

Conditions for caribou persistence in the wolf-elk-caribou systems of the Canadian Rockies

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Abstract: Woodland caribou populations are considered threatened in Alberta and have declined in the Canadian Rocky Mountain National Parks of Banff and Jasper despite protection from factors causing caribou populations to decline outside of parks. Recent research emphasizes the importance of the numeric response of wolves to moose in moose-caribou-wolf systems to caribou persistence. Moose are rare in the Canadian Rockies, where the dominant ungulate prey for wolves is elk. Few studies have explored wolf-elk dynamics and none have examined implications for caribou. We used data collected in Banff to estimate the numeric response of wolves to elk from 1985 to 2005. Because no caribou kill-rate data exist for the Rockies, we explore the consequences of a range of hypothetical kill-rates based on kill-rates of alternate prey collected from 1985 to 2000 in Banff. We then multiplied the numeric response of wolves by the estimated caribou kill-rates to estimate the wolf predation response on caribou as a function of elk density. Caribou predation rates were inversely density dependent because wolf numbers depend on prey species besides caribou in multiple prey species systems. We then combined this simple wolf-elk-caribou model with observed demographic and population estimates for Banff and Jasper caribou from 2003-2004 and solved for the critical kill-rate thresholds above which caribou populations would decline. Using these critical kill-rate thresholds, Jasper caribou are likely to persist when wolf densities are below 2.1 - 4.3 wolves/1000km² and/or when elk densities are below 0.015- 0.033 elk/km². Thresholds for Banff caribou persistence are much lower because of inverse density dependence. Future research is needed on some of the necessary assumptions underlying our modeling including multi-prey wolf numeric responses, wolf kill-rates of caribou, caribou mortality by other predators, and spatial aspects of wolf-elk-caribou dynamics.

Key words: ecosystem management, endangered species, inverse density dependence, long-term range of variation, park management, predation, species at risk.

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Introduction

Common causes of species endangerment include habitat loss, fragmentation or alteration, over-hunting, and competition by invasive species, all of which can alter trophic relationships (Sinclair & Byrom, 2006). Where changes to trophic dynamics occur, predator-prey theory has been useful to understand the mechanisms causing declines and strategies to reverse them (Sinclair & Byrom 2006). For example, endangered species are often an alternate prey for an introduced or native predator (Sinclair *et al.*, 1998). Where ecosystem changes increase primary prey density, predation rates can increase to the point where

endangered alternate prey can be driven to extinction (Sinclair *et al.*, 1998; Roemer *et al.*, 2002). A brief review of predator-prey theory for alternate prey reveals why.

Prey density influences both kill-rates (the functional response) and densities (the numeric response) of predators (Holling, 1959, Fig. 1). In single predator-prey systems, the functional response type (Fig. 1) determines whether predators regulate prey to low density (type II) or whether a high-density equilibrium is also possible (type III) (Messier, 1994). In single predator-prey systems predators can't drive

prey extinct because predator density declines with declining prey density. In multi-prey systems, however, predator density can remain high as alternate prey decline because of primary prey (i.e., the numeric response of predators to alternate prey has a positive Y-intercept, Fig. 1, Messier, 1995). The consequences of combining a type II or III functional response with a numeric response with and without a Y-intercept for an alternate prey species are shown in Fig. 1 (from Messier, 1995). Fig. 1a illustrates predation that is inversely density dependent for the type II functional response with, but not without, a Y-intercept. As alternate prey decline, predators kill a higher percentage of the alternate prey population, triggering further declines. Thus, alternate prey density must stay above a critical density (P) for the population to persist (Sinclair *et al.*, 1998). Fig. 1b shows that for a type III functional response, there exists some low-density threshold (P^*) below which the total predation rate is density dependent. This implies a low-density state for alternate prey at P^* is possible. Both illustrate that given a Y-intercept, once alternate prey species decline past some threshold, regardless of the functional response type, further population declines are likely.

Woodland caribou (*Rangifer tarandus caribou*) are an endangered alternate prey species most frequently found in moose (*Alces alces*)-caribou-wolf (*Canis lupus*) systems throughout the boreal forests and western mountains of Canada (COSEWIC, 2002). Classified as threatened under the Species at Risk Act (SARA) (COSEWIC, 2002), caribou are thought to be declining throughout their range because of anthropogenic activities that are altering predator-prey dynamics (COSEWIC, 2002; McLoughlin *et al.*, 2003; Wittmer *et al.*, 2005a,b). Among the main factors is commercial forestry that converts old forests to early seral habitats, which support higher moose densities (Bergerud, 1988; Seip, 1992). Because of the strong numeric response of wolves to ungulate prey (Fuller, 1989), logging is thought to increase wolf density and thus predation rates on caribou. Anthropogenic activities have also been hypothesized to increase the functional response by increasing the effective rate of search and hence kill-rates for caribou. Seismic exploration lines, paved roads, and compacted snow trails have all been linked to increased movement by wolves (James & Stuart-Smith, 2000; Whittington, *et al.*, 2005), but despite the potential for increased predator efficiency, effects on population dynamics of caribou are uncertain. Focusing on population dynamics, Wittmer *et al.* (2005b) found inverse density dependence in predation mortality for woodland caribou in British Columbia, consistent with a type II functional response combined with a numeric response with a

Y-intercept driven by increased densities of moose (Fig. 1a) (Messier, 1995). Under these conditions, caribou extinction below a critical population threshold is theoretically certain, regardless of changes to predator efficiency (Lessard, 2005).

While these mechanisms explain declines of woodland caribou outside protected areas, recent caribou declines in Banff and Jasper National Parks in the Canadian Rockies are puzzling. Anthropogenic activities such as forestry or oil and gas exploration do not occur within parks, yet caribou populations have declined since the mid 1980s paralleling provincial declines (Alberta Caribou Recovery Team, 2005, Parks Canada, unpubl. data). Furthermore, caribou in the Canadian Rockies exist in a wolf-elk (*Cervus elaphus*)-caribou system (Hebblewhite *et al.*, 2004), not in the more common moose-wolf-caribou system of the boreal and mountain caribou populations. Although wolf-elk dynamics have been studied in the Rockies (Hebblewhite *et al.*, 2004), they have received nowhere near the detailed study of moose-wolf dynamics (e.g. Messier, 1994). Thus it is uncertain whether results of wolf-moose-caribou studies can apply to the Canadian Rockies.

The purpose of this paper is to combine previous wolf-elk research with current caribou demography to understand conditions for caribou persistence in the Canadian Rockies. First, we modeled the numeric response of wolves to changing elk density using a 20-year time-series from a wolf-elk system overlapping the Banff caribou population (Hebblewhite *et al.*, 2002). Unfortunately, kill-rate data were unavailable to estimate the functional response of wolves preying on caribou. Instead, we varied kill-rates over a plausible range to explore the consequences of variation in caribou kill-rates on total predation rates for a given wolf and elk density. Finally, we compared the range of modeled caribou predation rates to observed caribou demographic data from Jasper for 2003-2004. By varying kill-rate and predation rate, we solved for the critical elk (and hence wolf) density above which present caribou populations in Banff and Jasper would decline (Sinclair *et al.*, 1998).

Study area

The study area was along the eastern slopes of the Canadian Rockies in Banff and Jasper National Parks (Banff and Jasper hereafter, Fig. 2) in the province of Alberta (AB) and a small adjacent area of British Columbia (BC). Topography is extreme, ranging from 1000 m to 3500 m in elevation, and climate is characterized by long, cold winters, and short summers with most precipitation occurring in spring. Banff is 6641 km² and Jasper is 10 500 km² in area. The land-

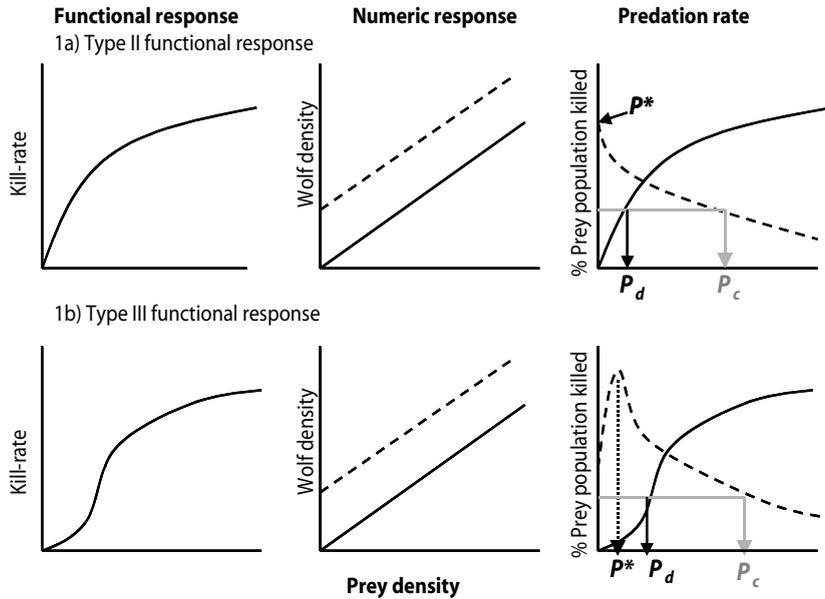


Fig. 1. Functional responses, numeric responses, and predation rates for a) type II and b) type III functional responses with (dashed line) and without (solid line) a numeric response with a Y-intercept, for a multiple prey system. For a given predation rate, some prey populations have a critical density below which their population will decline to extinction. Without a Y-intercept, the prey population is regulated to some low density, P_d , for a given critical % mortality rate (grey line). In the presence of a Y-intercept, however, predation rate is inversely density dependent, and for a given critical % mortality rate, P_c , prey density P^* declines to extinction under type II functional response, or a very low density in the presence of a type III functional response. Adapted from Messier (1994, 1995) and Dale *et al.* (1994).

scape is ecologically classified into the montane, subalpine, and alpine ecoregions (Holland & Coen, 1983). The montane ecoregion occurs in low elevation valley bottoms, contains the highest quality habitat for wolves and elk, and is characterized by lodgepole pine (*Pinus contorta*) and Douglas-fir (*Pseudotsuga menziesii*) forests interspersed with riparian white spruce (*Picea glauca*) – willow (*Salix* spp.) areas, aspen (*Populus tremuloides*) – parkland, and grassland systems. Sub-alpine and alpine ecoregions are comprised of Engelmann spruce (*Picea engelmannii*) – subalpine fir (*Abies lasiocarpa*) – lodgepole pine forest interspersed with willow-shrub meadow riparian communities, subalpine grasslands, and avalanche terrain, giving way to open shrub-forb meadows in the alpine ecoregion. In south Jasper and Banff, caribou seasonally migrate between alpine and subalpine ecoregions in the summer and winter, respectively. Elk migrate seasonally between the montane and alpine ecoregions in the summer. Wolves are the primary predator of elk, and other alternate prey species include white-tailed deer (*Odocoileus virginianus*), mule deer (*Odocoileus hemionus*), moose, bighorn sheep (*Ovis canadensis*), and mountain goats (*Oreamnos americanus*). See Holland &

Coen (1983) and Holroyd & Van Tighem (1983) for a more detailed description of the study area.

Caribou occur in four separate sub-populations in the Canadian Rockies National Parks: one in northern Banff, one in northern Jasper, and two in southern Jasper (Fig. 2) (Alberta Woodland Caribou Recovery Team, 2005). Caribou occurring in northern Jasper (the A La Peche sub-population) migrate to winter range in the province of AB and their conservation is considered elsewhere (Smith 2004; Alberta Woodland Caribou Recovery Team, 2005). The North Banff sub-population is very small (approximately five animals) and has much lower genetic variability than the two larger south Jasper sub-populations (Parks Canada, unpubl. data). Historically, it was assumed caribou moved between the Banff and Jasper populations and adjacent provincial populations, but dispersal between subpopulations has never been confirmed (Parks Canada, unpubl. data). From a Parks Canada management perspective, management of the Jasper and Banff herds are considered part of the Alberta recovery strategy (Alberta Woodland Caribou Recovery Team, 2005), and action plans for caribou recovery are presently being developed in Jasper and Banff (Van Tighem *et al.*, 2005).

Methods

Numeric response

We estimated the numeric response of wolves to only their primary prey, elk, in a study area for which wolf and elk densities were recorded from 1987-2005 in only the Bow Valley study area (Fig. 2). Wolf numbers were assumed to respond only to the density of their primary prey, elk, not alternate prey. This approach was used instead of using a wolf- total ungulate biomass equation (Fuller, 1989) for the following reasons; 1) wolf abundance in Canadian Rockies is largely driven by elk density (Hebblewhite, 2000), 2) wolves in the Rockies are highly selective for elk (Huggard, 1993), and other studies confirmed the density of preferred prey strongly influences the multi-species wolf numeric response (Dale *et al.*, 1995, Mech *et al.*, 1998); and 3) the rugged terrain of the Rockies allows strong spatial separation of some relatively abundant secondary prey species (e.g., bighorn sheep) from elk (Holroyd & Van

Tigham, 1983), limiting their influence on wolf numbers (e.g., Dale *et al.*, 1995; Mech *et al.*, 1998). Poor model fit between elk and wolf density would invalidate these assumptions and suggest alternate prey density should be included.

We defined the Bow Valley study area for 1985-2005 using the 100% minimum convex polygon (MCP) of all locations from 3 wolf packs. We estimated wolf numbers within this area following Hebblewhite *et al.* (2002), and elk density using aerial surveys during late winter (Hebblewhite *et al.*, 2002). We only considered elk west of the Banff townsite available to wolves, because Hebblewhite *et al.* (2002) showed Banff townsite elk were regulated by food, not wolf predation, and were generally unavailable to wolves. We corrected for incomplete sightability of elk following an aerial sightability adjustment of 87% developed by Hebblewhite (2000). We then estimated the numeric response of wolf density (reported in wolves/1000km²) to elk density by fitting linear and non-linear (type II and III) regression using least-squares in STATA (StataCorp, 2003). The highest-ranking model was selected using AIC_c (Burnham & Anderson, 1998).

Functional response - kill-rate variation

In the absence of caribou kill-rates, we selected a realistic range of alternate prey kill-rates to explore the consequences for caribou dynamics. We evaluated the effects of caribou kill-rates from 0 to 0.01 caribou/day/wolf (~0 to 13 caribou/pack/ 181 day winter). For comparison, these were close to observed kill-rates for the next rarest prey species, moose (Hebblewhite *et al.*, 2004).

Total predation response

We multiplied the number of wolves predicted by the numeric response (as a function of elk density) by the range of hypothetical caribou kill-rates to predict the total number of caribou killed per unit time. We then calculated the proportion of the total caribou population killed per winter (i.e., mortality rate) as a function of the Banff and Jasper caribou densities (see below) following:

$$(eq. 1) \quad M_{ww} = \frac{D_w K}{D_c}$$

where M_{ww} is the wolf-caused winter mortality rate, D_w is the wolf density as predicted from the numeric response to elk density, K is the caribou kill rate per wolf, and D_c is the caribou density.

Caribou demography and population size

We evaluated the effects of the mortality rates from eq. 1 on caribou population growth rate given demography for the south Jasper sub-population (not Banff

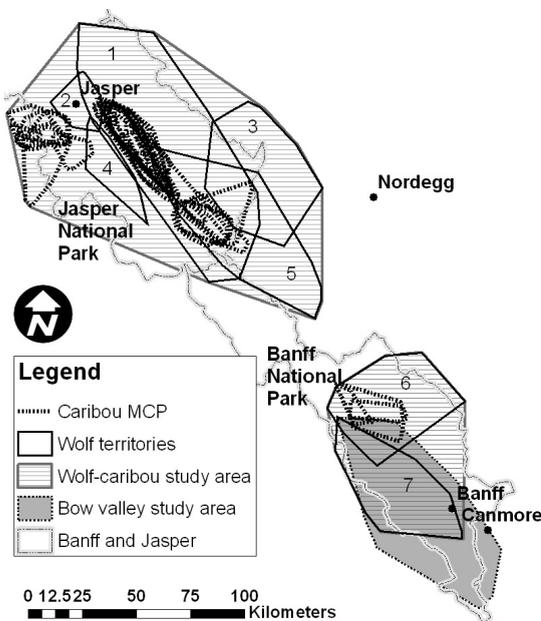


Fig. 2. Study area location in western Canada (see inset) showing annual winter home ranges for caribou (dashed) and multi-annual winter wolf territories (solid), respectively, from 2003 - 2004 in Banff National Park (Banff) and southern Jasper National Park (Jasper), Alberta, Canada. Cross-hatched areas are the Banff and Jasper wolf-caribou study areas used to estimate densities, and the shaded area is the Bow Valley study area in which wolf and elk densities were recorded from 1985 to 2003 to estimate the numeric response (see text). Numbers represent wolf packs; 1) Maligne, 2) Signal (town), 3) Brazeau, 4) Sunwapta, 5) Medicine, 6) Red Deer, and 7) Bow Valley.

because of low sample size) using the approach of Hatter & Bergerud (1991). Lambda (λ), population growth rate in year t was estimated during biological years 2003 and 2004 following:

$$(eq. 2) \quad \lambda_t = \frac{(1-M_t)}{(1-R_t)}$$

where M_t is adult female mortality rate (or $1-S_t$, the survival rate) and R_t is the recruitment rate of female calves:100 cows (assuming a 50:50 sex ratio) at 12 months of age. Confidence intervals for λ were calculated using 95% confidence intervals for M_t and R_t .

To estimate adult female survival we captured female caribou in from 2001-2005 using helicopter netgunning. GPS collars (Lotek GPS 2200 collars, Aurora, ON) were deployed from 2002-2005 on 18 caribou which were monitored 1.6 years each ($SD \pm 0.4$). We analyzed survival using Cox-proportional hazards regression (Therneau and Grambsch 2000) for one pooled survival rate. The sample size of collared caribou in any year ($\sim n=11$) was $\sim 29\%$ of the total adult female population size, thus we adjusted standard errors of survival estimators with a finite population correction factor of $((N-n)/N)$ where N was the average number of females during the study (2003-2004), and n was the average annual sample of radio-marked females (Thompson, 1992). The number of adult females using population estimates and calf:cow ratios (see below), assuming 35% of adult caribou were male (Smith, 2004). We also determined cause specific mortality (wolf, other) rates from radio-collared females in this and an earlier study (Brown *et al.*, 1994).

We estimated the size of Banff and Jasper caribou populations during fall 2004 and 2005 using helicopter (Bell 206 Jet Ranger) aerial surveys when sightability was highest because of the rut (Brown *et al.*, 1994; Parks Canada, unpubl. data). In Jasper we corrected for incomplete sightability by using the proportion of radio-marked caribou observed, and calculated 95% confidence intervals using the joint hyper-geometric maximum likelihood estimator (White & Garrott, 1990). Banff surveys were considered a complete census because of low sample sizes. We determined March recruitment rates using fall calf:cow ratios obtained on aerial surveys and then adjusting for an additional 15% overwinter mortality following Smith (2004). We adopted this approach because of the difficulty of distinguishing subadult males from females during March calf:cow surveys. Fall classification was conducted after observing caribou on aerial surveys (see below) by landing close enough to classify individuals using a 60x spotting scope, and thus represented true calf:cow ratios. Standard errors on calf:cow ratios were calculated assuming binomial

error distribution (Czaplewski *et al.*, 1983). Standard errors were adjusted using a finite population correction factor based on the number of females following the approach described above for survival.

Calculating caribou, elk, and wolf density

We defined the entire wolf-caribou study area (Fig. 2) using a minimum convex polygon (MCP) surrounding all caribou MCP's and overlapping winter wolf MCP's from 2003-2005 to define densities at the appropriate scale of wolf packs occupying caribou ranges (Lessard, 2005). We estimated 100% multi-winter MCP's from GPS collar (LOTEK GPS 3300sw, and ATS GPS 2000) locations from wolves and caribou in Jasper (Parks Canada, N. Webb, University of Alberta, unpubl. data) and Banff (Hebblewhite *et al.*, 2006). Caribou density within the study area was obtained from the aerial surveys described above. We estimated wolf density using radio-telemetry based methods (Burch *et al.*, 2005). Wolf radio-telemetry data was collected from the two Banff packs and three of the five Jasper wolf packs (Signal, Brazeau, and Medicine) in 2003/04 and 2004/05. The Maligne Pack was only radio-collared in 2004/05, and the Sunwapta Pack not until 2005/06. Because snow-tracking data (unpubl.data) confirmed these 2 packs used the same areas during 2003-2005, we used the 2004/05 MCP for the Maligne pack and the 2005/06 MCP for the Sunwapta pack. We estimated winter wolf pack counts from aerial observations and ground snow tracking to calculate wolf density within this wolf-caribou study area following Burch *et al.* (2005), but did not adjust for lone wolves.

In Banff, elk density was calculated from aerial survey data in the western Bow Valley and Red deer valleys (Hebblewhite *et al.*, 2002; Hebblewhite *et al.*, 2006), corrected for aerial sightability as described above. Elk in Jasper were only surveyed from the ground during early winter in 2004 and 2005. We used a ground sightability model developed in west Yellowstone by Eberhardt *et al.* (1998) to correct ground counts. One further problem was dealing with elk unavailable to wolves surrounding the town of Jasper. Based on research in Banff, we assumed 200 elk surrounding the town of Jasper were unavailable to Jasper wolves (e.g., Hebblewhite *et al.*, 2002).

Evaluating consequences for caribou persistence

We substituted wolf, elk and caribou densities from Jasper and Banff into eq. 1 to calculate wolf-caused caribou mortality rates over a range of kill-rates. We then combined eq. 1 and eq. 2 to solve for caribou kill-rates that predicted $\lambda = 0$ by making two assumptions. First, the proportion of caribou killed by wolves in winter was estimated based on data as

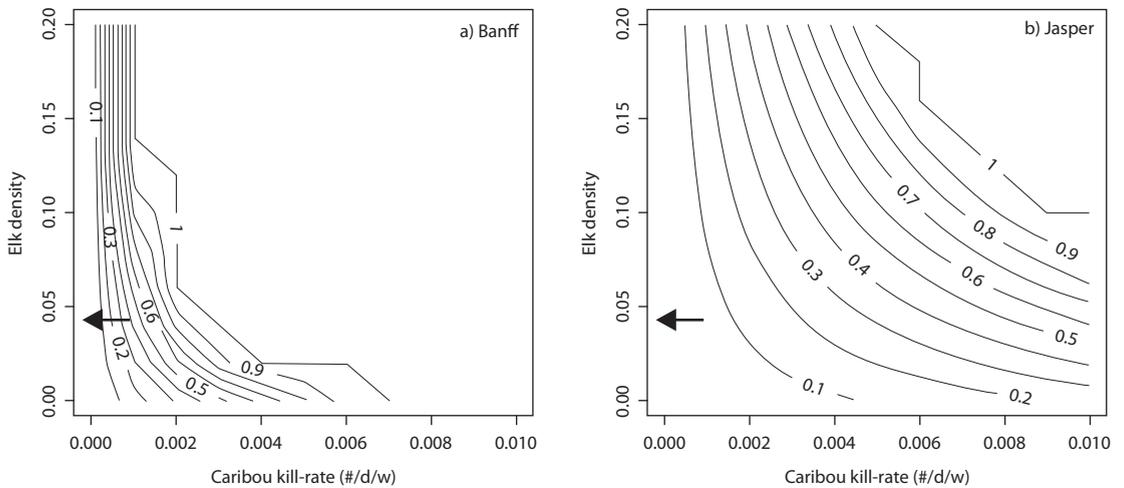


Fig. 3. Proportion of the a) Banff and b) Jasper caribou populations killed per winter (contours) by wolves as a function of elk density and a range of hypothetical wolf kill-rates (caribou killed per day per pack). Given current demography, caribou decline above a threshold of 0.15 and 0.20 wolf-caused mortality rate in Banff and Jasper. Differences between Banff and Jasper arise because of inverse density dependence in total predation rate driven by elk density (arrows mark current elk density).

0.75 (see below) to convert to annual rates. Second, the proportion of adult caribou killed that was female was assumed to be 0.75 (based on Adams *et al.*, 1995). Calf mortality was accounted for by recruitment. Combining eq. 1 and 2, we solved the following equation for $\lambda_i = 0$

$$(eq. 3) \quad \lambda_i = \frac{\left[1 - \frac{M_{ww}}{\alpha} \tau + \omega(1 - S_i)\right]}{(1 - R_i)}$$

where M_{ww} is from eq. 1, α is the proportion of caribou killed in the winter (0.75), τ is the proportion of adult caribou killed by wolves that are female (0.75), ω is the proportion of baseline mortality that is non-wolf related, S_i is the adult female survival rate, and R_i is from eq. 2. We used radiocollared mortalities from this (2001–2006) and an earlier study (Brown *et al.*, 1994) to estimate ω . The first term in the numerator is the annual wolf caused mortality rate and the second term is the non-wolf caused mortality rate. Setting $\lambda = 0$ yields the threshold kill-rate above which caribou decline, given current elk and wolf densities, and can also be expressed as the maximum wolf-caused mortality rate. Using this threshold kill-rate, and setting $\lambda = 0$, we then solved for the wolf (D_w) and elk density (D) above which caribou would decline.

In any modeling effort, uncertainty and sensitivity of model parameters on final model conclusions should be addressed (e.g., Wisdom & Mills, 1997). We addressed uncertainty in threshold estimates of kill-rate and elk/wolf densities by incorporating uncertainty in R_i and M_i in eq. 3. Sensitivity of

equation 4 was assessed by examining the % change in λ as a result of infinitesimally small, one-at-a-time changes (e.g., Wisdom & Mills, 1997) in parameters for Jasper and Banff populations using PopTools (Hood, 2001). Sensitivity is standardized so that values sum to 1 for ease of comparison between populations.

Results

Numeric and functional responses

A linear numeric response was the best fitting of the three models fit to the wolf and elk density data; linear $\Delta AICc = 0$, decelerating type II $\Delta AICc = 1.66$, and the sigmoid type III $\Delta AICc = 4.83$. Elk density explained 74% of the variance in wolf density ($F_{1,17} = 49.2$, $P < 0.0005$), according to the following model $D_w = 0.00082 + 0.0374D_i$. The strong relationship supported our approach to model wolf density using only primary prey density. Critically, the Y-intercept was significant (SE = 0.00032, $P = 0.020$). Note that Messier (2005) confirmed the Y-intercept was the most important aspect of the numeric response for multi-prey systems: considering a type II numeric response with a Y-intercept would not change our results (Messier, 2005).

Effects of caribou kill-rates and elk density on the total predation response

Results of using eq. 3 to explore the relationship between caribou kill-rates, wolf and elk density from Table 1 on caribou predation rate for the two caribou populations are summarized in Fig. 3. Generally, as

Table 1. Summary table of caribou demography and caribou, wolf and elk density for the Banff National Park and Jasper National Park caribou sub-populations, 2003 – 2004. The Banff and Jasper study areas were 4283 km² and 12 512 km² in size, respectively.

Caribou	Banff			Jasper		
	2003	2004	Mean	2003	2004	Mean
Number	4	5	4.50	107 (86-174) ^c	100 (56-336) ^c	103.5
Proportion of population collared	0.25	0.20		0.10	0.07	
Density (# / 1000km ²)	0.93	1.17	1.05	8.55	7.99	8.27
Adult female survival ^a	1	1	1.00	0.93 (0.81 – 0.98)		
Recruitment ^b	0.25	0	0.13	0.42 (34-51)	0.32 (24-32)	0.37
Lambda ^c	--	--	--	1.18 (0.92- 1.32)	1.11 (0.87- 1.24)	1.14
Elk						
Number ^d	130	169	149	406	539	473
Density (# / km ²)	0.030	0.039	0.03	0.032	0.043	0.038
Wolf						
Number	14	16	15	30	41	35.5
Density (# / 1000km ²)	3.27	3.74	3.50	2.40	3.28	2.84

^a Adult female survival SE adjusted for finite population size.

^b Number of calves per 100 cows in March calculated assuming 15% mortality overwinter from Fall calf:cow surveys, 90% confidence interval adjusted for finite population size.

^c Lambda calculated for Banff as N_{t+1}/N_t (unreported caribou count in 2006 used for 2005 lambda was 4), and eq. 3 following Hatter & Bergerud (1991).

^d Banff aerial elk counts adjusted for aerial sightability following Hebblewhite (2000), Jasper ground elk roadside counts adjusted for ground sightability following Eberhardt *et al.* (1998).

^e Hypergeometric 95% confidence interval on mark-resight population estimator.

caribou kill-rates increase, regardless of density (or vice versa), the total predation rate increased for both populations (Fig. 3). However, the dramatically higher susceptibility of the Banff population to increasing kill-rate (Fig. 3a) is because lower caribou density (Table 1) causes strong inverse density dependence with changes to elk density in predation rate, a function of the Y-intercept in the numeric response (e.g., Fig. 1a). In contrast, the Jasper population can withstand much higher elk and caribou kill-rates because of their relatively higher density (Table 1, Fig. 3b).

Caribou demography and population size

Banff surveys counted 4 and 5 total caribou in 2003 and 2004 (Table 1). In Jasper, caribou population size appeared stable throughout the study, at 107 and 100 (Table 1). Confidence intervals from mark-recapture estimates were wide as a result of sparse counts and the low collared proportion resighted in 2004 (3 of 7, vs 8 of 11 in 2003). Survival for 29-caribou years over

the pooled two-year period was 0.932 (Table 1) with wide confidence intervals despite the finite population correction (22% of adult females were collared). Wolves killed ~50% of radiocollared caribou during both the early (6 of 12) and present (2002-2006) studies (3 of 7). Other predators (bears), road-kills, and accidents (drowning, avalanches) comprised the remaining sources of mortality. Thus, we set $\omega = 0.5$ in Eq. 3. Furthermore, in contrast to many other populations (e.g., Wittmer *et al.*, 2005a), 6 of 8 (75%) wolf-caused caribou mortalities occurred during winter, thus we set $\alpha = 0.75$ in Eq. 3. Fall recruitment rates adjusted for 15% overwinter mortality were 42 calves:100 cows in 2003, and 32:100 in 2004 (Table 1). A higher proportion of females were observed during recruitment surveys, 40% and 48% in 2003 and 2004, respectively, narrowing confidence intervals (Table 1). Population growth rates (λ) were 1.18, and 1.14 in 2003-2005, with confidence intervals overlapping zero (Table 1).

Table 2. Threshold elk and wolf densities above which caribou populations decline (i.e., $\lambda < 1$) at kill-rate values (see subscripts) that caused mortality to exceed recruitment for the southern Jasper National Park and Banff National Park caribou populations. Differences in Jasper thresholds between years were a result of higher calf recruitment in 2003. See eq. 3 and text for how thresholds were calculated.

	Elk density (# / km ²)	95% CI ^d	Wolf density (#/1000km ²)	95% CI ^d
JNP 2003 ^a	0.078	0.04 – 0.14	4.3	1.9 – 7.9
JNP 2004 ^b	0.033	0.02 – 0.06	2.1	1.0 – 3.7
BNP 2003/04 ^c	0.015	0 – 0.20	1.8	1.0 – 2.0

^a Evaluated at a kill-rate of 0.0034 caribou/day/wolf from eq. 3.

^b Evaluated at a kill-rate of 0.0068 caribou/day/wolf from eq. 3.

^c Evaluated at a kill-rate of 0.00035 caribou/day/wolf, and Banff thresholds were calculated assuming adult female survival and juvenile recruitment were equal to Jasper.

^d 95% confidence intervals reported by evaluating eq. 3 using 95% CI for R_i and M_i .

Table 3. Sensitivity analyses for eq. 3 revealing the proportion of the variance in population growth rate, λ , explained by parameters, for the southern Jasper and Banff caribou sub-populations, 2003-2004. Sensitivity was evaluated using one at a time proportional changes to each parameter holding effects of other parameters constant at the values reported in Table 1, and are reported as standardized sensitivities summing to 1.

Parameter	Description	Jasper		Banff	
		Sensitivity	Rank	Sensitivity	Rank
a	% Caribou killed in the winter	0.001	8	0.001	8
t	% Adult female caribou killed by wolves	0.001	7	0.001	7
w	% Non-wolf mortality	0.025	6	0.006	6
St	Adult female caribou survival	0.187	2	0.045	5
Rt	Recruitment rate	0.447	1	0.098	4
Dw	Wolf density	0.158	3	0.128	3
Dc	Caribou density	0.054	5	0.425	1
K	Caribou kill-rate/ wolf/ day	0.128	4	0.298	2

Caribou, elk, and wolf density

For the Banff wolf-study area, caribou density was extremely low, less than 1.2 caribou/1000 km². Caribou density in Jasper was seven times higher around 8 caribou/1000 km² (Table 1). Elk densities were similar in Jasper and Banff (Table 1). We report elk densities in Banff for both the Red Deer and Bow Valley - elk densities in the Bow Valley were more than 50% lower in 2005 (0.016 elk/km²) than that of the Red Deer Valley (0.038 elk/km², Table 1).

Evaluating consequences for caribou persistence

Substituting observed wolf, elk, and caribou density and demography from Jasper into equation 3 yielded a threshold of 0.0034 caribou/day/wolf in 2004 to 0.0068 in 2004, or 4-9 caribou/winter/pack above which caribou would decline at present recruitment rates. We assumed adult female survival in Banff was the same as Jasper because there was too few collared caribou for survival estimation. Using Jasper survival rates with Banff recruitment yielded a threshold

caribou kill-rate of 0.0006 caribou/day/wolf, or <1 caribou/winter/wolf pack. These kill-rate thresholds corresponded to maximum sustainable annual caribou mortality rates caused by wolves of 0.15 and 0.17 in Jasper during 2004 and 2003, respectively, and 0.05 in Banff. Thus, rearranging equation 3 using this general wolf-caused mortality threshold to solve for elk (and thus wolf density) yielded threshold elk and wolf densities (averaged for 2003 and 2004) in Jasper of 0.056 elk/km² and 3.2 wolves/ 1000 km², respectively (Table 2). In Banff, thresholds were much lower following Fig. 1 such that caribou populations would be expected to decline above elk and wolf densities of 0.02 elk/km² and 1.8 wolves / 1000 km² (Table 2).

Sensitivity and uncertainty

Thresholds for caribou persistence were quite variable given wide variation in survival recruitment (Table 2). Jasper caribou would be expected to decline given the upper 95% confidence interval for R_i and S_i once elk

densities exceeded 0.14 elk/km², with a corresponding wolf density of 7.9 wolves/1000 km² (Table 2). In Banff, even assuming the upper 95% CI for demographic rates yielded upper thresholds of 0.21 elk/km² and 2.1 wolves/km² (Table 2). Sensitivity analysis revealed differences between Jasper and Banff in the consequences of perturbations in parameter values to λ . With higher caribou density in Jasper (Table 1), λ was most sensitive to changes in recruitment (the proportion of the variance in λ explained by this parameter = 0.447), adult survival (0.187), wolf density (0.158) and wolf kill-rates of caribou (0.129, Table 3). Other parameters had sensitivities <0.05. In contrast, under low caribou density in Banff, λ was most sensitive to changes in caribou density (0.425), wolf kill-rate of caribou (0.127), wolf density (0.127), and recruitment (0.099), with other parameters having <0.05 effects on λ (Table 3). Notably, parameters for which data were assumed for both populations, i.e., α , τ , ω , had minimal effect on λ in sensitivity analyses.

Discussion

Our simple modeling approach used caribou vital rates, the numeric response of wolves to elk density, and caribou, wolf, and elk density to solve for the critical kill-rates that would predict stable growth rates of caribou. We then calculated the threshold for elk and wolf densities above which caribou growth rates would decline. At present densities, given even modest wolf predation rates, extirpation of caribou in Banff is likely, while the higher density Jasper caribou population appears to be within the ranges of viability. The difference between the Banff and Jasper populations is consistent with inverse density dependence in predation rates by wolves subsisting on primary prey (elk) as caribou decline (Fig. 1a). These results echo other recent studies of endangered prey species. Sinclair *et al.* (1998) showed several species of endangered Australian marsupials being driven extinct by predators because of high densities of primary prey. On the Channel Islands off the coast of California, Roemer *et al.* (2002) found predation by golden eagles (*Aquila chrysaetos*) was driving endangered channel island fox (*Urocyon littoralis*) extinct because eagles were numerically buoyed by abundant feral pigs (*Sus scrofa*). These cases are clear examples of apparent competition between a primary and secondary prey species driven by human-caused perturbations.

A consensus that caribou abundance is mediated by the abundance of primary prey is emerging from both empirical (Bergerud, 1988; Seip, 1992; Kinley & Apps, 2001; Wittmer *et al.*, 2005a) and theoretical grounds (Lessard, 2005; Lessard *et al.*, 2005). As perhaps the strongest evidence for this, Wittmer *et al.* (2005b)

clearly demonstrated inverse density dependence in caribou population growth rates immediately west of our study area in southeastern BC. Only one caribou sub-population with less than 200 caribou had positive population growth rates over a 10-year period (Wittmer *et al.*, 2005a; b). Wittmer *et al.* (2005b) concluded predator density, buoyed by high moose and deer density, and not food limitation related to habitat loss of old growth forests, were driving caribou declines.

Recent modeling suggest our thresholds for caribou persistence in wolf-elk systems may be lower than boreal or foothills populations. In the foothills of the Rockies, Lessard (2005) showed caribou declined when wolf densities exceeded ~8 wolves/1000 km² following increases in moose because of forestry. This was remarkably close to Bergerud's (1988) threshold of 6.5 wolves/1000 km² for caribou declines amongst boreal caribou populations. Reasons for the difference between boreal and foothills thresholds and ours could arise from differences between moose and elk, lower net primary production, and lower caribou density in the Rockies. Almost 50% of the Canadian Rockies is rock and ice, and are likely more spatially complex than boreal systems. Patchy mountain landscapes may lead to higher travel and encounter rates for predators because predators searching for patches of primary prey (elk) are more likely to travel through areas of alternate prey (caribou) (Huggard, 1993; Lessard, 2005). Solitary living moose may also ensure frequent encounters relative to group living elk. Elk may have lower per-capita encounter rates because groups, not individuals, are encountered, and wolves would experience group-level patch depression (Huggard, 1993). This could also contribute to higher wolf encounter rates with caribou (Huggard, 1993; Lessard, 2005). Reduced net primary productivity in mountain environments would reduce productivity of both elk and caribou populations, leading to higher vulnerability to predation (Lessard, 2005).

Sensitivity analyses further support the role of inverse density dependence in predation rate. Caribou growth rates showed remarkably different sensitivity between Jasper and Banff (Table 3). At higher caribou density in Jasper, key parameters influencing λ were recruitment rate, adult female survival, wolf density and wolf kill-rate of caribou. Recruitment rate and adult survival explained ~65% of the variance in λ . In contrast, λ for the low density Banff caribou was most sensitive to caribou density, wolf kill-rates, and wolf density. Recruitment rate and survival of adults explained less than one-fifth the variance in λ in Banff as in Jasper (Table 3). Because caribou density is determined at the wolf pack scale, the top three factors influencing λ in Banff were wolf predation related.

Jasper caribou vital rates and demography were similar or higher than other mountain and boreal caribou populations. Southern Jasper adult survival, calf recruitment and population growth rate was similar to the northern Jasper A La Pêche herd, where survival was 0.919, calf recruitment 28:100, and population growth was 1.061 (Smith, 2004, Table 1). Outside of National Parks in the foothills of Alberta, however, caribou populations were stable ($\lambda \sim 1.0$) in the Red Rock-Prairie Creek area or rapidly declining in the Little Smoky river ($\lambda = 0.88$). And on the western slopes of the Canadian Rockies in British Columbia, survival varied from 0.55 to 0.96 and calf: adult ratios averaged $\sim 12:100$, and these low vital rates were causing ~ 7 of 10 populations to decline (Wittmer *et al.*, 2005b). Boreal caribou populations in Alberta had similar or slightly lower survival rates of 0.86 – 0.93 (McLoughlin *et al.*, 2003), and variable recruitment of 11–22 calves:100 cows that resulted in 2 of 6 populations declining. For calf recruitment, Bergerud & Elliot (1998) reported that under wolf densities of 6.5, caribou calf:cow ratios would need to be $> 19:100$. Thus, Jasper vital rates were higher than in landscapes influenced by oil and gas exploration and forestry, consistent with hypotheses for anthropogenic influences on caribou decline in Alberta and British Columbia. While caribou in Jasper have certainly declined from the late 1980s when population size was approximately 200, the population may be increasing or stable at present. Survival rates were 0.66 during an earlier study (Brown *et al.*, 1994) when most mortality was wolf related and regional wolf numbers were high following recolonization (e.g., Hebblewhite *et al.*, 2006). One interpretation is recolonizing wolves reduced caribou densities in Banff and Jasper in the 1980's, but following declines in elk in Jasper at least, wolves stabilized to below thresholds for caribou declines. Regardless, given the grim state of caribou outside parks (Smith, 2004; Wittmer *et al.*, 2005b), the relatively high growth rates observed in this study suggests an important potential role of Jasper as a regional source population in the future.

Persistence of the Banff population is unlikely considering results of previous studies (Kinley & Apps, 2001; McLoughlin *et al.*, 2003; Wittmer *et al.*, 2005a; b). Of the smaller subpopulations of caribou in southeastern BC reported by Wittmer *et al.* (2005b), the southern Purcells ($n=6$) and George mountain herds ($n=4$), were extirpated by 2006 (R. Serrouya, pers. comm.). These two subpopulations had intrinsic growth rates (r) of -0.18 (Wittmer *et al.*, 2005b). Based on maximum counts of the Banff caribou population of 25–40 in 1988 (Parks Canada, unpubl. data) and 4 in 2005 (Table 1), r for Banff for this

period = -0.13. Given present wolf and elk densities, especially in the Red Deer Valley, extirpation appears likely. Furthermore, demographic stochasticity will significantly reduce expected growth rates even more, making extinction almost certain (Boyce *et al.*, 2006). To recover Banff caribou, active recovery strategies such as those adopted for other small endangered caribou populations in the Alberta and British Columbia recovery plans will be required (e.g., Alberta Woodland Caribou Recovery Team, 2005).

Such grim predictions seem warranted because neither empirical studies (Wittmer *et al.*, 2005a) nor modeling (Lessard *et al.*, 2005) found evidence for the low-density spatial refugia scenario in Fig. 1b under a type III functional response. A spatial refuge would ensure that wolves were not able to extirpate alternate prey like caribou at high primary prey densities such as seen in Fig. 1b where P^* is > 0 ; P^* represents the density surviving because of the spatial refuge. Lessard (2005) described conditions that would favor existence of spatial refugia: habitat differentiation between elk and caribou, favored habitats (e.g., old-growth) by caribou must not be limiting, low spatial overlap between caribou and elk, elk density must be higher than caribou density, and the ratio of the scale of predator search behavior is small relative to both ungulate and habitat patch scales. Lessard (2005) indicated that in foothills caribou existing with industrial development, many conditions would be violated. In the Canadian National Parks, however, the first four conditions may arguably be met, dependent on the spatial structure of prescribed fire management. In the absence of human development, fire is the dominant natural process that influences the spatial arrangement of favored caribou habitat (late seral), habitat overlap, and patch size (Shepherd, 2006). Restoration of the role of fire in maintaining vegetation communities is an important objective of Parks Canada's management plans (White *et al.*, 1998; Parks Canada, 1997). Shepherd (2006) showed that Jasper caribou selected forests older than 150 years. Prescribed burning should maintain the long-term spatial patterns of fire frequency that favored persistence of old growth forests at higher elevations and on north-east aspects (Tande, 1979; Rogeau *et al.*, 2004). Implementation of a widespread and diffuse prescribed fire program that burned in or near preferred caribou habitat would reduce spatial overlap and create smaller habitat patches increasing predation rates on caribou. The most difficult condition for a refuge, however, is the spatial structure of wolf search behavior relative to size of forest patches and overlap between caribou and elk. Generally, Lessard (2005)'s results imply prescribed fire should occur in large patches far from caribou ranges. But how far will depend on the spatial scale

of wolves, and whether the large-scale numeric response of wolves to elk density following fire could eliminate small-scale spatial refugia for caribou. Spatial extensions of the modeling framework developed here with elk and wolf spatial models (e.g., Hebblewhite *et al.*, 2005a) will be required to test for the presence of spatial refugia and the interaction with prescribed fire.

Our simple modeling approach pooled caribou from two separate subpopulations within southern Jasper, the Tonquin and Maligne-Brazeau herds. Density thresholds presented here assume the southern Jasper herd is not subdivided, and are therefore likely optimistic. Movements between these two herds have not been observed (Parks Canada, unpubl. data). Effective caribou density could therefore be lower in each of these sub-herds than our modeling results for the pooled 'population'. This would render both herds more susceptible to inverse density dependence in wolf predation depending, again, on the spatial overlap of wolves, elk and caribou. Future analyses should examine spatial caribou meta-population dynamics.

The simple approach we took to modeling caribou population dynamics clearly has room for other improvements. The lack of kill-rate data of wolves on caribou in the Rockies and elsewhere (Lessard, 2005) poses a major problem to modeling predator-prey dynamics, and is surely a major weakness in our analysis. New approaches could be used to estimate kill-rates of wolves using GPS locations for wolves to predict prey species kill-rates (Sand *et al.*, 2005). Diet composition studies through scat analysis could aid interpretation of GPS kill-rate analyses. Another major limitation was obviously low confidence in adult female survival and density estimates, deficiencies being presently addressed with increased VHF collar deployment on Caribou in Jasper. Furthermore, calculation of elk density in Jasper was problematic because of the unknown availability of townsite elk to wolves, and research to determine how to adjust Jasper elk density for unavailable elk would be helpful. Also, eq. 3 assumes calf mortality is independent of wolf density, a necessary, but weak, assumption given present data limitations. While sensitivity analysis supported the parameter values we used for α , τ , and ω in our model (Table 2), low sample sizes were used to estimate cause-specific mortality. Perhaps the greatest limitation of our approach has to do with alternate mortality, ω . Many studies illustrate the critical role of grizzly bear predation on neonate caribou calf survival (Adams *et al.*, 1995). Our assumption of constant mortality by other 'predators' including grizzly bears despite changing elk density makes our thresholds for caribou persistence optimistic (Bergerud & Elliot, 1998). Unfortunately, few data exist to model grizzly bear numeric responses to prey density. Certainly,

prescribed fire in or near caribou ranges could increase predation rates from grizzly bears foraging on productive post-fire vegetation (Hamer, 1999).

When these results are combined with studies of the long-term range of variability in the Canadian Rockies, a convergent theme emerges of low-density elk populations as the long-term norm. Our thresholds for caribou persistence are close to those required for willow and aspen persistence (White *et al.*, 1998; Hebblewhite *et al.*, 2005b). Evidence for low elk densities are also found in early explorer's journals (Kay *et al.*, 2000) or archaeological evidence (Lange-mann & Perry, 2002). The only remaining difficulty is reconciling how elk density was maintained at low density under higher frequencies of forest fire (Rhemtulla *et al.*, 2002; White *et al.*, 2003) that would indirectly increase predation on caribou. Predation by multiple predators, including wolves, grizzly bears, and humans would have been required to limit elk to low enough densities that wolf densities would be low enough for caribou persistence. Regardless of debates over long-term ecosystem states, management policies that maintain elk, and hence wolf density in the Canadian Rockies, appear a prudent management direction for caribou restoration.

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