



Evaluating viability of woodland caribou in Banff and Jasper National Parks

**Final Report: Submitted to Parks Canada
06 April 2010**

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Abstract: Recovery of endangered species may require a combination of protection and conservation action. In Banff National Park, the southernmost population of woodland caribou in Alberta was extirpated by an avalanche in April 2009. Concurrently, two of three populations in neighboring Jasper National Park have declined to alarming numbers (≤ 10). These trends reflect an uncertain future for these populations of woodland caribou despite protection within Canada's Rocky Mountain national parks. We used population viability analysis to assess the potential for caribou persistence in Banff and Jasper National Parks with and without translocation-based management. We constructed a female-based projection matrix to model caribou life history and population growth among the Banff, Brazeau, Maligne, and Tonquin populations. Input vital rates included population-specific estimates of mean adult female survival and calf/cow ratio-based estimates of mean fecundity, with process variance isolated for each. Our results suggested the Tonquin caribou population within Jasper is likely to remain viable without management action. However, almost certain extirpation is predicted for the Brazeau and Maligne populations, with median times to extinction of 16 years and low likelihoods of persistence even after translocation efforts. Simulations reintroducing 45 female caribou into Banff resulted in a 66–99% chance of ≥ 8 females remaining after 20 years, making Banff a candidate for reintroduction. However, before translocations are adopted as a recovery tool, we encourage validation of our assumptions that the original causes of extirpation have been addressed and consideration of the challenges of conducting reintroductions to the edge of species' climatic niches.

Keywords: population growth, PVA, *Rangifer tarandus*, recovery plan, SARA, survival, translocation, woodland caribou

Suggested Citation:

DeCesare, N. J., J. Whittington, H. S. Robinson, M. Hebblewhite, M. Bradley, L. Neufeld, and M. Musaini. 2010. Evaluating viability of woodland caribou in Banff and Jasper National Parks. Final Report, University of Montana, Missoula.

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Introduction

Caribou and reindeer (*Rangifer tarandus*) populations are declining globally, with primary threats hypothesized to be the direct and indirect effects of anthropogenic landscape disturbance and climate change. Vors and Boyce (2009) recently reviewed published *Rangifer* literature and found that of 42 populations with sufficient data, 34 (81%) were declining. Populations of woodland caribou (*R. t. caribou*) at the southern fringe of *Rangifer* range in North America may be especially vulnerable in landscapes with higher human presence and disturbance (Schaeffer 2003, Vors et al. 2007, Wittmer et al. 2007). In 1983 Woodland caribou were listed under the United States Endangered Species Act as *Endangered* within the contiguous US, where numbers have since dropped to <5 individuals (Wakkinen et al. 2009). Since then, both the Boreal and Southern Mountain ecotypes of woodland caribou have been subsequently listed as *Threatened* under Canada's Species at Risk Act (COSEWIC 2002). Such legal mandates for protection and recovery present many challenges (Gerber and Hatch 2002), especially as additional threats to persistence mount when populations become small and vulnerable to the extinction vortex (Gilpin and Soulé 1986).

Population viability analysis (PVA) provides one tool for conservation managers to evaluate trends in population growth, and to predict future trends in population size and extinction probability under different management scenarios (Crouse et al. 1987, Doak et al. 1994, Morris and Doak 2002). The data required for accurate PVA predictions are typically unavailable for endangered species (Dennis et al. 1991), which has led to scrutiny of absolute predictions (Caughley 1994) and emphasis instead on using PVA for relative comparisons of future scenarios and population effects (Beissinger and Westphal 1998). However, when long-term and high quality data sets are available, PVA predictions can be quite accurate (Brook et al. 2000). This places increased emphasis upon demographic monitoring of rare or threatened species before populations reach immediate risk of extinction.

In Banff National Park, Canada's oldest and flagship national park, the southernmost population of woodland caribou in Alberta was collectively wiped out by a single avalanche in April, 2009 (Hebblewhite et al. 2010). This population had been historically small, composed of 25 - 40 animals from 1935 to 1993, and dwindled to less than 10 animals by 2003, before its recent extirpation. The leading explanation for this caribou decline hinges on artificially high elk (*Cervus elaphus*) densities throughout the park during the 1980's, which became the primary prey for a consequently high wolf (*Canis lupus*) population in the 1990's following wolf recolonization of Banff National Park (Hebblewhite et al. 2002, Hebblewhite et al. 2007). Peak wolf densities corresponded to a period of caribou decline during the 1990's (Hebblewhite et al. 2010). Elk and wolves eventually stabilized at low density, but their earlier eruptions may have left caribou in an inescapable vortex towards extirpation (Hebblewhite et al. 2010). Four woodland caribou populations, the A la Pêche, Brazeau, Maligne, and Tonquin populations, occur in neighboring Jasper National Park. Two of these populations, the Brazeau and Maligne, have declined to numbers akin to those in Banff prior to the avalanche event, with 2009 minimum population estimates of $N=4$ and $N=9$ caribou, respectively. The remaining two populations, the Tonquin and A la Pêche, are slightly larger, with population estimates of $N=74$ (minimum count) and $N=150$ (Smith 2004), respectively.

Collectively, three of five caribou populations in Canada's Rocky Mountain National Parks are either extirpated or have declined to fewer than 10 individuals, and the future of woodland caribou in this protected landscape is uncertain. At the same time, wolf densities in Banff have subsided since their post-recolonization peak (Hebblewhite et al. 2010), and apparently suitable habitat remains (Robinson et al. 2010). Thus conditions for caribou in Banff may be improved, and reintroduction may be a feasible management option. Translocation and reintroduction are common management strategies (Griffith et al. 1989), particularly in the recovery of ungulate populations such as bighorn sheep (Hansen et al. 1980, Singer et al. 2000), elk (Larkin et al. 2003, Anderson et al. 2005), and caribou

(Zager et al. 1995, Kinley 2009). Translocations of caribou in western North America have met mixed success. In a recent review, Kinley (2009) reported that of 37 programs identified, 67% were successful while 30% had zero caribou at last report. Specifically, the presence of novel parasites, predators, or food sources within the receiving ranges had negative implications for survival of translocated individuals.

Here we use PVA to assess the potential for caribou persistence in Banff and Jasper National Parks with and without translocation-based management. Hebblewhite et al. (2010) lamented that demographic monitoring of Banff caribou did not commence until the population had already declined, at which point most population ecologists would have considered woodland caribou effectively, or “quasi-,” extinct in Banff (Ginzberg et al. 1982, Wittmer et al. 2010). However, concurrent monitoring efforts were also spent in Brazeau, Maligne, and Tonquin populations of Jasper National Park. Given the importance of reliable demographic data in PVA, such monitoring of extant populations is paramount to our ability to forecast the future of a threatened species in the Canadian Rockies.

Methods

Study area and caribou status

The study area included portions of the Canadian Rockies within Banff and Jasper National Parks (Banff and Jasper hereafter) in Alberta, Canada (Fig. 1; 52°N, 117°W). Banff and Jasper combine with adjacent federal and provincial protected areas to form one of the largest protected landscapes (>20,000 km² of park area) in North America. Topography is extreme, ranging from 1000 to 3500 m in elevation, and climate is characterized by long, cold winters, and short summers with most precipitation occurring in spring. The landscape is ecologically classified into the montane, subalpine, and alpine ecoregions. In addition to wolves, the predator community also includes mountain lions (*Puma concolor*), grizzly bears (*Ursus arctos*), black bears (*Ursus americanus*), and wolverine (*Gulo gulo*). Wolf

diet includes elk, moose, and other ungulates such as white-tailed deer (*Odocoileus virginianus*), mule deer (*Odocoileus hemionas*), bighorn sheep, mountain goats (*Oreamnos americanus*) and woodland caribou.

In addition to the extirpated Banff population, caribou occur in four populations in Jasper, including the A la Pêche population in northern Jasper ($\hat{N} \approx 150$), and the Brazeau ($N_{min}=10$), Maligne ($N_{min}=4$), and Tonquin ($N_{min}=74$; M. B. & L.N., unpublished data) populations. The A la Pêche caribou in northern Jasper traditionally migrate to winter range outside the national parks and their conservation and recovery is considered elsewhere (Alberta Woodland Caribou Recovery Team 2005). Historically, caribou moved between these and adjacent provincial populations, but current levels of dispersal may be decreased (McDevitt et al. 2009). Mitochondrial DNA among caribou in the Canadian Rockies revealed a hybrid swarm among glacially separated barren ground and woodland lineages (McDevitt et al. 2009). However, analysis of nuclear DNA indicated population structure at a finer scale, with caribou in Banff and Jasper collectively delineated as distinct from neighboring populations (McDevitt et al. 2009). Here, we focus on the Banff population and the Brazeau, Maligne, Tonquin populations in Jasper (Fig. 1).

Caribou within the Rocky Mountain national parks are federally classified as belonging to the threatened Southern Mountain ecotype (COSEWIC 2002). Environment Canada is responsible for producing a recovery strategy for all Southern Mountain caribou, with Parks Canada considered a participating agency in the process, but no such plan yet exists. Caribou in Jasper and Banff are also included in the Alberta Recovery Plan (Alberta Woodland Caribou Recovery Team 2005), and management in Jasper is further guided by an existing park-specific action plan.

Recovery scenarios

To parameterize population viability simulations, we summarized the means and variances of key vital rates, adult survival and fecundity, as monitored among populations in Banff and Jasper during

2001–2009. We initially used these vital rates to project the current conditions of extant Jasper populations for 20 years into the future. We then simulated translocation-based recovery effort by reintroducing caribou to Banff and augmenting Jasper populations using translocation to increase initial population sizes.

Estimating vital rates

Adult Survival.

To monitor adult female survival we deployed GPS or VHF collars (Lotek Engineering Ltd., Aurora, ON) on female caribou (1.5+ yrs. old) from 2001–2009 with helicopter net-gunning (University of Montana, Animal Use Protocol 059-09MHWB-122209). For the Brazeau ($N=13$), Maligne ($N=10$), and Tonquin ($N=22$) populations, we used the Kaplan-Meier nonparametric product limit estimator (Kaplan and Meier 1958) in the survival analysis package in program Stata 10 (StataCorp 2007) to estimate population-specific annual survival across the study period based on a biological year (1 June–31 May). For Banff ($N=2$ of 5 total adults), sample size was insufficient to estimate a herd-specific survival rate. Thus we considered two scenarios in Banff, using both a pooled mean rate across all populations as a “Medium” survival scenario and the mean survival of the Tonquin population in Jasper as a “High” survival scenario. We assumed that conditions for caribou in Banff are improved enough to allow adult female survival at or above the pooled mean observed across populations in Jasper. As demonstrated by Hebblewhite et al. (2007), the conditions for caribou persistence in the Canadian Rockies can be theoretically estimated as a function of wolf and primary prey densities alone. Justification for assuming Medium to High adult female survival in Banff was drawn from the 75% decline in primary prey (elk) populations and subsequent and equivalent decline in wolf density (Hebblewhite 2006; Hebblewhite et al. 2010). Additionally, multi-species resource selection analyses suggest that suitable habitat with

spatial separation from predators and primary prey remains (Hebblewhite et al. 2007; Robinson et al. 2010).

Variance estimation for stochastic modeling should isolate process from sampling variance (White 2000), which is possible when estimates of both within- and among-year variances are available (Morris & Doak 2002). We estimated within-year variance of annual survival estimates, pooled among all populations, according to Greenwood's (1926) formula:

$$\widehat{\text{var}}(\hat{S}(t)) = (\hat{S}(t))^2 \sum_{t(i) \leq t} \frac{d_i}{n_i(n_i - d_i)} \quad (1)$$

where $\hat{S}(t)$ = annual survival estimate, n_i = the number of caribou at risk at the time of each death, and d_i = the number of deaths. We then used White's (2000) method to isolate process variance (V_c) of annual survival among all populations.

Cause-specific mortality rates were calculated using cumulative incidence functions (Coviello and Boggess 2004, Heisey and Patterson 2006). Cause of mortality for each caribou death were estimated using a combination of field evidence, including predator sign, carcass articulation and condition, and lab necropsies to assess trauma, parasite loads, and fat reserves. In cases when field visits were not timely enough to reliably determine cause of death, an 'unknown' status was recorded (Neufeld and Bradley 2009). Annual probability of mortality due to wolf predation, bear predation, avalanche, unknown, and other/natural causes were calculated separately for the periods 1988 to 1991 (Brown et al. 1994) and 2001 to 2009. These mortality rates were not used in population modeling but simply calculated to illustrate mortality patterns of caribou in the mountain national parks.

Fecundity.

Fecundity rates (\hat{F}) in female-based pre-birth pulse matrix models are the product of multiple vital rates, including pregnancy rate, fetal survival, fetal sex ratio, and calf survival through the first year. While calf survival of woodland caribou is poorly studied, recruitment is commonly monitored in woodland caribou

(McLoughlin et al. 2003) populations with spring aerial surveys of the calf/cow ratio (\hat{R}). Calf/cow ratios are adaptable to pre-birth matrix models by effectively combining multiple vital rates into a single matrix element parameterizing the contribution of 1-year-old calves at the end of each time step per adult that entered the time step. We conducted annual March calf/cow ratio surveys during 2004–2009, and used data pooled across Jasper populations to estimate the mean and process variance of fecundity. We estimated within-year mean ratios from survey counts as:

$$\hat{R}_i = \frac{\sum \text{calves}_i}{\sum \text{cows}_i} \quad (2)$$

We estimated within-year variance of ratio estimates with the binomial estimator (Thompson 1992):

$$\widehat{\text{var}}(\hat{R}_i) = \left(\frac{N_i - n_i}{N_i} \right) \frac{\hat{R}_i(1 - \hat{R}_i)}{n_i - 1} \quad (3)$$

where n_i = the number of cows counted during annual surveys, and N_i = the annual population estimate of cows developed with population-wide surveys and a joint hypergeometric maximum likelihood estimator to account for imperfect sightability (White 1996). We then used White's (2000) method to estimate process variance of \hat{R} across the study period.

March calf/cow ratios estimate the number of either-sex calves and cows that survived 10 months since the birth pulse. This does not correspond directly to fecundity (\hat{F}) for matrix projections, so we adjusted stochastically drawn values of \hat{R} in three ways. First, we divided the denominator of the ratio by a concurrent stochastic value for 10-month adult survival ($S_a^{10/12}$), which adjusted the cows counted each March to an estimate of cows that entered the time step the previous June. Second, we multiplied the numerator by the same stochastic value for adult survival adjusted to 2-month survival, which converted the calves counted each March to an estimate of calves surviving to the end of the time step the following May (assuming calf survival = adult survival in April/May). Third, we multiplied the numerator by 0.5, to account for an estimated sex-ratio of 50% female calves. Thus we estimated fecundity from simultaneously drawn stochastic March calf/cow ratio and adult survival rates as:

$$\hat{F}_{(i)} = \hat{R}_{(i)} \times \frac{\hat{S}_{a(i)}^{2/12} \times 0.5}{1/\hat{S}_{a(i)}^{10/12}} \quad (4)$$

which reduced to:

$$\hat{F}_{(i)} = \hat{R}_{(i)} \times \hat{S}_{a(i)} \times 0.5 \quad (5)$$

The effects of age on both survival and fecundity of individuals are well-documented for some ungulate species (Loison et al. 1999), though Gaillard et al. (1994) found evidence of senescence in just 25 out of 59 mammal populations surveyed. Age-specific survival and fecundity rates were not collected during our study and are not well-documented for woodland caribou in general. We did not model senescence in survival or fecundity of adult caribou, and instead assumed that our estimated mean vital rates were representative of a natural age distribution and could be applied equally across yearlings and adults.

Viability under current conditions

We constructed a stochastic, female-based, age-structured, pre-birth pulse Leslie matrix to model caribou life history and population growth for each of Banff, Brazeau, Maligne, and Tonquin populations (Leslie 1945). We used code adapted from Morris and Doak (2002) to conduct stochastic simulations in program MATLAB (R2009a, The MathWorks, Natick, MA). We drew random values of adult survival and March calf/cow ratios (adjusted to fecundity using Eq. 5) from beta distributions with estimated means and process variances. We included explicit modeling of demographic stochasticity for all simulations to treat vital rates as probabilistic individual outcomes rather than population-level averages (Morris and Doak 2002). We projected all populations 20 years into the future, and ran 10,000 simulations of each scenario. We selected a projection time of 20 years as a feasible planning horizon for recovery management in the parks, and as a conservative time frame with which to project vital rates with variances estimated from 6–8 years of input data.

Both positive (Wittmer et al. 2005) and negative (Skogland 1985) density dependence of demography has been demonstrated in *Rangifer*. We did not vary vital rates with population density for two reasons: 1) the small populations in our study area were assumed to remain below habitat-defined carrying capacity, and 2) we had insufficient data to confidently parameterize a density-dependent response to predation pressure, food, or other factors. Based on low levels of empirically observed inter-population movement of radio-collared individuals (N=1 dispersal event in 105.7 animal-years of monitoring), we treated populations as demographically isolated. Extant populations were reduced to female-only vectors by distributing minimum 2009 counts of adult females into a stable age distribution according to the right eigenvector of the mean matrix, and by assuming a 50:50 sex-ratio of calves. We estimated within- and among-year vital rate correlations using eight annual estimates of adult survival, and six concurrent estimates of March calf/cow ratios, each pooled across populations. Because correlations were not statistically significant and the simulation of correlated vital rates had minimal effects on results, we report simulation results assuming zero correlation among vital rates.

Small populations may undergo additional stressors (e.g., inbreeding depression or susceptibility to catastrophic events) that accelerate the risk of extinction below a quasi-extinction threshold (Ginzberg et al. 1982; Gilpin & Soulé 1986). Evidence in Banff suggests that extinction risk may increase when populations are reduced to a single group, because a single avalanche or predation event could feasibly cause population-level extirpation. During 2003–2008 winter population surveys, female caribou group size in Jasper ranged from 1–8 ($\bar{x}=3.1$, $N=81$ groups), similar to trends in summer group size of southern mountain caribou observed in British Columbia ($\bar{x}=3.8$, $N=2099$ groups; McLellan et al. 2010). We incorporated a quasi-extinction threshold equal to our maximum observed group size of 8 females, to recognize the increased risk faced at the population level when females are likely to be consolidated to a single group. This threshold of eight females also may be representative of the

minimum total population sizes at which recovery efforts were shown to be feasible in other populations (Compton et al. 1995; Stronen et al. 2007).

We summarized all simulations according to three measures of outcome: 1) the cumulative probability of quasi-extinction ($N \leq 8$ females at any point in the trajectory) over the 20-year time span, 2) the median number of female caribou per population at year 20, and 3) the stochastic population growth rate (λ_s), estimated as a geometric mean across simulations. Lastly, we conducted life-stage simulation analysis (LSA) to assess the correlation between each stochastically simulated vital rates and the resulting population growth rate as form of sensitivity analysis that incorporates both vital rate elasticity and observed variance (Wisdom et al. 2000).

Assessing translocation-based recovery

Following similar methods as above, we also simulated recovery scenarios implementing the translocation of caribou into each of the four considered populations (Banff, Brazeau, Maligne, Tonquin). Successful caribou translocations have typically involved the translocation of 30–60 caribou over one to three years (Jones 1966; Stronen et al. 2007). We accordingly simulated the translocation of 15, 30, or 45 female caribou to each population over one, two, or three years, respectively, which represented the total translocation of 20, 40, or 60 animals assuming a 75:25 sex ratio. Translocated caribou were also assumed to fit the stable age distribution. Translocated animals can experience lower survival rates than residents due to both mortality and emigration, though these rates can gradually improve to equal resident survival (Warren et al. 1996; Nickelson et al. 2003). We modeled three years of post-translocation survival depression, with 30%, 20%, and 10% decreases in adult survival, for the first three years when projecting populations of translocated individuals, and we assessed its effect by performing simulations both with and without survival depression for all scenarios.

Results

Viability under current conditions

Pooled mean annual survival of adult female woodland caribou was $\hat{S}=0.874$ during the study period, with raw variance $s^2=0.00985$ and isolated process variance $V_c(\hat{S})=0.00693$. Mean survival rates showed differences among populations and years (Tables 1, 2), though 95% confidence intervals overlapped among all populations. The pooled mean calf/cow ratio was $\hat{R}=0.284$, with raw variance $s^2=0.01230$ and process variance $V_c(\hat{R})=0.01030$. Simulations of extant population trajectories with herd-specific starting population sizes and vital rates forecasted a relatively certain probability of quasi-extinction for three of four populations, with caribou remaining only in the Tonquin population within Jasper (Table 3, Figs. 2, 3). The Banff population was extirpated in 2009, and the Brazeau (current $N_f = 3$) and Maligne (current $N_f = 6$) populations are currently at population sizes below our quasi-extinction threshold of 8 females. These two populations also had low adult female survival (Brazeau $\hat{S}_i=0.806$; Maligne $\hat{S}_i=0.842$), and showed declining stochastic population growth rates, $\bar{\lambda}_s$, of 0.884 and 0.922, respectively. The median time to complete extirpation ($N=0$) for both the Brazeau and Maligne populations was 16 years. The Tonquin population contained the largest extant population size (current $N_f = 33$) with the highest observed survival rates ($\hat{S}_i=0.944$), which suggested a growing population in the short-term future ($\bar{\lambda}_s = 1.041$). Consistent with these relationships between population-specific measures of \hat{S}_i and $\bar{\lambda}_s$, life-stage simulation analysis revealed that adult survival explained most of the variation in annual population growth ($r^2=0.81$) and calf/cow ratios a smaller amount ($r^2=0.19$).

Cause-specific mortality rates of adult female caribou were highest for wolf (0.106) and unknown sources of predation (0.155) during the 1988–1991 study period, declining to 0.045 (wolf) and 0.054 (unknown predation) during the 2001–2009 study period. Other sources of mortality included avalanches, other natural causes, and unknown causes (Table 4).

Assessing translocation-based recovery

The addition of different numbers of translocated female caribou also affected simulation results for reintroduction to Banff and supplemental translocation to Jasper populations (Table 3; Figs. 2, 3). Translocations into the Tonquin population yielded the greatest population size at year 20 and the lowest probability of region-wide quasi-extinction. Translocations into the Banff, Brazeau, and Maligne populations, instead, resulted in smaller numbers of caribou remaining in multiple populations, with translocations to Banff providing the greatest probability of conserving caribou in both national parks. For example, the simulated reintroduction of 45 female caribou (15 per year for 3 years) to Banff using the Medium survival scenario resulted in a median population of 13 females after 20 years, and a 34% likelihood of having 8 or fewer female caribou remaining. Increasing survival to the High scenario increased median population size to 61 and decreased the probability of $N \leq 8$ to 2%. On the other hand, adjusting the number of caribou to 30 (over 2 years) or 15 (in 1 year) under the Medium survival scenario decreased median population sizes to 9 and 4, and increased the likelihood of $N \leq 8$ to 91% and 94%, respectively. We assumed low initial survival rates for all translocation simulations, and parameterization of three years of post-translocation survival depression resulted in an average 40% decrease in the median number of females in 20 years.

Discussion

Our results paint the grim picture that, given current conditions, Jasper will have lost 50% of its caribou populations, and the Canadian Rocky Mountains national parks 3 of 5 populations in 20 years. Observed adult female survival rates in the Brazeau and Maligne populations in Jasper are low enough that stochastic simulations suggest likely extirpation of these populations in less than 20 years without recovery action. Reflecting the recent extirpation event in Banff, protection alone may not be enough to stave off caribou extinctions in the national parks. This mirrors conditions for other small woodland

caribou populations across Canada, where habitat protection, reduction of predators and primary prey, and translocation have all been used for conservation (Compton et al. 1995, Mosnier et al. 2003, 2008, Stronen et al. 2007). Significant and sustained efforts may be required to maintain current populations.

Translocations to augment caribou populations may be a valuable means to “buy time” until underlying threats to populations can be mitigated. Our results highlight this effect by showing that translocations do not alter population trends but instead affect only the initial population size from which trends play out. Given current vital rates among caribou populations in Jasper, translocation still yielded a low likelihood of recovery in the Brazeau and Maligne populations because wolf and primary prey densities there likely exceeded thresholds for viability (Hebblewhite et al. 2007). Our simulations of translocation into Banff were founded on the assumption that the lower predator and primary prey densities observed there would increase viability (Hebblewhite et al. 2007), making Banff the preferred destination for caribou translocation in our study area. The nearest caribou translocation program to our Canadian Rockies study area occurred in the Selkirk Mountains of northern Idaho and southern British Columbia, where caribou were translocated to augment an already small population (Compton et al. 1995). In the Selkirks, translocated animals experienced initially low survival due largely to predation (Kinley & Apps 2001) and uncertain success (Zager et al. 1995). Subsequent targeted predator control (on cougars and wolves) and habitat management may have been responsible for recent population increases (Wakkinen et al. 2009); this population has been growing at approximately 4%/year for the last 5 years. The Selkirk example suggests that management of threats may need to occur adaptively following translocations. Although we did not model density dependence or Allee effects of population density upon vital rates, translocation may also aid endangered populations in escaping Allee effects if vital rates are especially impacted at low density (Angulo et al. 2007; McLellan et al. 2010).

The IUCN’s recommendations regarding species reintroduction emphasize that reintroductions should only take place when threats are removed and habitat requirements are suitable (IUCN 1987).

Given that global caribou declines have been linked to climate change (Vors and Boyce 2009) and predator-mediated indirect effects of anthropogenic habitat disturbance (Wittmer et al. 2007), it is difficult to know with certainty that the initial cause of extirpation in Banff has been removed. Predator and primary prey densities have declined (Hebblewhite et al. 2010), and multi-species habitat suitability analysis suggests favorable caribou habitat in Banff with high spatial separation from primary prey (Robinson et al. 2010). Cautious translocation action may be justified if accompanied by rigorous monitoring and adaptive recovery protocols to address threats of direct human impacts and indirect ecosystem conditions such as primary prey and predator density (Kinley & Apps 2001; Serrouya & Wittmer 2010). For example, recovery of endangered island foxes on California's Channel Islands has achieved success as a result of intensive primary prey (feral pigs; *Sus scrofa*) control and translocation-based removal of protected predators (golden eagles; *Aquila chrysaetos*) from the islands (Courchamp et al. 2003). This level of direct community manipulation may be required for woodland caribou populations under the grip of proximate threats of apparent competition, though long-term results may only come with managing the ultimate source of abundant primary prey and predators rather than their abundance *per se* (DeCesare et al. 2010). IUCN guidelines also recommend consideration of social implications of translocation, which in this case may include benefits to education within the parks or costs to local peoples inhabiting areas of potential source populations. In fact, Wolf et al. (1996) found that the success of species translocations was correlated with both ecological factors such as habitat conditions, predation, and habitat improvement (recovery) actions, and with the degree of public acceptance and support.

Debate surrounds the conservation of species in peripheral portions of their range on both demographic (Wolf et al. 1996; Lomolino & Channell 1998) and genetic (Lesica & Allendorf 1995; Schwartz et al. 2003) grounds. Peripheral populations theoretically occur at the edge of tolerable environmental conditions (*sensu* Hutchinson's "fundamental niche"; Hutchinson 1957). A quantitative

assessment of the relationship between range position and population demography is lacking for *Rangifer*. Vors and Boyce (2009) highlight that global declines are primarily the result of two factors: climate warming and anthropogenic landscape change. These impacts may affect individual populations disproportionately across species' ranges, as shown in the relationships between anthropogenic disturbance and caribou distribution in Ontario (Schaeffer 2003) and globally between climate warming and at least barren-ground caribou and elk demography (Post et al. 2009). Populations of caribou in Banff and Jasper National Park might be those most susceptible to climate warming, due to their locations at the southern geographic extent of caribou range in North America. However, if changes in woodland caribou distribution are driven more by spatial patterns of human disturbance than climate factors (Environment Canada 2008), protection of these populations within federally-designated national parks might outweigh concerns of climate change. Regardless, given the rapid pace of ongoing landscape disturbance outside of protected areas in both Alberta and British Columbia, national parks may be the only realistic habitats for caribou recovery in the coming decades (McLoughlin et al. 2003; Environment Canada 2008).

Uncertainty is difficult to overcome, but it seems likely that woodland caribou may become a conservation-reliant species in Canada (Scott et al. 2010), especially if suitable habitat is eventually relegated only to protected areas in which they are still vulnerable. Protection and recovery efforts under SARA are still in their infancy. Current recovery efforts for woodland caribou and other potentially conservation-reliant and listed species such as sage grouse (*Centrocercus urophasianus*) and the Vancouver island marmot (*Marmota vancouverensis*) will likely set the stage for conservation and recovery of threatened and endangered species across Canada into the future. Zager et al. (1995) emphasized increasing both the spatial and temporal scales over which conservation efforts for endangered species are directed. Broadening spatial scales require consideration of range-wide population status and the effect of translocation management on both source and receiving

populations. Broadening temporal scales challenge conservationists to build long-term recovery strategies, and acknowledge that ecological conditions are dynamic and require adaptive protocols. Implementation of protection and recovery actions for woodland caribou outside of the federal parks face many challenges under Canada's relatively new and untested Species at Risk Act. Given the protection bestowed to Banff and Jasper, as well the region's symbolic importance to the nation's natural landscape, the maintenance of populations of woodland caribou within these national parks may have both ecological and social benefits for long-term species persistence.

Acknowledgements

We thank Parks Canada for many years of collaboration and support, and the views expressed herein are those of the authors, and not necessarily of Parks Canada. Funding for our research program has been provided by the Alberta Conservation Association, Alberta Department of Sustainable Resource Development, British Columbia Ministry of the Environment, Canadian Association of Petroleum Producers, Shell Canada, University of Calgary, University of Montana, Weyerhaeuser Company, and World Wildlife Fund. We thank S. Cleveland, J. Goldberg, L. Greene, M. Hurley, C. Miller, W. Peters, J. Polfus, and B. Weckworth for thoughtful discussion and assistance with literature review when developing this project. We acknowledge all attendees of the Banff Caribou Translocation Technical Meeting in February, 2010 for constructive criticism. We also thank our research collaborators including but not limited to C. Carroll, C. Callaghan, A. Dibb, D. Hervieux, L. Morgantini, M. Russell, F. Schmiegelow, D. Seip, R. Serrouya, K. Smith, D. Stepnisky, C. White, and J. Wilmshurst.

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Table Captions

Table 1. Vital rates from Southern Mountain Woodland Caribou pooled across all monitored individuals in Banff and Jasper National Park, 2001 – 2008, including estimates of variance, sample size, and process variance. Annual estimates were based in a biological year from June 1 – May 31, with calf/cow ratios estimated each March of the following year.

Table 2. Population-level adult female survival (\hat{S}_i) and pooled mean March calf/cow ratio (\hat{R}), and pooled process variance (V_c) estimates for southern mountain woodland caribou in Banff and Jasper National Park, 2001–2009, including the number of females monitored ($N_{monitored}$), the number of mortalities ($N_{mortalities}$), the survival analysis time (days).

Table 3. Median female population size at year 20 ($\hat{N}_{f,t=20}$), probability of quasi-extinction ($\text{pr}(N_f \leq 8)$), extant female population sizes (N_f), and geometric mean stochastic growth rate ($\bar{\lambda}_S$) under different translocation and survival scenarios from PVA simulations of translocations to reintroduce (Banff) or augment (Brazeau, Maligne, Tonquin) caribou populations in the Canadian Rockies, Banff and Jasper National Parks, Alberta, Canada.

Table 4. Cause-specific mortality rates for adult female caribou estimated from cumulative incidence functions in Banff and Jasper National Parks, 2001-2009.

Table 1.

Year	Adult female survival			March calf:cow ratio		
	Survival	VAR	N_{Adults}	Calves/Cows	VAR	N_{Cows}
2001	1	.	4			
2002	1	.	11			
2003	0.917	0.00637	12	0.318	0.00759	22
2004	0.849	0.00997	15	0.231	0.00483	26
2005	0.911	0.00359	22	0.133	0.00109	45
2006	0.832	0.00588	25	0.422	0.00235	45
2007	0.875	0.00456	24	0.213	0.00108	47
2008	0.694	0.00926	22	0.387	0.00417	31
Mean, Process Variance	(0.8744, 0.0069)			(0.284, 0.0103)		

Table 2.

Population	$N_{monitored}$	$N_{mortalities}$	Analysis time	<u>Adult female survival</u>		<u>March calf/cow ratio</u>	
				\hat{S}_i	$V_c(\hat{S}_i)$	\hat{R}	$V_c(\hat{R}_i)$
Banff	2	2	1996
Brazeau	13	7	2425	0.8057	.	.	.
Maligne	10	5	2792	0.8418	.	.	.
Tonquin	22	5	2425	0.9441	.	.	.
Pooled	47	19	2792	0.8744	0.0069	0.284	0.0103

Table 3.

Number of translocated females	<u>Brazeau</u> extant $N_f = 3$ $\bar{\lambda}_S^* = 0.884$		<u>Maligne</u> extant $N_f = 6$ $\bar{\lambda}_S = 0.922$		<u>Tonquin</u> extant $N_f = 33$ $\bar{\lambda}_S = 1.041$		<u>Banff (Medium)</u> extant $N_f = 0$ $\bar{\lambda}_S = 0.958$		<u>Banff (High)</u> extant $N_f = 0$ $\bar{\lambda}_S = 1.041$	
	$\bar{N}_{f,t=20}$	$\text{pr}(N_f \leq 8)$	$\bar{N}_{f,t=20}$	$\text{pr}(N_f \leq 8)$	$\bar{N}_{f,t=20}$	$\text{pr}(N_f \leq 8)$	$\bar{N}_{f,t=20}$	$\text{pr}(N_f \leq 8)$	$\bar{N}_{f,t=20}$	$\text{pr}(N_f \leq 8)$
0	0	1.000	0	1.000	75	0.008
15	1	0.993	2	0.969	96	0.003	4	0.937	20	0.550
30	2	0.965	5	0.830	115	0.002	9	0.606	40	0.073
45	3	0.916	7	0.650	137	0.001	13	0.344	61	0.016

*Years during which population sizes were affected by translocation-added animals and post-translocation survival depression were excluded from the estimation of stochastic growth rates ($\bar{\lambda}_S$).

Table 4.

Cause of mortality	<u>1988–1991</u>		<u>2001–2009</u>	
	CIF	SE	CIF	SE
Wolf predation	0.1056	0.0507	0.0448	0.0179
Unknown predation/scavenged	0.1548	0.0821	0.0541	0.0200
Avalanche	0.0000	0.0000	0.0209	0.0119
Other	0.0526	0.0512	0.0162	0.0114
Unknown	0.0273	0.0270	0.0550	0.0283

Figure Captions

Figure 1. Kernel home ranges of GPS-collared caribou for three extant populations in Jasper National Park the recently extirpated population in Banff National Park in the Canadian Rocky Mountains, Alberta, 2001–2009.

Figure 2. Median number of female caribou over time from 10,000 population projection simulations for each of several scenarios representing different populations of woodland caribou, survival scenarios (Banff only), and translocation management (15 females added per year for three years) in Banff and Jasper National Parks, Alberta.

Figure 3. Probability of quasi-extinction ($N_t \leq 8$) over time from 10,000 population projection simulations for each of several scenarios representing different populations of woodland caribou, survival scenarios (Banff only), and translocation management (15 females added per year for three years) in Banff and Jasper National Parks, Alberta.

Figures

Figure 1.

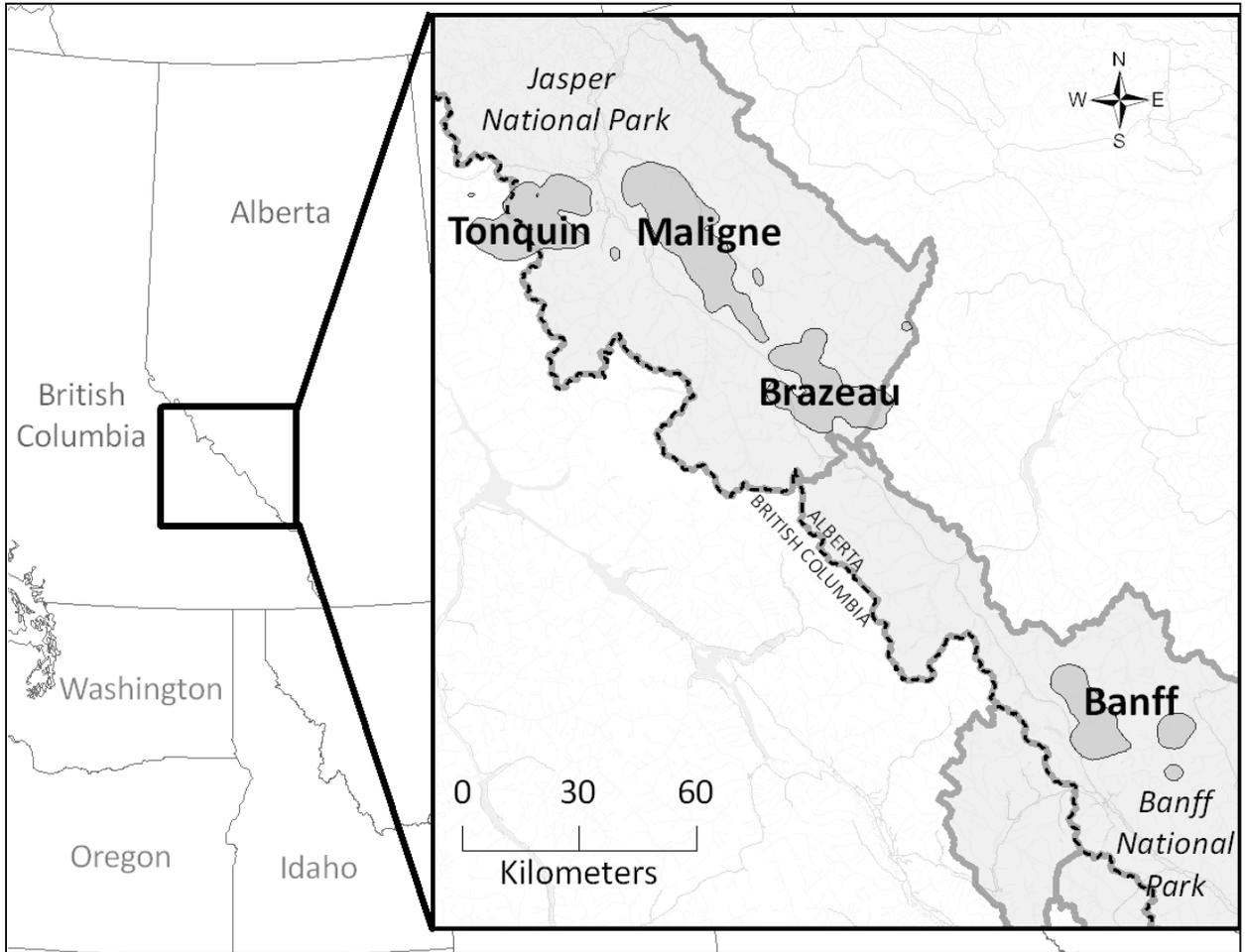


Figure 2.

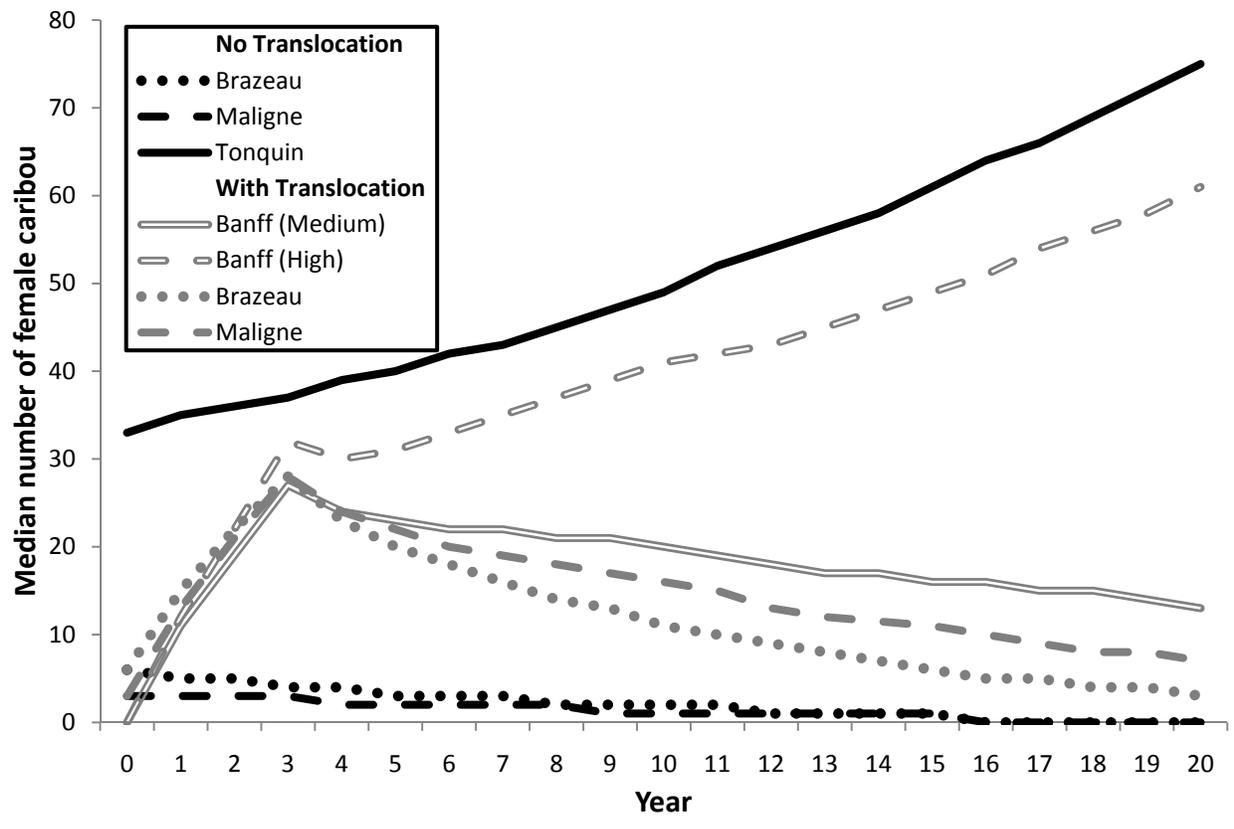


Figure 3.

