably over the past century. The ultimate reason for their decline is habitat alterations by industrial activities. The proximate causes are predation and, to a lesser extent, overharvest. The most southerly populations of “Mountain” caribou are at imminent risk of extirpation. Mountain caribou are threatened by similar industrial activities as Boreal caribou, and face increasing harassment from motorized winter recreational activities. Most populations of “Migratory Tundra” caribou are currently declining. Although these caribou fluctuate in abundance over decades, changing harvest technologies, climate change, increasing industrial development and human presence in the North raise doubts over whether recent declines will be followed by recoveries. The Peary caribou (*Rangifer tarandus pearyi* J.A. Allen, 1902), a distinct subspecies endemic to Canada’s High Arctic, has suffered drastic declines caused by severe weather, hunting and predation. It faces an increasing threat from climate change. While some questions remain about the reasons for the decline of Migratory Tundra caribou, research has clearly identified several threats to the persistence of “Boreal”, Mountain, and Peary caribou. Scientific knowledge, however, has neither effectively influenced policies nor galvanized public opinion sufficiently to push governments into effective actions. The persistence of many caribou populations appears incompatible with the ongoing pace of industrial development.

Résumé : Le caribou (*Rangifer tarandus* (L., 1758)) occupe une place centrale dans l’écologie et la culture de plusieurs régions du Canada. Bien que le caribou ait déjà été le cervidé le plus abondant au Canada, la plupart des populations sont présentement en déclin et certaines font même face à l’extinction. Dans les régions du sud du Canada, la distribution du caribou a diminué considérablement au cours du dernier siècle. Le facteur ultime responsable du déclin est la modification des habitats par les activités industrielles, alors que les causes proximales sont la prédation et, dans une moindre mesure, la surexploitation. Les populations les plus méridionales de caribou Montagnard font face à un risque imminent d’extinction. Le caribou Montagnard est menacé par les mêmes activités industrielles que le caribou de l’écotype sédentaire et fait face à une augmentation du harcèlement par les activités de récréation motorisées en hiver. La plupart des populations de caribou Migrateur sont présentement en diminution. Bien que ces populations fluctuent en abondance au cours des décennies, les modifications des techniques de chasse, les changements climatiques, ainsi que l’augmentation du développement industriel et de la présence humaine dans les milieux nordiques sèment le doute sur la possibilité que les populations récupèrent des déclinés récents. Le caribou de Peary (*Rangifer tarandus pearyi* J.A. Allen, 1902), une sous-espèce endémique au Haut Arctique canadien, a subi des déclinés drastiques causés par des conditions climatiques difficiles, la chasse et la prédation, et fait présentement face à la menace des changements climatiques. Bien que certaines interrogations demeurent sur les raisons du déclin du caribou Migrateur, la recherche a identifié plusieurs menaces pour la persistance du caribou des écotypes sédentaires, Montagnard et de Peary. Les résultats de la recherche, toutefois, n’ont pas influencé la législation efficacement, ni canalisé l’opinion publique suffisamment pour forcer des actions concrètes de conservation de la part du gouvernement. Le maintien de plusieurs populations de caribou apparaît incompatible avec le niveau de développement industriel actuel.

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Introduction

The status of caribou (*Rangifer tarandus* (L., 1758)) in Canada is deteriorating, with most current conservation efforts apparently unable to reverse this trend. While concern for this species at both its southern and northern range limits has been ongoing for the last 20 years, recently it has extended to other populations. Most populations from Newfoundland to the Yukon are declining and some are at record low numbers (CARMA 2009; Environment Canada 2009). In addition, a recent review reported that the species is in decline globally (Vors and Boyce 2009). Therefore, a review of the conservation status of caribou in Canada is timely. Caribou once ranged from Newfoundland to the Queen Charlotte Islands in British Columbia and from southern British Columbia to Ellesmere Island in Nunavut. Within the last 150 years, however, caribou disappeared from the Maritime provinces leaving only a small and declining herd of less than 200 in Gaspésie, southeastern Quebec. Their distribution in all other provinces has receded (Hummel and Ray 2008). In Ontario, the southern limit of caribou distribution has moved northwards by about 34 km per decade in response to settlement and the expansion of commercial forestry (Schaefer 2003), a pattern repeated across Canada (McLoughlin et al. 2003; Environment Canada 2009). Here, we will critically review hypotheses to explain caribou declines. We will also examine why currently little is being done to stop anthropogenic sources of caribou endangerment, and why most attempts to ensure recovery appear to have failed.

In much of northern Canada, caribou are a keystone species supporting predator populations (Dale et al. 1994; Mowat and Heard 2006; Musiani et al. 2007), as well as affecting vegetation structure and nitrogen cycling. Caribou are also fundamental for the culture, spirituality, and diet of northern aboriginal peoples (Hummel and Ray 2008; Kendrick et al. 2005), for whom the cultural and subsistence value of caribou remain high. The replacement value of the annual harvest of the Beverly and Qamanirjuaq caribou herds alone is valued at more than \$20 million, shared between Nunavut (\$12 million), Manitoba (\$4 million), Saskatchewan (\$3 million), and the Northwest Territories (\$1 million) (InterGroup Consultants 2008).

Caribou declines

One measure of the declining conservation status of caribou is the gradual increase in number of caribou populations and ecotypes assessed as wildlife species at risk by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) (Fig. 1). In 1979, Peary caribou (*Rangifer tarandus pearyi* J.A. Allen, 1902) were the first to be designated at risk, with the rating of Threatened. The small isolated population in Gaspésie was assessed as Threatened in 1984 and as Endangered in 2000. Peary caribou were most recently reassessed as Endangered (COSEWIC 2004). In 2002, COSEWIC assessed as Threatened caribou in the boreal forest from Labrador to British Columbia, as well as the "Southern Mountain" populations of British Columbia and Alberta. At the same time, COSEWIC (2002) rated "Northern Mountain" caribou of British Columbia, the Northwest Territories, and Yukon as Special Concern. Caribou also appear on provincial

and territorial species-at-risk lists. Recently, concerns have been expressed about the status of this species in designatable units not yet assessed by COSEWIC.

The numbers of Migratory Tundra caribou typically rise and fall over a time scale of decades (Gunn 2003; Payette et al. 2004; Bergerud et al. 2008). Analysis of hoof scars on black spruce (*Picea mariana* (Mill.) B.S.P.) roots exposed across caribou trails revealed trends similar to those described by Aboriginal Traditional Knowledge (Zalatan et al. 2006). Migratory tundra caribou numbers were low for most herds in the 1950s and 1960s (Kelsall 1968), then increased. Many herds peaked in the mid-1980s to mid-1990s. Across continental northern Canada, 9 out of 10 major herds are currently declining. Since the late 1980s, the Rivière George herd in Quebec–Labrador declined and the Rivière-aux-Feuilles herd increased until the most recent census in 2001 (CARMA 2009).

Other declining Migratory Tundra herds include the Cape Bathurst herd that dropped from 20 000 in 1992 to 1 800 in 2006 and 2009, suggesting a 17% annual rate of decline. The Bluenose East herd declined by almost half in 6 years, from 104 000 in 2000 to 66 000 in 2006. The Bluenose West herd declined by over 80% in 14 years, from 112 000 in 1992 to about 18 000 in 2006 and 2009; the Ahik and Qamanirjuaq herds are currently declining (CARMA 2009). The Bathurst herd peaked in 1986 at 470 000 caribou. It declined to 32 000 by 2009 (Government of the Northwest Territories 2009). The Beverly herd, estimated at 270 000 in 1994, was apparently reduced to a few hundreds by 2009 (CARMA 2009). The halving rate for these herds ranged from 3 to 7 years. The lack of corresponding increases in neighbouring herds rules out the notion that such declines can be attributed to movements of individuals among herds.

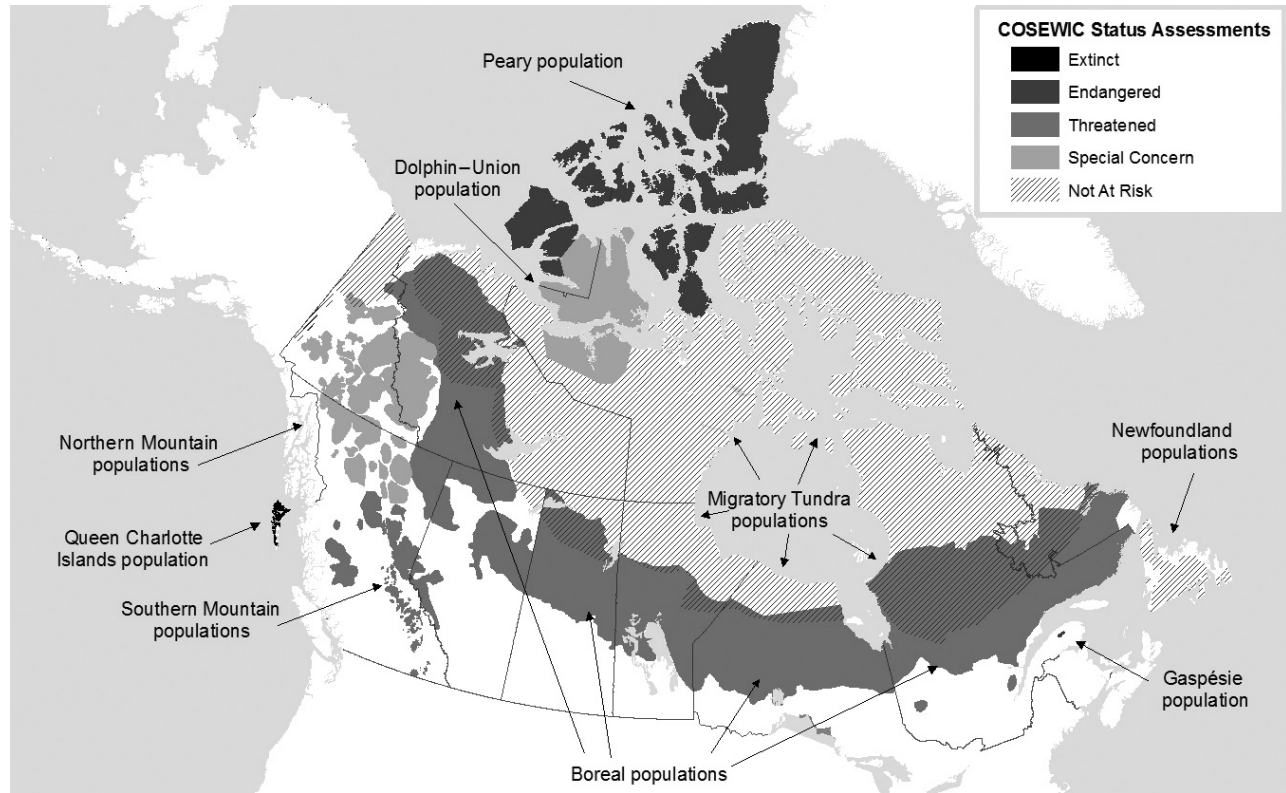
In the southern part of their range in Canada, caribou are extirpated from about 60% of historic extent of occurrence in Alberta, 50% in Ontario, and 40% in British Columbia (Hummel and Ray 2008). Some herds in the western mountains have stopped migrating between traditional seasonal ranges (Edmonds 1988), and 6 out of 13 herds in the southern Rockies are reduced to fewer than 50 individuals, facing dire prospects for even short-term persistence (Environment Canada 2009; Wittmer et al. 2010). Numbers on the island of Newfoundland have declined by 60%, from 90 000 estimated in 1996 to only 32 000 in 2008 (Government of Newfoundland and Labrador 2009).

Peary caribou on the Arctic Archipelago have mostly continued to decline since the 1960s, although declines on some islands have been interspersed with periods of recovery aided by reduced harvest by Inuit and Inuvialuit (COSEWIC 2004). The formerly large population inhabiting Prince of Wales and Somerset Islands has disappeared (Gunn et al. 2006).

The complicated subspecific classification of caribou

Before reviewing the conservation status of caribou, it is necessary to examine the different ways in which scientists, managers, and others refer to types of caribou. There is only one species of caribou (called reindeer in Europe and Asia) ranging over northern North America, Europe, and Asia. In Canada, the physical, behavioural, and ecological diversity

Fig. 1. Location of populations of caribou (*Rangifer tarandus*) assessed by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC), and the populations (Migratory Tundra and Newfoundland) that COSEWIC did not assess and are assumed to be Not at Risk. These populations are referred to as Wildlife Species in the context of the *Species at Risk Act* (SARA). Modified from map 1.4 of Hummel and Ray (2008) and reproduced with permission of Dundurn Press Ltd.



and postglacial history of caribou present a challenge for classification below the species level. Various ecotypes and subspecies have been suggested (Table 1). Banfield (1961) recognized four extant North American subspecies, based on appearance and skeletal measurements: *Rangifer tarandus groenlandicus* (L., 1767) and *Rangifer tarandus granti* (J.A. Allen, 1902) (generally referred to as “Canadian barren-ground” and “Alaskan barren-ground”, respectively, but also called “migratory” or “tundra”), *Rangifer tarandus caribou* (Gmelin, 1788) (“woodland”), and *R. t. pearyi* (“Peary”). These are for the most part separated geographically, although there is some overlap between *pearyi* and *groenlandicus* in the Boothia Peninsula and between *groenlandicus* and *caribou* in the territories and northern parts of the prairie provinces in winter. The Dolphin–Union herd on Victoria Island combines *pearyi* characteristics with the size of *groenlandicus*. Another subspecies, Dawson’s caribou (*Rangifer tarandus dawsoni* (Thompson-Seton, 1900)) may have occurred in the Haida Gwaii islands of British Columbia. The subspecific designation is based on very few specimens and these caribou may not have been genetically distinct (Byun et al. 2002).

This formal taxonomy used methods that are now outdated and has been inconsistently applied (Hummel and Ray 2008). These shortcomings triggered reliance on ecotypes, defined based on behaviour and ecology, for conservation purposes. Two broad ecotypes—sedentary and migratory—were proposed based on spacing strategy during calving (Bergerud et al. 2008). In Quebec–Labrador, the two large migratory herds

classified as *R. t. caribou* are ecologically similar to *R. t. groenlandicus* and differ from sedentary *R. t. caribou* with which they overlap in winter (Couturier et al. 2010), despite gene flow between migratory and sedentary populations (Boulet et al. 2007). Similarly, within the subspecies *caribou*, at least two herds in Ontario and Manitoba calve gregariously and migrate over long distances, similarly to barren-ground caribou. Ecotypes based on terrain or habitat often align more closely than taxonomy with anthropogenic threats faced by caribou in Canada. Because the classification schemes used by different management agencies are not always consistent with one other, we will refer to four ecotypes, wherever possible adhering to the terminology used by COSEWIC (COSEWIC 2002, 2004) (Fig. 2). We will first present these ecotypes, then consider their conservation status and threats separately.

Ecotypes

We use “Boreal caribou” to refer to sedentary caribou in the boreal forest from Newfoundland to the northeast of British Columbia and the Northwest Territories (Fig. 2), a huge range covering four ecozones. These caribou are mostly distributed as individuals and small groups. They disperse widely at calving and are sedentary only compared with Migratory Tundra caribou. Some populations have seasonal home ranges of hundreds or thousands of square kilometres (Schaefer et al. 2000), with northern populations generally having the largest ranges (Schaefer 2008). Caribou in New-

Table 1. A classification scheme for subspecies and ecotypes of caribou (*Rangifer tarandus*).

Migratory pattern	Ecotype	Subspecies	Examples of herds or populations	COSEWIC
Migratory	Migratory Tundra	Peary (<i>R. t. pearyi</i>)	Banks Island (Nunavut), Melville Island (Nunavut)	Peary (EN)
		Barren-ground (<i>R. t. groenlandicus</i>)	Bathurst (Northwest Territories), Bluenose East (Northwest Territories)	Dolphin–Union (population) (SC)
	Mountain	Grant's (<i>R. t. granti</i>)	Porcupine (Alaska–Yukon), Western Arctic (Alaska)	
		Woodland (<i>R. t. caribou</i>)	Pen Islands (Ontario–Manitoba), George River (Quebec–Labrador)	
Sedentary	Mountain	Grant's (<i>R. t. granti</i>)	Muchatna (Alaska), Fortymile (Alaska)	Southern Mountain (TH)
		Woodland (<i>R. t. caribou</i>)	Wolverine (British Columbia), Narraway (Alberta)	
	Boreal	Woodland (<i>R. t. caribou</i>)	Owl Lake (Manitoba), Little Smoky (Alberta)	Boreal forest ecotype of woodland caribou (TH)
		Mountain	Grant's (<i>R. t. granti</i>)	Northern Mountain (SC)
		Woodland (<i>R. t. caribou</i>)	South Selkirk (British Columbia), Narrow Lake (British Columbia)	Southern Mountain (TH)

Note: Committee on the Status of Endangered Wildlife in Canada (COSEWIC) assessments are in parentheses and are defined as follows: EN, Endangered; SC, Special Concern; TH, Threatened.

foundland can form large groups and until recently existed at high densities.

Based on recognized ecozones, COSEWIC assessed caribou that primarily reside in the mountains of western Canada as two units. We will use “Mountain caribou” when referring to both Northern and Southern Mountain ecotypes. (Fig. 2). Mountain caribou migrate up to 100 km between seasonal ranges (Edmonds 1988). Calving at high elevations, they can have both migratory and sedentary behaviour: small herds tend to calve in subalpine forests, while larger herds calve and summer in open alpine areas and migrate over longer distances (Seip and McLellan 2008). In winter, Northern Mountain caribou typically forage on terrestrial lichens and migrate over both elevation and horizontal distances. Migrations by the Southern Mountain caribou are mostly elevational, and because of the deep snowpack, these caribou depend on arboreal lichens on old growth trees for forage (Seip and McLellan 2008).

The migratory herds in northern Canada, from Labrador to the Yukon, are the “Migratory Tundra caribou” (Table 1; Fig. 2). They are gregarious during calving, can form groups of thousands to tens of thousands, and migrate between seasonal ranges that are often hundreds of kilometres apart. Many large herds migrate across the tree line to spend the winter in boreal forests of the Taiga Shield and Taiga Plains. We included the Dolphin–Union herd on Victoria Island in the Migratory Tundra ecotype. It migrates seasonally and occupies tundra ranges, but at calving, females distribute themselves widely, unlike the gregarious calving of continental Migratory Tundra caribou.

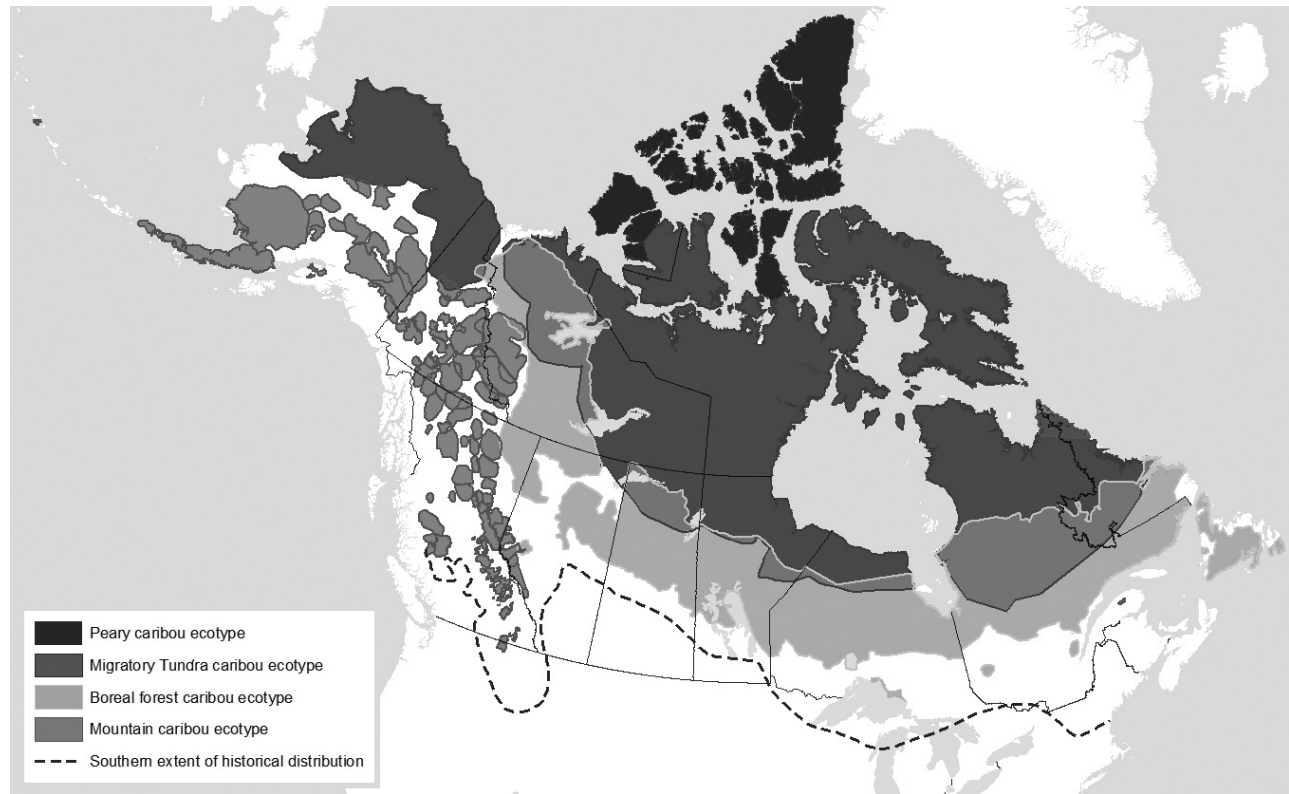
Peary caribou are considered a separate subspecies (Manning 1960) and are recognized as a different entity by Aboriginal peoples (COSEWIC 2004). They are adapted to the High Arctic deserts, with extreme cold but little precipitation and a short growing season, at the northern limits of plant growth. Typically, group sizes are small; even postcalving groups are small with tens of caribou. Their migratory behaviour varies from annual migrations between seasonal ranges on different islands to year-round occupation of relatively small home ranges (Miller and Gunn 2003a). Although Peary caribou migrate to calving ranges, their calving grounds are characterized by relatively low densities so calving is dispersed.

Caribou management and conservation in Canada

The jurisdictional structure of caribou management in Canada is complex. In addition to wildlife management provisions, caribou conservation involves Species at Risk legislation at the federal, territorial, or provincial levels. In northern Canada, governmental responsibilities for wildlife management are shared with aboriginal partners through co-management boards.

The *Species at Risk Act* (SARA) provides for separate scientific assessment and legal listing. COSEWIC assess the conservation status of wildlife species based solely on biological information, but only species that are listed under SARA receive legislative protection. The federal government may use social or economic arguments to refuse to list a species assessed by COSEWIC at some level of endangerment.

Fig. 2. Distribution of ecotypes of caribou (*Rangifer tarandus*) as discussed in this review. The spatial overlap between the Boreal ecotype and the Migratory Tundra and Mountain ecotypes is indicated by intermediate shading. Modified from map 2.11 of Hummel and Ray (2008) and reproduced with permission of Dundurn Press Ltd.



Under this framework, northern species have been particularly unlikely to be listed (Mooers et al. 2007). In 2004, COSEWIC assessed Peary caribou as Endangered based on a 72% decline over 21 years (approximately three caribou generations). The Government of Canada at first did not accept that assessment. In 2010, however, the Minister of the Environment recommended legal listing of Peary caribou under SARA. The Government of Canada accepted COSEWIC's recommendations on the status of several other populations of caribou that are now listed under SARA (Table 2).

A SARA listing, however, does not necessarily imply any additional conservation measures for outside lands directly under the control of the federal government. Boreal caribou from Labrador to the Yukon and Southern Mountain caribou in British Columbia and Alberta were listed as Threatened under SARA 7 years ago, but no National Recovery Strategy has been accepted. A final Recovery Strategy was legally required for June 2007, but lack of identification of Critical Habitat delayed its release (Environment Canada 2009). A "preface" to the recent assessment of Critical Habitat for Boreal caribou hints at continued delay of the recovery strategy until 2011, almost 10 years after legal recognition of the Threatened status.

SARA became a law only in 2002. Although this partially explains the lack of action beyond listing of species, there are fundamental limitations to the powers of this legislation. In contrast to the emphasis on regulation inherent in the U.S. *Endangered Species Act*, for example, the approach in Canada is more discretionary, relying on government-subsidized stewardship. This means that most costs of species protection

are borne by government, rather than by the private sector, through regulation (Illical and Harrison 2007). Additionally, responsibility for the conservation of most species, other than aquatic species and migratory birds, is deferred to provincial and territorial governments, not all of which have endangered species legislation. Many jurisdictions, particularly in western Canada, instead rely on other legislation and policy related to wildlife management. Therefore, while the provincial or territorial status of species at risk such as caribou is often acknowledged and recovery strategies are formulated, the ability to enact meaningful measures for the protection of these species, particularly as they relate to habitat, can be severely constrained. Provinces, such as Ontario and Quebec, that have endangered species legislation have more authority to confer habitat protection measures. Most jurisdictions manage caribou habitat through guidelines developed to protect this species for particular industrial processes such as forestry.

Caribou hunting regulations are set by provinces or territories and co-management boards. Generally, caribou management is based on defining herds or populations (named after calving grounds for migratory populations, geographical range for others) as management units. Currently, there are sport hunting seasons for Migratory Tundra or Mountain caribou in all territories and several provinces, but over the last few decades, sport hunting of Boreal caribou has been closed in Alberta, Saskatchewan, Manitoba, the Northwest Territories, and Quebec. There has been no sport hunting of Boreal caribou in Ontario since 1929.

Subsistence hunting by Aboriginal people of all caribou

Table 2. Conservation status of different caribou “designatable units” in Canada.

Designatable unit	COSEWIC*	SARA†	Occurrence‡
Peary	Endangered	Endangered§	Northwest Territories, Nunavut
Dolphin–Union	Special Concern	Special Concern§	Northwest Territories, Nunavut
Migratory Tundra	Not assessed	None	Yukon, Northwest Territories, Nunavut, Saskatchewan, Manitoba, Ontario, Quebec, Newfoundland (Labrador)
Haida Gwaii	Extinct	None	British Columbia
Northern Mountain	Special Concern	Special Concern	Yukon, British Columbia
Southern Mountain	Threatened	Threatened	British Columbia, Alberta
Boreal	Threatened	Threatened	Yukon, Northwest Territories, Nunavut, British Columbia, Alberta, Saskatchewan, Manitoba, Ontario, Quebec, Newfoundland (Labrador)
Atlantic (Gaspé)	Endangered	Endangered	Quebec
Newfoundland	Not at Risk	None	Newfoundland (island)

*The status given to each population by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC).

†The legal status of each caribou population under Canada’s *Species at Risk Act* (SARA).

‡The provinces or territories where each population occurs. Provinces and territories indicated in boldface type are those that have recognized particular populations (or parts of those populations) as At Risk under specific jurisdictional legislation.

§In July 2010, Canada’s Minister of the Environment recommended the listing under SARA of Peary and Dolphin–Union caribou. Based on past practice, the recommendation above is likely to be accepted by the Government of Canada.

ecotypes is constitutionally guaranteed by treaty rights and land-claim agreements and is typically not monitored by provincial or territorial wildlife management agencies. In the territories, Labrador, and northern Quebec, caribou hunting is also regulated by co-management boards, established under land-claim agreements. Restrictions on Aboriginal harvesting can be imposed when there are serious conservation concerns and agreement on the extent of declines. For example, Inuvialuit accepted to limit their harvest of Peary caribou on northwest Victoria and Banks Islands in the 1990s (COSEWIC 2004) and on the migratory Cape Bathurst and Blue-nose West herds in 2007. In early 2010, both the Northwest Territories and Yukon governments implemented interim conservation measures to reduce harvest of the Bathurst and Porcupine herds, respectively.

Nonaboriginal hunters resident in the province or territory may harvest a restricted number of Migratory Tundra caribou. Harvest reporting is compulsory in some jurisdictions, voluntary in others. Hunters not residing in a particular province or territory can hunt caribou in some populations through the services of guides and outfitters and reporting is required. The price of a guided caribou hunt, excluding license and transportation, ranges from about \$3 000 to \$16 000, depending on the site and duration.

Many Migratory Tundra caribou populations cross jurisdictional boundaries during seasonal migrations. The Porcupine herd, for example, ranges within the Northwest and Yukon territories, as well as into the state of Alaska. Its management is subject to an international agreement with an international co-management board advising on the herd’s conservation. Similarly, the Beverly Qamanirjuaq Caribou Management Board advises the governments of Nunavut, the Northwest Territories, Manitoba, and Saskatchewan about the two herds of migratory caribou they share. These two boards are advisory only and there are no legislated interjurisdictional boards to ensure cooperative management. The Rivière George caribou move seasonally between Quebec and Labrador, and their conservation requires cooperation between two provinces and two wildlife management boards. Several herds

of Migratory Tundra caribou winter in the boreal forests of Saskatchewan, Manitoba, Labrador, and Quebec, mixing with sedentary Boreal caribou, leading to a risk of harvest of Threatened Boreal caribou by subsistence hunters seeking Migratory Tundra caribou.

Threats to caribou

A fundamental issue for caribou conservation is the extent to which ongoing declines are caused by human influences. In the context of this review, we categorize human influences as direct and indirect. Within indirect influences, we separate climate change from past and current habitat changes owing to settlement and industrial activities such as forestry or oil and gas. Our categorization of threats is not absolute, because threats interact with one other. For example, a warming climate will affect all aspects of caribou ecology and exacerbate the impact of other threats.

We treat hunting as a direct influence. Caribou population dynamics are similar to those of other large herbivores in being sensitive to even small changes in the mortality of adult females (Gaillard et al. 1998). Although hunting is not the only cause of mortality, we isolate it as an influence because it is, in theory, relatively straightforward to modify and reverse.

We suggest that much of the decline in numbers and in geographical range of caribou in boreal forests and mountains of southern Canada can be explained by indirect effects of human activities that act in concert to change caribou habitat (Vistnes and Nellemann 2008). Timber extraction and other industrial activities trigger a cascade of effects from removal of forest cover and creation of road or cutline access for hunters and predators. Caribou are vulnerable to landscape-scale habitat changes, being adapted to escape from high levels of predation and parasites by spatial separation from predators and alternative prey (Bergerud et al. 2008; Courbin et al. 2009). They live at low densities in large, contiguous tracts of muskegs or mature coniferous forests where other ungulates (e.g., moose (*Alces alces* (L., 1758)) and white-tailed deer (*Odocoileus virginianus* (Zimmermann, 1780)))

are less prevalent (Rettie and Messier 1998; Bowman et al. 2010).

Boreal and Mountain caribou

Declines in most Boreal and Southern Mountain caribou populations are due directly or indirectly to human activities. We will discuss several threats to these caribou, but we underline that habitat alterations that affect the predator–prey balance are by far the most important.

Prior to industrial activities, Boreal caribou existed at naturally low densities, possibly because high densities led to increases in predator numbers and unsustainable predation rates (Bergerud et al. 1990). Currently, Boreal caribou populations appear to decline and their ranges contract when forestry activities, hydrocarbon exploration, and mining affect their habitat (McLoughlin et al. 2003). Caribou respond to these activities by changing their use of habitat. For example, Boreal caribou avoid the vicinity of hydro, oil and gas, mining, and forestry activities over a scale of several kilometres (Bradshaw et al. 1997; Dyer et al. 2002; Mahoney and Schaefer 2002; Sorensen et al. 2008; Vistnes and Nellemann 2008; Courbin et al. 2009), although the direct effect of this reduced habitat use on population dynamics has not been quantified. One study in Norway that monitored the impact of infrastructure development over 10 years showed that wild reindeer density declined by as much as 92%, use of areas within a 4 km radius of infrastructure was reduced, and reproductive parameters were negatively affected. Over time, development fragmented a once-continuous population into 26 isolated subpopulations (Nellemann et al. 2003). In Ontario, Boreal caribou do not use areas within 13 km of recent cutovers and are extirpated in about 20 years from within 50 km of cutovers, likely as a result of changes in predator–prey relationships (Vors et al. 2007).

The impact of habitat loss on carrying capacity may be magnified beyond the proportion of total caribou range that becomes unavailable, especially considering that caribou rely on a spacing-out strategy to limit predation risk. The meta-analysis of radio-collared caribou in 25 populations across Canada presented in the Critical Habitat Report (Environment Canada 2009) demonstrated a strong linear relationship between caribou recruitment and level of disturbance (anthropogenic and natural) within caribou ranges. This suggests a threshold of habitat alteration beyond which caribou populations appear unable to persist (Sorensen et al. 2008; Environment Canada 2009).

Although habitat changes are the ultimate and indirect cause of Boreal and Mountain caribou declines, the proximate cause of decline is either predation or combination of predation and human harvests. Predation is mostly by gray wolves (*Canis lupus* L., 1758) but also by bears (genus *Ursus* L., 1758) (Wittmer et al. 2005a), coyotes (*Canis latrans* Say, 1823) (Ouellet et al. 1996), and lynx (*Lynx canadensis* Kerr, 1792) on the island of Newfoundland (Bergerud et al. 1983); cougars (*Puma concolor* (L., 1771)) for the Southern Mountain caribou (Kinley and Apps 2001); and wolverines (*Gulo gulo* (L., 1758)) on Mountain caribou (Gustine et al. 2006; Wittmer et al. 2005a). Generally, the impact of predation is greater than that of human harvest, with exceptions in eastern Canada (Schmelzer et al. 2004; Courtois et al. 2007). In Quebec, hunting and predation were higher in areas disturbed by

logging and forest fires (Courtois et al. 2007). Caribou tended to avoid disturbed areas, similar to findings elsewhere. Avoidance of disturbed areas is an extension of the typical caribou strategy to reduce predation risk. For example, even in the absence of timber extraction in northern British Columbia, caribou avoid areas with high vegetation productivity that attract other herbivores and their predators, presumably to reduce the risk of predation on neonates (Gustine et al. 2006).

Additionally, Mountain and Boreal caribou often require large tracts of mature forest (Terry et al. 2000; Courbin et al. 2009; Bowman et al. 2010), and suffer a direct loss of foraging habitat following forestry operations (Smith et al. 2000). Some populations of Mountain caribou in particular are heavily dependent on lichens growing on mature trees (Rominger et al. 1996). Negative effects on caribou populations by land-use change are compounded by time lags of up to several decades, as numerical responses by both caribou and their predators are not immediate (Vors et al. 2007).

It has been suggested that insufficient research has been done on caribou nutrition to exclude inadequate nutrition as an alternative hypothesis for Boreal and Mountain caribou declines (Brown et al. 2007). The question of nutrition was explicitly addressed for caribou in the British Columbia Mountains where Wittmer et al. (2005b) found that caribou populations declined even at very low density; pregnancy rates were high and caribou were more likely to die during the summer when food was abundant. Elsewhere, studies that examined productivity showed that most adult females are pregnant every year (Table 3). Where data on age-specific reproduction are available, they suggest an early age of primiparity (Rettie and Messier 1998). That is a strong clue that populations are not limited by resource abundance, as a delay in primiparity is among the most sensitive indicators of food limitation in mid-sized ungulates (Gaillard et al. 1998; Gaillard et al. 2000). Declines are strongly associated with human-caused habitat alterations, and predator control increases recruitment (Hayes et al. 2003). Although selection for rich lichen feeding areas (particularly in winter) can be an important driver of caribou distribution (Mayor et al. 2009), caribou habitat selection is hierarchical, with the priority to avoid predation at the coarsest level possible (Rettie and Messier 2001).

Timber harvesting in the boreal forest may improve habitat for other cervids, particularly moose, within and near caribou range (Rettie and Messier 1998; Bowman et al. 2010). Moose have substantially expanded their range in British Columbia and Quebec (Darimont et al. 2005; Bergerud et al. 2008) and deer (*Odocoileus* spp.) have moved north into the boreal forest (Latham 2009; Rooney 2001). That expansion has increased the prey base for large predators, mostly wolves. While caribou occupy low productivity mature forest or peatlands, moose (and in some areas deer and elk (*Cervus canadensis* (Erxleben, 1777))) benefit from the vegetation regeneration that follows the harvest of mature trees (Maier et al. 2005). The life-history strategy of moose appears adapted to early seral stages of the boreal forest, such as those created by fires: they regularly twin when nutrition is adequate; grow quickly; females can first conceive at 18 months of age (Garel et al. 2009); and juveniles disperse over long distances (Labonté et al. 1998).

Table 3. Vital statistics of declining populations of Boreal and Mountain caribou in Canada since 1970.

Location	Gestation		Juvenile survival (%)	Adult female survival		Calf:cow ratio	References
	%	<i>n</i>		%	<i>n</i>		
Saskatchewan	94	51		84	64	28:100	Rettie and Messier 1998
Labrador			24	70	36	17:100	Schaefer et al. 1999
Québec	95	55		81	68	31:100	Courtois et al. 2007
Alberta	90–100	93		88	332	17:100	McLoughlin et al. 2003
British Columbia	92	134		67–93	338	12:100	Wittmer et al. 2005a, 2005b, 2007

Note: Calf:cow ratios were collected in March or later and are representative of yearling recruitment. Sample size (*n*) is the number of caribou or number of caribou-years. When sample size is not indicated, estimates are based on comparing age ratios. A range of values is provided for studies of multiple herds.

Caribou require large tracts of low-productivity coniferous forest or peatland characterized by low densities of other ungulates and wolves (James et al. 2004; Latham 2009; Bowman et al. 2010). Caribou tend to select habitats different from those preferred by moose (James et al. 2004; Hins et al. 2009). The resulting interspecific spatial separation appears to reduce but not completely prevent wolf predation on caribou, even if wolves mostly hunt moose (James et al. 2004). A key question therefore is the extent of the positive effect of forestry practices on moose density. Early-seral forest stages benefit moose populations (Fisher and Wilkinson 2005), although population growth may be prevented if logging roads increase hunter access (Rempel et al. 1997). In the absence of habitat alterations owing to forestry, however, Hayes et al. (2003) suggested that declines in moose densities in the Yukon may increase wolf predation on caribou. Therefore the relationship between moose, caribou, and their predators is complex and may not be uniform over the entire range of caribou, particularly in regards to habitat changes. For the Red Wine herd of Boreal caribou in Labrador, subpopulations with substantial spatial overlap with either moose or the large Rivière George herd of Migratory Tundra caribou declined faster than those that did not overlap with other cervids, presumably because sympatry increased the risk of predation and hunting (Schaefer et al. 2001; Schmelzer et al. 2004).

Relations between caribou, predators, and alternative prey are complex (Gasaway et al. 1983), and in much of Canada, wolves, caribou, moose, other potential prey, and predators such as bears co-existed for centuries, usually exposed to Aboriginal harvest. Although we know nothing about the possible spatial and temporal scale of caribou declines and local extinctions that may have occurred in the past, persistence over large spatial and temporal scales does not necessarily imply small-scale and short-term equilibria. Local extinctions or declines could have been followed by recolonizations. Currently, however, habitats are increasingly fragmented; migration routes are sometimes blocked; and human activities have altered the habitat structure, abundance of alternative prey, and the travel efficiency of wolves.

The transportation network associated with industrial activities substantially increases accessibility to hunters and poachers (Courtois et al. 2007; Rettie and Messier 1998; Schaefer 2003). Many areas where caribou have recently been extirpated or are declining were mostly inaccessible to human harvesters before the development of a road network. Additional to hunting access, transportation corridors associated with industrial developments, including roads, cutlines,

snowmobile trails, hydro transmission lines, and pipeline rights-of-way, can allow for more efficient travel by wolves, leading to greater predation rate on caribou. For example in Alberta, wolves made frequent use of human-made travel routes and often killed caribou near them (James and Stuart-Smith 2000). The development of a transportation network may partly explain why forestry operations have a much greater negative impact on caribou populations than equivalent losses of mature forests caused by fires (Environment Canada 2009). Both fires and forestry create seral habitat favored by other cervids, but unlike forest fires, forestry leaves a road network that facilitates travel by wolves.

Motorized winter tourism has increased in many areas with Mountain caribou, especially in British Columbia and the Yukon. Advances in snowmobile technology now allow access to remote areas that were previously undisturbed in winter (Powell 2004). The increase in winter motorized recreation in caribou habitat is an important conservation concern for populations already facing other human-induced environmental stressors for two reasons. First, heavy use of caribou winter ranges by snowmobiles can lead directly to range abandonment (Seip et al. 2007). Second, snowmobile trails increase accessibility to caribou habitat by wolves (Bergerud 1988). Similar to arctic Canada, mountain tops in the western Rockies held relatively little interest for developers until recently. This situation has changed dramatically over the past decade, with activities ranging from coal mining, gas exploration and development to major wind-farm developments and accompanying roads being constructed, planned, or proposed on caribou winter ranges. Windswept alpine ridges are important winter feeding grounds for some Mountain caribou populations that obtain ready access to terrestrial lichen in these snow-free sites (Seip and McLellan 2008). Windpower developments are now being considered for almost every caribou winter range. A further relatively new threat to caribou habitat in central British Columbia is due to the mountain pine beetle (*Dendroctonus ponderosae* Hopkins, 1902). A major outbreak began in the 1990s, crossed the Rockies a decade later. It killed large expanses of pine-lichen habitat and stimulated large-scale salvage logging operations (Ritchie 2008).

Hunting remains a source of mortality for some Boreal and Mountain caribou populations. Currently, sport harvest of Boreal or Mountain caribou is limited to the island of Newfoundland (where quotas have been severely curtailed in recent years), British Columbia, and the Yukon. Harvest by Aboriginals continues in most jurisdictions and there is little information on its extent (Courtois et al. 2007; Hayes et al.

2003), because reporting requirements are usually nonexistent. Some Boreal caribou populations, such as the Red Wine herd in Labrador, can be hunted accidentally when they overlap with populations of Migratory Tundra caribou (Courtois et al. 2007; Schmelzer et al. 2004). Because they show no evidence of negative density-dependence, and instead appear to show strong Allee effects (Wittmer et al. 2005b), small populations of caribou cannot sustain any harvests, suggesting that hunting mortality of declining populations is additive. Although human harvests may accelerate the decline of threatened populations, the limited information on harvests makes it difficult to assess the relative impacts of hunting and of predation. For other ungulates, human hunters typically harvest prime-aged individuals so that their negative impact on population growth is much greater than that of predators, which are more likely to remove old individuals or young of the year (Festa-Bianchet 2007; Wright et al. 2006).

It is likely that some Boreal caribou populations in eastern Canada were negatively affected by human-induced habitat changes that led to range expansion of white-tailed deer infected by meningeal worms (*Parelaphostrongylus tenuis* Dougherty, 1945), a parasite lethal to caribou (Trainer 1973). Although eventually these populations may have been extirpated even without the new parasite, the presence of infected white-tailed deer has been blamed for the failure of reintroduction attempts in Cape Breton and in other former caribou ranges in eastern North America where wolves are absent (Bergerud and Mercer 1989). Changes in moose distribution and abundance may also increase the prevalence of *Echinococcus* Rudolphi, 1801 (Rausch 2003), which links moose, wolves, and caribou.

The situation we described for Boreal caribou is mirrored for Southern Mountain caribou where research has established a direct link between habitat alteration and caribou mortality (Wittmer et al. 2007). Population-specific female mortality increased steeply as the proportion of regenerating forest within a population's range exceeded 10%, based on a retrospective analysis of almost 400 radio-collared caribou between 1984 and 2004. Of 17 subpopulations identified, 15 were decreasing. Six populations were declining by more than 10% a year, with an overall decline estimated at 8% per year (Wittmer et al. 2005a). That decline occurred despite pregnancy rates of about 94% and was caused by high mortality of calves and especially of adult females (range 0.07–0.33) mostly due to predation. Mortality rates were higher in smaller populations, revealing a clear Allee effect: low density and population size were correlated with lower adult female survival and reduced population growth (Wittmer et al. 2005b). Predator populations subsidized by other cervids led to an increased predation risk as caribou density decreased, probably because caribou are easier prey than other species. Consistent results of research in British Columbia (Wittmer et al. 2010), Alberta (Sorensen et al. 2008), Saskatchewan (Rettie and Messier 1998), Ontario (Vors et al. 2007), Quebec (Courtois et al. 2007), and Labrador (Schaefer et al. 1999) suggest that Boreal and Mountain caribou are at risk of extirpation where industrial activities alter habitat causing a shift in predator–prey dynamics.

The effects of a changing climate are becoming increasingly important for species like caribou dwelling in northern

boreal and mountain environments. Caribou have lived with weather and climate fluctuations, but the current pace and trajectory of change causes concern for irreversible impacts. A trend towards hotter and drier summers, increasing fire events, and unpredictable snow conditions has the potential to reduce both recruitment and survival.

Migratory Tundra caribou

For Migratory Tundra caribou, we are only just beginning to understand how human activities including harvesting interact with other ecological processes. Large-scale demographic fluctuations are characteristic of this ecotype (Gunn 2003; Zalatan et al. 2006; Payette et al. 2004) and are likely explained by nonequilibrium interactions of weather and forage availability (Behnke 2000; Caughley and Gunn 1993; White 2008) that affect fecundity and calf survival, especially on calving and summer ranges (Griffith et al. 2002). Those relationships may be shaped by decadal climate patterns (Gunn 2003; Griffith et al. 2002): regionally, climate interacts with forage growth and availability. Forage availability in turn influences caribou body condition, which then determines birth rates and calf survival. Predation and harvesting have a driving role in declines as small reductions in adult female mortality strongly influence population trends, which is typical of ungulates (Gaillard et al. 2000). The factors that initiate the transition from peak herd size to the decline phase and those that accelerate decline or prolong recovery are likely different. For example, harvest and predation play a stronger role in the later phases (Bergerud et al. 2008).

Hunting is not invariably a cause of decline. Migratory Tundra caribou have declined and recovered in the past, despite aboriginal hunting (Zalatan et al. 2006), and Aboriginal people see their hunting as part of caribou ecology (Kendrick et al. 2005). Hunting may become a threat to population persistence when technological changes modify the feedback between caribou abundance and hunting effort, or when a population is already declining because of other causes. Payette et al. (2004) described how a reduced rate of increase in the present-day Rivière-aux-Feuilles herd coincided with increased hunting by Nunamuit in the late 1800s and early 1900s when rifles were introduced. The disappearance of the small Harp Lake herd in northeastern Quebec in the late 1970s coincided with the time when snowmobiles were introduced and hunting increased (Bergerud et al. 2008).

The habitat of most Migratory Tundra caribou remains largely intact, and it is not yet affected by commercial forestry, agriculture, or extensive settlement and accompanying road networks. The tendency of migratory caribou to aggregate in traditional areas for calving and postcalving does, however, increase their vulnerability to disturbances at that time of year (Gunn and Miller 1986; Griffith et al. 2002; Bergerud et al. 2008). The industrial footprint in Canada's North is increasing quickly, especially hydrocarbon and mining, as are winter and all-year road access. Mineral exploration is occurring in some Migratory Tundra caribou calving and postcalving areas, and both roads and mines are proposed for these sensitive areas, with only two calving grounds in the Northwest Territories and Nunavut under permanent protection (Hummel and Ray 2008). Aboriginal Traditional Knowledge suggests that industrial developments and an increasing frequency of fires may affect the migration pat-

terns and reduce the numbers of caribou (Kendrick et al. 2005). The frequency of forest fires is largely determined by decadal changes in climate such as the Arctic Oscillation (Overland and Wang 2005). Migratory Tundra caribou avoid industrial sites, roads, pipelines, and buildings (Cameron 2005; Vistnes et al. 2008), and move away from vehicle and aircraft (Wolfe et al. 2000). The demographic effects of these behavioural responses are unknown, but they could increase energy expenditure and reduce forage intake so that body reserves would be reduced especially when already facing other environmental stresses. The severity of the current declines for several Canadian Migratory Tundra caribou herds raises questions about whether hunting has become a pivotal influence as caribou confront ever-increasing human activities within their ranges.

Global warming is predicted to have a strong signal in the Arctic and current trends already reveal strong warming, especially in winter (Sharma et al. 2009). The timing of the onset of plant growth relative to snow melt is expected to change and may be beneficial to caribou (Pettorelli et al. 2005; Cebrian et al. 2008). Over the next few years, threats to Migratory Tundra caribou in most of their distribution in Canada will substantially increase in complexity as climate change will have opposing and cascading effects on forage growth and availability, the severity and duration of insect harassment, exposure to parasites, and vulnerability to predation (Sharma et al. 2009).

Peary caribou

Peary caribou occupy remote and vast ranges, and so are difficult and costly to monitor. Trends from populations in individual islands suggest sporadic die-offs that coincide with severe winter weather events. These die-offs can be severe: for example, three successive winters (1995–1997) of heavy snow and icing events resulted in a 98% decline of Peary caribou on Bathurst Island (Miller and Gunn 2003b). Other declines may have more complex and interacting causes, including predation and harvesting such as is likely for the Prince of Wales – Somerset Island population that may have been extirpated (Gunn et al. 2006). On other large islands (Banks, northwest Victoria, Prince of Wales, and Somerset), hunting and predation likely contributed to declines (COSEWIC 2004; Miller et al. 2007). Although Inuit report earlier declines and recoveries, Peary caribou recovery after recent declines has been slow or nonexistent, especially on the larger southern islands.

Overall, the estimated number of Peary caribou decreased by about 72% between 1980 and 2001 (COSEWIC 2004). Climate projections suggest that in the near future the high Arctic will experience warmer temperatures and greater precipitation (Rinke and Dethloff 2008), leading to more frequent icing events and die-offs of Peary caribou. This Canadian endemic subspecies is at risk of extinction under existing scenarios of global warming.

Caribou conservation

We present here specific actions required over both the short and long term to stave off caribou losses throughout Canada. First, we offer short-term remedies to deal with the high mortality that drives many declines. Some of these ac-

tions are aimed at ensuring that existing legislation is implemented effectively. Second, we describe longer-term remedies that will be necessary to address the underlying causes of caribou declines: cumulative changes to its habitats. Longer-term solutions involve land management at a very large spatial scale to incorporate caribou into management prescriptions. That includes providing for their requirement to space themselves to avoid predation (and some parasites) without compromising foraging opportunities. Third, we comment on prevailing environmental trends, especially global warming. Lastly, falling into the classical response of wanting more data, we identify key technical gaps in information.

A key for both short- and long-term remedies to conserving caribou lies in how scientific and other relevant knowledge is used to influence policy and public opinion. If caribou are not to go the way of other formerly abundant Canadian species, such as plains bison (*Bison bison* (L., 1758)), passenger pigeon (*Ectopistes migratorius* (L., 1766)), or Atlantic cod (*Gadus morhua* L., 1758), researchers must ensure that their results reach the public, the agencies, and co-management boards responsible for conservation decisions. People who live with caribou have the most to lose if conservation fails (Hummel and Ray 2008). The public needs to be involved because caribou conservation implies difficult choices. Similar to most remaining populations of long-distance migratory ungulates in the world, caribou face increasing threats from escalating levels of human activities (Harris et al. 2009).

Our emphasis on involving people is because a pervasive threat to the conservation of Migratory Tundra and Peary caribou is best summarized as failures in communication, including those brought about by differences between wildlife managers and hunters. Caribou management is not unique in this respect (Weeks and Packard 1997). Differences of opinions between managers and hunters about declines and their causes have hindered progress on recovery actions (Gunn 2001; Gunn et al. 2006). The reality that caribou numbers fluctuate can add further complications because “natural” fluctuations are not ordinarily a conservation concern as long as conditions exist to allow recovery in the future. Periodic declines and recoveries are well understood by harvesters, encouraging the assumption that caribou will inevitably recover from their current declines. This may not be the case, however, given the strong signals for changing trends in weather across caribou ranges, as well as the increasing intensity and scale of the human footprint. In particular, recovery of caribou populations will require collaborations among biologists, co-management boards, and harvesters, such as the CircumArctic Rangifer Monitoring and Assessment Network (CARMA 2009). Because changes in population growth rates occur over decades, a long-term multi-herd approach is essential.

Over the short term, caribou conservation must focus on reducing mortality. That means reducing hunting and predation where required. Hunting is a pivotal influence and can be both a threat and a benefit to conservation (Gunn 2001). Currently, even though most Migratory Tundra populations are declining, predation and harvesting levels remain mostly unchanged, except for the Bluenose West and Cape Bathurst herds where co-management boards have taken steps to proactively reduce harvests. There is an urgent and immediate

need to establish effective harvest monitoring programs, as the current levels of harvest are mostly uncertain, with the exception of sport harvests. Effective conservation of declining populations cannot be achieved if managers do not know how many caribou are harvested.

Experience has demonstrated that once population range conditions for Boreal and Mountain caribou have shifted to those that favour proliferation of predators and alternative prey, it is not possible to stave off caribou declines without sustained and intensive management actions. Predator control programs, over the short term, are necessary under these conditions to increase caribou survival, particularly for adult females and calves (Hayes et al. 2000). Other short-term management strategies that have been attempted include fencing of pregnant females to protect newborn calves from predators and increased harvest of other species such as moose that support a high density of wolves. All these initiatives, however, require constant human intervention over sustained periods of time and are very expensive (Potvin et al. 1992). Effective predator control generally requires the removal of over 80% of wolves over a large area and over many years (Hayes et al. 2003). At the spatial scale of most Boreal or Mountain caribou populations, effective predator control requires annual removals of hundreds of wolves. Mosnier et al. (2008) warn that for very small caribou populations, the wide-ranging habits of some predators also imply that control well beyond the areas used by caribou may be necessary, because predators from neighbouring areas may rapidly move into removal areas. Hence, although predator removals are often promoted as short-term emergency measures, in reality they need to be conducted year after year. Wolf control programs lasting only 3–5 years may allow caribou numbers to stabilize or increase, but the pattern returns to one of decline as soon as predator control stops because wolf numbers recover quickly (Hayes and Harestad 2000; Potvin et al. 1992).

Predator control programs present two societal problems: (1) they are unpopular with the public, and (2) by attacking the proximate (predation) rather than the ultimate (habitat destruction) cause of caribou declines, they may instill a false sense of security among people, particularly those that live within caribou range. Most members of the public are unaware of the measures required to ensure caribou survival in such circumstances. Over the short term, however, it seems highly unlikely that many southern and western Boreal and Mountain caribou populations in Canada will persist without intensive predator control. Even if all industrial activity was to stop and recovery of habitat following forest cutting or energy sector development was accelerated in these ranges, most herds would continue to decline because of the time lag of forest succession. Our review suggests that it is currently impossible for high levels of industrial activity and Boreal or Mountain caribou to co-exist. Wolf control can “buy time” for caribou. Unless there are efforts to create and maintain large areas of low industrial activity, however, predator control merely delays extinction. Where levels of disturbance have been more restrained, caribou declines can be prevented through proactive land management approaches.

Short-term remedies also include working within the context of species at risk legislation, which to date has been ineffective in serving caribou conservation. The 6 years that passed between COSEWIC’s assessments of Peary and

Dolphin–Union caribou and the acceptance of that assessment by the Canadian government illustrates the communication failures already mentioned. We also note the slow progress in addressing the Critical Habitat provisions under SARA. Moreover, although many provinces and territories have released caribou recovery strategies or conservation plans in recent years, progress towards implementation of recovery actions has been slow. Recently, however, caribou conservation has received a higher priority for natural resource management agencies in many jurisdictions, with increased levels of investment in research and monitoring. At the federal level, meaningful action beyond listing is unlikely given the deferral of federal legislative authority to provincial and territorial entities. A case in point is offered by Southern Mountain caribou, listed under SARA since 2002. Eight years later, the process for recovery planning and critical habitat identification has not even been initiated by Environment Canada. One population in Banff National Park is now extinct (Hebblewhite et al. 2010). In contrast, the British Columbia recovery planning process (Government of British Columbia 2002) has resulted in a suite of aggressive actions, including restrictions to commercial forestry and attempts to reduce both predators and alternative prey.

Land-use management is needed to protect calving and postcalving ranges of Migratory Tundra caribou. Although Canada has called on the U.S. to protect the Porcupine herd’s calving grounds, within Canada little progress has been made to protect calving caribou and their habitat from disturbance. Canada has only one national park (Tuktu Nogait) that partially protects the calving grounds of the Bluenose West herd. The Queen Maud Gulf Migratory Bird Sanctuary serves as a measure of protection for the Ahiak herd’s calving grounds, but the calving and postcalving ranges of all other herds remain unprotected. We should note that sedentary caribou adopt the opposite strategy at this time of year, in that females space themselves far apart from one another to minimize predation risk on calves (Schaefer 2008). This scattered distribution of females, often across the entire population range, means that protection of calving sites will do little on its own to ensure population persistence for nonmigratory caribou.

Long-term steps are needed to address changes in land use on caribou ranges. In the southern part of its distribution in Canada, the decline of Boreal and Mountain caribou is due to human activities. Research from Labrador to British Columbia has identified the cumulative effects of forestry operations and other activities such as hydrocarbon exploration, motorized winter recreation, and unsustainable harvest as the ultimate reasons for the decline (Environment Canada 2009; Seip and McLellan 2008). When the causes of a species’ decline are known, society must decide whether or not it wishes to slow or stop that decline by making long-term choices about land-use planning, restraining development, and maintaining areas of intact habitat. Currently, it appears that Canadians, or at least their governments, are uncertain about the choices that need to be made to stop the declines of Boreal and Mountain caribou populations. Therefore, the decline will continue, with local extirpations and further range contraction towards the north. As industrial activities move north, herds in northern boreal regions will experience

the conservation problems now affecting herds in southern regions.

The effects of industrial activities on Migratory Tundra caribou habitat are currently not as intense as in the boreal forest and the western mountains. Since the 1970s, however, the human population in the Arctic and subarctic has doubled, reaching about 107 200 people in 2006. Changing socio-economic conditions and technology are influencing caribou harvesting patterns. Increasing exploration and development, including all-weather roads, mining, and hydroelectric projects, are likely to increasingly affect Migratory Tundra caribou, but an assessment of cumulative effects has not yet taken shape.

In the background but growing in importance is global warming. It is particularly important to determine how climate change may affect the complex interactions between snow cover (that may increase in some places and decrease in others), forage availability, and use by caribou (Pettoelli et al. 2005; Sharma et al. 2009). The distribution and abundance of predators, alternate prey, and parasites or diseases may also be affected by climate change. Several species may move northwards as is occurring with moose (Norment et al. 1999) and white-tailed deer (Veitch 2001). For Migratory Tundra caribou, it is urgent to understand how current and projected environmental trends in arctic Canada may affect population recovery. For example, the Dolphin–Union herd has likely declined in recent years partly because of increasing mortality when caribou migrate across the sea ice from Victoria Island to the mainland. Freeze-up is progressively later and mortality from breaking through thin ice may be compounded by high harvest levels (COSEWIC 2004). Yet, no management plan to adjust aboriginal harvest to the changing environment has been completed.

Extirpations of Peary caribou from several islands are possible within decades if changes in the arctic climate continue as predicted (Anisimov et al. 2007; Rinke and Dethloff 2008) and are compounded by other stresses, including changes in predation, land use, and hunting. Listing this subspecies under SARA, however, will signal that Canadians and their governments recognize the seriousness of the status of Peary caribou and the need to work together to ensure effective recovery planning. Unfortunately, media reports about the impacts of climate change in Canada's Arctic rarely mention Peary caribou.

We conclude by underlining two major gaps in information that must be filled to ensure caribou conservation. First, there are serious gaps in information on population size, trends, and geographical ranges. The logistics of monitoring the population dynamics of caribou are challenging and costly. Yet, the costs of missed population declines can be much higher, especially for the people depending on the caribou. We point to the 15-year gap in monitoring Peary caribou on Somerset and Prince of Wales islands. In 1980, caribou numbers were estimated at about 6000, but the next survey in 1995 showed almost no caribou (Gunn et al. 2006). On the Nunavut mainland, the Beverly herd was estimated at 270 000 in 1994, but then there was almost no monitoring until 2007–2009. By then, the herd had collapsed, as only a few females were counted on the calving grounds (Beverly and Qamanirjuaq Caribou Management Board 2009). Similar logistic problems

affect the monitoring of some remote populations of Boreal caribou.

Second, our knowledge of how caribou population dynamics are affected by habitat alterations and other ecological changes remains inadequate. Notwithstanding the observation that various levels of government appear unwilling to restrain industrial activities to protect caribou, there is also a large gap in our understanding of how much habitat must be protected to ensure survival of caribou populations, or what minimum levels of predator control (both in terms of duration and intensity) may allow caribou populations to persist. There is currently no research on whether artificial control of alternative prey may affect changes on predation pressure on caribou in the face of habitat alterations that favor other cervids. We know little about temporal variations in the sex and age structure of populations and how those changes may affect trends in population sizes and their ability to sustain human harvests (Coulson et al. 2001, 2005; Festa-Bianchet et al. 2003). There is little information on age-specific survival and reproduction of wild caribou (Adams and Dale 1998; Cameron and Hoef 1994; Couturier et al. 2009a, 2009b; Crête et al. 1996), and on the age–sex structure of caribou harvested by people or killed by predators.

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References

- Adams, L.G., and Dale, B.W. 1998. Reproductive performance of female Alaskan caribou. *J. Wildl. Manage.* **62**(4): 1184–1195. doi:10.2307/3801982.
- Anisimov, O.A., Vaughan, D.G., Callaghan, T.V., Furgal, C., Marchant, H., Prowse, T.D., Vilhjálmsson, H., and Walsh, J.E. 2007. Polar regions (Arctic and Antarctic). *CIn* Contribution of Working Group II to the the Fourth Assessment Report of the Intergovernmental Panel on Climate Change, 2007. *Edited by* M.L. Parry, O.F. Canziani, J.P. Palutikof, P.J. van der Linden, and C.E. Hanson. Cambridge University Press, Cambridge. pp. 653–685.
- Banfield, A.W.F. 1961. A revision of reindeer and caribou, genus *Rangifer*. National Museum of Canada, Ottawa, Ont.
- Behnke, R.H. 2000. Equilibrium and non-equilibrium models of livestock population dynamics in pastoral Africa: their relevance to Arctic grazing systems. *Rangifer*, **20**(2–3): 141–152.
- Bergerud, A.T. 1988. Caribou, wolves and man. *Trends Ecol. Evol.* **3**(3): 68–72. doi:10.1016/0169-5347(88)90019-5. PMID:21227095.
- Bergerud, A.T., and Mercer, W.E. 1989. Caribou introductions in eastern North America. *Wildl. Soc. Bull.* **17**: 111–120.
- Bergerud, A.T., Nolan, M.J., Curnew, K., and Mercer, W.E. 1983. Growth of the Avalon Peninsula, Newfoundland caribou herd. *J. Wildl. Manage.* **47**(4): 989–998. doi:10.2307/3808157.

- Bergerud, A.T., Ferguson, R., and Butler, H.E. 1990. Spring migration and dispersion of woodland caribou at calving. *Anim. Behav.* **39**(2): 360–368. doi:10.1016/S0003-3472(05)80882-6.
- Bergerud, A.T., Luttich, S.N., and Lodewijk, C. 2008. The return of caribou to Ungava. McGill–Queen’s University Press, Montréal.
- Beverly and Qamanirjuaq Caribou Management Board. 2009. Press release: Continuing drop in caribou numbers makes a “Recipe for Recovery” to help the ailing Beverly herd more important than ever. Available from http://www.arctic-caribou.com/press_releases/July_09.html [accessed 30 November 2009].
- Boulet, M., Couturier, S., Côté, S.D., Otto, R.D., and Bernatchez, L. 2007. Integrative use of spatial, genetic, and demographic analyses for investigating genetic connectivity between migratory, montane, and sedentary caribou herds. *Mol. Ecol.* **16**(20): 4223–4240. doi:10.1111/j.1365-294X.2007.03476.x. PMID:17784914.
- Bowman, J., Ray, J.C., Magoun, A.J., Johnson, D., and Dawson, F.N. 2010. Roads, logging, and the large-mammal community of an eastern Canadian boreal forest. *Can. J. Zool.* **88**(5): 454–467. doi:10.1139/Z10-019.
- Bradshaw, C.J.A., Boutin, S., and Hebert, D.M. 1997. Effects of petroleum exploration on woodland caribou in northeastern Alberta. *J. Wildl. Manage.* **61**(4): 1127–1133. doi:10.2307/3802110.
- Brown, G.S., Landriault, L., Sleep, D.J.H., and Mallory, F.F. 2007. Comment arising from a paper by Wittmer et al.: hypothesis testing for top-down and bottom-up effects in woodland caribou population dynamics. *Oecologia (Berl.)*, **154**(3): 485–492. doi:10.1007/s00442-007-0855-3. PMID:17891419.
- Byun, S.A., Koop, B.F., and Reimchen, T.E. 2002. Evolution of the Dawson caribou (*Rangifer tarandus dawsonii*). *Can. J. Zool.* **80**(5): 956–960. doi:10.1139/z02-062.
- Cameron, R.D. 2005. Central Arctic caribou and petroleum development: distributional, nutritional, and reproductive implications. *Arctic*, **58**: 1–9.
- Cameron, R.D., and Hoef, J.M.V. 1994. Predicting parturition rate of caribou from autumn body mass. *J. Wildl. Manage.* **58**(4): 674–679. doi:10.2307/3809681.
- CARMA. 2009. CircumArctic Rangifer Monitoring and Assessment Network: status of herds. Available from <http://www.carmanetwork.com/display/public/Herds> [accessed 20 November 2009].
- Caughley, G., and Gunn, A. 1993. Dynamics of large herbivores in deserts: kangaroos and caribou. *Oikos*, **67**(1): 47–55. doi:10.2307/3545094.
- Cebrian, M.R., Kielland, K., and Finstad, G. 2008. Forage quality and reindeer productivity: multiplier effects amplified by climate change. *Arct. Antarct. Alp. Res.* **40**(1): 48–54. doi:10.1657/1523-0430(06-073)[CEBRIAN]2.0.CO;2.
- COSEWIC. 2002. COSEWIC assessment and update status report on the woodland caribou *Rangifer tarandus caribou* in Canada. Committee on the Status of Endangered Wildlife in Canada (COSEWIC), Ottawa, Ont.
- COSEWIC. 2004. COSEWIC assessment and update status report on the Peary caribou *Rangifer tarandus pearyi* and the barren-ground caribou *Rangifer tarandus groenlandicus* (Dolphin and Union population) in Canada. Committee on the Status of Endangered Wildlife in Canada (COSEWIC), Ottawa, Ont.
- Coulson, T., Catchpole, E.A., Albon, S.D., Morgan, B.J.T., Pemberton, J.M., Clutton-Brock, T.H., Crawley, M.J., and Grenfell, B.T. 2001. Age, sex, density, winter weather, and population crashes in Soay sheep. *Science (Washington, D.C.)*, **292**(5521): 1528–1531. doi:10.1126/science.292.5521.1528. PMID:11375487.
- Coulson, T., Gaillard, J.M., and Festa-Bianchet, M. 2005. Decomposing the variation in population growth into contributions from multiple demographic rates. *J. Anim. Ecol.* **74**(4): 789–801. doi:10.1111/j.1365-2656.2005.00975.x.
- Courbin, N., Fortin, D., Dussault, C., and Courtois, R. 2009. Landscape management for woodland caribou: the protection of forest blocks influences wolf–caribou co-occurrence. *Landsc. Ecol.* **24**(10): 1375–1388. doi:10.1007/s10980-009-9389-x.
- Courtois, R., Ouellet, J.-P., Breton, L., Gingras, A., and Dussault, C. 2007. Effects of forest disturbance on density, space use, and mortality of woodland caribou. *Ecoscience*, **14**(4): 491–498. doi:10.2980/1195-6860(2007)14[491:EOFDOD]2.0.CO;2.
- Couturier, S., Côté, S.D., Huot, J., and Otto, R.D. 2009a. Body condition dynamics in a northern ungulate gaining fat in winter. *Can. J. Zool.* **87**(5): 367–378. doi:10.1139/Z09-020.
- Couturier, S., Côté, S.D., Otto, R.D., Weladji, R.B., and Huot, J. 2009b. Variation in calf body mass in migratory caribou: the role of habitat, climate, and movements. *J. Mammal.* **90**(2): 442–452. doi: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. *J. Wildl. Manage.* **74**(3): 395–404. doi:10.2193/2008-384.
- Crête, M., Couturier, S., Hearn, B.J., and Chubbs, T.E. 1996. Relative contribution of decreased productivity and survival to recent changes in the demographic trend of the Rivière George caribou herd. *Rangifer*, **16**(4; Special Issue No. 9): 27–36.
- Dale, B.W., Adams, L.G., and Bowyer, R.T. 1994. Functional response of wolves preying on barren-ground caribou in a multiple-prey ecosystem. *J. Anim. Ecol.* **63**(3): 644–652. doi:10.2307/5230.
- Darimont, C.T., Paquet, P.C., Reimchen, T.E., and Crichton, V. 2005. Range expansion by moose into coastal temperate rainforests of British Columbia, Canada. *Divers. Distrib.* **11**(3): 235–239. doi:10.1111/j.1366-9516.2005.00135.x.
- Dyer, S.J., O’Neill, J.P., Wasel, S.M., and Boutin, S. 2002. Quantifying barrier effects of roads and seismic lines on movements of female woodland caribou in northeastern Alberta. *Can. J. Zool.* **80**(5): 839–845. doi:10.1139/z02-060.
- Edmonds, E.J. 1988. Population status, distribution, and movements of woodland caribou in west central Alberta. *Can. J. Zool.* **66**(4): 817–826. doi:10.1139/z88-121.
- Environment Canada. 2009. Scientific review for the identification of critical habitat for woodland caribou (*Rangifer tarandus caribou*), boreal population, in Canada. Environment Canada, Ottawa, Ont.
- Festa-Bianchet, M. 2007. Ecology, evolution, economics, and ungulate management. In *Wildlife science: linking ecological theory and management applications*. Edited by T.E. Fulbright and D.G. Hewitt. CRC Press, Boca Raton, Fla. pp. 183–202.
- Festa-Bianchet, M., Gaillard, J.-M., and Côté, S.D. 2003. Variable age structure and apparent density-dependence in survival of adult ungulates. *J. Anim. Ecol.* **72**(4): 640–649. doi:10.1046/j.1365-2656.2003.00735.x.
- Fisher, J.T., and Wilkinson, L. 2005. The response of mammals to forest fire and timber harvest in the North American boreal forest. *Mammal Rev.* **35**(1): 51–81. doi:10.1111/j.1365-2907.2005.00053.x.
- Gaillard, J.-M., Festa-Bianchet, M., and Yoccoz, N.G. 1998. Population dynamics of large herbivores: variable recruitment with constant adult survival. *Trends Ecol. Evol.* **13**(2): 58–63. doi:10.1016/S0169-5347(97)01237-8. PMID:21238201.
- Gaillard, J.-M., Festa-Bianchet, M., Yoccoz, N.G., Loison, A., and Toïgo, C. 2000. Temporal variation in fitness components and population dynamics of large herbivores. *Annu. Rev. Ecol. Syst.* **31**(1): 367–393. doi:10.1146/annurev.ecolsys.31.1.367.
- Garel, M., Solberg, E.J., Sæther, B.E., Grøtán, V., Tufto, J., and

- Heim, M. 2009. Age, size, and spatiotemporal variation in ovulation patterns of a seasonal breeder, the Norwegian moose (*Alces alces*). *Am. Nat.* **173**(1): 89–104. doi:10.1086/593359. PMID:19072136.
- Gasaway, W.C., Stephenson, R.O., Davis, J.L., Sheperd, P.E.K., and Burris, O.E. 1983. Interrelationships of wolves, prey, and man in interior Alaska. *Wildl. Monogr.* No. 84. pp. 1–50.
- Government of British Columbia. 2002. A strategy for the recovery of mountain caribou in British Columbia. B.C. Ministry of Water, Land and Air Protection, Victoria.
- Government of Newfoundland and Labrador. 2009. News releases: Caribou resource committee established to bring stakeholder perspective to the table. Available from <http://www.releases.gov.nl.ca/releases/2009/env/0908n02.htm> [accessed 30 November 2009].
- Government of the Northwest Territories. 2009. Current news: Survey confirms continued decline in Bathurst caribou. Available from http://www.exec.gov.nt.ca/currentnews/prDetails.asp?varPR_ID=1393 [accessed 30 November 2009].
- Griffith, B., Douglas, D., Walsh, N., and Young, D. T. M., Russell, D. E., White, R.G., Cameron, R., and Whitten, K. 2002. The Porcupine caribou herd. In *Arctic refuge coastal plain terrestrial wildlife research summaries*. Edited by D. Douglas, P. Reynolds, and E. Rhode. U.S. Geol. Surv. Biol. Sci. Rep. No. BSR-2002–0001.
- Gunn, A. 2001. Conservation and resource use in Arctic ecosystems. In *Conservation of exploited species*. Edited by R.D. Reynolds, G. M. Mace, K.H. Redford, and J.G. Robinson. Cambridge University Press, Cambridge. pp. 424–439.
- Gunn, A. 2003. Voles, lemmings and caribou: population cycles revisited? *Rangifer*, **23**(Special Issue No. 14): 105–112.
- Gunn, A., and Miller, F.L. 1986. Traditional behaviour and fidelity to caribou calving grounds by barren-ground caribou. *Rangifer*, **6**(2; Special Issue No. 1): 151–158.
- Gunn, A., Miller, F.L., Barry, S.J., and Buchan, A. 2006. A near-total decline in caribou on Prince of Wales, Somerset and Russell Islands, Canadian Arctic. *Arctic*, **59**: 1–13.
- Gustine, D.D., Parker, K.L., Lay, R.J., Gillingham, M.P., and Heard, D.C. 2006. Calf survival of woodland caribou in a multi-predator ecosystem. *Wildl. Monogr.* No. 165. pp. 1–32.
- Harris, G., Thirgood, S., Hopcraft, J.G.C., Cromsigt, J.P.G.M., and Berger, J. 2009. Global decline in aggregated migrations of large terrestrial mammals. *Endanger. Species Res.* **7**: 55–76. doi:10.3354/esr00173.
- Hayes, R.D., and Harestad, A.S. 2000. Demography of a recovering wolf population in the Yukon. *Can. J. Zool.* **78**(1): 36–48. doi:10.1139/cjz-78-1-36.
- Hayes, R.D., Baer, A.M., Wotschikowsky, U., and Harestad, A.S. 2000. Kill rate by wolves on moose in the Yukon. *Can. J. Zool.* **78**(1): 49–59. doi:10.1139/cjz-78-1-49.
- Hayes, R.D., Farnell, R., Ward, R.M.P., Carey, J., Dehn, M., Kuzyk, G.W., Baer, A.M., Gardner, C.L., and O'Donoghue, M. 2003. Experimental reduction of wolves in the Yukon: ungulate responses and management implications. *Wildl. Monogr.* No. 152. pp. 1–35.
- Hebblewhite, M., White, C., and Musiani, M. 2010. Revisiting extinction in National Parks: mountain caribou in Banff. *Conserv. Biol.* **24**(1): 341–344. doi:10.1111/j.1523-1739.2009.01343.x. PMID:19843126.
- Hins, C., Ouellet, J.-P., Dussault, C., and St-Laurent, H. 2009. Habitat selection by forest-dwelling caribou in managed boreal forest of eastern Canada: evidence of a landscape configuration effect. *For. Ecol. Manage.* **257**(2): 636–643. doi:10.1016/j.foreco.2008.09.049.
- Hummel, M., and Ray, J.C. (Editors). 2008. *Caribou and the North: a shared future*. Dundurn Press Ltd., Toronto, Ont.
- Illicial, M., and Harrison, K. 2007. Protecting endangered species in the US and Canada: the role of negative lesson drawing. *Can. J. Polit. Sci.* **40**: 367–394.
- InterGroup Consultants. 2008. Economic valuation and socio-cultural perspectives of the estimated harvest of the Beverly and Qamanirjuaq caribou herds. Beverly and Qamanirjuaq Caribou Management Board, Winnipeg, Man. Available from http://www.arctic-caribou.com/PDF/Economic_and_Socio-Cultural_Value_of_Bev+Qam_Caribou_01May08.pdf.
- James, A.R.C., and Stuart-Smith, A.K. 2000. Distribution of caribou and wolves in relation to linear corridors. *J. Wildl. Manage.* **64**(1): 154–159. doi:10.2307/3802985.
- James, A.R.C., Boutin, S., Hebert, D.M., and Rippin, A.B. 2004. Spatial separation of caribou from moose and its relation to predation by wolves. *J. Wildl. Manage.* **68**(4): 799–809. doi:10.2193/0022-541X(2004)068[0799:SSOCFM]2.0.CO;2.
- Kelsall, J.P. 1968. *The caribou*. Queen's Printer, Ottawa, Ont.
- Kendrick, A., and Lyver, P.O.B. Lutsel K'E Dene First Nation. 2005. Denésoliné (Chipewyan) knowledge of barren-ground caribou (*Rangifer tarandus groenlandicus*) movements. *Arctic*, **58**: 175–191.
- Kinley, T.A., and Apps, C.D. 2001. Mortality patterns in a subpopulation of endangered mountain caribou. *Wildl. Soc. Bull.* **29**: 158–164.
- Labonté, J., Ouellet, J.-P., Courtois, R., and Bélisle, F. 1998. Moose dispersal and its role in the maintenance of harvested populations. *J. Wildl. Manage.* **62**(1): 225–235. doi:10.2307/3802282.
- Latham, A.D.M. 2009. Wolf ecology and caribou-primary prey-wolf spatial relationships in low productivity peatland complexes in northeastern Alberta. Ph.D. thesis, Department of Biological Science, University of Alberta, Edmonton.
- Mahoney, S.P., and Schaefer, J.A. 2002. Hydroelectric development and the disruption of migration in caribou. *Biol. Conserv.* **107**(2): 147–153. doi:10.1016/S0006-3207(02)00052-6.
- Maier, J.A.K., Ver Hoef, J.M., McGuire, A.D., Bowyer, R.T., Saperstein, L., and Maier, H.A. 2005. Distribution and density of moose in relation to landscape characteristics: effects of scale. *Can. J. For. Res.* **35**(9): 2233–2243. doi:10.1139/x05-123.
- Manning, T.H. 1960. The relationship of the Peary and barren ground caribou. *Arctic Inst. N. Amer. Tech. Pap.* No. 4.
- Mayor, S.J., Schaefer, J.A., Schneider, D.C., and Mahoney, S.P. 2009. The spatial structure of habitat selection: a caribou's-eye-view. *Acta Oecol.* **35**(2): 253–260. doi:10.1016/j.actao.2008.11.004.
- McLoughlin, P.D., Dzus, E., Wynes, B., and Boutin, S. 2003. Declines in populations of woodland caribou. *J. Wildl. Manage.* **67**(4): 755–761. doi:10.2307/3802682.
- Miller, F.L., and Gunn, A. 2003a. Status, population fluctuations and ecological relationships of Peary caribou on the Queen Elizabeth Islands: implications for their survival. *Rangifer*, **23**(Special Issue No. 14): 213–226.
- Miller, F.L., and Gunn, A. 2003b. Catastrophic die-off of Peary caribou on the western Queen Elizabeth Islands, Canadian High Arctic. *Arctic*, **56**: 381–390.
- Miller, F.L., Barry, S.J., and Calvert, W.A. 2007. Near-total loss of caribou on south-central Canadian Arctic Islands and the role of seasonal migration in their demise. *Arctic*, **60**: 23–36.
- Mooers, A.Ø., Prugh, L.R., Festa-Bianchet, M., and Hutchings, J.A. 2007. Biases in legal listing under Canadian endangered species legislation. *Conserv. Biol.* **21**(3): 572–575. doi:10.1111/j.1523-1739.2007.00689.x. PMID:17531035.
- Mosnier, A., Boisjoly, D., Courtois, R., and Ouellet, J.-P. 2008. Extensive predator space use can limit the efficacy of a control

- program. *J. Wildl. Manage.* **72**(2): 483–491. doi:10.2193/2006-462.
- Mowat, G., and Heard, D.C. 2006. Major components of grizzly bear diet across North America. *Can. J. Zool.* **84**(3): 473–489. doi:10.1139/Z06-016.
- Musiani, M., Leonard, J.A., Cluff, H.D., Gates, C., Mariani, S., Paquet, P.C., Vila, C., and Wayne, R.K. 2007. Differentiation of tundra/taiga and boreal coniferous forest wolves: genetics, coat colour and association with migratory caribou. *Mol. Ecol.* **16**(19): 4149–4170. doi:10.1111/j.1365-294X.2007.03458.x. PMID: 17725575.
- Nellemann, C., Vistnes, I., Jordhoy, P., Strand, O., and Newton, A. 2003. Progressive impact of piecemeal infrastructure development on wild reindeer. *Biol. Conserv.* **113**(2): 307–317. doi:10.1016/S0006-3207(03)00048-X.
- Norment, C.J., Hall, A., and Hendricks, P. 1999. Important bird and mammal records in the Thelon River Valley, Northwest Territories: range expansions and possible causes. *Can. Field Nat.* **113**: 375–385.
- Ouellet, J.P., Ferron, J., and Sirois, L. 1996. Space and habitat use by the threatened Gaspé caribou in southeastern Quebec. *Can. J. Zool.* **74**(10): 1922–1933. doi:10.1139/z96-217.
- Overland, J.E., and Wang, M. 2005. The Arctic climate paradox: the recent decrease of the Arctic oscillation. *Geophys. Res. Lett.* **37**: L06701, doi:067. doi:10.1029/2004GL021752.
- Payette, S., Boudreau, S., Morneau, C., and Pitre, N. 2004. Long-term interactions between migratory caribou, wildfires and Nunavik hunters inferred from tree rings. *Ambio*, **33**(8): 482–486. PMID:15666677.
- Pettorelli, N., Weladji, R.B., Holand, Ø., Mysterud, A., Breie, H., and Stenseth, N.C. 2005. The relative role of winter and spring conditions: linking climate and landscape-scale plant phenology to alpine reindeer body mass. *Biol. Lett.* **1**(1): 24–26. doi:10.1098/rsbl.2004.0262. PMID:17148119.
- Potvin, F., Jolicœur, H., Breton, L., and Lemieux, R. 1992. Evaluation of an experimental wolf reduction and its impact on deer in Papineau-Labelle Reserve, Quebec. *Can. J. Zool.* **70**(8): 1595–1603. doi:10.1139/z92-220.
- Powell, T. 2004. Réponse comportementale des caribous des bois au harcèlement par les motoneiges. M.Sc. thesis, Département de biologie, Université de Sherbrooke, Sherbrooke, Que.
- Rausch, R.L. 2003. Cystic echinococcosis in the Arctic and subarctic. *Parasitology*, **127**(Suppl. 7): S73–S85. doi:10.1017/S0031182003003664. PMID:15027606.
- Rempel, R.S., Elkie, P.C., Rodgers, A.R., and Gluck, M.J. 1997. Timber management and natural-disturbance effects on moose habitat: landscape evaluation. *J. Wildl. Manage.* **61**(2): 517–524. doi:10.2307/3802610.
- Rettie, W.J., and Messier, F. 1998. Dynamics of woodland caribou populations at the southern limit of their range in Saskatchewan. *Can. J. Zool.* **76**(2): 251–259. doi:10.1139/cjz-76-2-251.
- Rettie, W.J., and Messier, F. 2001. Range use and movement rates of woodland caribou in Saskatchewan. *Can. J. Zool.* **79**(11): 1933–1940. doi:10.1139/z01-156.
- Rinke, A., and Dethloff, K. 2008. Simulated circum-Arctic climate changes by the end of the 21st century. *Global Planet. Change*, **62**(1–2): 173–186. doi:10.1016/j.gloplacha.2008.01.004.
- Ritchie, C. 2008. Management and challenges of the mountain pine beetle infestation in British Columbia. *Alces*, **44**: 127–135.
- Rominger, E.M., Robbins, C.T., and Evans, M.A. 1996. Winter foraging ecology of woodland caribou in northeastern Washington. *J. Wildl. Manage.* **60**(4): 719–728. doi:10.2307/3802370.
- Rooney, T.A. 2001. Deer impacts on forest ecosystems: a North American perspective. *Forestry*, **74**(3): 201–208. doi:10.1093/forestry/74.3.201.
- Schaefer, J.A. 2003. Long-term range recession and the persistence of caribou in the taiga. *Conserv. Biol.* **17**(5): 1435–1439. doi:10.1046/j.1523-1739.2003.02288.x.
- Schaefer, J.A. 2008. Boreal forest caribou. *In* Caribou and the North: a shared future. Edited by M. Hummel and J. Ray. Dundurn Press Ltd., Toronto, Ont. pp. 223–237.
- Schaefer, J.A., Veitch, A.M., Harrington, F.H., Brown, W.K., Theberge, J.B., and Luttich, S.N. 1999. Demography of decline of the Red Wine Mountains caribou herd. *J. Wildl. Manage.* **63**(2): 580–587. doi:10.2307/3802646.
- Schaefer, J.A., Bergman, C.M., and Luttich, S.N. 2000. Site fidelity of female caribou at multiple spatial scales. *Landsc. Ecol.* **15**(8): 731–739. doi:10.1023/A:1008160408257.
- Schaefer, J.A., Veitch, A.M., Harrington, F.H., Brown, W.K., Theberge, J.B., and Luttich, S.N. 2001. Fuzzy structure and spatial dynamics of a declining woodland caribou population. *Oecologia (Berl.)*, **126**(4): 507–514. doi:10.1007/s004420000555.
- Schmelzer, I., Brazil, J., Chubbs, T., French, S., Hearn, B., Jeffery, R., LeDrew, L., Martin, H., McNeill, A., Nuna, R., Otto, R., Phillips, F., Mitchell, G., Pittman, G., Simon, N., and Yetman, G. 2004. Recovery strategy for three woodland caribou herds (*Rangifer tarandus caribou*; boreal population) in Labrador. Department of Environment and Conservation, Government of Newfoundland and Labrador, Corner Brook.
- Seip, D., and McLellan, B. 2008. Mountain caribou. *In* Caribou and the North: a shared future. Edited by M. Hummel and J. Ray. Dundurn Press Ltd., Toronto, Ont. pp. 240–255.
- Seip, D.R., Johnson, C.J., and Watts, G.S. 2007. Displacement of mountain caribou from winter habitat by snowmobiles. *J. Wildl. Manage.* **71**(5): 1539–1544. doi:10.2193/2006-387.
- Sharma, S., Couturier, S., and Côté, S.D. 2009. Impacts of climate change on the seasonal distribution of migratory caribou. *Glob. Change Biol.* **15**(10): 2549–2562. doi:10.1111/j.1365-2486.2009.01945.x.
- Smith, K.G., Ficht, E.J., Hobson, D., Sorensen, T.C., and Hervieux, D. 2000. Winter distribution of woodland caribou in relation to clear-cut logging in west-central Alberta. *Can. J. Zool.* **78**(8): 1433–1440. doi:10.1139/cjz-78-8-1433.
- Sorensen, T., McLoughlin, P.D., Hervieux, D., Dzus, E., Nolan, J., Wynes, B., and Boutin, S. 2008. Determining sustainable levels of cumulative effects for boreal caribou. *J. Wildl. Manage.* **72**(4): 900–905. doi:10.2193/2007-079.
- Terry, E.L., McLellan, B.N., and Watts, G.S. 2000. Winter habitat ecology of mountain caribou in relation to forest management. *J. Appl. Ecol.* **37**(4): 589–602. doi:10.1046/j.1365-2664.2000.00523.x.
- Trainer, D.O. 1973. Caribou mortality due to the meningeal worm (*Parelaphostrongylus tenuis*). *J. Wildl. Dis.* **9**(4): 376–378. PMID: 4784327.
- Veitch, A.M. 2001. An unusual record of a white-tailed deer (*Odocoileus virginianus*) in the Northwest Territories. *Can. Field-Nat.* **115**: 172–175.
- Vistnes, I., and Nellemann, C. 2008. The matter of spatial and temporal scales: a review of reindeer and caribou response to human activity. *Polar Biol.* **31**(4): 399–407. doi:10.1007/s00300-007-0377-9.
- Vistnes, I.I., Nellemann, C., Jordhøy, P., and Støen, O.-G. 2008. Summer distribution of wild reindeer in relation to human activity and insect stress. *Polar Biol.* **31**(11): 1307–1317. doi:10.1007/s00300-008-0468-2.
- Vors, L.S., and Boyce, M.S. 2009. Global declines of caribou and

- reindeer. *Glob. Change Biol.* **15**(11): 2626–2633. doi: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. *J. Wildl. Manage.* **71**(4): 1249–1256. doi:10.2193/2006-263.
- Weeks, P., and Packard, J.M. 1997. Acceptance of scientific management by natural resource dependent communities. *Conserv. Biol.* **11**(1): 236–245. doi:10.1046/j.1523-1739.1997.95433.x.
- White, T.C.R. 2008. The role of food, weather and climate in limiting the abundance of animals. *Biol. Rev. Camb. Philos. Soc.* **83**(3): 227–248. doi:10.1111/j.1469-185X.2008.00041.x. PMID:18557977.
- Wittmer, H.U., McLellan, B.N., Seip, D.R., Young, J.A., Kinley, T. A., Watts, G.S., and Hamilton, D. 2005a. Population dynamics of the endangered mountain ecotype of woodland caribou (*Rangifer tarandus caribou*) in British Columbia, Canada. *Can. J. Zool.* **83**(3): 407–418. doi:10.1139/z05-034.
- Wittmer, H.U., Sinclair, A.R.E., and McLellan, B.N. 2005b. The role of predation in the decline and extirpation of woodland caribou. *Oecologia (Berl.)*, **144**(2): 257–267. doi:10.1007/s00442-005-0055-y. PMID:15891849.
- Wittmer, H.U., McLellan, B.N., Serrouya, R., and Apps, C.D. 2007. Changes in landscape composition influence the decline of a threatened woodland caribou population. *J. Anim. Ecol.* **76**(3): 568–579. doi:10.1111/j.1365-2656.2007.01220.x. PMID:17439473.
- Wittmer, H.U., Ahrens, R.N.M., and McLellan, B.N. 2010. Viability of mountain caribou in British Columbia, Canada: effects of habitat change and population density. *Biol. Conserv.* **143**(1): 86–93. doi:10.1016/j.biocon.2009.09.007.
- Wolfe, S.A., Griffith, B., and Gray Wolfe, C.A. 2000. Response of reindeer and caribou to human activities. *Polar Res.* **19**(1): 63–73. doi:10.1111/j.1751-8369.2000.tb00329.x.
- Wright, G.J., Peterson, R.O., Smith, D.W., and Lemke, T.O. 2006. Selection of northern Yellowstone elk by gray wolves and hunters. *J. Wildl. Manage.* **70**(4): 1070–1078. doi:10.2193/0022-541X(2006)70[1070:SONYEB]2.0.CO;2.
- Zalatan, R.A., Gunn, A., and Henry, G.H.R. 2006. Long-term abundance patterns of barren-ground caribou using trampling scars on roots of *Picea mariana* in the Northwest Territories, Canada. *Arct. Antarct. Alp. Res.* **38**(4): 624–630. doi:10.1657/1523-0430(2006)38[624:LAPOBC]2.0.CO;2.