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Application of Herd Viability Models for Boreal Woodland Caribou (*Rangifer tarandus caribou*) to a Northern Mountain Caribou Herd

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Abstract

Caribou (*Rangifer tarandus*) herds of the northern mountain population in British Columbia and Yukon are facing increased human development and habitat alteration. Managers need to better understand at what stage these changes will become a conservation issue. Historical declines in numerous herds of the Boreal Woodland Caribou population prompted development of three models relating herd viability to human footprint and proportion of the land base changed to early-seral conditions by natural or human disturbance. We applied these models to the range of a northern mountain herd, the Carcross Caribou Herd (CCH), in south-central Yukon, to understand whether and how the boreal models could be used in a northern mountain context. Two of the boreal models, one based on Canada-wide (CW) herds and one on Alberta (AB) herds, produced reasonable approximations of the current population status of the CCH (increasing). The minimal secure patch area requirement of the third model, based largely on Northwest Territories (NT) herds, could not be satisfied in the CCH range, if such secure patches necessarily include substantial winter range. The boreal models could not deal with the widespread and permanent shrub and sparsely vegetated habitats, often at high elevations, in Northern Mountain Caribou range, nor with the spatial segregation of the herds' seasonal ranges, especially high-value winter ranges. The most robust conservation approach for Northern and Southern Mountain Caribou would be to develop new models based on the demographic and habitat profiles of numerous herds from these populations.

Key Words: Boreal, Caribou, Carcross, Northern Mountain, Population Viability, Rangifer tarandus.

INTRODUCTION

Woodland Caribou (Rangifer tarandus caribou) in Canada occupy

primarily forested ranges through British Columbia and east across the boreal forest to Newfoundland and Labrador (Thomas and Gray 2002; Hummel and Ray 2008). Woodland Caribou herds occupying the boreal forest regions east of the cordillera are classified as the boreal population. Woodland Caribou herds in the mountainous

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Page 68 REID et al.

cordillera of the west (British Columbia, Yukon and parts of Alberta and Northwest Territories) are classified as the mountain population. Mountain population herds are subdivided into northern mountain and southern mountain populations based on substantial differences in forage types and seasonal habitat use (Thomas and Gray 2002; COSEWIC 2011). In this paper, we focus on the distinctions between the northern mountain population and the boreal population, and their responses to landscape change.

Northern Mountain Population Caribou herds in northern British Columbia and much of Yukon Territory occupy boreal forest landscapes, but also range extensively in subalpine forests and shrublands, and in alpine tundra (Environment Canada 2012). They often differ from boreal population herds by having non-overlapping seasonal ranges with migrations between ranges. Like the boreal population, northern mountain herds tend to be more gregarious on their restricted rut and winter ranges and more widely spaced during calving and summer seasons, supposedly to reduce predation risk (Schaefer 2008; Seip and McLellan 2008). Their means of spacing out generally include travel to high elevations for calving and summer (Bergerud et al. 1984; Seip 1992; Gustine et al. 2006). Northern Mountain Caribou are part of a more complex food web than that in most of the boreal population range, including additional predators (Grizzly Bear, Ursus arctos) and ungulate prey (Thinhorn Sheep, Ovis dalli), and Mountain Goat (Oreamnos americanus)). However, the diets of the two ecotypes are similar, with heavy reliance on lichens in winter, and inclusion of more diverse new plant growth in the growing seasons (Seip and Cichowski 1996; Schaefer 2008; Seip and McLellan 2008).

Listed as Threatened under the Canadian Species at Risk Act in 2003, many herds or subpopulations of the boreal population are suffering a conservation crisis with severe declines in abundance, while other herds remain fairly stable or are increasing (COSEWIC 2002; Hummel and Ray 2008; Environment Canada 2008, 2011; Festa-Bianchet et al. 2011). Research implicates human industrial activities in the population declines because caribou avoid linear corridors (roads, seismic lines and rights-of-way) and industrial infrastructure (Smith et al. 2000; Dyer et al. 2001; Nellemann et al. 2003), and because predators (notably Gray Wolf, Canis lupus) and Black Bear (Ursus americanus) may increase their kill rate by using the network of linear corridors to more efficiently locate and attack caribou (James and Stuart-Smith 2000; Smith 2004; Latham et al. 2011a; Dussault et al. 2012). In addition, wild fires and forest cutblocks are implicated in some declines because they reduce the area of mature and old forest stands, which are the highest quality caribou habitat, thereby reducing the carrying capacity of the range (Schaefer and Pruitt 1991; Schaefer and Mahoney 2007; Vors et al. 2007). The change from undisturbed, old forest to early-successional stands also produces high quality habitat for alternative prey species such as White-tailed Deer (Odocoileus virginianus), mule deer (Odocoileus hemionus) and Moose (Alces alces), and this added prey biomass can support higher predator

densities and greater predation risk for caribou in the same landscapes (James and Stuart-Smith 2000; Thomas and Gray 2002; Latham *et al.* 2011b; Wasser *et al.* 2011).

The detailed research, along with the divergent trends in population abundance among herds, prompted biologists to investigate what intensities of human activity and habitat alteration a caribou herd could sustain before it began to decline. Habitat loss or change as a result of human activity is often called the human footprint. This human footprint includes habitat permanently lost to human uses such as settlements, rural residences, agricultural and industrial land conversion, as well as linear corridors including roads, seismic lines, trails, and rights-of-way. It also includes mature forest habitat temporarily changed by stand-replacing timber harvesting to a poorer quality (for the caribou) vegetation condition. Wild fires also shift forests to a younger successional stage from which they gradually revert to mature forest. Researchers have developed at least three models relating the intensity of the human footprint and the extent of habitat alteration by fire to the population trajectory of the herd (Table 1). These models indicate levels of habitat change at which herds shift from stable or increasing abundance to declining abundance.

The Environment Canada model (hereafter termed CW) was based on a Canada-wide sample of 57 boreal caribou herds, and was developed to define critical habitat for this species-at-risk (Environment Canada 2008, 2011). The Alberta model (hereafter termed AB) focuses specifically on 12 herds in the Boreal Plains ecozone where hydrocarbon exploration and extraction coupled with forest harvesting have resulted in the highest total disturbance in boreal Canada (Sorensen *et al.* 2008; Schneider *et al.* 2010). The Northwest Territories model (hereafter termed NT) focuses mostly on herds in the Mackenzie River drainage of northwest Alberta and Northwest Territories (Nagy 2011), with variable total disturbance.

In general, Northern Mountain Caribou ranges have experienced less human-induced habitat change, and less human footprint, than the boreal ranges. However, this situation is changing with rapid increases in mineral and oil and gas exploration and development, increased interest in forest harvesting, conversion of forests to agriculture, and new development of backcountry recreation travel routes and facilities. Given the dire conservation status of many boreal and most southern mountain herds, managers in Yukon have been searching for models or tools that would define the level of risk projected for Northern Mountain Caribou herds as the human footprint expands (e.g., Francis and Hamm 2011). This means anticipating the levels of habitat alteration and linear feature development that Northern Mountain Caribou herds might be able to sustain before declining. In the absence of any scientific guidance from studies of Northern Mountain Woodland Caribou herds, the first inclination is to use the models from Boreal Woodland Caribou herds. Given the different ecologies of these two ecotypes (Schaefer 2008; Seip and McLellan 2008), we were sceptical that the boreal models would apply in a northern mountain setting, but felt the need to test the idea so as to

Table 1.Parameters and decision criteria used by each of the three boreal ecotype models to assess caribou herd viability. Clearcuts are termed "temporary" in that they can return to usable habitat within decades depending on silvicultural practices.

		Human Footprint	Natural Disturbance			
Model	Linear Features Permanent	Polygonal Permanent	Polygonal Temporary (Clearcuts)	Wild Fire	Decision Criterion	
Canada-wide (CW): (Environment Canada 2011)	Total non- overlapping area including 500 m buffer on all sides	overlapping area overlapping area including 500 m including 500 m		Total unbuffered area of fires ≥200 ha and ≤40 years since burn, classed as "disturbed"	Total area human footprint + total area "disturbed" as a % of total herd range. This % converted to probability that λ≥1(Environment Canada 2011:37). Also, recruitment related to % disturbance (Environment Canada 2011:25)	
Alberta (AB): (Schneider et al. 2010 Appendix)	Total unbuffered length (km) as a density throughout herd range (km/km²)	Not considered	Total unbuffered area of clearcuts ≤30 years old as % of total herd range, classed as "disturbed"	Total unbuffered area of all fires ≤30 years old as % of total herd range, classed as "disturbed"	Linear Model: Herd growth rate = 1.0184 - (0.0234 x linear feature density) - (0.0021 x Disturbed)	
Northwest Territories (NT): (Nagy 2011)	linear and p on all s	bitat lacking security a olygonal features (inclusides + total unbuffered abitat is: (Total herd ra	Herds are viable only if ≥46% of herd range is "Secure" AND 54% of Secure habitat is in patches > 500 km² in size			

identify a useful approach to this pressing management question.

Our study asks whether we can apply any or all of the boreal population models of herd viability, based on human footprint and habitat age, to northern mountain population herds. We chose one northern mountain herd, the Carcross Caribou Herd (CCH), as our focus. This is the best studied herd in Yukon, with previous research on seasonal movements and habitat selection (Florkiewicz et al. 2007), population abundance (Florkiewicz 2008), and impact of human activities in its winter range (Applied Ecosystem Management 2002, 2004). Therefore, certain necessary data sets were already available. In addition, CCH is a useful indicator herd because its range is immediately adjacent to the city of Whitehorse where it is subject to a substantial human footprint that raises immediate conservation concerns (Applied Ecosystem Management 2004; Florkiewicz 2008). The herd undergoes seasonal movements typical of most northern mountain herds, feeding on ground lichens in low elevation winter ranges, and using a wider array of habitats including alpine regions in other seasons (Farnell et al. 1998). The CCH was historically harvested, but is under a no-harvest agreement between the Carcross-Tagish First Nation and the Government of Yukon for the past decade (Florkiewicz 2008).

Our objectives were to apply each of the three published models

of herd viability for the boreal population to the range of the CCH to determine: (i) whether the models adequately predicted the current population trend for the CCH (increasing); (ii) if one or other of the models was more compatible with the patterns of habitat differentiation and human footprint typical in the general distribution of the northern mountain herds; and (iii) what particular steps in data interpretation and analysis would be necessary for using the boreal models in a northern mountain setting.

STUDY AREA AND METHODS

Study Area

The approximately 12,000 km² range of the CCH straddles the Yukon – British Columbia border, southeast of Whitehorse, Yukon (Figure 1). The range boundaries were mapped to encompass all radiotelemetry relocations (mix of VHF and GPS) of primarily adult female caribou from 1994 to 2006 (Florkiewicz *et al.* 2007; Florkiewicz 2008). Centred at approximately 60°30'N and 134°00'W, this is a transitional mountain landscape with the southern one-third (mostly in British Columbia, but as far north as Carcross and Tagish Lake in Yukon) being part of the Yukon-Stikine Highlands ecoregion with extensive alpine and subalpine landscapes in the coastal mountains (Yukon Ecoregions Working Group 2004; Demarchi 2011). The central and

Page 70 REID et al.

northern two-thirds of the CCH range lie in the Yukon Southern Lakes ecoregion with more subdued mountains and more extensive boreal forests (Yukon Ecoregions Working Group 2004). The coastal mountains receive 300-500 mm of precipitation annually, with deep

snow, whereas the Southern Lakes ecoregion is more in a precipitation shadow with 200 to 250 mm annually. Mean annual temperatures in valley floors vary from -1 $^{\circ}$ C to -3 $^{\circ}$ C, and snow typically covers the ground at lower elevations from October through April. The region is

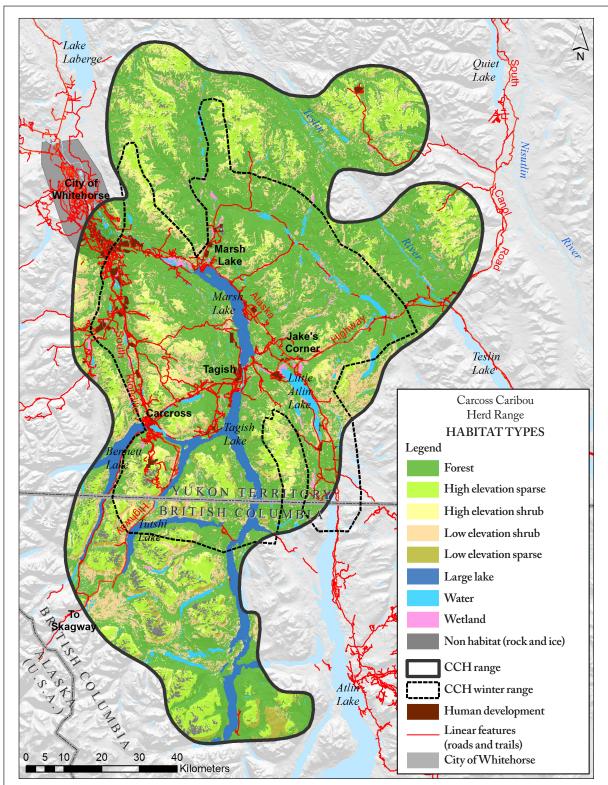


Figure 1. Map of the Carcross Northern Mountain Caribou Herd annual and winter ranges illustrating the prominent human footprint features, the major topographic and hydrological features, and the derived land cover classes (habitats) use in the model runs.

noteworthy for a number of large lakes (Figure 1), generally oriented north to south.

In the Yukon Stikine Highlands, forest trees are most often White Spruce (Picea glauca) and Subalpine Fir (Abies balsamea) with Trembling Aspen (Populus tremuloides) on disturbed sites and dry slopes. Permanent (edaphic climax) shrublands of willows (Salix spp.) and shrub birch (Betula spp.) are extensive both in the subalpine and in many valley floors, associated with cold air seepage (Pojar and Stewart 1991). Tree line is at about 1,200 m elevation (Yukon Ecoregions Working Group 2004). In the Yukon Southern Lakes, forests are a complex mix of White Spruce, Lodgepole Pine (Pinus contorta) and Trembling Aspen, depending on the disturbance history, soil types, moisture regime and exposure. There are extensive permanent shrublands (Betula and Salix spp.) in the subalpine and associated with wetlands. Trembling Aspen often forms edaphic climax stands on drier slopes, in association with grasslands (Yukon Ecoregions Working Group 2004). Strong (2013) indicates that this ecoregion covers portions of three ecoclimatic regions, differentiated elevationally and each with different climax communities across the moisture gradient. These ecoclimatic regions are Mid-Cordilleran Boreal, Mid-Cordilleran Subalpine, and Mid-Cordilleran Alpine.

Members of the CCH move seasonally. Individuals occupy valley-bottom winter range in mature White Spruce and Lodgepole Pine forests in the Yukon Southern Lakes ecoregion from November through mid-April, feeding primarily on ground lichens (e.g., *Cladina* spp.) (Florkiewicz *et al.* 2007). The herd generally moves to higher elevations in both ecoregions for the rest of the year. Females seem to spread out, often in rugged alpine areas, to calve, and alpine and subalpine tundra and shrublands sustain the herd in summer and fall (Florkiewicz 2008).

The CCH is part of a complex boreal montane food web, with principal predators being Gray Wolf, Grizzly Bear, Black Bear, and Wolverine (Gulo gulo), similar to other northern mountain ecotype herds (Environment Canada 2012). Wolf density in the Yukon Southern Lakes region had declined from 2004 to 2009, at which time it was about 1 wolf/204 km² (Baer 2010). This is relatively low for boreal and boreal-montane regions where densities generally range from 1 wolf/40 km² to 1 wolf/250 km² (Paquet and Carbyn 2003; Latham et al. 2011b). Grizzly Bear density was estimated in 1990 at 15.4 bears / 1,000 km², but an ongoing study suggests density has declined and is lower than the Kluane ecosystem 200 km to the west (Southern Lakes Wildlife Coordinating Committee 2012). The main other prey to caribou is Moose, based on total biomass and on importance in the diet of Gray Wolves (Larsen et al. 1989). Moose densities in recently surveyed portions of the CCH range in Yukon vary from 0.15 to 0.28 Moose/km2 (Yukon Environment, unpubl. data), well within the range of densities (0.05 – 0.42 Moose / km2) for Moose regulated by Gray Wolf populations in the northern boreal mountains (Gasaway et al. 1992). Dall's Sheep (Ovis dalli dalli) occupy the Yukon Stikine Highlands in British Columbia, but in Yukon they

are only common in the southwest portions of the CCH range and rare to absent in some other areas (Russell and Hegel 2011). Both species of deer (*Odocoileus* spp.) are still relatively uncommon in the Yukon Southern Lakes ecoregion; they are increasing in abundance but density estimates are lacking (Southern Lakes Wildlife Coordinating Committee 2012).

The human footprint within the CCH annual range is restricted mostly to valley floors, with the highest density of features occurring in the CCH winter range (Figure 1). Linear corridors are comprised of major highways (Alaska and South Klondike Highways), secondary and residential access roads, and recreational trails. Permanent land conversions include agricultural parcels, urban and country residential subdivisions, and aggregate quarries (Figure 1). The region has experienced relatively few large fires in the past 50 years, partly due to fire suppression, and has also had very limited clearcut timber harvesting. Consequently, these temporary forest alterations to younger successional stages are not extensive.

Study Design

The population trend models for Boreal Woodland Caribou herds are based on empirical data showing that an improving population trend is correlated with lower amounts of human footprint and lower proportions of the land base in younger forest stages (Schneider et al. 2010; Environment Canada 2011). The indication of population trend in the caribou (response variable) varies by model: probability that rate of population growth (lambda, herein λ) is greater than or equal to one (CW model: Environment Canada 2011); average annual estimates of female survival and recruitment converted to rate of population growth (AB model: Sorensen et al. 2007; Schneider et al. 2010); population growth rate (NT model: Nagy 2011). The underlying causal mechanism behind these correlations is believed to be predation mortality, with increasing human footprint and larger area of disturbed forest supporting enhanced densities of alternative prey (mainly Moose and deer) and consequently higher predator densities and/or higher hunting efficiency (Latham et al. 2011a, 2011b). In addition, certain older forest stands support the essential lichen growth for caribou, which is generally not found in young forests (Schaefer 2008).

We ran the models independently using the mapped habitat conditions in the CCH range. We then compared the models' outputs (estimates of population condition) to the latest empirical estimate of finite annual rate of population increase (an approximation of λ) for the CCH of 1.062 (90% C.I. of 1.016-1.116), based on aerial estimates of population size in 1997 (400; 90% C.I. 280-540) and 2008 (775; 90% C.I. 642-935) (Florkiewicz 2008). We also compared the expected recruitment rate from the CW model (Environment Canada 2011, Appendix 7.5) to the empirical data on recruitment in the CCH.

Each Woodland Boreal Caribou model requires three key inputs: (i) human footprint or disturbance mapping, (ii) the area of undisturbed, old forest, and (iii) the area of disturbed, young forest regenerating since forest harvesting or fire (Table 1). To apply the boreal models to the CCH range, we developed a GIS database of mapped features in

Page 72 REID et al.

two major categories: the human footprint, and land cover classes to assess forest cover and stand age.

Human footprint mapping

The boreal models differed somewhat in their mapping methods: CW — satellite imagery (Environment Canada 2011); AB — air photos to 5 m resolution (Sorensen et al. 2007). Human footprint mapping for most of our study area was originally completed in 2003 (Applied Ecosystem Management 2004). This consisted of all humanaltered land cover types including linear features (roads, railway, utility rights-of-way, mineral exploration trails, cut lines and recreational trails) and polygonal features (agricultural leases, gravel and aggregate quarries, urban and country residential subdivisions, forest harvest blocks and historically operating mine sites). Data were derived from orthophotos to 1 m resolution, government cadastral databases, and ground surveys (Applied Ecosystem Management 2004). In 2011, we updated this database and mapping to circa 2010 by conducting GPS mapping of new and previously unmapped roads and trails with the assistance of a suite of citizens familiar with the backcountry, and by searching Yukon Government (Geomatics Yukon) GIS databases for human footprint features. Most new features were recreational trails, agricultural parcels, gravel quarries or country residential properties and associated roads. Recreational trails are an added component of the human footprint not mapped by the CW or AB models; they make the linear corridor component of our human footprint more extensive by about 10%. New land uses that require applications or permits are subject to government review and approval processes and are therefore available as GIS data and updated frequently. Wherever possible, new GIS features were checked against satellite imagery, orthophotos and recent aerial photographs. Clearcut timber harvesting was extensive in our study area in the early 20th century but those forests are now mature. Within the past 50 years such harvesting has been uncommon and is readily identifiable on aerial photos. Our footprint mapping is likely of slightly higher to similar detail as that produced for other models.

Land cover classification

The Land Cover of Canada (Natural Resources Canada 2010) was selected as the best representation of habitat classes for the CCH range analysis due to complete and consistent coverage across the entire study area (both Yukon and British Columbia), appropriate spatial resolution, and adequate representation of high elevation and non-forested habitat types. Fire maps were obtained from Yukon and British Columbia fire mapping databases, current to 2010. We included fires up to 50 years old because forests regenerating after local fires in 1958 are still in the pole-sapling stage without much regeneration of ground lichens.

The Land Cover of Canada contains 31 cover classes comprised of coniferous, deciduous and mixedwood forest, plus shrub, herb, sparsely vegetated, rock and water. The boreal models require these to be simplified (partially amalgamated) and discriminated as undisturbed (mature forest) or disturbed (early succession forests). To satisfy these requirements, we had to: (i) differentiate types that might change

considerably with elevation; (ii) decide whether any classes were non-habitat (excluded from the analysis because caribou would not use them); (iii) deal with shadowed polygons; (iv) decide how to categorize classes as undisturbed or disturbed (as per model criteria in Table 1), in particular dealing with non-forested cover classes. Our derived habitat classes are summarized and mapped (Table 2; Figure 1) with rationale as follows.

Table 2. Summary of the spatial extent of all derived habitat classes used in the analysis of the Carcross Nothern Mountain Caribou Herd range.

Habitat Class	Area (ha)	Area (%)
High elevation sparsely	130,143	10.7
vegetated (alpine tundras)		
Low elevation sparsely vegetated	30,714	2.5
(steep slopes and grasslands)		
High elevation shrub (sub-alpine)	96,422	7.9
Low elevation shrub	173,303	14.2
Forest	675,837	55.3
Wetlands	10,821	0.9
Large lakes*	53,768	4.4
Other open water	28,209	2.3
Non-habitat (rock and ice)	22,283	1.8
Total study area	1,221,449	100.0

^{*} Note: Large lakes include Marsh, Tagish, Bennett and Tutshi Lakes

To better stratify sparsely vegetated (alpine tundra vs. grasslands) and shrub (sub-alpine vs. valley-bottom shrubs) classes, we intersected a bioclimate elevation boundary with the land cover mapping, creating different high and low elevation habitat classes. These are analogous to the distinctions between alpine and forested biogeoclimatic zones in the British Columbia classification system (Banner *et al.* 1993) or ecoclimatic regions proposed by Strong (2013).

The permanent ice (glaciers) and rock (exposed bedrock, cliffs and talus) were mostly in the high elevation stratum and were considered non-habitat because they offer very little habitat value to caribou (1.8% of study area; Table 2). They primarily occurred in the Yukon Stikine Highlands ecoregion. It was debatable whether large lakes (Marsh, Bennett and Tagish; > 2.0 km across on shortest axis) should be included as habitat. In the boreal caribou models, large lakes formed the boundaries of herd ranges (e.g., Environment Canada 2008, 2011), and smaller lakes were otherwise included in herd ranges because caribou are known to use them in winter to rest and to lick minerals from re-frozen seepage and overflow (Miller 2003). Most of the surface area of the large lakes, however, likely offers little habitat value to CCH caribou, except for the narrows between Bennett and Tagish Lakes that were kept in all model runs. Because the large lakes were central to the CCH range and comprised a fairly large proportion of the herd range (4.4%; Table 2, Figure 1), we decided to run the models once with these water bodies included (as was done with the CW model), and once with them excluded. All other smaller water bodies

were included as useable habitat for all model runs.

Shadows (north facing) were mostly cliff terrain in the high elevation stratum, and were treated as rock and ice. When in the low elevation stratum, they were considered to be undisturbed forest.

Northern Mountain Caribou ranges cover various vegetated habitat classes not found in the typical boreal population range, specifically shrub-dominated classes or sparsely vegetated habitats (steep mountain slopes and grasslands). The boreal models distinguish all vegetated classes as undisturbed or disturbed, equivalent to good or poor habitat based on predation risk and forage availability. Disturbed stands in the boreal models are forest types in early succession. They are distinct, being relatively short-lived (a few decades) because they are seral stages after stand-replacing disturbances (such as fire or clearcut logging), but otherwise rare. In the northern mountain range, such herb and shrubdominated conditions also form after stand-replacing disturbances. In addition, they are common as edaphic climax or permanent vegetation communities in the subalpine, in valley bottoms with cold air seepage, on dry south-facing aspects, and in wetlands (Pojar and Stewart 1991; Yukon Ecoregions Working Group 2004). For Northern Mountain Caribou, these shrub-dominated habitats cover large areas and have considerable forage value in spring and summer when caribou feed on forbs, grasses and willows (Oosenbrug and Theberge 1980; Environment Canada 2012). They are often patchily distributed within alpine tundra habitats and open canopy spruce stands that support lichen forage (Pojar and Stewart 1991), including the range of the CCH (Florkiewicz et al. 2007). They are high quality habitats for Moose (Bowyer et al. 2003), the primary alternative prey, and reasonably good foraging habitat for Grizzly Bears, so we assume they have high predation risk for caribou.

Collectively, shrub-dominated and low-elevation sparsely vegetated habitats comprise 25.5 % of the CCH range, consisting of sub-alpine shrub (7.9%; mature birch and willow shrub stands), low elevation

shrub (14.2%; also birch and willow shrub stands, often reflecting cold air seepage into valley floors and steep mountain slopes), low elevation sparsely vegetated (2.5%; mostly grasslands and gravelly steep slopes), and wetlands (0.9%; a mix of fens and willow shrub lands) (Table 2). This is a substantial area, with both high forage values and high predation risk. Consequently we ran each of the models twice, once with these edaphic climax shrub communities as undisturbed forest, and once as disturbed forest.

One other class, high elevation sparsely vegetated, represented alpine tundra with varying degrees of cover. We considered this undisturbed or good habitat as it is used by all caribou, and specifically by reproductive cows in reducing predation risk (Gustine *et al.* 2006; Environment Canada 2012).

In sum, we ran each of the models four times (Table 3). Two runs were with permanent shrub plus low elevation sparsely vegetated and grassland communities considered either undisturbed or disturbed. This dichotomy was repeated with large lakes either included or excluded from the study area.

RESULTS

With the CW model classifying permanent shrub, sparsely vegetated and grassland habitats as undisturbed, the total area of disturbance was 12.5% (large lakes included) and 13.1% (large lakes excluded). With those habitats considered disturbed, the total disturbance was 38.5% (large lakes included) and 40.3% (large lakes excluded). The inclusion or exclusion of large lakes in the herd range made little difference to the model outcomes (Table 3). Inclusion slightly enhanced the projected population growth rate or level of security by adding a small increment to the total area of good quality habitats.

The classification of permanent (edaphic climax) shrub, sparsely vegetated and grassland classes as either undisturbed (good quality)

Table 3. Summary of the projected population growth rates for the Carcross Northern Mountain Caribou Herd based on each of the boreal ecotype model runs. Large lakes were included or excluded as potential habitat, then each boreal ecotype model was run twice, considering all the shrub and open habitats as either undisturbed ("undist") or disturbed ("dist") habitat. For the Alberta (AB) model, population growth is represented by λ ("lambda", value>1.0 represents an increase and value <1 a decrease). For the Canada-wide (CW) model, the statistic is the probability that population growth will be positive. This is interpreted as risk of population decline as follows: probability >0.9 is very low risk, probability of 0.6 to 0.9 is low risk, probability of 0.4 to 0.6 is moderate risk, and probability below 0.4 is high risk (Environment Canada 2011:12). For the Northwest Territories (NT) model, "Secure" habitat is defined in Table 1, and number of patches >500 km² also comprising 54% of secure habitat were counted in GIS.

Large lakes included					Large lakes excluded						
CW		AB		NT		CW		AB		NT	
Shrub undist	Shrub dist	Shrub undist	Shrub dist	Shrub undist	Shrub dist	Shrub undist	Shrub dist	Shrub undist	Shrub dist	Shrub undist	Shrub dist
0.87 - 0.88	0.52 - 0.53	1.013	0.958	89% is Secure; Patches (n=2) large enough	63% is Secure; Patches (<i>n</i> =2) large enough	0.86 - 0.87	0.49 - 0.50	1.012	0.955	88% is Secure; Patches (n=2) large enough	61% is Secure; Patches (<i>n</i> =2) large enough

Page 74 REID et al.

habitat or disturbed (poor quality) habitat strongly altered the outcomes of the Canada-wide (CW) and Alberta (AB) models, and also the amount of secure habitat in the Northwest Territories (NT) model (Table 3). When these classes were considered disturbed, the AB model projected a declining population (λ < 1.0), the CW model projected close to 50% probabilities of positive growth (moderate risk of population decline), and the NT model indicated a low extent of secure habitat (c. 62%) though still sufficient to support a viable herd. When classed as undisturbed, the AB model projected an increasing population (λ = 1.012), the CW model approximately 86% probability of positive growth (low risk of population decline), and the NT model indicated widespread secure habitat (c. 88%). The NT model's second necessary criterion, minimum patch size of secure habitat, was satisfied in all model runs and the number of patches did not change among runs (Table 3).

The permanent shrub, sparsely vegetated and grassland classes were extensive in the CCH range, so their classification as undisturbed or disturbed drove a big shift in total proportion of the range disturbed from 12.5% to 38.5%. These proportions convert to caribou recruitment rate estimates of 38.9 calves/100 cows (95% C.I. 34 – 44) and 27.7 calves/100 cows (95% C.I. 24 – 31), respectively, based on the disturbance-recruitment regression that drives the CW model (Environment Canada 2011, Appendix 7.5, Figure 70). Mean recruitment rates for the CCH were 25 calves/100 cows (corresponding to 44.9% disturbance) over the time period for which population growth rate was estimated (Florkiewicz 2008). The field data show lower recruitment than the CW model would suggest, but within the 95% confidence intervals at the higher disturbance rate when these shrub and open habitats are considered disturbed (with high predation risk).

An implicit assumption in the NT model is that the secure habitat patches cover significant amounts of each seasonal habitat close enough together that caribou do not have to migrate seasonally. This assumption was not met in the CCH range. The most extensive definition of the CCH winter range includes all winter locations from a radio-telemetry study (Figure 1; Florkiewicz *et al.* 2007), but this range was not well represented in any secure habitat patches >500 km² in area. Considering that this herd primarily uses valley floor habitats within the broader winter range shown in Figure 1 (Florkiewicz *et al.* 2007), the core areas of winter range are completely separate from any secure habitat patches.

DISCUSSION

The CW and AB boreal population viability models, when applied to the Carcross Caribou Herd (CCH) range, produced fairly similar estimates of population trend (good chance of growth) and growth rate (positive λ) as the latest empirical estimate of finite rate of population increase (an approximation of λ) for the CCH of 1.062 (Florkiewicz 2008), but only when the permanent shrub, sparsely vegetated and grassland habitat classes were considered to be undisturbed, or

good habitat, for caribou. When these shrub, sparsely vegetated and grassland habitats were considered disturbed, or poor habitat, the CW and AB models underestimated the current population growth rate and apparent viability compared to recent empirical data.

However, the empirical data on CCH recruitment only showed reasonable fit with the CW model's recruitment-disturbance relationship when the permanent shrub, sparsely vegetated and grassland habitat classes were considered disturbed. This lack of coherence between the two measures of CCH population condition (λ and recruitment rate) and the disturbance levels suggests that the CW recruitment-disturbance relationship developed for boreal population herds is inaccurate for Northern Mountain Caribou.

The NT model was not so sensitive to our classification of permanent climax shrub, sparsely vegetated and grassland habitats as either disturbed or undisturbed. It has a relatively high tolerance for total range-wide habitat disturbance, and a built in assumption that the secure patches of >500 km² contain considerable undisturbed habitat for all seasonal ranges. Making this assumption explicit, we would have to conclude that the CCH is not viable because its winter range only marginally overlaps the secure habitat patches. This leads to two interpretations: (i) Northern Mountain Caribou populations may not require secure habitat patches containing substantial areas of all seasonal habitats; and (ii) there is something particular about the CCH that makes its winter range relatively secure despite the heavy human footprint. We suspect the latter interpretation is most true because the hunting ban and the relatively low predator densities in the CCH range (Baer 2010) both support the recent population growth.

We conclude that using the CW and AB boreal models in the northern mountain context is invalid because such use would depend heavily on poorly documented interpretation of the quality of permanent shrub, sparsely vegetated and grassland habitats, and on a potentially inaccurate recruitment-disturbance relationship. We also conclude that the application of the NT model is invalid in the northern mountain context because we cannot meet that model's implicit assumption that secure habitat patches cover substantial amounts of all seasonal ranges, and the validity of that assumption for Northern Mountain Caribou herds is undocumented.

Each boreal model has some features of value in the northern mountain context. The CW model buffers the human footprint, more effectively mimicking caribou avoidance of these features than the AB model (Applied Ecosystem Management 2004; Vors *et al.* 2007). Also, it explicitly considers permanent removals of alienated habitat, such as residential, industrial or agricultural parcels; all of these need to be dealt with in northern mountain population range (Environment Canada 2012). Regarding the secure habitat patch concept in the NT model, future work needs to investigate the minimum undisturbed proportion of the most limiting seasonal range that needs to remain contiguous with other seasonal ranges in each secure patch.

We gained some insights by relating the response variables of the three models to the estimates of λ and recruitment for the CCH,

our first objective. However, this was not a sufficient test because demography of one herd can change annually whereas the three models provide decision rules based on average conditions across many herds. The more substantive insights relate to the classification decisions the three models require for shrub, sparsely vegetated and grassland habitats (which are extensive in Northern Mountain Caribou population range), and also for the proportion of limiting seasonal range(s) left undisturbed by human footprint.

General Interpretation

There is general agreement that boreal and northern mountain populations of Woodland Caribou are proximally limited by predation mortality, with Gray Wolves and bears being the dominant predators (James and Stuart-Smith 2000; Hayes et al. 2003; Schaefer 2008; Environment Canada 2012). Predator avoidance has shaped the caribou's large scale habitat selection, while intermediate and small scale selection seems more oriented to good quality foraging habitats and patches (Rettie and Messier 2000; Johnson et al. 2004). Caribou select older forests and peatlands where other ungulate prey species, and therefore predators, are generally uncommon. They space out at the vulnerable calving season to reduce detection by predators (Bergerud et al. 1984; Schaefer 2008). Alteration of undisturbed forest to disturbed successional stands (by fire or timber harvest) enhances densities of other prey, especially Moose and deer, with consequent increases in predation risk for caribou (Latham et al. 2011b). In addition, disturbance often removes high quality foraging habitat for a number of decades, thereby reducing the carrying capacity of the entire herd range (Schaefer and Pruitt 1991; Joly et al. 2003). The Boreal and Northern Mountain Caribou populations generally face similar circumstances with respect to the population effects of human and natural disturbances.

Boreal and Northern Mountain Caribou populations may differ in how they can respond to risks associated with human footprint. To do so, both populations need sufficient space well away from linear features where predation risk and disturbance are elevated (Latham et al. 2011a). This is the premise behind the NT model's requirement for large blocks of secure habitat, the AB model's focus on linear features, and the CW model's assessment of total area disturbed including buffering of linear features. Linear features in the boreal population range tend to be more uniformly distributed because the terrain is less rugged, and hydrocarbon exploration and development (seismic lines, well pads and associated roads) and timber harvesting are fairly evenly dispersed. Linear features in Northern Mountain Caribou population range are more constrained to valley bottoms in rugged terrain, leaving larger blocks of unfragmented habitat, often at higher elevations. Topography appears to offer northern mountain herds more options to avoid linear features, except in the valley floors which they often use as winter range (Environment Canada 2012). Both the AB and CW models may underestimate the impact of linear features in valleybottom winter ranges because they calculate this parameter across the entire range.

The two populations may differ in how they can respond to changes in seral stage after fire or timber harvesting, depending on the spatial scale at which seasonal habitats are distributed and temporal patterns of habitat availability. By migrating seasonally, most Northern Mountain Caribou herds may enhance their predator avoidance by spacing away from some core predator ranges (Bergerud et al. 1994; Environment Canada 2012), but late snow melt at high elevations may thwart the spacing out in spring and allow predators improved chances of finding calves (Hegel et al. 2010). Also, some Northern Mountain Caribou herds may be able to change one or other of their seasonal ranges. For example, some winter in alpine tundra and subalpine forests, instead of using low elevation undisturbed forests (Environment Canada 2012). When this occurs, as with the Ibex herd in southern Yukon (Florkiewicz 2008) or the Telkwa Mountains herd in central British Columbia (Vik Stronen et al. 2007), the original winter range has been largely lost to fire or clearcutting and has not regenerated to mature forest with lichen forage. Winter ranges are often viewed as the most limiting portion of a northern mountain herd's range (Florkiewicz et al. 2007; Environment Canada 2012). The ability to change winter range, even to one of lower quality, may offer some Northern Mountain Caribou herds enhanced choices for dealing with forest disturbance. By contrast, each seasonal range for boreal herds appears to be divided into separate patches, such that ranges for different seasons are more intergraded and less spatially disjunct (Schaefer 2008). Boreal Woodland Caribou appear to have fewer opportunities to space away from predators and alternative prey, and fewer choices of alternative range following changes in forest seral stage.

Permanent shrub, sparsely vegetated and grassland habitats support quite high to intermediate forage values for caribou in summer and winter (Florkiewicz *et al.* 2007; Florkiewicz 2008). They may also be relatively risky habitats, being heavily used by Moose in many seasons and often close to Thinhorn Sheep range, so frequently visited by Gray Wolves, Wolverines and Grizzly Bears. The overall quality of these habitats for caribou would seem to be intermediate between disturbed and undisturbed, and they were neither selected for nor avoided by the CCH (Florkiewicz *et al.* 2007). There is no defensible way to deal with these habitats within the boreal population models. This emphasizes the need for a new model focussing exclusively on the Northern Mountain Caribou population.

Some particular features of the CCH are important to consider in the northern mountain context. Recruitment, at about 25 calves/100 cows (Florkiewicz 2008), is on the threshold between stable and declining for Boreal (Environment Canada 2012) and Northern Mountain (Bergerud and Elliott 1998) Caribou herds, indicating that population growth is proximally limited by relatively high calf mortality (Florkiewicz 2008). Calf mortality in Northern Mountain Caribou range may be simply a result of healthy predator populations supported by diverse and productive ungulate populations (Bergerud and Elliott 1998). However, as we report here, the CCH range

Page 76 REID et al.

supports relatively low densities of caribou predators and of alternative ungulate prey. Studying northern mountain herds in Yukon, including CCH, Hegel et al. (2010) concluded that climate conditions during winter and at calving strongly influenced recruitment of young the subsequent autumn. Mechanisms could include deep snow limiting access to forage, and late snow melt forcing caribou to calve in restricted high elevation range; both lead to more vulnerable calves (Hegel et al. 2010). The human footprint is extensive in CCH winter range and caribou strongly avoid much of this footprint, so considerable winter forage is not accessed by caribou (Applied Ecosystem Management 2004; Florkiewicz et al. 2007). This habitat alienation is likely to have energetic costs somewhat similar to those imposed by deep snow. The overall point is that snow conditions can strongly affect northern mountain caribou demography, and they may add considerable variance within any application of the boreal disturbance-recruitment paradigm to northern mountain population herds.

Limitations of the boreal models need to be considered. None deals adequately with what proportion of any sensitive seasonal range needs to be conserved without human or natural disturbance. None of the models deals adequately with the permanent shrub, sparsely vegetated and grassland communities that are common in northern mountain range. The most robust approach to Northern Mountain Caribou habitat conservation would be to develop a specific disturbance-population model for this population, including an assessment of the effects of variation in snow conditions on demography. This could be achieved using demographic and habitat data from many of the herds found from central British Columbia to central Yukon.

One key consideration will be the responses of ground lichens and caribou to timber harvesting and fire across this large region. Responses may vary with disturbance type, climate zone, and silvicultural practice (e.g., history of broadcast burning; seasonal timing of harvest; regeneration time for ground lichens on different sites, harvest rotation period) (Coxson and Marsh 2001; Hart and Chen 2006; Waterhouse et al. 2011). Fire and timber harvest disturbances may differ in their effects on lichen regeneration (Hart and Chen 2006). The boreal models only classify forest stands <30-50 years old as disturbed. However, pine woodlands typical of caribou winter range in boreal montane forests often support rich ground lichen growth only 50 years after fire with prime growth from 80-120 years (Coxson and Marsh 2001). Another key consideration will be the specific mechanisms of predation limitation across caribou age-classes (seasons), alternative prey distributions, and habitat scale (Hayes et al. 2003; Hegel et al. 2010; Peters et al. 2013), and how these might differ by disturbance type.

Modelling should be done separately for the Southern Mountain Caribou population whose ecology is sufficiently different (more frequent natural shrub lands in avalanche chutes; winter forage limited to arboreal lichens; reduced availability of alpine habitats in winter; Seip and McLellan 2008) from the Northern Mountain Caribou population that the role of non-forested habitats and human footprint

within sensitive seasonal ranges would need separate assessment.

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Page 78 REID et al.

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