

Implications of body condition on the unsustainable predation rates of endangered mountain caribou

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Abstract Both top-down and bottom-up processes influence herbivore populations, and identifying dominant limiting factors is essential for applying effective conservation actions. Mountain caribou are an endangered ecotype of woodland caribou (*Rangifer tarandus caribou*) that have been declining, and unsustainable predation has been identified as the proximate cause. To investigate the role of poor nutrition, we examined the influence of sex, season, age class, and available suitable habitat (i.e., old-growth forest >140 years) per caribou on bone marrow fat content of caribou that died ($n = 79$). Sex was the only strong predictor of marrow fat. Males that died during and post rut

had lower marrow fat than females or males at other times of year. Old-growth abundance per caribou, season, and age class did not predict marrow fat. Caribou killed by predators did not have less marrow fat than those that died in accidents, suggesting that nutritionally stressed caribou were not foraging in less secure habitats or that predators selected nutritionally stressed individuals. Marrow fat in endangered and declining populations of mountain caribou was similar to caribou in other, more viable populations. Our results support previous research suggesting that observed population declines of mountain caribou are due to excessive predation that is not linked to body condition.

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Introduction

Population dynamics of herbivores are influenced both by their interactions with forage (bottom-up) and predators (top-down) and the relative importance of these limiting factors which likely vary over time (Meserve et al. 2003; Owen-Smith and Mills 2006). Recent studies that have concurrently evaluated both processes in populations of rare species have often found the proximate cause of population decline to be excessive predation (e.g., Sweitzer et al. 1997; Wittmer et al. 2005b). Evaluations of bottom-up processes for these populations, however, have relied on indirect proxy variables such as population density, climate, or amount of suitable habitat without direct body condition measurements of individuals, particularly of those that died. This is a concern because indirect variables measured at the population scale may not represent the

nutritional status of individuals that died or the possible interactions between body condition and predation risk that may have contributed to the death.

To maximize fitness, individuals must balance predation risk with securing adequate forage to meet nutritional demands (Owen-Smith 2002). Individuals may alter their use of space, increase vigilance, and change foraging patterns according to perceived risk of predation (Krebs 1980; Lima and Dill 1990). Nutritionally stressed individuals are expected to take increased risks to access food sources and may thus be disproportionately exposed to predation [referred to as predation-sensitive foraging (PSF) hypothesis] (Sinclair and Arcese 1995). In addition, predators may select more vulnerable individuals including those in poor condition (Parker and Lutich 1986; Mech et al. 2001; Smith et al. 2004; Bender et al. 2007). Therefore, an unsustainable predation rate may not eliminate the possibility of food being the ultimate factor limiting or even regulating the population, but is being expressed as an interaction of top-down and bottom-up processes. If a lack of food or inefficient foraging is compromising the condition of individuals and these are either making riskier foraging decisions (PSF) or are simply more vulnerable to predators, then a higher proportion of animals killed by predators should have compromised body conditions compared to surviving animals (Sinclair and Arcese 1995; Mech et al. 2001).

The decline of endangered mountain caribou (*Rangifer tarandus caribou*) found in southeastern British Columbia, Canada, appears primarily due to unsustainable predation rates and apparent competition (Holt 1977) is currently the hypothesis with most support (Seip 1992; Wittmer et al. 2005b, 2007). The mechanism underlying this hypothesis is that expanding early seral conditions caused by forest harvesting and, in some areas, forest fires, has led to increased numbers of other prey species such as moose (*Alces alces*) and deer (*Odocoileus* spp.) that thrive in early-seral habitats (Latham et al. 2011; Serrouya et al. 2011). More of these ungulates have resulted in a numerical response in predators such as wolves (*Canis lupus*) (Messier 1994) and cougars (*Puma concolor*), and more predators have led to greater encounter and kill rates of caribou (Latham et al. 2011). Because predator numbers depend on the abundance of other prey species than caribou, apparent competition can cause the extinction of caribou, as their decline has little or no feedback to predator numbers. This ecological pathway leading to population decline and extirpation appears common with other ecotypes of woodland caribou when early seral conditions have increased (e.g., Bergerud and Elliot 1986; Stuart-Smith et al. 1997; Schaefer et al. 1999; Latham et al. 2011).

Mountain caribou also depend on old-growth (i.e., >140-year-old) conifer forests to meet nutritional

requirements throughout much of the year (Terry et al. 2000; Apps et al. 2001), and large reductions of old forest stands from logging may have compromised their ability to meet these needs. Observed high predation rates may thus simply mask nutritional deficiencies and potential bottom-up limiting factors that could result in prescription of ineffective recovery strategies (Brown et al. 2007). Wittmer et al. (2005b) tested the food regulation and PSF hypotheses as causes of mountain caribou declines. The authors rejected these hypotheses because: (1) predation was the primary cause of mortality and most caribou died in summer and fall when food was relatively abundant; (2) pregnancy rates were high in all populations; and (3) population rates of increase were positively related to the density of caribou. Brown et al. (2007), however, speculated that forage quantity and/or quality on summer and fall ranges may now be insufficient for individual females to maintain body condition needed to avoid predators or for their calves to gain sufficient mass to survive the following winter. They suggested that the data of Wittmer et al. (2005b) were insufficient to properly evaluate the PSF hypothesis without also incorporating information on seasonal forage quality and availability plus plane of nutrition of these endangered animals.

In this study, we determine whether low body condition increases the likelihood that individual mountain caribou died from predation. We also examine whether the per capita availability of old-growth forest affected their body condition at time of death. More generally, we use information on the nutritional status of individuals that died to test for interactions between bottom-up and top-down mechanisms that affect the status of this endangered herbivore.

For our analyses, we rely on the fat content of bone marrow from animals that died from a variety of causes and at various times of the year. The commonly accepted belief that during periods of food shortage animals first deplete subcutaneous fat, followed by visceral fat, and finally, when all other fat deposits are exhausted, bone marrow deposits are mobilized is an oversimplification (Parker 2003). Subcutaneous reserves are not exhausted before marrow deposits are mobilized (Cederlund et al. 1989; Parker 2003). In caribou, the relationship between marrow fat and body fat is linear below about 9% body fat, but poorly related at higher body fat levels that reach a maximum of 17% in non-reproductive caribou in September (Allay Chan-McLeod et al. 1995, 1999). Unlike other body fat measures, bone marrow fat samples can be taken from animals that have been mostly consumed. Bone marrow fat deposits are thus well suited to test the hypothesis that caribou killed by predators are in worse nutritional condition than the living population.

Several confounding factors, however, may affect bone marrow fat content of caribou, particularly from those that

were not sampled randomly but found dead, and we first investigated these factors. First, we expect adult males that died during or shortly after the rut would have low bone marrow fat content (Skoog 1968; Cederlund et al. 1989; Mech et al. 1995). Second, we expect young and very old animals to have lower bone marrow fat levels than prime-aged animals (Parker 1981; Kojola et al. 1998). Third, animals that appeared to die of malnutrition should have the lowest bone marrow fat content. Fourth, we test the hypothesis that there is an interaction between top-down and bottom-up limiting factors, either because caribou in poor body condition forage in risky locations (PSF hypothesis) or simply because predators select prey in compromised body condition. We predicted caribou killed by predators would have lower bone marrow fat content than those killed in accidents such as avalanches and collisions with vehicles, that we assumed would represent the living population. Finally, it remains possible, that mountain caribou in general have compromised condition, so we also compare our measurements to other, more viable caribou populations.

Materials and methods

Study area

Our study area spanned the distribution of mountain caribou in the interior wet-belt of British Columbia between the USA–Canada border at Idaho to the Hart Ranges northeast of Prince George (49°–55°N) and included 10 of the 16 remaining subpopulations (Wittmer et al. 2005a; van Oort et al. 2011). The distribution of the 10 subpopulations included here covers an area of about 150,000 km², but caribou are largely confined to approximately 30,000 km² within this area. The topography of subpopulation ranges is mountainous with elevation ranging from 350 to 3,500 m. High precipitation and infrequent forest fires result in wet, largely old-growth-dominated forests. Lower elevations of the study area are in the Interior Cedar Hemlock (ICH) zone in the southern portion and the Sub-Boreal Spruce (SBS) zone in the north (Meidinger and Pojar 1991). Throughout the caribou range, mid-elevations are dominated by the Engelmann Spruce–Subalpine Fir zone (ESSF) and high elevation habitat extends into the Alpine Tundra zone (AT). High-elevation caribou late winter range occurs near tree line (>1,800 m) usually on more gently sloping plateaus and ridges where subalpine fir (*Abies lasiocarpa*) grows in patches (Terry et al. 2000; Apps et al. 2001). Forestry has been the primary human land use activity across the study area for the last 50 years.

Between 1984 and 2009, 541 mountain caribou were captured using a net gun from a helicopter during late

winter when >85% of caribou were in subalpine forests where they are readily visible from the air and easily captured on the deep snowpack (Wittmer et al. 2005a). Animals were captured across their entire remaining distribution in British Columbia. Capture teams determined the sex and approximate age of the sampled animals and fitted them with VHF radiocollars with mortality sensitivity. Due to concerns about the negative impacts of tooth extractions (Festa-Bianchet et al. 2002), teeth were not removed from these endangered herbivores during capture so accurate ages determined by cementum annuli (Mattson's Lab, Milltown, Montana) were only available for dead animals whose teeth were found. Caribou were captured using approved provincial animal care capture protocols.

Age and cause of death

Radiocollared animals were located from fixed-wing aircraft and their status assessed approximately every 2 weeks. Stationary collars were investigated as soon as possible. Cause of death was categorized as accident, malnutrition, predation, non-predation but cause unknown, or unknown. Accidents included collisions with vehicles or trains, avalanches, plus more obscure events such as falls or being struck by falling trees. Predation was differentiated from scavenging by oxygenated blood in the snowpack, on the ground, foliage or radiocollar, or sign of a struggle, bite wounds, position of carcass, and the presence of predators and scavengers. Non-predation but cause unknown was where the caribou was not killed by predators but the cause of death was uncertain. When there was insufficient evidence to tell if the caribou was killed by a predator or scavenged, the death was recorded as unknown cause. Cause of death was classified as malnutrition if the animal did not appear to be killed by a predator or accident but a necropsy suggested that it was emaciated. We did not use marrow fat values to determine cause of death. In addition to dead collared caribou, we included marrow samples from caribou killed by vehicles and those killed by radiocollared predators. Sex and age estimates of these animals were recorded when possible, and age was classified into three groups relative to female reproductive status (Adams and Dale 1998): yearlings (1–2 years), prime adults (3–12 years), and old adults (>12 years).

Season and available old-growth in caribou range

Forest age was extracted from the British Columbia 1:20,000 forest inventory data (Resources Inventory Branch 1995) and 1:20,000 vegetation resources inventory data (Ministry of Sustainable Resource Management 2002). The amount of old-growth (>140 years) forest available per caribou was estimated by the amount of

old-growth within the 95% cumulative kernel home range determined from all radio-locations from all collared caribou in each subpopulation (see Wittmer et al. 2005b for details) divided by the estimated number of caribou in the subpopulation in 2002 (van Oort et al. 2011). In the case of caribou within the Hart Ranges, all marrow samples were collected from a portion of the subpopulation (i.e., the Parsnip Herd), and therefore we adjusted the amount of old forest and population size for the reduced sampling area.

Seasons were derived from mountain caribou foraging strategies in the Columbia Mountains (Apps et al. 2001) and were classified as: Summer (SU) 21 May–21 October, early winter (EW) 22 October–11 January, late winter (LW) 12 January–23 April, and spring (SP) 24 April–20 May.

Animal condition and marrow extraction

Whenever possible, one or both femurs were collected at mortality sites, but sometimes femurs had been broken or removed and other long bones were collected. We followed the methods of Neiland (1970) to determine marrow fat content. No correction was made for mineral residue (Davis et al. 1987). In cases where more than one femur bone per individual was analyzed, the average value was used for the sample value. We converted bone marrow fat proportions from bones other than femurs to a femur standard following Davis et al. (1987).

Statistical analyses

We conducted two analyses. First, we selected four predictor variables that potentially influence body condition in caribou: sex (SEX), age class (AGE_CL), season (SEASON) and available old-growth (i.e., old-growth per caribou: PC_OLDGR) and used linear mixed effects models to identify their independent, cumulative, and interactive relationships with bone marrow fat of dead caribou. We used a generalized linear model with marrow fat (arcsine-transformed) as the dependent variable. Pseudo-replication was avoided by specifying which subpopulation caribou were from as a random effect (random intercept and fixed slope). We then used an information theoretic approach with a conditional Akaike Information Criterion corrected for small sample size (AIC_c) to rank a set of 11 a priori candidate models based on the above predictor variables (Burnham and Anderson 2002). We compared the selected best model and the other candidate models using AIC_c differences (Δ_i) and Akaike weights (ω_i) (Burnham and Anderson 2002). The fit of the best model was evaluated by plotting observed data against the predicted results.

Our second analysis was to investigate relationships between marrow fat and cause of death. Here, we used

ANOVA and then orthogonal contrasts for our a priori hypotheses: (1) bone marrow fat of caribou with deaths attributed to malnutrition was lower than those that died from predation, accident, unknown or unknown causes that are not predation; and (2) caribou that died from predation had lower marrow fat than those that died from accidents (i.e., the PSF hypothesis). We used bootstrapping to estimate 95% CIs. Analyses were performed using R (R Development Core Team 2010).

Results

Between 1984 and 2010, bone marrow samples were collected from 67 radiocollared caribou, 8 animals killed in vehicle or train collisions, 3 that were killed by radiocollared predators, and 1 dead caribou found opportunistically (Table 1). Samples included 68 femurs, 5 humeri, 2 radiuses, 3 tibias, and 1 mandible. Three caribou femurs from animals with unknown sex were excluded from model selection analyses but were used for cause of death analysis.

Of the models used to predict bone marrow fat in mountain caribou, SEX alone was the strongest candidate model having an AIC weight of 0.86 with all other models ranked 0.01 or less (Table 2; Fig. 1). The parameter estimates for the best model (SEX) was -0.42 (SE 0.11, $p = 0.003$) for males in the rut, and 0.07 (SE 0.13, $p = 0.583$) for males, with females as the reference category. This result was because males had much less marrow fat than other caribou in the early winter that included the rut and post-rut period (Table 1; Fig. 1). When we excluded males that died during the rut, the null model had most support (Table 3), indicating that neither sex, age class, season nor the amount of old forest available per caribou were useful predictors of bone marrow fat. The mean amount of marrow fat by subpopulation, ranged from 41% ($n = 6$, 95% CI 22–63) in the Hart Ranges to 87% ($n = 3$, 95% CI 85–89) in the Frisby–Boulder subpopulation (Fig. 1), although the per capita old growth availability within each subpopulation was not supported as a predictor of marrow fat (Table 3).

Because rutting males that died had less than half the marrow fat of other dead caribou, these males were excluded from cause of death analyses and all data were pooled regardless of sex, season of death, and age of death. Cause of death was a significant predictor of bone marrow fat ($F_{4,65} = 8.03$, $p < 0.0001$). Caribou with a death attributed to malnutrition had lower average marrow fat ($\bar{x} = 20.1\%$, $n = 7$, 95% CI 9.5–30.5) than caribou that died from accidents ($\bar{x} = 73.7\%$, $n = 20$, 95% CI 69–80), predation ($\bar{x} = 68.7\%$, $n = 27$, 95% CI 58–78), unknown causes ($\bar{x} = 66.4\%$, $n = 12$, 95% CI 50–75), and unknown

Table 1 Mean femur marrow fat (%) from mountain caribou (*Rangifer tarandus caribou*) found dead in southeastern British Columbia between 1993 and 2009 in relation to sex, season, and cause of death (*n*, 95% CI)

Season	Sex	Cause of death					Total
		Accident	Malnutrition	Predation	Unknown	Unknown-not predation ^b	
Early winter	F	75 (2, 56–93)	16 (2, 12–19)	59 (6, 34–75)	57 (4, 26–74)	79 (2, 76–82)	58 (16, 41–71)
	M	30 (6, 26–39)		27 (2, 18–36)	42 (1)		31 (9, 24–37)
Late winter	F	79 (8, 70–85)	7 (1)	79 (3, 71–85)	89 (1)		74 (13, 56–83)
	M	63 (1)					63 (1)
Spring	F	68 (3, 44–84)		73 (1)	69 (2, 63–75)		69 (6, 58–77)
	M	73 (1)				73 (1)	73 (2, 73–73)
Summer	F	65 (3, 38–83)	25 ^a (4, 10–51)	70 (13, 56–82)	75 (3, 42–97)	78 (3, 64–87)	64 (26, 53–75)
	M	87 (1)		90 (1)	49 (1)		75 (3, 49–90)
Total	F	74 (16, 65–80)	20 ^a (7, 10–36)	69 (23, 57–79)	68 (10, 52–81)	79 (5, 72–85)	65 (61, 59–72)
	M	45 (9, 30–60)		48 (3, 18–90)	46 (2, 42–49)	73 (1)	48 (15, 35–60)

^a Includes one caribou that had 65% marrow fat and was 16 years old

^b The cause of death was not predation but otherwise unknown

Table 2 Top models using linear mixed effect models to predict caribou femur marrow fat, with caribou subpopulation as the random effect; models sorted by increasing Akaike information criteria (AIC_c); only models with ΔAIC_c < 10 included

Model ^a	AIC _c	<i>k</i>	Log(L)	ΔAIC _c	AIC _c ω
SEX	54.62	5	−21.88	0	0.86
Null model	58.94	3		4.32	0.10
SEX + AGE_CL	63.13	7	−23.74	8.51	0.01
SEX + PC_OLDGR	63.46	6	−25.12	8.84	0.01

^a SEX includes males, females and males in the rut; age class (AGE_CL) consists of either juvenile (1–2 year) adults (3–13 years), and old (13+ years); per capita old growth (PC_OLDGR) is the amount of old growth within an animal’s subpopulation divided by the number of caribou in that subpopulation

AIC_c Akaike units corrected for small sample size, *k* number of parameters, Log(L) maximized log likelihood function, ΔAIC_c difference in AICc units between the top model and the model of interest, AIC_cω are Akaike weights

causes that were not predation ($\bar{x} = 77.6\%$, $n = 6$, 95% CI 70–84; all $p < 0.0001$; Table 1). One 16-year-old caribou with a death attributed to malnutrition had 68% marrow fat. The apparent emaciation of this animal may have been due to age. When this animal is excluded, the average marrow fat of caribou with deaths attributed to malnutrition was 12.6%. There was no significant difference in marrow fat among caribou killed by predators and those that died in accidents ($F_{1,65} = 0.424$, $p = 0.517$) or by unknown and unknown but not predation causes ($F_{1,65} = 0.316$, $p = 0.576$; Table 1). Bone marrow fat contents from animals dying from vehicle collisions ($\bar{x} = 71\%$, $n = 4$, 95% CI 62–84) were also not different from all other animals whose deaths were attributed to accidents ($\bar{x} = 74\%$, $n = 10$, 95% CI 66–84).

Discussion

The development of suitable conservation strategies for endangered species depends on the identification of the underlying causes of observed population declines (Caughley 1994). Results from this and previous studies on the ecology of endangered mountain caribou (Wittmer et al. 2005b, 2007) highlight the importance of considering bottom-up nutritional effects simultaneously with possible top-down effects. Based on these results, we conclude that food limitation is unlikely to be the cause for the dramatic declines of mountain caribou across their range in British Columbia.

Our objective was to use bone marrow fat content from animals that died to examine whether the decline of mountain caribou was exacerbated by poor body condition. We found that bone marrow fat content was sufficiently sensitive to detect compromised body condition of rutting males and clearly identified animals whose death was attributed to poor nutrition. Our results, however, did not reveal patterns suggesting compromised body condition. Sex was the only a priori factor that predicted marrow fat, and it was due to rutting males, a result that is consistent with other studies (Skoog 1968; Cederlund et al. 1989; Mech et al. 1995). Our limited samples from males suggest that their bone marrow fat content recovered over late winter, spring, and through the summer.

Old-growth forests are selected by caribou in every season and are critical in winter because arboreal lichens are most abundant in these stands (Servheen and Lyon 1989; Terry et al. 2000; Apps et al. 2001). The amount of old growth forest per caribou, however, did not predict the bone marrow fat content of animals that died. One-third of the range of the Columbia South subpopulation of caribou

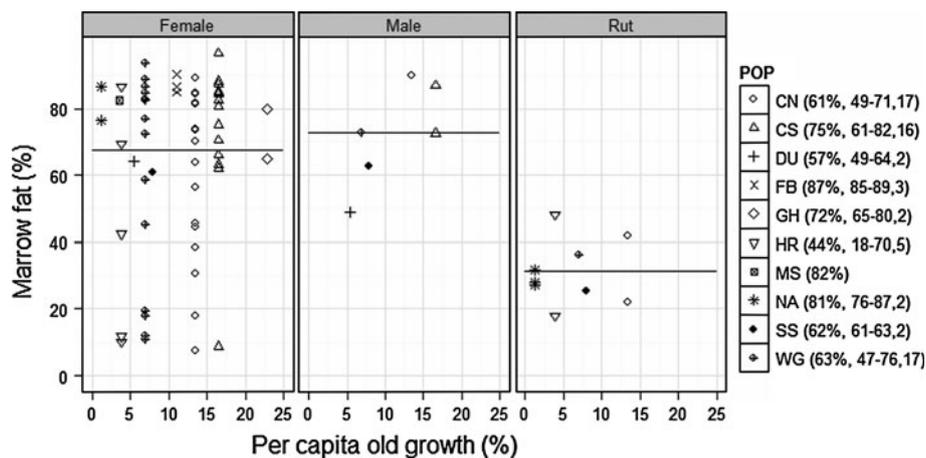


Fig. 1 The relationship between marrow fat of mountain caribou (*Rangifer tarandus caribou*) partitioned by sex (female, males, males in rut) and per capita available old growth. The mean marrow fat by subpopulation shown in the legend excludes 9 males in the rut (\bar{x} , 95% CI, n). Analysis were done with arcsine transformed data and presented here as percent values. Horizontal line represents the top

Table 3 Top models using linear mixed effect models to predict caribou femur marrow fat, with caribou subpopulation as the random effect

Model	AIC _c	<i>k</i>	Log(L)	ΔAIC _c	AIC _c ^ω
Null model	48.78	3		0	0.86
SEX	52.91	4	-22.13	4.13	0.11
AGE_CL	57.02	5	-23.02	8.24	0.01
PC_OLDGR	57.54	4	-24.45	8.76	0.01

SEX includes males, females and males in the rut; age class (AGE_CL) consists of either juvenile (1–2 years) adults (3–13 years), and old (13+ years); per capita old growth (PC_OLDGR) is the amount of old growth within an animal's subpopulation divided by the number of caribou in that subpopulation

Males in the rut were excluded from this analysis. Models sorted by increasing Akaike information criteria (AIC_c). Only models with ΔAIC_c < 10 included

AIC_c Akaike units corrected for small sample size, *k* number of parameters, log(L) maximized log likelihood function, ΔAIC_c difference in AIC_c units between the top model and the model of interest, AIC_c^ω are Akaike weights

includes two National Parks where there has been no logging, and these animals had relatively high bone marrow fat but still experienced one of the fastest rates of decline (Wittmer et al. 2005a; Serrouya and Wittmer 2010). Similarly, Wittmer et al. (2005b) found that the per capita rate of increase was positively related to caribou density in suitable, old-growth habitat, or populations with more old-growth per caribou are decreasing fastest. These results, when combined with the rates of population decline even within protected areas, suggest that caribou are not being directly regulated by the amount of old-growth forest through food availability.

model prediction from Table 2 using Wells Gray (WG) as the reference population. POP is the mountain caribou subpopulations defined by Wittmer et al. (2005a); CN (Columbia North), CS (Columbia South), DU (Duncan), FB (Frisby-Boulder), GH (Groundhog), HR (Hart ranges), MS (Monashee South), NA (Nakusp), SS (South Selkirks), WG (Wells Gray)

An interaction between top-down and bottom-up processes such as the PSF hypothesis predicts a disproportionate number of animals killed by predators would be in poor enough condition for them to make risky decisions (Sinclair and Arcese 1995), particularly during summer and fall when most predation occurs (Wittmer et al. 2005a, b; Brown et al. 2007). Obtaining adequate nutrition during summer is important because lactation demands are high (Parker et al. 2009), and there are additional demands of molt, antler growth, and replenishing body reserves for reproduction and the upcoming winter. Indeed, adult females in some large migratory herds gain little or even lose body fat during summer (Allaye Chan-McLeod 1999; Couturier et al. 2009) due to density-dependent competition on heavily grazed ranges (Crête and Huot 1993). Because the marrow fat content of animals killed by predators was similar to those that were killed in accidents or other causes, this hypothesis was not supported.

It is possible that most mountain caribou are in poor condition and that is why we found little difference among those killed by various causes. Average bone marrow fat content of female caribou killed by wolves in Denali National Park during winter (66%) and summer/fall (71%; Mech et al. 1995) was similar to females killed from all causes excluding malnutrition in our study (71% both seasons). During the rut, the 7 males killed by wolves in Denali averaged 24% bone marrow fat while 9 males averaged 30% in this study. Similarly, femur fat of female barren-ground caribou collected over the year averaged 69% (Allaye Chan-McLeod et al. 1995) and 52% for all ages and both sexes collected mostly during winter in Alaska (Davis et al. 1987). Two-year-old and adult females from the Qamanirjuaq herd had average marrow fat of 55

and 66%, respectively, in April, while the same aged females also collected in April from the George River herd had 82 and 88% marrow fat, respectively, when that population was rapidly increasing in 1980 (Parker 1981). Given the constraints on bone marrow fat to detect animals with high body fat, these comparisons suggest that mountain caribou have similar marrow fat values as other, much more viable, caribou populations.

Combining our results on the bone marrow fat content of mountain caribou with the results of Wittmer et al. (2005b) on pregnancy rates, cause, and timing of deaths, and the relationship of population trend with respect to old-growth forests and longer term trends of mountain caribou and moose populations (Spalding 2000), suggests continued support for the apparent competition hypothesis over food regulation or predation-sensitive foraging. Concluding that apparent competition is the mechanism of decline does not indicate that there are no “bottom-up” effects (Brown et al. 2007). There are always stochastic, density-independent limiting factors that affect access to food (Sæther 1997; Gaillard et al. 1998), particularly in rugged mountains with heavy snowfall and perhaps even during summer, even though at that time of year caribou can disperse widely across the extensive subalpine and alpine meadows in wet-belt ecosystems of British Columbia. Early writings describe groups of many hundreds, and in some cases over a thousand caribou observed, suggesting much larger historic populations compared to today where the largest of 5,565 groups seen over the past 20 years was 62 animals (Spalding 2000; McLellan et al. 2010). Stochastic factors would have affected the much larger populations of caribou that recently lived in these mountains just as they affect the <20 animals found on most of these ranges today. But a general reduction of food or decline in quality is unlikely the major cause of the continued mountain caribou declines.

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