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Climate and management interact to explain the decline of woodland caribou (*Rangifer tarandus caribou*) in Jasper National Park

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Abstract: Woodland caribou in the southern portion of Jasper National Park have declined from an estimated 435 in the mid 1970s to a population estimate of 87 in the fall of 2009. We examined the available historical information to determine why caribou have declined. We compared three main hypotheses for caribou decline in JNP: human disturbance, climate change, and wildlife management. We used historical human use statistics, climate data, and animal abundance information to weigh the evidence for these competing hypotheses over two time scales. Caribou decline could not be attributed to changes in climate over the long-term, or an increase in human use (our proxy for disturbance). Caribou decline was attributed to a combination of climate and wildlife management. Recovery of caribou in Jasper National Park will likely be contingent on managing the interaction between the predator/prey dynamic and climate change.

Key words: climate; elk; Jasper National Park; wolves; woodland caribou.

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Introduction

Woodland caribou (*Rangifer tarandus caribou*) are declining across Canada. The prevailing theory behind the decline is that industrial development of formerly intact caribou range has altered predator/prey interactions to the detriment of caribou (Bergerud & Ballard, 1988; Stuart-Smith *et al.*, 1997; Rettie & Messier, 1998; Mcloughlin *et al.*, 2003; Mcloughlin *et al.*, 2004; Wittmer *et al.*, 2005b). The altered interactions have been described as apparent competition, identified by Holt (1977), in which the decline of one prey species (e.g. caribou) is caused by higher-than-normal predator densities (e.g. wolf) that are influenced by the abundance of a second prey species (e.g. elk).

Southern mountain caribou (a population of woodland caribou federally designated as Threatened) are among the most vulnerable of Canada's woodland caribou. In 2005, 14 of 16 monitored southern mountain herds were in decline in British Columbia (Wittmer *et al.*, 2005a), while in 2008-09 all but one southern mountain herd were declining in Alberta (Alberta Sustainable Resource Development and Alberta Conservation Association, 2010). Furthermore, the southern-most caribou herds were thought to be in imminent danger of extirpation (Thomas & Gray, 2002). Unfortunately, these dire predictions were fulfilled by the extirpation of caribou in Banff National Park (Hebblewhite *et al.*, 2010b), as well as the extirpation of two herds in British Columbia (Hatter, 2006). As with woodland caribou across Canada, the primary reason for declines in the southern mountain population is attributed to apparent competition driven by human alteration of the land-

scape for industrial purposes and resulting increases in wolf-caribou encounters and predation (Wittmer *et al.*, 2005a; Wittmer *et al.*, 2005b).

But why have caribou in Jasper National Park also declined? Caribou in the southern part of Jasper National Park numbered approximately 435 animals in the mid-1970s (Stelfox, 1974) but today only 87 remain (90% confidence limits 87 to 96, unpublished Parks Canada data). Compared to the industrial landscape, human alteration of the landscape in Jasper National Park has been modest, and the decline of the park's caribou cannot be explained solely by the industrial landuse/apparent competition hypothesis. Recent monitoring (2001 to 2009) has shown wolf predation to also be important to Jasper caribou population dynamics. A study of collared adult female caribou in Jasper found that wolf predation (cumulative incidence function or CIF = 0.045) and unknown predation (CIF = 0.054) were the most important causes of mortality; however, unknown causes of mortality were also important (CIF = 0.055) (Decesare *et al.*, 2010).

We used the historical record of elk, wolf, and caribou abundance, wildlife management, human use, and weather to examine the decline of caribou in Jasper National Park. In particular, we weighed the evidence to discriminate among three general hypotheses of caribou decline in Jasper National Park: climate change, human disturbance, and wildlife management. The hypothesis of caribou decline due to climate change is that warmer temperatures and shallower snow should favour elk (Creel & Creel, 2009, Hebblewhite et al., 2002) to the detriment of caribou via apparent competition. The hypothesis of caribou decline due to human disturbance is that large numbers of people using wilderness areas can displace caribou from important habitat, thus causing population decline. The hypothesis of caribou decline due to wildlife management is that people have influenced the abundance of elk and wolves, which has in turn affected caribou numbers via apparent competition.

Study area

Caribou inhabit two disjunct areas of Jasper National Park (hereafter referred to as Jasper), one in the north and the other in the south (Fig. 1). The northern caribou, the A La Peche herd, have traditionally migrated between the protected mountain environments of Jasper and Willmore Wilderness Park in the summer to the adjacent industrial landscapes of the Alberta foothills in the winter. The management of the A La Peche caribou has been primarily the jurisdiction of the Alberta provincial government, and will not be considered further in this paper. Jasper's southern caribou live largely within the bounds of Jasper, but their range also extends into British Columbia's Mount Robson Provincial Park, and Alberta's White Goat Wilderness Area. We focused our analyses on the caribou of south Jasper.

The Jasper landscape can be classified into montane, subalpine, and alpine ecoregions (Holland *et al.*, 1983). The low elevation montane ecoregion is primarly lodgepole pine (*Pinus contorta*), with some Douglas fir (*Pseudotsuga menziesii*), willow (*Salix* spp.), aspen (*Populus tremuloides*), and riparian white spruce (*Picea glauca*) areas, interspersed with small grasslands. The mid-elevation subalpine ecoregion consists mainly of subalpine fir (*Abies lasiocarpa*) – Engelmann spruce (*Picea engelmanii*) - lodgepole pine forests with limited grasslands. The alpine ecoregion is largely open shrub-forb meadows. Both alpine and subalpine ecoregions can have avalanche terrain, relatively non-vegetated ridgetops, and areas of rock and ice.

In addition to caribou, the ungulate community consists of elk (*Cervus elaphus*), moose (*Alces alces*), white-tailed deer (*Odocoileus virginianus*), mule deer (*O. hemionus*), bighorn sheep (*Ovis canadensis*), and mountain goats (*Oreamnos americanus*). Wolves (*Canis lupus*) prey on all of these ungulates, but elk abundance has been considered to be a primary driver of wolf density in the Rocky Mountains (Huggard, 1993; Hebblewhite, 2000). Other predators of large mammals in Jasper include cougar (*Felis concolor*), coyote (*Canis latrans*), wolverine (*Gulo gulo*), black bear (*Ursus americanus*) and grizzly bear (*Ursus arctos*).

Because we were interested in predation impacts on caribou populations in south Jasper, our study area encompassed caribou range, plus the ranges of wolf packs that overlapped with caribou based on current habitat use as determined by current VHF and GPS radio-telemetry (Fig. 2).

Methods

Wildlife abundance data

We examined available records of animal abundance from 1811 (the arrival of the first Europeans) to the present. Data on historical wildlife and wildlife management come from the published literature, Parks Canada's unpublished literature, and from our search of the Parks Canada archives in the Town of Jasper's Yellowhead Museum. Recent wildlife data were from Parks Canada's ongoing research and monitoring efforts. Only wildlife abundance within our study area was considered. Weather variables were obtained from Environment Canada.

Caribou abundance has been estimated in several ways over the years. The 1973 estimate was a subjective combination of aerial and ground-based counts (Stelfox, 1974). The estimate from 1988 was an aerial count adjusted for sightability based on expert opinion (Brown *et al.*, 1994). The estimates for 1993, 1998, and 2000 were aerial counts adjusted for sightability using the average sightability from 2003 to 2009. Estimates from 2003 to 2009 were calculated using a joint hypergeometric mark-recapture procedure, based on a sample of radio-collared females (White, 1996; Neufeld & Bradley, 2009). Caribou population estimates for 2006 to 2008 were corroborated using genotyping data and capture-mark-recapture techniques described by Hettinga *et al.* (2011).

We used historical accounts to estimate elk abundance for years when count data were not available. Otherwise, elk estimates were based on counts conducted from roadsides each winter when a large proportion of the total elk population was observable. The number of elk killed by humans (primarily by highway/railway mortality) was obtained from park records. Park records also informed human use data (number of user nights for backcountry camping) and wolf abundance data.

Data quality

Relying on historical data for long-term abundance was challenging, as meth-

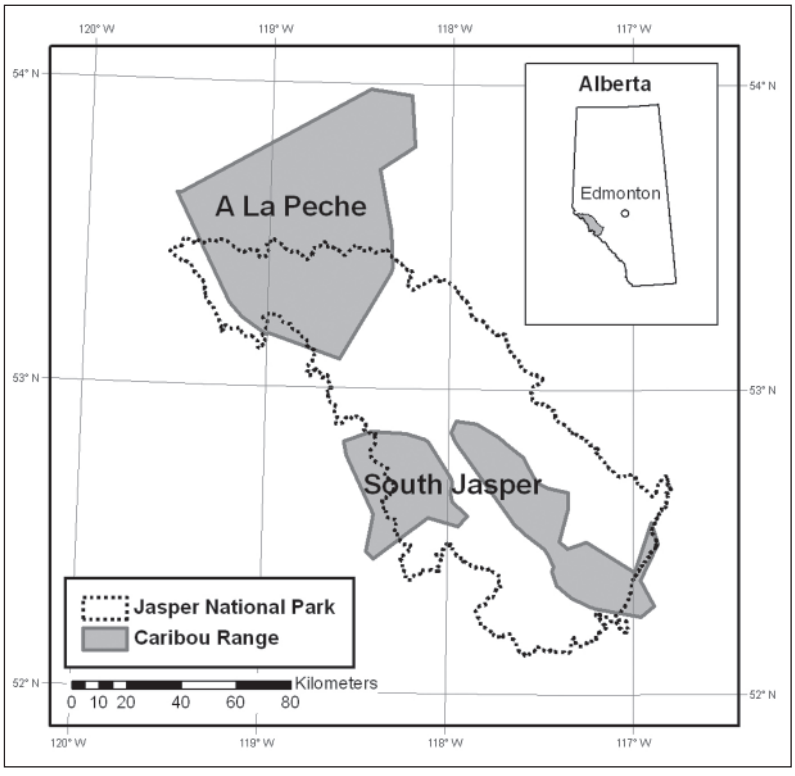

Fig. 1. Caribou ranges in Jasper National Park and surrounding areas.

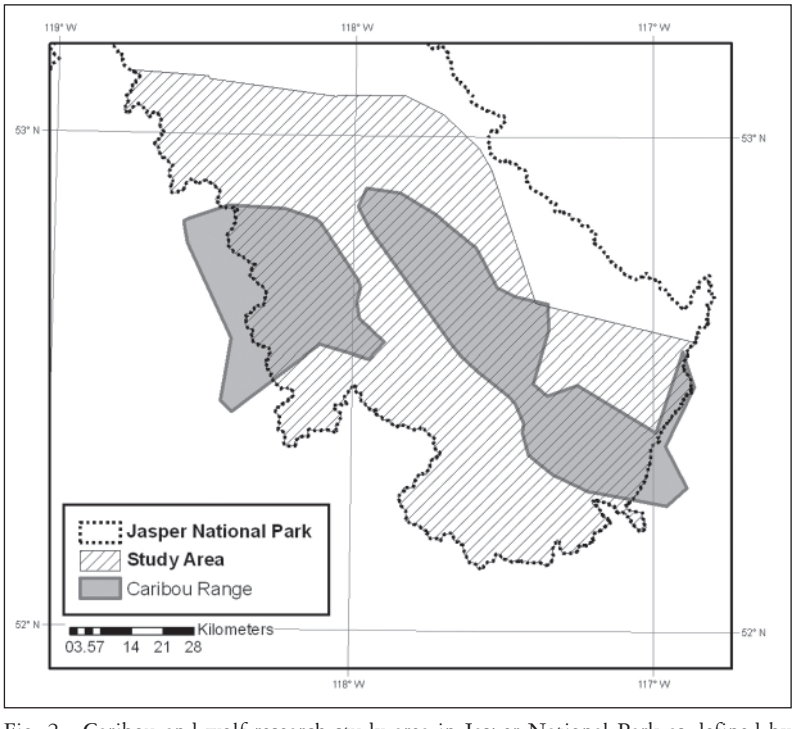

Fig. 2. Caribou and wolf research study area in Jasper National Park as defined by caribou range and associated wolf pack territories.

ods and effort have changed over time. For elk, abundance was mainly derived from expert opinion until 1975, when infrequent aerial counts began. Annual roadside elk counts began in 1997. Historical wolf and caribou data are of lesser quality than historical elk data, because unlike elk, wolves and caribou are difficult to survey without intensive effort.

Despite these shortcomings, major trends in elk abundance can be reliably summarized because elk gather in large groups in open areas, and casual observation can result in the observation of a high proportion of the elk population. For wolves and caribou, year-to-year historical data should be interpreted with caution, but we feel that the general trends are likely representative of changes over time.

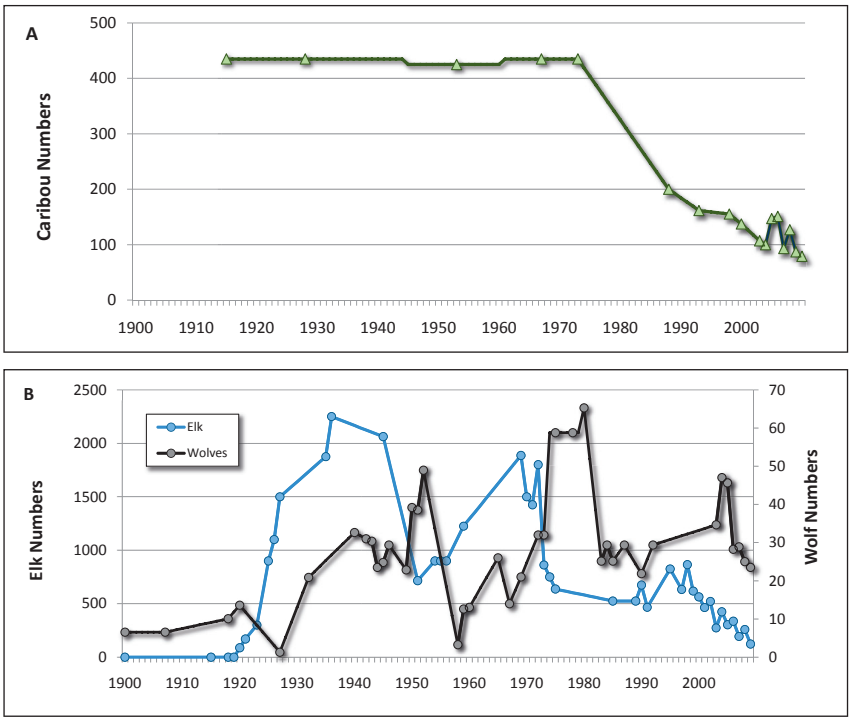

Fig. 3. Trends in approximate abundance of caribou (A), elk (B), and wolves (B), in Jasper National Park from 1900 to 2009. Elk were reintroduced in 1920 while predator control was ongoing (1900-1959). Severe winters affected the elk population in the late 1940s and early 1970s.

Analyses

Because techniques and data collection intervals varied widely throughout the years, we present the data mainly as a description of the wildlife abundance timelines. We also identify some unique turning points in Jasper's wildlife management history that are not amenable to analysis, but offer insight for interpreting trends.

For the long-term time-scale (1900 to 2009), we were not confident in the historical record's capacity to detect annual changes in wildlife abundance and therefore identified two multi-year eras of relatively consistent wildlife trends and management practices. We compared climatic variables between the two eras, using univariate parametric statistical testing (t-tests). Human use data were not available for the early era and therefore were not comparable between the two eras.

For the short-term time scale, from 1973 to 2009, there were more frequent and more objective surveys for all three species (elk, wolf, and caribou), unfortunately, there were still considerable gaps in the data. Moreover, these gaps were not synchronized among the species, so a statistical analysis of the annual changes in all three species in this shorter time-scale was not possible.

Results

Wildlife abundance and wildlife management context

Caribou prior to 1973 were considered relatively abundant in south Jasper - approximately 435 (range 275 to 550; Fig. 3A, (Stelfox, 1974)). The first aerial count of caribou in 1988 was 158, and the authors speculated that there were probably 200 caribou in total (Brown *et al.*, 1994). The 2009 population estimate was 87 caribou (90% confidence limits of 87 to 96).

Seven key events in the elk time series should be noted (Fig. 3B): 1) no or very few elk until the re-introduction of 88 elk in 1920; 2) a population increase to over 2000 elk by 1936; 3) a winter die-off in 1948 and 1949; 4) the subsequent population

rebound to approximately pre-1948 numbers by 1969; 5) a second winter die-off in 1972; 6) population stability from 1972 to 1995 (i.e. no population rebound from the winter die-off); and, 7) a linear decrease in elk from 1995 to approximately 200 elk near caribou habitat in 2009 (Lloyd, 1927; Mctaggart-Cowan, 1946; Robinson et al., 2009; Stelfox, 1971a; Stelfox, 1974; Dekker *et al.*, 1995; Parks Canada records). It is worth noting that the number of elk killed by humans probably influenced wolf abundance in Jasper because the practice of disposing of elk carcasses in gravel pits contributed substantial additional food to wolves. Carcass dumping ended in 2006.

As with elk, wolves were rare in the early 1900s (Fig. 3B) (Stelfox, 1971b; Dekker *et al.*, 1995). Wolf control in Jasper, ongoing at the turn of the century, intensified in 1920 in an attempt to aid elk recovery. Following the elk increase, wolves increased from 1930 to 1950, prompting a more aggressive poisoning campaign in 1952 in an attempt to eradicate rabies, and to augment ungulate numbers (this time sheep were the major concern). By 1958 wolves had been reduced to very low numbers before wolf control officially ended in 1959. The end of wolf control marked the beginning of a 20 year increase in wolf numbers. In 1983, wolves experienced a rapid decline attributed, at the time, to the decline of elk. Recovery in wolf numbers occurred between 1990 and 2003, but since 2004, wolves have again declined, this time concurrent with recent elk declines and also with the cessation of leaving road-killed ungulate carcasses in gravel pits for wolf consumption (Mctaggart-Cowan, 1946; Carbyn, 1975; Kaye & Roulet, 1980; Dekker *et al.*, 1995, Parks Canada records).

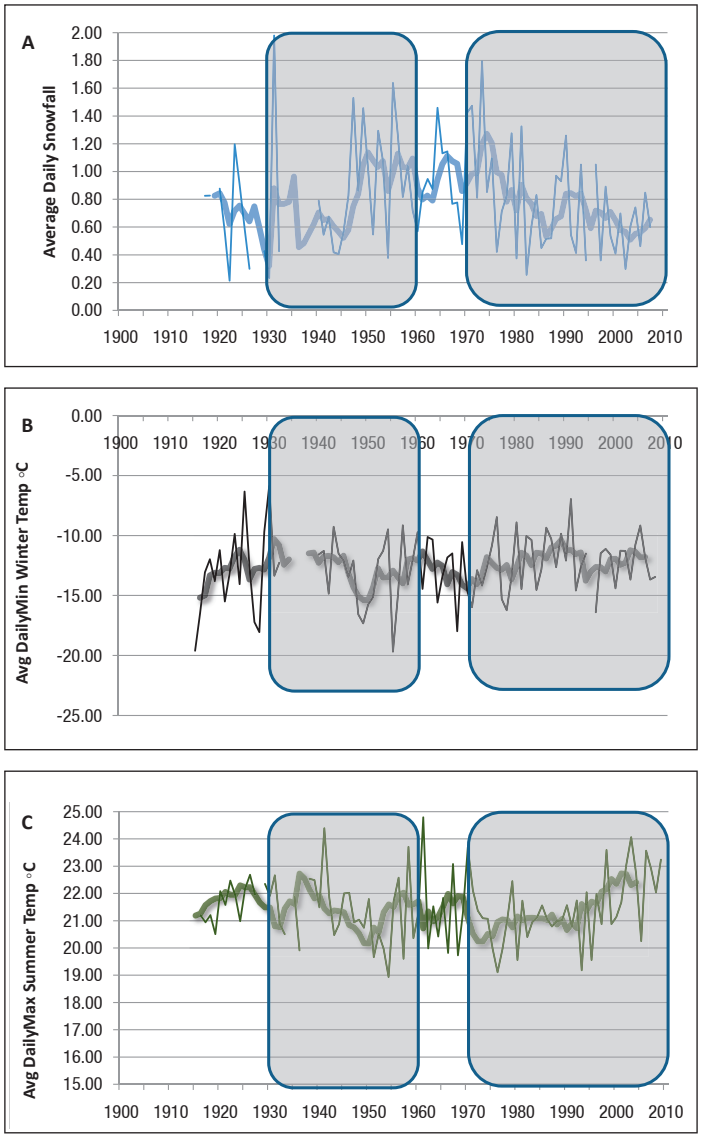

Fig. 4. A) Snowfall, B) average daily minimum winter temperature, and C) average daily maximum summer temperature for Jasper National Park 1900-2009. Grey polygons represent eras within which wildlife abundance trends were consistent. Thick lines depict five year running averages.

The long-term time scale: comparing two eras

We defined two eras of consistent wildlife abundance and management trends based on the historical context: *1930 to 1960:* high elk numbers, high caribou numbers, low wolf numbers, wolf control. *1970 to 2009:* declining elk numbers, declining caribou numbers, higher wolf numbers, no wolf control.

None of the climate variables (average daily winter snowfall (Fig. 4A), average daily minimum winter temperatures (Fig. 4B), and average daily maximum summer temperatures (Fig. 4C)) were significantly different between the two eras (winter temperature $P = 0.6$, winter snowfall $P = 0.6$, summer maximum temperature $P = 0.5$). Multi-year averages can mask

trends however, so we also examined weather data within each era. Snowfall tended to increase during the first era (Fig. 4A, P = 0.02), and decrease during the second era (Fig 4A, P < 0.01). Winter minimum temperatures and summer maximum temperatures showed no trends within either era (Fig 4B and 4C, P > 0.05) although later in the second era there is a positive slope for summer maximum temperature.

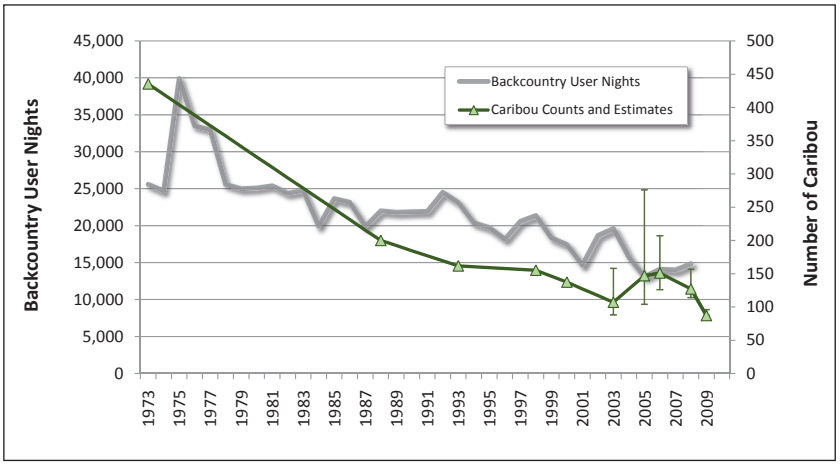

Fig. 5. Number of caribou and number of backcountry user nights in Jasper National Park from 1973-2009.

The Recent Era: 1970 to 2009

Since 1970, elk (Fig. 3), caribou, and human use have all declined (Fig. 5).

While number of elk were declining between 1970 and 2009, for much of that period the number of elk killed (mostly by vehicles), was increasing (Fig. 6). Although the number of elk killed has been stable since 2004, at about 45 animals, carcasses are now disposed in a fenced transfer station away from carnivores.

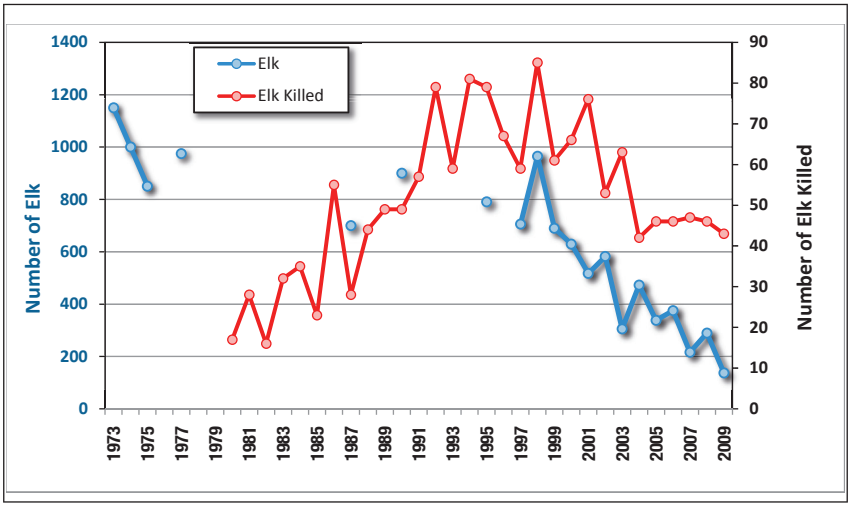

Fig. 6. Number of elk and number of elk killed by humans (vehicles, railway, aggressive elk) in Jasper National Park from 1973 to 2009.

Discussion

We set out to examine three general hypotheses of caribou decline: disturbance by humans, climate, and wildlife management. First, we concluded that the history of human use of Jasper's wilderness areas does not support the idea that disturbance by humans has caused caribou decline. Since 1970, human use of Jasper wilderness areas has declined concurrently with the decline in caribou abundance – i.e. if disturbance were important, we would have expected an increase in human use as caribou declined.

Our conclusion was to some extent unexpected, given that Stelfox (1974) judged human use of Jasper's wilderness areas to be a detriment to caribou in the 1970s, and that a recent behavioural study in Jasper has shown that people can cause a flight response in individual caribou (McKay, 2007). Human use however is currently only a fraction of what it was in the 1970s, so the potential for population level disturbance effects is less. Therefore, while individual caribou may react strongly to encounters with humans, our basic observation of concurrent declines in both human use and caribou leads us to believe

that negative consequences to individual caribou have not accumulated into population level effects.

Climate change also did not appear to be solely responsible for the historical decline in caribou abundance. The long-term trend in caribou abundance did not correlate with climate variables. In general, caribou are assumed to use snow to avoid predation (Telfer & Kelsall, 1984; Courbin *et al.*, 2009), and indeed the recent era of caribou decline has also been a time of declining snowfall. However, there have been similar periods of declining snowfall in the past (e.g. 1930 to 1940) that did not result in detectable caribou decline. The difference was that during the early era of milder winters, suppression of predation was occurring through poisoning campaigns. Since excessive predation during shallow snow years will not occur if there are few predators, this interaction between climate and predation is probably important.

Elk cope poorly with deep snow and severe winter weather (Creel & Creel, 2009, Hebblewhite *et al.*, 2002), and in Jasper, severe winter weather did cause two elk population crashes. The crash of the late 1940s occurred during an era of intense predator control, and the elk population subsequently recovered. The crash of the early 1970s however, occurred after predator control had ended and, in the presence of predation, elk populations were not able to fully recover despite declining snowfall since 1973. Thus, for both caribou and elk, we propose that the historical record demonstrates the importance of the interaction between human management practices, predation, and climate.

There has been an intricate connection between elk and wolf populations elsewhere in the Rocky Mountains (Huggard, 1993; Hebblewhite *et al.*, 2002). The trends in Jasper elk and wolf numbers, although imprecisely measured, can at least notionally be attributed to a strong interaction between the two species: at the time of European settlement there were very few elk and few wolves; the re-introduction of elk and concurrent poisoning of wolves resulted in a prolonged period of high elk numbers in an ecosystem; the decline of wolves in the late 1940s occurred after a winter elk die-off; the subsequent rise in elk numbers during the 1960s was mirrored (with a lag) by a rise in wolves; the decline of elk numbers since 1970 has been roughly mirrored (with a lag) by another decline in wolf numbers.

Today, elk abundance is almost an order of magnitude lower than it has been in the past, and it is possible that Jasper is in the process of transitioning away from an elk/wolf driven system. Our current research focus is, in part, addressing questions around predator/prey dynamics in Jasper (Hebblewhite *et al.*, 2010a).

An additional historical management factor is elk highway mortality. The post-1970 data suggest that the number of elk killed by humans (highway and railway deaths) may be as influential as elk abundance alone. The number of elk has declined steadily since 1970, so one might have expected apparent competition to wane, and caribou to increase. The number of elk killed by humans (almost all by vehicles on the highways) however, rose dramatically between 1979 and 1998 (Fig. 6). Prior to 2006, many of these road-killed elk were left in gravel pits for wolves (and other animals) to scavenge, almost certainly contributing to larger pack sizes and subsequent dispersal of young wolves, which could have prevented apparent competition effects on caribou from decreasing. Although it is impossible to be precise, the annual quantity of elk biomass left for wolves would have been almost 10 000 kilograms at its peak in the late 1990s. The origins of elk carcasses being left for wolves was not well recorded, but we found references to the practice as far back as 1980 (Kaye & Roulet, 1980). Since the practise of dumping carcasses was halted, wolf abundance has been halved (Fig. 3b) – we will continue monitoring to see if these lower numbers endure.

What do our results mean for the future of caribou management in Jasper? Parks Canada's first priority is the maintenance or enhancement of ecological integrity as described in the Canada National Parks Act (2000). Maintaining biodiversity is an important component of ecological integrity, and preventing the extirpation of a large mammal is important for preserving biodiversity. Current caribou population trends suggest that they are the large mammal species most likely to disappear from both Jasper and the greater ecosystem. Maintaining ecological processes is another imperative for achieving ecological integrity as identified in the Canada National Parks Act (2000). We believe that Jasper's history has illustrated the negative effect humans have had on predator/prey processes, so in promoting the persistence of caribou, Parks Canada will strive to remove negative or "unnatural" human influences from ecological processes, rather than directly manipulate predator and prey numbers. Excluding elk from the Jasper town site, and restricting unnatural predator access to winter caribou habitat via packed snow trails will be two of our top priorities. We believe that Jasper's history has shown us that predator control promotes hyper-abundance of wolves' primary prey (e.g., Jasper elk in the middle of last century), with disastrous consequences for caribou via apparent competition once predator control ends.

Given Parks Canada's mandate and principles, which human influences are most important to miti-

gate in order to reverse caribou declines? Our conclusion that climate change is not solely responsible for caribou decline has implications for caribou management. Previous efforts to conserve caribou in Jasper have been criticized because of the belief that climate change would render our efforts fruitless. While we cannot meaningfully reverse climate change directly, Jasper's history suggests that it is the *interaction* of climate and predation that is important. Thus, we can continue to promote caribou recovery by mitigating negative human influences on predation variables. The historical record suggests that past wildlife management practises in Jasper have heavily influenced the relationship between predators and their prey, therefore mitigating human influences and returning the ecosystem to a self regulating condition with minimal human subsidies has a good chance of positively affecting caribou persistence.

We also found no support for the hypothesis that high backcountry human use is directly related to the caribou decline. This is also important, because it allows us to concentrate our efforts on management efforts that have a higher probability of recovering caribou. For example, it is probably more important to devise ways to help caribou avoid unnaturally high predation than it is to attempt to keep hikers and campers away from caribou.

Even with very long-term, extremely detailed predator/prey data, explaining past population trends has been far easier that accurately foretelling the future (Vucetich, 2010). Our examination of historical data of limited quality is therefore unlikely to give us a precise prescription for restoring caribou in Jasper National Park. We believe however, that Jasper's history helps us to better understand the origins of our current situation, and provides broad direction for research and management that will promote caribou persistence.

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