The Seventh North American Caribou Conference,
Thunder Bay, Ontario, Canada,
19–21 August, 1996.

Demographic characteristics of circumpolar caribou populations: ecotypes, ecological constraints, releases, and population dynamics

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Abstract: Data on the status of caribou (*Rangifer tarandus*) herds throughout the circumpolar region during the last 20 years were obtained from the literature and personal communication with researchers. Information was analysed in relation to ecotype (insular, montane, barren-ground, and woodland/forest), population status (increasing, stable, decreasing), herd size, human impact, and temporal change in number. The data support the conclusions (1) that each ecotype is exposed to different ecological constraints and releases, which influence the demographic characteristics of their populations, (2) that subspecific (genotypic) classification does not explain the demographic characteristics of caribou populations, (3) that insular and montane ecotype populations are relatively stable, (4) that barren-ground ecotype herds are currently experiencing synchronous population growth throughout the circumpolar region and may undergo population cycles, (5) that in North America, the woodland caribou subspecies (genotype) forms the largest barren-ground ecotype herd in the world and is not endangered nor at risk, (6) that populations of woodland/forest ecotypes are declining and threatened throughout the circumpolar region, possibly due to the interaction of human disturbance and predation, and (7) that no relationship exists between herd size and risk of being classified as threatened by researchers.

Key words: caribou, reindeer, ecology, demography, status, subspecies.

Rangifer, Special Issue No. 10, 49–60

Introduction

Banfield (1961) hypothesized that extant caribou and reindeer evolved from three forms that survived in isolation during the last Wisconsin glaciation. These Holarctic subspecies include; the arctic forms evolving in tundra refugia north of the continental ice-sheets on the Queen Elizabeth Islands and Greenland, the continental tundra forms originating in Beringia (eastern Siberia/Alaska/Yukon), and the woodland or forest forms that survived in temperate refugia, south of the continental ice-sheets.

Reindeer and caribou (*Rangifer tarandus*) have been divided into subspecies based on morphological (Banfield, 1961) and genetic analysis (Røed *et al.,* 1991). The Arctic Island subspecies include the Svalbard reindeer, *R. t. platyrhynchus,* and the Peary caribou, *R. t. pearyi* from Canada. The continental tundra subspecies include, the Eurasian tundra reindeer, *R. t. tarandus*, the Alaska caribou, *R. t. granti*, and the Canadian barren-ground caribou, *R. t. groenlandicus.* Woodland caribou/reindeer subspecies include the Eurasian forest caribou, *R. t. fennicus,* and the American woodland caribou, *R. t. caribou.*

Although these taxonomic designations may reflect evolutionary events; they do not appear to reflect current ecological conditions. In numerous instances, populations of the same subspecies have evolved different demographic and behavioural adaptations, while populations from separate subspecies have evolved similar demographic and behavioural patterns.

For example, in North America populations of the woodland caribou subspecies typically form small isolated herds in winter, but are relatively sedentary and migrate only short distances (50 - 150 km), during the rest of the year (Euler *et al.,* 1976; Seip, 1992). Gravid females most often calve in the spring on islands or in bogs separate from the rest of the population and frequently remain solita-

ry until mid-winter. In contrast, the caribou of the George River herd, Quebec, Canada, which morphologically and genetically belongs to the woodland caribou subspecies, represents the largest caribou herd in the world (Williams & Heard, 1986), migrating thousands of kilometers from boreal forest to open tundra, where most females calve within a three week period (Messier *et al.*, 1988). This behaviour is typical of most barren-ground caribou/reindeer subspecies, which inhabit the Northwest Territories and northern Eurasia.

For wildlife managers dealing with caribou across a wide range of habitats and continents, understanding the ecotype in relation to existing ecological constraints and releases may be more important than the taxonomic relationships between different populations.

For these reasons, the primary objectives of this study were:

(1) to review demographic data on caribou/reindeer populations throughout the circumpolar region,

(2) to analyse the data in relation to ecotype (insular, montane, barren-ground, and woodland/forest), and

(3) to analyse the data in relation to population status (increasing, stable, decreasing), herd size, and temporal change in number.

Table 1. Circumpolar herds classified as insular caribou[1] ecotypes: I = increasing; S = stable; D = declining; TH = threatened.

No.	Name	Trend	Population Estimate	Location
1	Slate Is.	D	250	Ontario
2	Belcher Is.	I	700	NWT
3	Coates Is.	S	2 100	"
4	Southampton Is.	I	1 100	"
5	Banks Is.	S	5 000	"
6	Inglefield Land	I	<100	Greenland
7	Orlik Fiord	I	300	"
8	Nienavik	D,TH	400	"
9	Nusussuaq	I	300	"
10	Qegertassuaq	I	250	"
11	Nassuttuup	D	3 300	"
12	Sismut	D	5 500	"
13	Nuuk	D	10 200	"
14	Qoornoq	S	75	"
15	Ameralek	S	2 000	"
16	Sermilik	S	400	"
17	Qassit	S	300	"
18	Neria	S	500	"
19	Tasiilaq	S	120	"
20	Iceland	S	3 000	Iceland
21	Svalbard Is.	S	4 500	Svalbard Is.
22	Svalbard Is.	S	500	"
23	Svalbard Is.	S	2 500	"
24	Adak Is.	S	300	Russia
25	Novaya Zemlya Is.	I	6 500	"
26	Novosibirsk Is.	I	10 000	"
27	Sakhalin Is.	D,TH	3 000	"

(modified from Williams & Heard, 1986).

[1] Subspecies: #1 *R. t. caribou*; #2 - 4 & 6 - 20 *R. t. groenlandicus*; #5 *R. t. groenlandicus/pearyi*; #21 - 23 *R. t. plathyrhynchus*; #24 - 26 *R. t. tarandus*; and #27 *R. t. fennicus*.

Methods

Data were obtained from the literature (Davis, 1980; Meldgaard, 1986; Williams & Heard, 1986; Messier *et al.*, 1988; Shtele & Pavlov, 1990) and by communicating directly with researchers listed in the Acknowledgments. The data represent estimates of herd size, population status (increasing, stable, decreasing), and temporal change in circumpolar caribou populations during the last 20 years. However, data on some populations, especially from islands in the Canadian High Arctic were not available. Each population was classified as one of four ecotypes (insular, montane, barren-ground, woodland/forest) and analysed separately.

Insular caribou ecotypes were defined as populations restricted to isolated small to medium sized islands (*i.e.* Slate Islands; Coates Island) with physical barriers limiting movement. Primary predators and potential competitors (other ungulates) are most often absent from these systems (Table 1).

Montane caribou ecotypes were defined as populations found in the alpine and boreal zones of mountainous regions with ecological barriers (valleys) often limiting movement to adjacent areas. Primary predators and potential competitors (other ungulates) are most often present in these systems (Table 2).

Barren-ground caribou ecotypes were defined as populations associated with large land areas that migrate annually over relatively long distances between boreal forest and open tundra. Primary predators and potential competitors are present in these systems (Table 3).

Woodland or forest caribou ecotypes were defined as populations associated exclusively with the boreal forest, which are relatively sedentary and often found solitary or in small groups. Primary predators and potential competitors are present in these systems (Table 4).

Ecological releases were defined as parameters that tend to promote population growth and included; large land mass (islands or continents), no or few physical or ecological barriers, opportunity for range expansion, opportunity for forage diversification (boreal and tundra), the absence of potential ungulate competitors (moose and muskoxen), absence of predators (humans, wolves, and bears), and limited human disturbance (logging, roads, urban centres etc.).

In contrast, ecological constraints were defined as parameters that tend to reduce or limit population growth and included; small land mass (small to medium sized islands), physical and ecological barriers (water and valleys), limited opportunity for range expansion, no opportunity for forage diversification, the presence of potential ungulate competitors (moose and muskoxen), the presence of primary predators (humans, wolves, and bears), and high levels of human disturbance (logging, roads, urban centres etc.).

It is recognized that different techniques were employed by researchers throughout the circumpolar region to monitor population numbers and that these data represent broad estimates. However, these data are the best available and the high quality of researchers makes these estimates highly probable. In addition, the authors feel that trends in data are the more important element and not the actual data themselves. The results are discussed in relation to current theories on caribou demography and management and the impacts of ecological releases and constraints.

Results

Insular caribou ecotypes isolated on small to medium islands characteristically experienced physical barriers to migration/dispersal, no opportunities for range expansion, no opportunity for forage diversification, no competition from other ungulates, no or limited predation, and limited human disturbance. Populations ranged in size from 75 to 10 200 animals, with 78% of the herds below 4 000 individuals. Percentage of the populations increasing, stable,

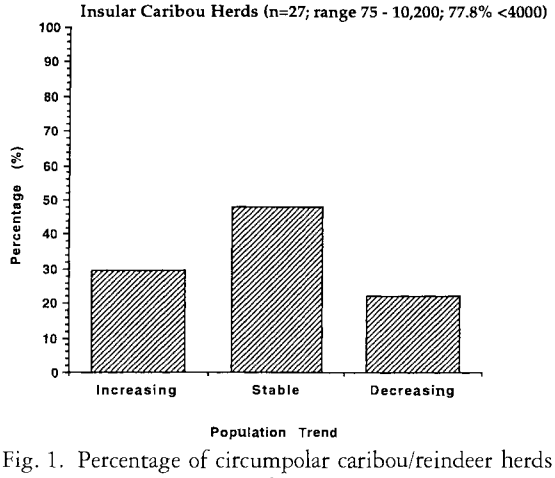


Fig. 1. Percentage of circumpolar caribou/reindeer herds designated as "insular ecotypes" thar have been identified as increasing, stable, or decreasing in number.

Table 2. Circumpolar herds classified as montane caribou[1] ecotypes: I = increasing; S = stable; D = declining; TH = threatened.

No.	Name	Trend	Population Estimate	Location
1	Altin	S	500	British Columbia
2	Kaudy-Level	D	800	"
3	Spatizi-Lawyers Pass	D	1 260	"
4	Horse Ranch	I	300	"
5	Pink Mt.	S	300	"
6	Laird Plateau	S	125	"
7	Telkwa	S	40	"
8	Tweedsmuir	I	200	"
9	Itcha-Iiqachuz	I	700	"
10	Caribou Mts.	D	1 500	"
11	Selkirk Mts.	S	30	"
12	Hart River	S	1 200	Yukon
13	Little Rancheria	D,TH	450	"
14	Carcross	S	600	"
15	Aishihik	S	1 500	"
16	Burwash	S	400	"
17	Big River	D	750	Alaska
18	Delta	S	8 000	"
19	Denali	S	2 100	"
20	Kenai Lowland	S	85	"
21	Kenai Mts.	S	300	"
22	Mentasta	S	3 000	"
23	Mulchatna	I	33 000	"
24	Welchina	I	25 000	"
25	Sunshine	D	750	"
26	Setesdal Vesthei	S	2 700	Norway
27	Saudafjella	S	75	"
28	Setesdal Austhei	S	2 000	"
29	Hardangervidda	S	20 000	"
30	Blefjell	S	130	"
31	Hallingskarvet	S	2 500	"
32	Raudafjell	S	30	"
33	Fjellheimen	S	850	"
34	Brattfjell-Vindeggen	S	600	"
35	Vest-Jotunheimen	S	720	"
36	Ottadalen Sor	S	460	"
37	Ottadalen Nord	S	3 100	"
38	Fordefjella	S	100	"
39	Sunnfjord	S	600	"
40	Svartebotnen	S	130	"
41	Snohetta	S	2 800	"
42	Rondane	S	1 200	"
43	Solnkletten	S	530	"
44	Forelhogna	S	1 800	"
45	Knutsho	S	914	"
46	Tolga Ostfjell	S	200	"
47	Rendalen	S	700	"
48	Altai-Sayan Mts.	S	10 000	Russia
49	W. Okhotsk	S	16 000	"
50	Kamchatka	S,TH	4 000	"

(modified from Williams & Heard, 1986).

[1] Subspecies: #1 - 11, 13 *R. t. caribou*; #12, 14 - 25 *R. t. granti*; #26 - 47 *R. t. tarandus*; #48 - 50 *R. t. fennicus*.

Table 3. Circumpolar herds classified as barren-ground caribou[1] ecotypes: I = increasing; S = stable; D = declining; TH = threatened.

No.	Name	Trend	Population Estimate	Location
1	Avalon	I	5 000	Newfoundland
2	Middle Ridge	I	8 000	"
3	Pot Hill	I	450	"
4	Sandy Lake	I	200	"
5	Grey River	I	4 500	"
6	Gaff Topsails	I	1 500	"
7	Buchans	I	2 000	"
8	LaPoile	I	8 500	"
9	Hampden	I	400	"
10	Humber	I	450	"
11	N. Peninsula	I	1 500	"
12	Mealy Mt.	I	700	Labrador
13	White Bear L.	D,TH	<100	"
14	Torngat Mt.	I	7 500	"
15	Red Wine Mt.	S	750	"
16	George River	I	700 000	Quebec
17	Leaf River	I	70 000	"
18	N.E. Mainland	I	130 000	NWT
19	Kaminuriak	450 000	"	
20	Beverley	I	420 000	"
21	Bathurst		I	450 000 "
22	Bluenose	S	80 000	"
23	Finlayson	I	2 500	Yukon
24	Central Arctic	I	12 500	Alaska
25	Fortymile	I	1 600	"
26	Porcupine	I	150 000	"
27	W. Arctic	I	200 000	"
28	Alaska Peninsula	I	30 000	"
29	Bonnet Plume	I	5 000	"
30	W. Kola Peninsula	I, TH	230	Russia
31	E. Kola Peninsula		I,TH	2 700"
32	Karelia	S	11 000	"
33	Archangel Forest	S,	14 000	"
34	Archangel Tundra		S,TH	4 000"
35	Komi Forest	S	4 000	"
36	Yamal Tundra	S,TH	2 000	"
37	Nadym-Pur River		D,TH	5 000"
38	Taimyr	I	530 000	"
39	Bulun	S	60 000	"
40	Yana-Indigir River	S	100 000	"
41	Sundrun		I	30 000 "
42	Chukotsk Tundra	S	5 500	"
43	Chukotsk Forest	I	4 000	"

(modified from Williams & Heard, 1986).

[1] Subspecies: #1 - 17 *R. t. caribou*; #18 - 23 *R. t. groenlandicus*; #24 - 29 *R. t.granti*; #30 - 43 *R. t. tarandus.*

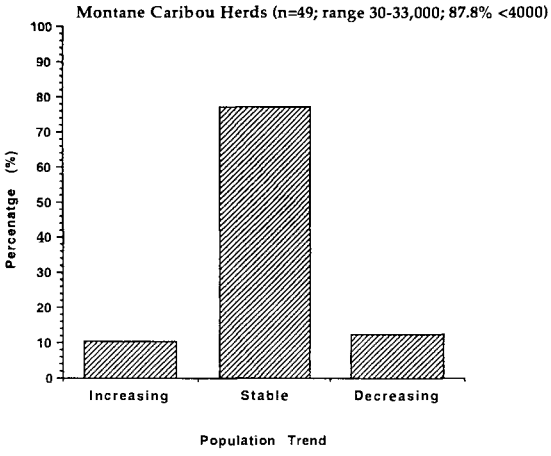


Fig. 2. Percentage of circumpolar caribou/reindeer herds designated as "montane ecotypes" that have been identified as increasing, stable, or decreasing in number.

and decreasing were 30, 48, and 22, respectively (Fig. 1).

Montane caribou ecotypes confined to the upper zones of mountains characteristically experienced ecological barriers to migration and dispersal, limited opportunities for range expansion, opportunities for forage diversification (alpine and boreal zones), potential competition from other ungulates, exposure to predators, and limited human disturbance. Populations ranged in size from 30 to 33 000 animals, with 89% of the herds below 4 000 individuals. Percentage of the populations increasing, stable, and decreasing were 10, 77, and 13, respectively (Fig. 2).

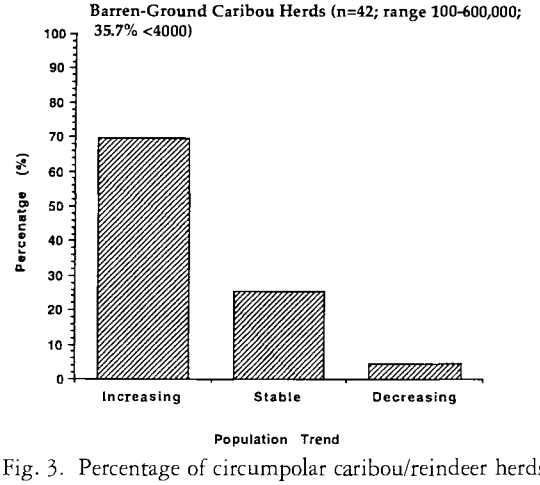


Fig. 3. Percentage of circumpolar caribou/reindeer herds designated as "barren-ground ecotypes" that have been identified as increasing, stable, or decreasing in number.

Barren-ground caribou ecotypes found on large islands or continents characteristically experienced no ecological or physical barriers, opportunities for range expansion, opportunities for forage diversification, competition from other ungulates, exposure to predators, and limited human disturbance. Populations ranged in size from 100 to over 700 000 animals, with 36% of the herds below 4 000 individuals. Percentage of populations increasing, stable, and decreasing were 70, 26, and 5, respectively (Fig. 3).

Woodland/forest caribou ecotypes limited to the boreal forest biome characteristically experienced no ecological or physical barriers, opportunities for range expansion, no opportunities for forage diversification (boreal habitat only), potential competition from other ungulates, exposure to predators, and

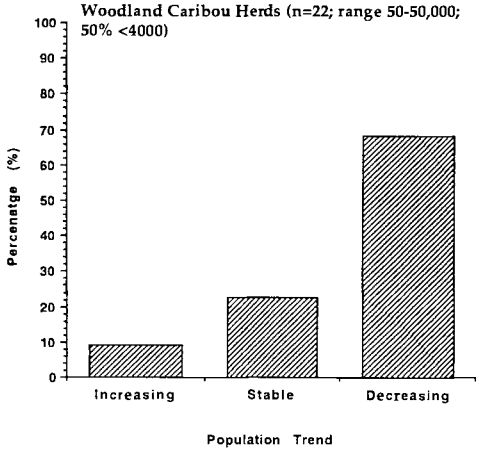


Fig. 4. Percentage of circumpolar caribou/reindeer herds designated as "woodland or forest ecotypes" that have been identified as increasing, stable, or decreasing in number.

high levels of human disturbance. Populations ranged in size from 50 to 50 000 animals, with 50% of the herds below 4 000 individuals. Percentage of the populations increasing, stable, and decreasing were 9, 23, and 68, respectively (Fig. 4).

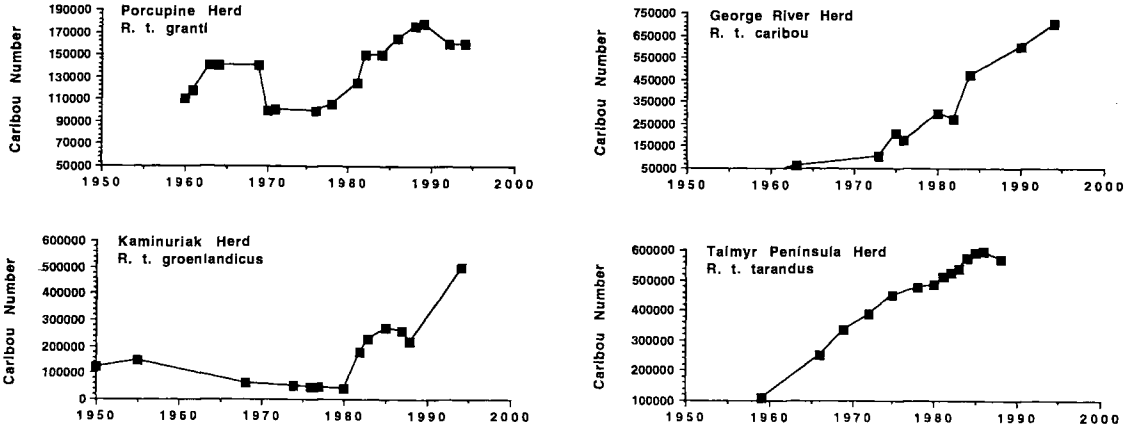
Analysis of the percentage of populations of each ecotype classified as threatened by researchers indicated that herds of the montane ecotype were least threatened and herds of the woodland or forest ecotype were most threatened (montane 8%; barren-ground 14%; insular 26%; woodland 27%). No correlation between percenatge of herds below 4 000 animals and percentage of herds classified as threatened was found (r=0.31; P>0.05).

Table 4. Circumpolar herds classified as woodland caribou[1] ecotypes: I = increasing; S = stable; D = declining; TH = threatened.

No.	Name	Trend	Population Estimate	Location
1	Lac Joseph	D,TH	<600	Quebec
2	Gaspesie Park	D	250	"
3	North Shore	D	2 000	"
4	Grand Jardins	I	67	"
5	Val d'Or	D,TH	50	"
6	James Bay	S	4 500	"
7	N.E. Ontario	D	4 500	Ontario
8	N. Lake Superior	D	<200	"
9	Manitoba	D	5 000	Manitoba
10	Saskatchewan	D,TH	2 500	Saskatchewan
11	Alberta	D,TH	2 250	Alberta
12	Finnish Forest	I	600	Finland
13	Konda-Sosva River	D	7 000	Russia
14	W. Siberia Forest	S,TH	5 000	"
15	Evenkiysk	D	50 000	"
16	Upper Angara River	D	10 000	"
17	Irkutsk	S	20 000	"
18	E. Baikal	S	8 000	"
19	Amur	D	3 000	"
20	Lena-Vilyui Rivers	D	20 000	"
21	Yukutsk Mt. Taiga	D	30 000	"
22	Taxinganling	S	980	China

(modified from Williams & Heard, 1986).

[1] Subspecies: #1 - 11 *R. t. caribou*; #12, 15, 20, 21 *R. t. fennicus/tarandus*; #13, 16, 19 *R. t. tarandus*.



Figs. 5–8. Comparison of population growth in 4 barren-ground ecotype herds during the past 5 decades.

In addition, comparison of population growth during the past 5 decades in 4 herds classified as barren-ground ecotypes (Figs. 5 - 8) indicated that herds grew synchronously throughout the circumpolar region and reached high population levels in the 1990s, although all represent different subspecies and genotypes, as defined by Banfield (1961) and Røed *et al.* (1991).

Table 5. A summary of ecological constraints (-) and releases (+) impacting the four caribou ecotypes.

Insular Caribou - confined to small and medium sized islands -
(1) experience physical barriers to migration/dispersal (-),
(2) no opportunities for range expansion (-),
(3) no opportunities for forage diversification (-),
(4) commonly no competition from other ungulates (+),
(5) limited or no predation (+),
(6) limited human disturbance (+).

Montane Caribou - confined to mountain tops -
(1) experience some ecological resistance to migration/dispersal (+/-),
(2) fewer opportunities for range expansion (+/-),
(3) opportunities for forage diversification (+),
(4) potential competition from other ungulates (-),
(5) exposure to predators (-),
(6) limited human disturbance (+)

Barren-ground Caribou - occupying large islands or continents -
(1) experience no or few barriers to migration/dispersal (+),
(2) range expansion opportunities available (+),
(3) opportunities for forage diversification (+),
(4) potential competition from other ungulates (-),
(5) exposure to predators (-),
(6) limited human disturbance (+).

Woodland/Forest Caribou - occupying large islands or continents -
(1) experience no or few barriers to migration/dispersal (+),
(2) opportunities for range expansion (+),
(3) no or few opportunities for forage diversification (-),
(4) potential competition from other ungulates (-),
(5) exposure to predators (-),
(6) high levels human disturbance (-).

Discussion

Insular ecotypes confined to isolated small and medium sized islands characteristically experience physical barriers to migration and dispersal; however, movement across ice/water barriers does occur on occasion (Euler *et al.*, 1976; R. Mulders, pers. comm.). Competition from other ungulates, such as moose or muskoxen is frequently absent and predation by primary predators is most often absent. In addition, human disturbances are most frequently absent or limited in these habitats. Typical examples of these types of ecosystems are the Slate Islands, Ontario and Coates Island, Northwest Territories, Canada. Both these sites represent one ungulate systems (caribou) with no competition or interactive impact from other ungulate species. Primary predators are or have been absent in these systems for long periods of time. Wolves have only arrived on the Slate Islands during the past few years and Inuit from Coral Harbour occasionally hunt on Coates Island. In addition, range expansion is not an option and nor is forage diversification, as island systems are usually limited to one relatively homogeneous habitat type (Coates Island-tundra/ Slate Islands -boreal forest). Evidence suggests that the primary dynamic controlling insular populations and their demographics is forage exploitation (Klein, 1968; Gates *et al.*, 1986). Forage depletion and habitat degradation have been identified as primary reasons for caribou population declines on the Slate Islands (W. J. Dalton, pers. comm.) and Coates Island, (Gates *et al.*, 1986). Populations of insular caribou ranged in size from 75 to 10 200 animals, with 78% of the herds below 4000 individuals. Percentage of the populations increasing, stable, and decreasing were 30, 48, and 22%, respectively (Fig. 1). These data indicate that approximately half of the insular populations are stable, while the other fifty percent are increasing or declining. Similar

demographic characteristics have been found in island populations of many mammalian species (Bonner, 1958; Mech, 1966; Klein, 1968; Krebs & Myers, 1974; Tamarin, 1977) and this type of non-cyclic, relatively stable population pattern appears to be typical of mammal populations in isolated systems. As 78% of these populations are increasing or stable, it can be concluded that insular caribou ecotype populations are relatively healthy at this time.

Montane ecotypes confined to the upper floristic zones on mountains frequently experienced ecological barriers (valleys) to migration and dispersal and range expansion is often limited. However, movement between mountain ranges does occur and forage diversification is an option in these populations. Potential competition from other ungulates, such as moose and predation by primary predators, such as wolves and bears typically impact in these populations (Seip, 1992). Human disturbances are usually limited to more southern populations in these habitats (Davis, 1980; Seip, 1992). Typical examples of these types of populations are the Wells Gray herd in southeastern British Columbia (Seip, 1992) and the Nelchina herd in Alaska (Eberhardt & Pitcher, 1992). Both these sites represent two ungulate systems (caribou and moose) and primary predators (wolves and bears) represent significant mortalities on these herds. Range expansion is generally limited due to ecological barriers; however, forage diversification does occur, as montane systems provide both alpine and boreal habitats, which can support caribou. In contrast to insular caribou populations, the primary dynamic controlling montane populations and their demographics appears to be predation and the interactive impact of other ungulate species (Seip, 1992). Forage exploitation and habitat degradation have not been identified as reasons for caribou population decline in montane regions (Davis, 1980); however, increased human activity (ie. logging) appears to be having some influence, by increasing moose numbers and caribou susceptibility to wolf predation (Bergerud & Elliot, 1986; Seip, 1992). Populations of montane ecotypes ranged in size from 30 to 33 000 animals, with 88% of the herds below 4000 individuals. Percentage of the populations increasing, stable, and decreasing were 10, 77, and 13, respectively (Fig. 2). These data indicate that montane caribou populations are in general more stable than insular populations, although they both have similar demographic attributes, common to isolated populations. The increased stability associated with montane ecotype populations appears to be related to (1) increased forage diversity, and (2) predation by primary predators, which minimizes the chance that numbers will exceed the carrying capacity of the range. As 88% of these populations are increasing or stable, it can be concluded that montane ecotype populations are healthy, although the majority of these herds are relatively small in number.

Barren-ground ecotypes found on large islands or continents experienced long seasonal migrations from boreal forest to open tundra, have few physical or ecological barriers to movement and disperse to ranges of other populations (Messier *et al.,* 1988; D. C. Heard, pers, comm.; R. Mulders, pers. comm.). At minimum, all of these ecosystems represent two ungulate systems, with moose in the boreal forest and muskoxen in the open tundra. This results in the potential for competition and the interactive impact of other ungulate species on predation (Bergerud & Elliot, 1986; Seip, 1992). Predation by primary predators, such as humans, wolves and bears is common in these populations (Parker, 1972; Hillis & Mallory, 1989; Lamothe & Parker, 1989; Lamothe, 1991). Human disturbances, such as logging, roads, and urban centres are usually limited (F.F.M, pers. obs.). Typical examples of these types of populations are the Kaminuriak herd found along the west coast of Hudson Bay, N.W.T. (Parker, 1972) and the George River herd found in northern Quebec (Messier *et al.,* 1988). Both these locations support two ungulate systems and primary predators (humans, wolves, and bears) represent constant mortalities on these populations. Range expansion has occurred during the last 40 years in both herds and forage diversification occurs (Heard & Calef, 1986; Messier *et al.,* 1988). The fact that these herds have opportunities for ecological release through range expansion and forage diversification may explain, in part, the massive increase in numbers found throughout the circumpolar region. In contrast, populations of insular and montane ecotypes seldom attain ecological release and remain relatively stable, due to physical and ecological barriers, which limit population size. Forage exploitation and habitat degradation have been suggested as major limiting factors effecting barren-ground ecotype population decline, while predation and human activity appear to have minimal impact during periods of population increase (Messier *et al.,* 1988; R. Mulders, pers. comm.).

Populations of barren-ground caribou ecotypes ranged in size from 100 to over 700 000 animals,

with 36% of the herds below 4000 individuals. Percentage of the populations increasing, stable, and decreasing were 70, 26, and 5, respectively (Fig. 3). These data indicate that most barren-ground ecotype populations are increasing synchronously throughout the circumpolar region, in contrast to the populations of other ecotypes. These changes may represent synchronous population cycles (Meldgaard, 1986), as has been found in many other mammal species (Mallory, 1987). As 95% of these populations are increasing or stable and the few declining populations have been overharvested, it can be concluded that populations of barren-ground ecotypes are very healthy, at this point in time. However, these populations will probably decline during the next decade, due to habitat exploitation and forage depletion.

Populations of woodland or forest ecotypes confined to the boreal forest, characteristically experience no limit to range expansion, no opportunities for forage diversification, potential competition from other ungulates, exposure to predators (humans, wolves, and bears), and relatively higher levels of human disturbance. Although few barriers to movement appear to exist in this habitat, woodland/forest ecotypes are relatively sedentary, commonly dispersing only short distances and returning to the same ranges annually (Edmonds, 1988; W. J. Dalton, pers. comm.). With few exceptions, these ecotypes are part of a two ungulate system, which results in potential competition and the interactive impact on predation of other ungulate species (Bergerud & Elliot, 1986; Seip, 1992). Predation by primary predators, such as humans, wolves, and bears is common in these populations (Edmonds, 1988; Seip, 1992) and fire and human disturbances, such as logging, roads, and urban development maintain large tracts of early successional forest ideal for moose, especially in the southern parts of the range (Bergerud, 1974; Jackson *et al.,* 1991).

Typical examples of these populations are the woodland caribou herds in west central Alberta (Edmonds, 1988) and the Quesnel Lake herd in southeastern British Columbia (Seip, 1992). Both these sites support two ungulate systems (caribou and moose) and primary predators (wolves and bears) represent significant mortalities on these populations (Edmonds, 1988). Range expansion is an option; however, forage diversification does not occur, as only boreal habitats are available. The primary dynamic controlling the demographics of woodland/forest populations appears to be predation and habitat loss due to human disturbance (Bergerud & Elliot, 1986; Seip, 1992). While woodland caribou have not been shown to over graze ranges in boreal habitats, habitat loss due to fire and logging appear to result in caribou population decline. Early successional boreal forest appears to increase moose numbers and caribou susceptibility to wolf predation (Bergerud & Elliot, 1986; Seip, 1992). Hunting by humans has historically impacted this ecotype significantly (Bergerud, 1974).

Populations of woodland/forest ecotypes ranged in size from 50 to 50 000 animals, with 50% of the herds below 4 000 individuals. Percentage of the populations increasing, stable, and decreasing were 9, 23, and 68, respectively (Fig. 4). As only 32% of these populations are increasing or stable, it can be concluded that populations of woodland/forest ecotypes are vulnerable and should receive intensive management effort at this time.

A summary of ecological contraints and releases impacting the four caribou ecotypes is presented in Table 5. These data illustrate that in the two ecotypes with relatively stable population patterns (insular & montane), equal numbers of positive (+) and negative (-) ecological factors are active. In barren-ground ecotype populations, 4 ecological parameters are positive (+) and 2 are negative (-) providing opportunity for ecological release and population growth until carrying capacity and new ecological contraints are reached. In contrast, in woodland/forest ecotype populations, 2 ecological parameters are positive (+) and 4 are negative (-) resulting in a general decline and loss of populations.

The data support the conclusions (1) that each ecotype is exposed to different ecological constraints and releases, which influence the demographic characteristics of their populations (2) that subspecific (genotypic) classification does not explain the demographic characteristics of caribou populations, (3) that insular and montane ecotype populations are relatively stable, (4) that barren-ground ecotype herds are currently experiencing synchronous population growth throughout the circumpolar region and may undergo population cycles, (5) that in North America, the woodland caribou subspecies (genotype) forms the largest barren-ground ecotype herd in the world and is not endangered or at risk, (6) that populations of woodland or forest ecotypes are declining and threatened throughout the circumpolar region, possibly due to the interaction of

human disturbance and predation, and (7) that no relationship exists between herd size and risk of being classified as threatened by researchers.

Acknowledgments

We thank: W. J. Dalton and G. E. Racey, Northwest Region Science & Tech Unit, Ontario Ministry of Natural Resources, Thunder Bay, Ontario, Canada and the Northwest Region Caribou Task Team for encouragement; F. V. Clulow, J. Hamr, G. H. Parker, and D. Thomas for reviewing the manuscript and R. Mulders, A. Gunn, M.A.D. Ferguson, M. Crête, D. E. Russell, and A. Fietch for provided essential information. Finanical support was provided by Abitibi Consolidated Inc., Avenor Inc., Buchanan Forest Products Ltd., Domtar Forest Products Inc., Kimberly-Clark Forest Products Inc., and the Boreal Ecosystem Science Co-operative (Lakehead University) with a grant from the Ontario Ministry of Natural Resources.

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