Fragmentation, dispersal and metapopulation function in remnant populations of endangered mountain caribou

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Abstract

Populations that are fragmented in space may persist because of metapopulation function that relies on dispersal among subpopulations. Assuming that a fragmented distribution means that the species operates as a metapopulation can lead to erroneous conclusions about population structure, unless the dispersal traits of the organism are understood. A wide-ranging large mammal with an increasingly fragmented distribution is the mountain caribou, found in the interior rain forests of British Columbia, Canada. These caribou are an endangered ecotype of woodland caribou *Rangifer tarandus caribou*, and, based on movements of adult caribou, their population has been divided into 18 subpopulations. Their numbers have declined over at least the last 25 years, and it is unknown if their fragmented distribution operates as a metapopulation linked by juvenile dispersal or is simply a step towards extinction. From a database of radio-locations collected over a 23-year period (1984–2007) from 358 caribou, we used a spatial index to define summer/fall composite ranges (breeding ranges) across their distribution. The 18 previously recognized subpopulations were fragmented further into 41 summer/fall composite ranges. Young animals (<1 year of age) were not observed to disperse among subpopulations (0/26 opportunities) or even among summer/fall composite ranges (0/7). Similar results were found for animals 2 and 3 years of age. Breeding dispersal by adult caribou occurred in 1.4% of the observed opportunities (8/587). These dispersal rates are insufficient to rescue the smaller and declining subpopulations. We conclude that the distribution of these mountain caribou is more fragmented than thought previously and is not functioning as a classic metapopulation due to a lack of dispersal; rather, it is better described as an extreme non-equilibrium metapopulation. Mountain caribou and other wide-ranging species fragmented into subpopulations by human actions may appear to be in a metapopulation but unless they have the innate ability to disperse among subpopulations, the distribution is more likely the geographic pattern of the extinction process.

Introduction

The distribution of a species may vary from one large contiguous population to many small, isolated subpopulations (Harrison, 1991; Stith *et al.*, 1996). The distribution of most species lies in a variety of patterns between these two extremes, providing diverse examples of metapopulations with varying levels of movement within them (Hanski & Gilpin, 1991; Harrison, 1991; Stith *et al.*, 1996). Because metapopulation structure and function affect the rate of population decline and probability of extinction, understanding the degree to which populations are fragmented, and rates of movement among subpopulations is important, particularly for endangered species.

Movement between subpopulations occurs via dispersal (Greenwood, 1980; Greenwood & Harvey, 1982). With mammals and birds, most dispersal occurs as juveniles and is referred to as natal dispersal (Greenwood & Harvey, 1982). Natal dispersal can be an innate behaviour but is sometimes socially stimulated (Nilsson, 1989; Drent, Van Oers & Van Noordwijk, 2003). Breeding dispersal, where adult animals switch breeding locations (Greenwood & Harvey, 1982), usually occurs at a lower frequency than natal dispersal but has similar ramifications. Both forms of dispersal may be adaptive as a way to avoid inbreeding and competition, particularly among kin (Hamilton & May, 1977; Bengtsson, 1978). Beyond benefits to the individual or their kin groups, dispersal is also important for the

persistence of populations. Species that evolved to disperse widely are better able to persist if their distribution becomes fragmented. The propensity to disperse can lead to demographic rescue of subpopulations that have declined to low numbers, or to re-colonization after extirpation (Simberloff, 1988; Hanski & Gilpin, 1991; Hanski *et al.*, 1995). Dispersal also promotes genetic mixing and reduces inbreeding in small populations (Simberloff, 1988; Madsen, Stille & Shine, 1996; Hitchings & Beebee, 1998; Keller & Waller, 2002). Although dispersal behaviour is important for conservation, the study of dispersal is challenging because it is often difficult to capture, mark and follow long-distance movements of young animals, or because there is insufficient genetic structuring to confidently identify putative migrants from genetic samples. This is a challenge even in large viable populations, but more so for endangered species found at low numbers over broad geographic areas (Elmhagen & Angerbjörn, 2001).

Mountain caribou *Rangifer tarandus caribou* (Heard & Vagt, 1998) are an endangered herbivore with an increasingly fragmented distribution (Wittmer *et al.*, 2005a; Wittmer, Sinclair & McLellan, 2005b; Apps & McLellan, 2006) that are found in the interior rain forests of British Columbia, Canada. These caribou are an ecotype of woodland caribou – a gregarious herbivore living in conifer forests across much of northern North America. The number of caribou in the interior rain forests is declining (Wittmer *et al.*, 2005a) and is estimated at fewer than 2000. Much of their historic distribution is no longer occupied (Apps & McLellan, 2006); Wittmer *et al.* (2005a) found them to be fragmented into 18 subpopulations with several of these consisting of <20 individuals, and two have since been extirpated (Hatter, 2006). The decline of these caribou has been greatest in the southern part of their distribution where subpopulations are smaller and more isolated than those further north (Wittmer *et al.*, 2005a; Wittmer, Ahrens & McLellan 2010).

The 18 subpopulations of mountain caribou identified by Wittmer *et al.* (2005a) using radio-telemetry on adult animals appeared largely discrete and represent a coarse scale of population structure. It remained unknown if natal dispersal provided potential for demographic rescue and gene flow among subpopulations, primarily because no juveniles were collared during past studies. Because subpopulations were defined previously by multi-year home range overlap that considered radio-locations from all times of the year, it was also unknown if the subpopulations were themselves comprised of multiple discrete breeding ranges and how frequently animals moved among such breeding ranges. Here, we radio-collared and monitored juvenile caribou plus expanded the radio-telemetry sample on adults. With the most recent information, we delineated the summer/fall distribution of mountain caribou (the seasonal range that includes the breeding period), and investigated natal and breeding dispersal at two spatial scales: among subpopulations, and among breeding ranges within subpopulations. Our goal was to describe the geographic distribution of these caribou on the ranges where they breed, and to determine if dispersal was sufficient for demographic rescue of the smaller subpopulations.

Materials and methods

The distribution of mountain caribou in the interior rain forests extends from the McGregor range in the Rocky Mountains – c. 80 km to the north-east of Prince George, BC (55°N) – to just south of the international border in Idaho, USA (48.5°N). Between these geographic endpoints, caribou are found in the Cariboo, Monashee, Selkirk, Purcell and Rocky Mountains. Their general distribution covers almost 150 000 km^2. The area is mountainous but varies from mostly forested, high-elevation plateaus or rounded mountains, to very rugged peaks with glaciers and long narrow valleys; elevations range from 350 to ≈ 3500 m. The interior rain forests include the wet and very wet subzones of the Engelmann Spruce – Subalpine Fir biogeoclimatic zone, the wet and very wet subzones of the Interior Cedar Hemlock zone and the very wet subzones of the Sub-Boreal Spruce zone (Meidinger & Pojar, 1991). Most precipitation comes from pacific weather systems falling in winter as snow. Snowpack in the mountains typically ranges between 2 and 5 m each winter.

Forestry, usually by clear-cutting, re-planting and management of competing vegetation is the dominant land use in the study area. Large reservoirs for hydroelectric power generation and associated transmission lines have had significant effects in some areas (Apps & McLellan, 2006). Because of the wet, rugged nature of the area, human settlement is relatively uncommon with a few towns of <10 000 people within occupied caribou habitat. Four major highways, including the Trans-Canada highway, cross the study area.

In addition to mountain caribou, moose *Alces alces*, white-tailed deer *Odocoileus virginianus*, mule deer *Odocoileus hemionus*, elk *Cervus elaphus* and mountain goats *Oreamnos americanus* occur at variable densities. Predators of ungulates include wolves *Canis lupus*, cougars *Puma concolor*, grizzly bears *Ursus arctos*, black bears *Ursus americanus* and wolverine *Gulo gulo*. Mountain caribou appear to be declining primarily because of apparent competition (Holt, 1977) with other co-habiting ungulate species (Seip, 1992; McLoughlin, Dunford & Boutin, 2005; Wittmer *et al.*, 2005a,b, 2007).

Here, we use radio-telemetry to investigate population structure. Genetic analysis was not used because the overall population has been declining (Wittmer *et al.*, 2005a) and half of the subpopulations have 30 or fewer animals. With necessarily small sample sizes per subpopulation and the declining population paradigm suggesting recent fragmentation, there was insufficient genetic structuring to identify putative migrants as has been carried out with other species with increasing movements (Proctor *et al.*, 2005; Dixon *et al.*, 2006; Paetkau *et al.*, 2009). Furthermore, small and rapidly declining populations are not at 'migration-drift' equilibrium making it inappropriate to estimate migrants using classic population genetics (Whitlock & McCauley, 1999). Thus, using radio-collared animals was the most

Table 1 Details of mountain caribou distribution is reviewed

Subpopulation	Number collared adults (calves)	Proportion of 2002 census	Census data 1990	2002	2006	2008	No. of SFCR
Allen Creek	5 (1)	0.16	–	38	33		1
Barkerville	14	0.24	55	58	51		1
Central Selkirks	31	0.30	211	103	85		2
Columbia-North	51 (10)	0.42	280	145	138	166	5
Columbia-South	25 (3)	0.82	114	34	29	20	3
Duncan	4	0.17	29	23	9		1
Frisby-Boulder	10 (1)	0.46	24	24	19	12	2
George Mountain	2	0.50	24	4	0		1
Groundhog	6 (2)	0.42	48	19	30		1
Hart Ranges	20	0.04	–	>450	717[a]		6
Kinbasket-South	5	1.00	25	5	2	3	3
Monashee-South	2 (1)	0.60	12	5	8	5	1
Narrow Lake	2	0.03	81	73	40		1
North Cariboo	11	0.04	279	284	267		3
Purcells-North	8	1.33	18	6	0		1
Purcells-South	23	1.35	77	17	20		2
South Selkirks	9 (1)	0.29	52	34	37		1
Wells Gray	129 (8)	0.27	620	516	422		6
TOTAL	357[b] (27)	0.21	1949	1838	1907		41

The number of adult caribou used to define composite summer/fall ranges (SFCR), and the number of newly collared calves in each subpopulation are provided. Census data were obtained from Hatter (2006) and McLellan et al. (2008). The number of SFCR are results from the current study.
[a]The 2006 census area was more extensive in the Hart Ranges and thus more animals were found.
[b]The single collared adult caribou from the unknown subpopulation (Pyramid drainage) is not included in this table.

appropriate method of estimating dispersal to make inferences about demographic rescue.

Between 1984 and 2007, telemetry-based research on mountain caribou occurred throughout their geographic range. Using a helicopter, we captured 432 caribou with a net-gun in March when they use high-elevation, open parkland habitat. Captured caribou were fitted with VHF or GPS collars, which operated for up to 6 years. Some study animals were re-collared and followed for up to 11 years. Collared animals were located by aircraft approximately every 16 days throughout the year. Before GPS units were used in aircraft to geo-reference locations, 95% of the telemetry locations were accurate to within 364 m ($\bar{x} = 148 \pm 98$; 1 SD) but recent VHF locations using GPS in aircraft are likely more accurate. Since previous analyses from this long-term dataset (Wittmer et al., 2005a, 2007), 41 additional caribou, including 27 calves, were captured and monitored (Table 1).

Of the 432 radio-collared caribou, 63 (15%) were male. Teeth of these endangered herbivores were not pulled at the time of capture, and hence age was not accurately known for most animals. Seventeen were classified as yearlings (22 months old), 112 were classified as adults, while 276 animals were unclassified but were either adults or yearlings (see below for how these animals were analysed), therefore 388 adults/subadults were collared. We also collared 27 calves to investigate natal dispersal between subpopulations, and fitted these with lightweight expandable VHF collars (Telonics Inc., Mesa, AZ, USA) to accommodate the growth of young animals. Population census and spatial data for the 18 recognized subpopulations are reviewed in Table 1.

Mountain caribou in the interior rain forests undergo well-defined migrations between ranges used for spring, summer/fall, early winter and late winter (Apps et al., 2001). Fidelity to seasonal ranges is greatest for the summer/fall composite ranges (Wittmer, McLellan & Hovey, 2006). Mountain caribou move to their summer/fall composite ranges (SFCR) in mid June shortly after calving has occurred; these ranges are on high-elevation mountainous ridges of alpine and sub-alpine parkland habitat and caribou mate on these ranges in October (Wittmer et al., 2005a) before their migration to early winter ranges. Because SFCR are used during the breeding period, the population structure can be defined by their distribution during this season and dispersal movements between SFCRs over time.

We were interested in spatially delineating SFCR and then determining the frequency that individuals move among these ranges to estimate the degree of spatial partitioning within subpopulations. We adapted the methods used by Wittmer et al. (2005a) to delineate SFCRs. We delineated 100% minimum convex polygons around the summer/fall telemetry locations (11 June–21 October; Wittmer et al., 2006) separately each year for every caribou; data from caribou that were located less than three times during a summer/fall season were not considered. For the purposes of SFCR delineation, we only included data from animals that were at least 3 years old, including all polygons from
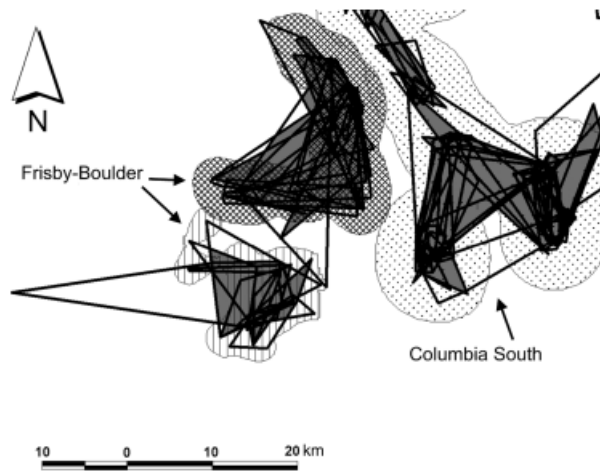
Figure 1 An example of how the composite summer/fall ranges were delineated in an area with some movement between ranges. Minimum convex polygons were fitted around the summer/fall locations for each individual caribou each year, which are represented here as hollow polygons. Contiguous areas of two or more overlapping ranges separate the composite summer/fall ranges (shaded grey). Each of the annual summer/fall polygons were assigned to a composite summer/fall range and the underlying telemetry were pooled to derive a 95% Kernel for mapping purposes (with variable fill patterns). There are three different summer/fall composite ranges from two subpopulations mapped in this figure.

caribou classified as adults at capture. Polygons from unclassified caribou were also included, but we omitted the first summer/fall polygons observed from these animals that were potentially 2 years old at capture.

Most of the minimum convex polygons were stacked tightly over top of each other forming clearly distinct SFCR clusters (Fig. 1), but there were cases where caribou locations were occasionally recorded outside of these well-defined SFCR areas. To delineate the primary areas used as SFCRs, we developed rules that enabled consistent and repeatable delineation of SFCRs and what constituted a dispersal event between these ranges. We delineated SFCRs as contiguous areas over which there were two or more overlapping polygons, thereby filtering out habitats that were rarely used during this season (Fig. 1). Each polygon was then assigned to the SFCR within which its telemetry locations were located. Because the number of SFCR estimated will depend on the proportion of the subpopulation sampled, we conducted sensitivity analyses on all subpopulations with >1 SFCR to ensure that we were not overestimating fragmentation within subpopulations. This analysis was performed by randomly removing individual radio-collared caribou from the analysis, one at a time, and recording the number of SFCR at each step to estimate the relationship between the proportion of the subpopulation collared and the number of composite ranges to determine when the number of ranges stabilizes. The proportion of the subpopulation sampled was based on the 2002 population estimate.

A dispersal event was defined to have occurred when an individual caribou was located in different SFCR between successive years. We calculated rates of dispersal as the number of dispersal events that occurred over the total number of dispersal opportunities. Incidences of dispersal among SFCR and subpopulations were examined separately for yearlings (dispersal between age 0 and 1), 2-year-olds (age 1 to age 2), 3-year-olds (age 2 to age 3) and adults. For yearlings, we did not directly observe their natal summer range (year 0) because they were captured when $c.$ 10 months of age, which was after they may have left their first SFCR. We therefore inferred the whereabouts of their first summer/fall locations from the subset of collared calves whose mothers' were collared in the previous year to test for dispersal among SFCR. To test for dispersal among subpopulations, we also examined data from all collared calves with functioning collars because they were still with their mothers when captured. We pooled all dispersal opportunities from all adults; hence, an animal monitored for eight consecutive summer/fall seasons provided seven dispersal opportunities. All spatial computing was performed using geo-referenced mapping software (ESRI ArcView 3.3). We computed 95% fixed kernel boundaries around locations of all summer/fall locations using a least squares cross validation smoothing parameter for mapping the SFCR after these had been delineated.

Results

Because there were <30 animals in half of the subpopulations (Table 1), the sample sizes of collared animals in some of these were small. However, even with the small sample sizes inherent with an endangered animal consisting of <2000 individuals, a total of 969 annual summer/fall polygons from 358 adults monitored between 1984 and 2007 were used to delineate 41 SFCR (Tables 1 and 2). There were insufficient data to delineate SFCRs from 30 adults, thus, they were excluded from analyses. One SFCR (Pyramid) was located outside the known population boundaries of Wittmer *et al.* (2005*a*). This small group of animals (four) had been reported previously in this area but they were not found during the capture programme until 2004. Half (nine) of the 18 subpopulations contained only one SFCR. The remaining 32 SFCRs were located within the other nine subpopulation boundaries (Fig. 2a–d). The Hart Ranges, Wells Gray, Kinbasket South and Columbia North subpopulations were each fragmented into more than two SFCRs.

The sensitivity analysis on our method to delineate SFCRs suggested that the number of SFCRs initially increased with an increasing proportion of the population radio-collared. When 10–15% of the population was collared, then too many ranges would sometimes be delineated, but the number of ranges would stabilize when about 20% of the subpopulation had been radio-collared (Fig. 3).

In all seven instances for which we had data, the annual summer/fall polygons of yearlings were in the same SFCR as was their mother during the previous year (when the yearlings were calves; Table 3). Out of 27 collared calves, 26 were

Table 2 Details of the summer/fall composite ranges (SFCR)

Subpopulation	SFCR	Distance to nearest	Collared caribou	No. of MCP	Number of opportunities by age			
					0	1	2	Adult
Allen Creek	Allen Creek	12	5	12				6
Barkerville	Barkerville	17.3	14	41				25
Central Selkirks	Halcyon	3.2	27	74				40
Central Selkirks	Lardeau	3.2	4	7				1
Columbia-North	Birch	2.8	1	4				3
Columbia-North	Cummins	4.5	11	26		1		15
Columbia-North	Mica	4.5	3	4				
Columbia-North	Pettipiece	3.9	29	83	2	3	4	60
Columbia-North	Soards	2.6	7	18	1		1	11
Columbia-South	Glacier	1.7	6	17			3	11
Columbia-South	Revelstoke	1.7	18	67		1	2	49
Columbia-South	Sorcerer	1.3	1	3				1
Duncan	Duncan	20.5	4	14				9
Frisby-Boulder	Boulder	2.8	4	11				7
Frisby-Boulder	Frisby	2.8	6	19				12
George Mountain	George Mountain	29	2	5				2
Groundhog	Groundhog	2.6	6	18		1		12
Hart Ranges	Farmstead	7.1	2	8				7
Hart Ranges	Herrick	7.1	1	4				2
Hart Ranges	Kenneth-Longworth	10.2	6	11				5
Hart Ranges	McGreggor	7.9	2	5				3
Hart Ranges	Parsnip	11.4	6	20				14
Hart Ranges	Pass lake	11.4	3	8				5
Kinbasket-South	Adamant	5.5	1	6				6
Kinbasket-South	Esplanade	16.1	2	4				2
Kinbasket-South	Windy	5.5	2	13			1	11
Monashee-south	Blanket	24.5	2	8				6
Narrow Lake	Narrow Lake	21.5	2	6				3
North Cariboo	Dome-Haggen	0.1	8	22				15
North Cariboo	North Bowron	0.1	2	4				
North Cariboo	South Bowron	15.5	1	3				1
Purcells-North	Purcells North	20.9	8	16				8
Purcells-South	East	6	20	35				15
Purcells-South	West	6	3	3				
South Selkirks	South Selkirks	25.4	9	30				20
Unknown	Pyramid	12.1	1	2				1
Wells Gray	Black Stuart	7.6	1	6			1	4
Wells Gray	Boss Mtn.	1	7	15				7
Wells Gray	Horsefly Lake	4.2	3	3				
Wells Gray	Miledge	2.6	9	29	1			18
Wells Gray	Plateau	2.6	107	283	3	3		169
Wells Gray	Trophy	13.5	2	2				1
TOTAL			358	969	7	9	12	587

The minimum distance to the nearest neighbouring SFCR, the number of collared caribou that were monitored, the total number of individual annual summer/fall minimum convex polygons (no. of MCP) in the dataset, and the number of dispersal opportunities are listed by caribou age for each SFCR.

followed through the calving season when they became yearlings (11 June) and into their second summer/fall season; 17 were followed until the end of this season (21 October). None of these dispersed to a new subpopulation during these periods and hence the probability of dispersal between subpopulation is <0.037 from birth to 1 year of age and <0.058 from birth to the beginning of their second winter. Nine collared calves were observed for both their yearling summer/

fall (age 1) and their subsequent summer/fall (age 2); again, no animals dispersed to a different SFCR or subpopulation (Table 3). No animals dispersed to different SFCR between their second and third year ($n = 12$ observed opportunities; Table 3).

Of the 587 breeding dispersal opportunities monitored (521 by females and 66 by males), dispersal to new SFCRs occurred eight times (1.4%; Table 3), and only by females. In two out of the eight dispersal cases, the dispersing females
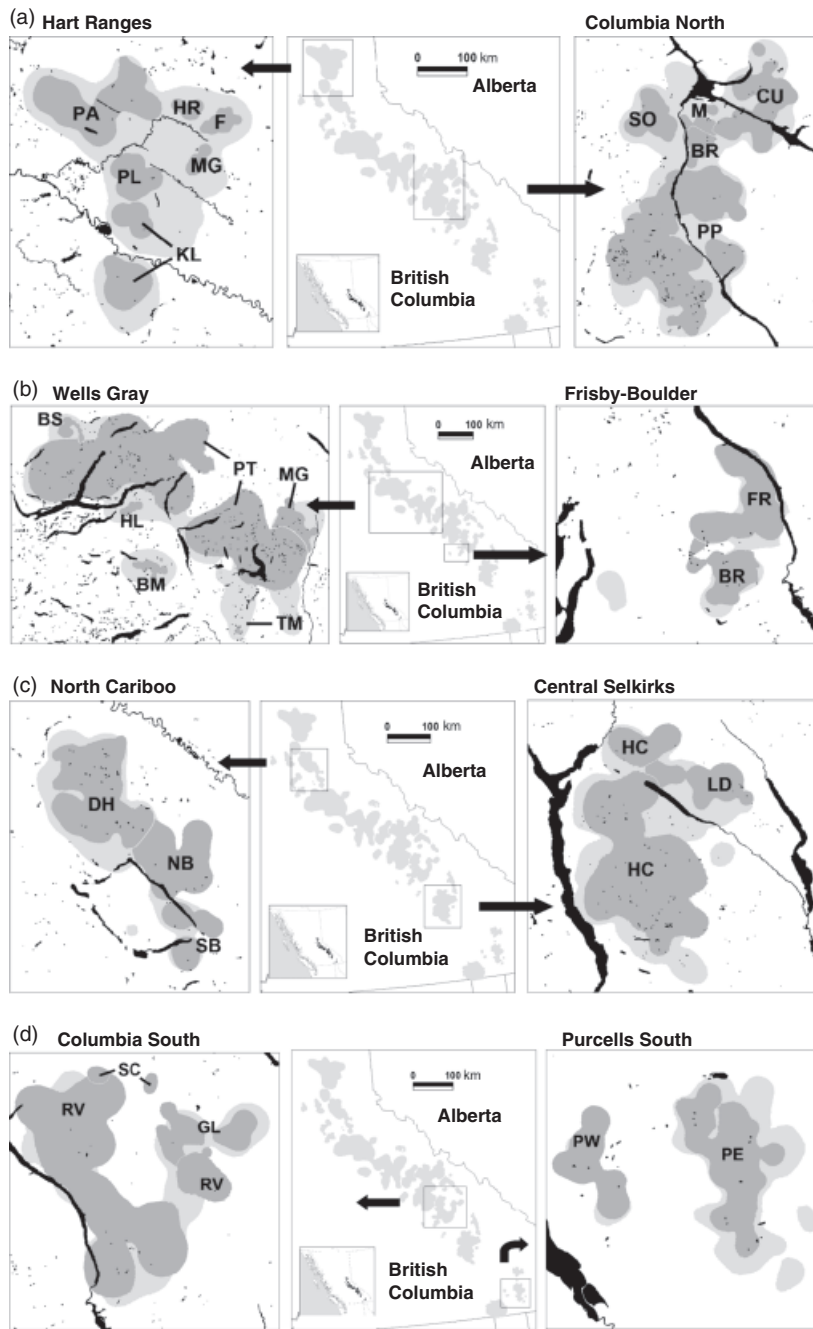
Figure 2 (a) The central panel shows the entire distribution of mountain caribou in the interior rain forests of British Columbia at two scales. Detailed maps on the side panels show the composite summer/fall ranges identified for the Hart Range (left panel) and Columbia North subpopulations (right panel). Light grey shading delineates the subpopulations (Wittmer *et al.*, 2005*a*), dark grey shading delineates the composite summer/fall range, and lakes are colored black. The composite summer/fall ranges were mapped as 95% Kernels around the telemetry locations (dark grey: PA, Parsnip; HR, Herrick; F, Farmstead; PL, Pass Lake; MG, McGreggor; KL, Kenneth/Longworth; SO, Soards; M, Mica; CU, Cummins; BR, Birch Creek; RB, Rudduck-Bench PP, Pettipiece). (b) Dark grey: BS, Black Stuart; HL, Horesfly Lake; PT, Plateau; MG, Miledge; BM, Boss Mountain; TM, Trophy Mountain; FR, Frisby; BR, Boulder. (c) Dark grey: DH, Dome-Hagen; NB, North Bowron; SB, South Bowron; HC, Halcyon; LD, Lardeau. (d) Dark grey: RV, Revelstoke; SC, Sorcerer; GL, Glacier; PW, Purcell West; PE, Purcell East.

moved to SFCR in a different subpopulation. These latter cases link the Wells Gray subpopulation to Allan Creek subpopulation, and Columbia North subpopulation to the Groundhog subpopulation (Table 3), movements that were not recorded previously by Wittmer *et al.* (2005*a*).

Discussion

Even in pristine areas with little human influence, organisms are not uniformly distributed across the landscape, but are found unevenly with some areas of higher density than

others (Levins, 1969; Harrison, 1991). A species' habitat requirements may naturally fragment their distribution among suitable patches and if several separate population units persists through asynchronous extinction of patches but eventual recolonization by dispersing individuals from other patches, they are referred to as a classic metapopulation (Hanski & Gilpin, 1991; Hanski *et al.*, 1995). Other species have a more continuous distribution in space and do not form a metapopulation. However, few areas remain pristine and many species that were once continuously distributed have now been forced into a series of habitat

patches resembling, at least superficially, a metapopulation (Clinchy, Haydon & Smith, 2002). For the conservation of these species, it is critical to know if they function as a metapopulation across their fragmented distribution with sufficient dispersal for demographic rescue or if the fragmented distribution is simply a predictable step towards extinction (Simberloff, 1988).

Mountain caribou are one of many species that were much more numerous and more widely and evenly distributed in
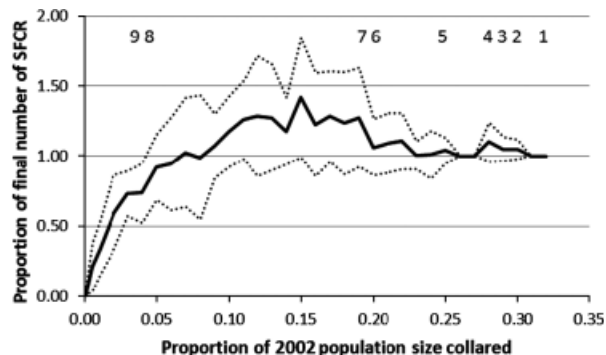

Figure 3 The proportion of the total number of summer/fall composite ranges (SFCR) as a function of the proportion of each subpopulation that was radio-collared, including 95% confidence intervals (dotted lines). Data from all subpopulations fragmented into >1 SFCR were included for this simulation. The proportion of the population radio-collared was based on the 2002 census, except two small and rapidly declining subpopulations (Purcells South and Kinbasket) where the number collared was greater than the 2002 estimate, and hence the 1990s estimate was used to calculate the proportion collared. The number of subpopulations (descending from nine to one) is shown across the top of the figure. For example, 20% or more of the caribou were sampled within each of six subpopulations.

the past (Spalding, 2000; Laliberte & Ripple, 2004; Apps & McLellan, 2006). These caribou are in decline (Wittmer *et al.*, 2005*a*) and are increasingly restricted to mountainous areas surrounded by low-lying regions of inhospitable habitat (sensu Brown, 1971). Using minimum convex polygons of radio-collared caribou >1 year of age captured across their distribution, Wittmer *et al.* (2005*a*) delineated 18 subpopulations with no recorded movements among them suggesting little metapopulation function. In many if not most species, the majority of dispersing individuals are juveniles (Greenwood, 1980; Sutherland *et al.*, 2000), hence, it remained unclear if the fractured distribution of mountain caribou was acting as a metapopulation with sufficient dispersal by juvenile animals for demographic rescue of the smaller subpopulations. Although our sample size of collared calves monitored for a full year was small, we found no tendency to disperse. None of the 26 calves were recorded to move among subpopulations, and from a more restricted dataset (seven calves plus nine yearlings), we also found that none moved between SFCR among years. Hence, our data do not provide evidence that immature mountain caribou have an innate tendency towards natal dispersal.

Because we found no movement among subpopulations or SFCR by the radio-collared calves/juveniles, and a very low incidence of dispersal by adults, it appears that mountain caribou are not functioning as a metapopulation or are a metapopulation in a state of non-equilibrium (Brown, 1971; Harrison, 1991). The inter-subpopulation dispersal rate of <0.5% is certainly insufficient to rescue subpopulations from their ongoing annual declines of up to 18% (Wittmer *et al.*, 2005*a*, Table 1), even if adjacent to the largest subpopulations, and unlikely adequate to recolonize the increasingly abundant amount of unoccupied habitats.

Table 3 Outcomes of all dispersal opportunities monitored from mountain caribou from the interior mountains of British Columbia, Canada

Age x	Age x+1	Sex	n (SFCR)	Dispersal among SFCR	n[a] (subpops)	Dispersal among subpopulations
0	1	F	5	0	16, 14	0
0	1	M	2	0	10, 3	0
0	1	All	7	0	26, 17	0
1	2	F	6	0	6	0
1	2	M	3	0	3	0
1	2	All	9	0	9	0
2	3	F	9	0	9	0
2	3	M	3	0	3	0
2	3	All	12	0	12	0
x	x+1	F	521	8 (1.5%)	521	2 (0.4%)
x	x+1	M	66	0	66	0
x	x+1	All	587	8 (1.4%)	587	2 (0.3%)

Each opportunity is a pair of consecutive years where the summer/fall locations of animals in year x are compared with their locations in year x+1. Ages of animals are provided in the columns Age x and Age x+1. Ages for adults are generally unknown and are therefore not specified. Dispersal rates are listed at 2 scales: (1) the number annual individual summer/fall polygons in different composite summer ranges; (2) the number annual summer/fall polygons of individuals located in different subpopulations in the mountain caribou distribution. For calves (age x=0) sample size (n) differed for analyses among SFCR, versus the analysis among subpopulations.
[a]For calves (age x=0) the first sample size represents the number of calves observed until the start of their second summer (11 June), and the second n denotes the number of calves observed until the end of their second summer (21 October).

The lack of evidence for dispersal not only suggests that the patchy distribution of mountain caribou is unlikely functioning as a metapopulation but we also found that the level of fragmentation is greater than previously suggested by Wittmer et al. (2005a). The 18 subpopulations delineated by Wittmer et al. (2005a) have been useful for geographically closed censuses to document population size and trends (Hatter, 2006; McLellan, Serrouya & Furk, 2008), but they are misleading because populations that overlap geographically outside of the breeding season were grouped as one subpopulation despite the apparent reproductive isolation found in this study. For example, the Columbia North subpopulation, which was estimated to have 166 individuals in 2008 (McLellan et al., 2008), actually consists of five largely isolated SFCRs (review Table 2 for more examples). Our results suggest that half of the 18 subpopulations are likely an amalgamation of several distinct and reproductively isolated groups. According to our measure of fragmentation during the summer/fall season, there were 41 SFCR that functioned during the study period, hence the distribution is c. 2.3 times more fragmented than suggested by Wittmer et al. (2005a). Some of the SFCR were identified using few animals and may, after more sampling, be found to be connected to others. In particular, we expected that the larger subpopulations with a smaller proportion of the population radio-collared may not be as well defined by our methods compared with the smaller subpopulations with a higher proportion collared. Our sensitivity analyses supported this prediction. Two larger subpopulations (Hart Ranges and North Cariboo) had < 5% of the 2002 population size collared and, if we had collared more animals, would likely have had a different number of SFCR defined. There was a sufficient sample size of collared animals in most subpopulations to identify SFCR using our method and to conclude that mountain caribou distribution is more fragmented than thought previously.

While low sampling effort may have increased error in our estimation of the number of SFCRs in a few cases, it is unlikely to impact our conclusion that dispersal is uncommon. Low sampling generally results in an over-estimation of the true average level of fragmentation, which would inflate the chances of detecting dispersal. Hence, it is possible that the true dispersal rates are even lower than what we report, but such a bias, if it exists, would not alter our conclusion.

Although our results suggest little dispersal by mountain caribou during our study, these animals did, at one time, arrive from somewhere so population radiation must have occurred. Hinkes et al. (2005) described the dispersal of caribou in south-western Alaska in detail over a 20-year period and more generally over the past 150 years. Isolated populations of these Alaskan caribou amalgamated during range expansion coinciding with rapidly increasing population size (Hinkes et al., 2005). In particular, the Mulchatna caribou herd increased from 10 000 individuals in 1977 to 200 000 in 1996 and their range expanded enormously, likely due to a combination of depleted food and social stimulus, and engulfed other herds. Hinkes et al. (2005) postulate that

under optimal weather and predator conditions, extirpation and recolonization by expanding populations of caribou, or a form of metapopulation function, may occur with more than a century between population maximums. Similarly, Boulet et al. (2007) suggest that large, more migratory populations may be responsible for augmenting smaller, sedentary populations. In the past, mountain caribou may have radiated by greatly increasing the population size causing range expansion as was described for the Mulchatna caribou herd by Hinkes et al. (2005). However, with the amount of habitat change in southern areas (Wittmer et al., 2007), and a general decline of woodland caribou, this form of dispersal is unlikely to occur again.

The lack of dispersal and high levels of fragmentation that we recorded has considerable implications for the conservation of mountain caribou and other species of conservation concern that, through recent human activities, have isolated subpopulations that superficially appear to exist as a metapopulation but do not have the inherent dispersal behaviour for a classic metapopulation to function. One example from the same area that we studied caribou is the grizzly bear. Near the southern edge of their distribution, they too are found in small, isolated subpopulations (Proctor, McLellan & Strobeck, 2002). Although some subpopulations are gradually expanding their range (Schwartz et al., 2006), limited dispersal, particularly by females, (McLellan & Hovey, 2001; Proctor et al., 2002, 2005), has prevented them from recolonizing any of 30 patches that contained bears a century ago (Merriam, 1922), despite complete protection in the US since 1975. Wolves, on the other hand, disperse widely (Fritts, 1983; Lehman et al. 1992; Forbes & Boyd, 1997), possibly an adaptation to avoid inbreeding as unlike bears or caribou, wolves are territorial. This dispersal ability has allowed wolves to recolonize many patches of suitable habitat across western North America where they had been eliminated by predator control (Hayes & Gunson, 1995; Oakleaf et al., 2006).

Incorporating the metapopulation paradigm in conservation is likely appropriate for species with a naturally fragmented distribution but should be used more cautiously with species that were recently more uniformly distributed (Brown, 1971; Noon & McKelvey, 1996). Understanding mechanisms influencing dispersal may further indicate which species should be of greatest concern when they are reduced to isolated subpopulations. Reducing inbreeding (Pusey & Wolf, 1996; Saccheri et al., 1998; Keller & Waller, 2002) and reducing competition for resources and mates among related individuals (Hamilton & May, 1977; Waser, 1985) or a combination of both are the dominant hypotheses underlying the cause of animal dispersal. Animals that live in territories (e.g. wolves), small colonies (e.g. ground squirrels Spermophilus spp.) or extended family groups must disperse to avoid inbreeding or competing with relatives. These species more likely have inherent dispersal ability that enables them to exist in a functioning metapopulation. Species that have large ranges that overlap with many conspecifics (e.g. caribou or bears), or which breed in very large colonies, may not need to

disperse to reduce the probability of inbreeding or competing with relatives because they have the potential to mate and/or compete with many unrelated conspecifics (McLellan & Hovey, 2001). Such species likely suffer greater consequences as a result of habitat degradation.

With the lack of dispersal among declining mountain caribou subpopulations and even little movement among composite summer ranges, the implications for recovery are serious, because managers cannot rely on natural rescue. To maintain small subpopulations over the short term, population augmentation, as has been carried out successfully in the South Selkirk subpopulation that crosses the Canada/USA border, will be needed (Warren *et al*., 2002). Longer term restoration of conditions that encourage population growth and expansion among subpopulations should also be a management goal.

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