



Viability of mountain caribou in British Columbia, Canada: Effects of habitat change and population density

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ABSTRACT

Population viability analyses (PVA) are frequently employed to develop recovery plans and inform management of endangered species. Translating results from PVA into meaningful management recommendations often depends on an understanding of how population parameters change with environmental conditions as well as population density. The decline of mountain caribou (*Rangifer tarandus caribou*) in British Columbia, Canada, is believed to be caused by apparent competition with alternative prey species following changes to the forest age structure from timber harvest and wildfire. In addition, populations have been shown to decline at faster rates at low population density. To evaluate the potential effects of habitat change and population density on population persistence, we used stochastic projection models for 10 distinct populations varying in initial size from <10 to approximately 150 females. In an initial model, we used estimates of vital rates based on information sampled from >350 radiocollared caribou between 1984 and 2004. We then compared the results of the initial model to a set of models that evaluated the effects of habitat conditions and population density via their expected relationships to female adult survival. Assuming that vital rates remain constant over a 200-year time frame, only three populations have high probabilities (>0.95) of extinction. When models incorporate the declines in adult female survival known to occur with increasing proportions of young forest and declining population densities, all 10 populations are predicted to decline to extinction within <200 years. Based on our results, we suggest that PVA models that fail to incorporate the effects of changes in vital rates with habitat and population density may lead to overly optimistic assessments of the probability of population persistence in endangered species.

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1. Introduction

Population viability analysis (PVA) refers to a group of analytical and modeling approaches for assessing the risk of population extinction (Shaffer, 1981; Beissinger, 2002). The main focus of contemporary PVA is usually not predicting absolute time to extinction but identifying factors and environmental conditions that most strongly affect the likelihood of extinction (Reed et al., 2002). Translating results from a PVA into meaningful management recommendations requires both substantial empirical data from the system of interest and an estimation of the stochasticity inherent in the system (Ludwig, 1999; Engen et al., 2001). When used in this manner, PVA can be a valuable tool for both scientists

and resource managers for predicting the probable fate of endangered populations under a variety of management scenarios.

Understanding how vital rates change with environmental conditions as well as with population density is critical for making accurate predictions about population persistence (Morris and Doak, 2002; Henle et al., 2004). While spatially explicit models have been widely used to quantify species-specific habitat requirements (e.g., Johnson et al., 2004; Brambilla et al., 2009), our ability to link changes in environmental conditions to population processes remains limited for most species (Akcakaya et al., 1995; Caughley and Gunn, 1996). Furthermore, our understanding of density-dependent processes is usually based on studies of large populations where the per capita growth rate typically decreases with increasing population density (i.e., density dependence) (Sinclair, 1989). At very small population sizes, however, Allee effects are common and the per capita growth rate may instead decrease with declining population density (reviewed in Courchamp et al., 2008).

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Seip (1992) and Wittmer et al. (2005a, 2007) concluded that the decline of the endangered arboreal lichen-feeding ecotype of woodland caribou (*Rangifer tarandus caribou*), commonly referred to as “mountain caribou” (Heard and Vagt, 1998), has been caused primarily by apparent competition (*sensu* Holt, 1977) due to ecological changes brought on by timber harvest and wildfires that result in an abundance of early seral stage forests. An increasing abundance of early seral conditions has led to widespread increases in alternative prey species such as moose (*Alces alces*) and deer (*Odocoileus* spp.) (Seip, 1992; Shackleton, 1999). Increased prey availability, together with cessation of predator control, also resulted in rebounding predator numbers, particularly wolves (*Canis lupus*) (Hayes and Gunson, 1995), but cougars (*Puma concolor*) also increased across western North America (Riley and Malecki, 2001) including at least the southern portion of mountain caribou distribution (Mowat, 2007). Due to high predation rates, most mountain caribou populations are in decline and survival rates of adult females are, as predicted by the apparent competition hypothesis, related to the proportion of early seral forest within a given population’s range (Wittmer et al., 2007).

However, the results of Wittmer et al. (2005a, 2007) also suggested that high predation rates may have resulted in an Allee effect. Models developed by McLellan et al. (in press) suggest that predator-mediated Allee effects may occur where predators rely on more than one prey species provided the secondary (i.e., rare) prey species lives in groups and the average group size declines as the population declines. In such a case, the rate at which the number of groups declines is less than the rate that the population declines. Thus the rate that predators encounter a group may remain relatively stable but when a predator kills one animal from smaller groups, the predation rate increases with declining density. These conditions appear likely for caribou (e.g., Dale et al., 1994; McLellan et al., in press) as well as other large herbivores living in social groups (e.g., Hebblewhite and Pletscher, 2002; Fryxell et al., 2007).

Here we use PVA to determine the sensitivity of extinction probabilities to uncertainties in the effect of habitat change and population density in a system where the relationship between vital rates and changes in environmental conditions and population density has been relatively well documented for an endangered herbivore. We evaluate these uncertainties by comparing extinction probabilities produced by stochastic population projection models for 10 distinct populations of mountain caribou varying in initial population size from <10 to approximately 150 females. First, we estimate extinction probabilities using models that do not incorporate influences of habitat conditions or population density (but do include demographic stochasticity and uncertainty in parameter estimates). We then contrast the results from this initial analysis with results from a set of alternative models where female adult survival changes as a direct function of the amount of early seral forests as well as population density because these were the independent variables that best explain variation in survival in mountain caribou (Wittmer et al., 2007). Outcomes of the PVA are then used to support appropriate recovery strategies for these endangered caribou.

2. Methods

2.1. Species distribution and biology

Mountain caribou are the southernmost remaining caribou in North America and are found only in mountainous ecosystems of southeastern British Columbia, Canada, and extreme northern Idaho, United States. A century ago, mountain caribou were abundant and sightings of single groups of >100 animals were recorded

across much of their distribution, including a few sightings of 1000 or more individuals in a group (Spalding, 2000; McLellan, 2009). In 2004, mountain caribou totaled fewer than 1900 individuals fragmented into 18 isolated populations with total population size declining by up to 8% per year (Wittmer et al., 2005a, 2005b). The distribution of these remaining populations is closely associated with the interior wet-belt ecosystem (Apps and McLellan, 2006) where high annual precipitation and cool climate result in deep snowpacks and large, historically continuous stands of old forests (Meidinger and Pojar, 1991). A detailed description of the vegetation communities in the interior wet-belt ecosystem was provided by Meidinger and Pojar (1991).

Mountain caribou are distinguished from other woodland caribou populations by their behavioral and ecological adaptations rather than by genetics (Zittlau, 2004). In particular, mountain caribou rely on old forests at high elevations for several life-history requirements including abundant arboreal lichens, their primary winter food (Rominger et al., 1996; Terry et al., 2000), and to avoid other ungulate species and their predators (Seip, 1992; Apps and McLellan, 2006; Wittmer et al., 2007). In contrast to other woodland caribou in North America, mountain caribou walk on top of the typically 2–4 m deep snowpack at high elevations to gain access to lichens that hang from branches of older trees. Mountain caribou move seasonally to lower elevations in parts of their distribution (Apps et al., 2001), but only to reach green vegetation in early spring and again in early winter when snow at higher elevations has yet to deepen and consolidate, making it difficult for animals to access arboreal lichens in the tree canopy.

2.2. Data collection and population structure

The population dynamics of mountain caribou have been monitored for >20 years. Between 1984 and 2004, >350 adult caribou were captured and fitted with telemetry collars equipped with mortality-motion sensors. Monitoring of individual caribou resulted in long-term estimates of vital rates as well as detailed information of causes of mortality across most of their distribution (Wittmer et al., 2005b, 2007). We did not extract teeth from these endangered animals for aging so age-specific rates are unavailable.

Systematic aerial surveys were conducted by helicopter over the entire distribution of mountain caribou since 1992 (Wittmer et al., 2005b). Aerial surveys were in late winter when the majority of mountain caribou use open, high elevation habitats (Apps et al., 2001) where tracks in the snow are clearly seen. Tracks could then be followed until the animals were sighted, and, because mountain caribou live in small groups, they were easily enumerated. The detection probability, determined by the proportion of radiocollared animals seen, was >90% (Wittmer et al., 2005b), and thus allowed for relatively accurate population estimates.

The population distribution of mountain caribou has been delineated from telemetry locations. Based on the extensive radiotelemetry data on >350 adult caribou, Wittmer et al. (2005b) identified 18 populations with no recorded movements among populations. Also, none of the 27 calves collared since 2004 have moved among populations (Van Oort et al., unpublished). Due to the small number of collared individuals in some populations, however, reliable estimates of vital rates required to perform a PVA were effectively restricted to 10 populations (Wittmer et al., 2005b, 2007). We therefore limited our analyses to these 10 populations with sufficient data.

2.3. Model parameters

Population growth rates and persistence in large herbivores are largely functions of female vital rates (Gaillard et al., 2000; Gordon et al., 2004). Consequently, we developed stochastic population

models to project population persistence restricted to female caribou.

All 10 populations included in this analysis were surveyed either in 2002 or 2004 (Wittmer et al., 2005b), and we used these estimates as starting points for the PVA models. We used the following estimates for model parameters (Table 1):

2.3.1. Number of females

During census flights in late March, antlered females were often difficult to distinguish from young males without excessive harassment (Wittmer et al., 2005b). Thus, in the absence of reliable estimates of sex ratios for individual populations, we assumed initial sex ratios of 58% females and 42% males, within the range of sex ratios commonly reported for woodland caribou (e.g., Schaefer et al. (1999): 61% females; Stuart-Smith et al. (1997): 53.5% females). We then adjusted the population estimates to obtain the initial number of female caribou.

2.3.2. Population density

We divided current population estimates of female caribou by the area of the population's range estimated from telemetry data (Wittmer et al., 2005b) to derive the density of females within each population.

2.3.3. Survival rates

Wittmer et al. (2007) estimated survival rates of adult (i.e., ≥ 3 -years old) females from radiocollared animals using known-fate mark-recapture models in program MARK (White and Burnham, 1999). Survival rates were estimated for all 10 populations and corrected for sampling variance (White et al., 2001). These corrected

survival estimates ensured that only process variance was included in our analysis (White et al., 2002). In the absence of actual data on survival rates of either yearlings (1-year old) or juveniles (2-years old), we assumed that the survival of these age classes equals adult survival. While likely an oversimplification, previous research has indicated that caribou ≈ 10 months of age are likely to experience similar mortality rates as older animals (Bergerud, 1980; Fuller and Keith, 1981).

2.3.4. Calf survival

We estimated calf survival from the ratio of observed calves per adult female during population censuses in late winter to total expected spring calf production using the same data as Wittmer et al. (2005b). Calf survival was bounded according to the relationship between observed calf survival rates and corresponding female densities (Fig. 1).

2.3.5. Age structure

We grouped animals into four age classes (i.e., calves, yearlings, juveniles, adults). The proportion of calves in each population was available from the survey data (Wittmer et al., 2005b). Yearlings and juveniles were indistinguishable from adults during population surveys. Thus we estimated initial numbers of these classes at the start of each simulation based on population-specific survival rates drawn at random assuming a normal distribution with means and standard deviation presented in Table 1 and using the linear regression for calf survival (Fig. 1). These rates determine the proportion of the population in each age class. Individuals were assigned randomly to each age class.

Table 1
Summary of vital rates \pm SD used to initialize the PVA for mountain caribou in British Columbia, Canada.

Population	Area (km ²)	% Forest 1–40 years	Population estimate (year) ^a	Females/ calves ^b	Female density (km ²)	Corrected survival estimates ^c	Birth rate ^d
Purcells-South	771	18.29	16 (2002)	8/1	0.010	0.67 \pm 0.14	0.69 \pm 0.02
Nakusp	2340	9.53	108 (2002)	53/6	0.023	0.85 \pm 0.04	0.69 \pm 0.02
Columbia-South	1761	6.07	38 (2004)	19/3	0.011	0.86 \pm 0.03	0.69 \pm 0.02
Frisby-Boulder	613	6.69	25 (2004)	10/3	0.016	0.90 \pm 0.05	0.69 \pm 0.02
Columbia-North	4526	8.82	129 (2004)	64/9	0.014	0.81 \pm 0.03	0.69 \pm 0.02
Groundhog	1277	12.62	20 (2004)	9/2	0.007	0.79 \pm 0.07	0.69 \pm 0.02
Wells Gray	8141	5.74	307 (2004)	144/29	0.018	0.85 \pm 0.02	0.69 \pm 0.02
Barkerville	742	6.32	52 (2004)	27/2	0.036	0.88 \pm 0.04	0.69 \pm 0.02
North Cariboo Mtn.	1779	10.72	271 (2002)	143/11	0.080	0.90 \pm 0.05	0.69 \pm 0.02
Hart Ranges	3890	7.42	316 (2002)	153/30	0.039	0.93 \pm 0.03	0.69 \pm 0.02

^a Population estimates used as starting point for the PVA models from Wittmer et al. (2005b).

^b Number of female calves (assuming a sex ratio of 50:50) per adult female (assuming a female to male ratio of 58:42).

^c Survival rates corrected in program MARK to only include process variation from Wittmer et al. (2007).

^d Birth rates adjusted for age of first reproduction of 3 years from Wittmer et al. (2005b).

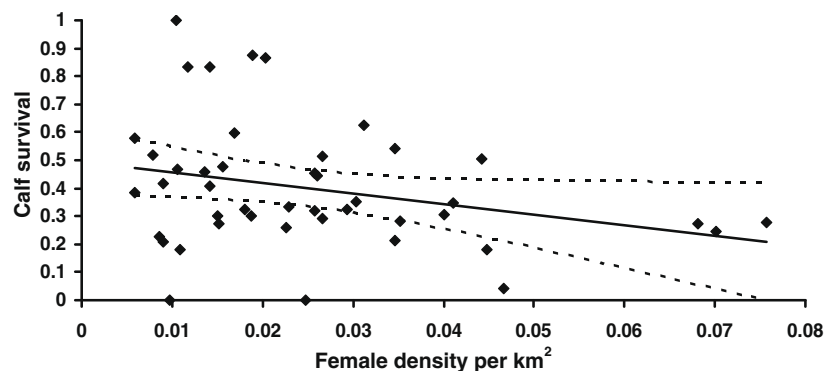


Fig. 1. Relationship between calf survival and female density estimated from multiple census results for 10 populations of mountain caribou in British Columbia; line indicates goodness of fit curve from regression analysis as $y = -3.7842 (\pm 1.9798) * x + 0.4968 (\pm 0.0598)$ with 95% confidence intervals.

2.3.6. Age of first reproduction

Woodland caribou can give birth as early as 2 years of age (Rettie and Messier, 1998). However, age of first reproduction is often 3 years for caribou in arctic environments (e.g., Whitten et al., 1992). In the absence of reliable empirical data for mountain caribou, we conservatively estimated age of first reproduction at 3 years but determined the sensitivity of extinction probabilities to uncertainty in age of first reproduction by setting the proportion of 2 year-old animals giving birth at 0, 0.2 and 0.8.

2.3.7. Birth rate

Birth rates of mountain caribou were estimated from pregnancy rates determined from blood progesterone levels consistent with pregnancy (Wittmer et al., 2005b). Blood samples were taken from 134 adult females across 8 populations and 11 different years. Pregnancy rates of mountain caribou averaged $92.4\% \pm 2.24$ during the last trimester and did not differ among years or populations (Wittmer et al., 2005b). We then estimated the expected number of female calves ($N_{0,t}$) born in a given year as

$$N_{0,t} = \sum_a Pr_t p_a N_{a,t} \quad (1)$$

Each breeding season, expected pregnancy rate (Pr_t) for mature individuals were drawn randomly from a normal distribution with mean and standard deviation described above. Females ($N_{a,t}$) were randomly assigned as mature with probability p_a . Note that such a calculation can result in individuals deemed mature 1 year being classified as immature the next. Mature individuals were then randomly assigned, with probability Pr_t , as pregnant. Finally, for pregnant individuals and assuming a 50:50 sex ratio at birth, calf sex was determined.

2.4. Model structure and simulations

The age specific female population in early spring each year, shortly before parturition, $N_{a,t}$ (for females age 1 year and older) was simulated using the following simple balance model:

$$N_{a,t} = s_{a-1,t-1} N_{a-1,t-1} \quad (2)$$

where $s_{a-1,t-1}$ are the annual population and age specific female survival rates for ages greater than one that were randomly drawn from a normal distribution with means and standard deviation based on the data in Table 1 (density-dependent for calves surviving to become yearlings) applied to all individuals of the previous year ($N_{a-1,t-1}$). We then determined the number of years a population persisted (up to 200 years) and the probability of a population going extinct after a certain number of years.

2.4.1. Initial models

In the initial models we estimated time to extinction assuming that the mean and variance of female survival rates remained constant over time. At each time step demographic stochasticity was included following Caughley and Gunn (1996, page 156) where each individual survives to the next time step if a random number drawn from a uniform distribution bounded by 0 and 1 falls under the population's survival probability. Adult mean survival rates were bounded at 0.95 because average annual adult survival rates >0.95 have not been previously reported for woodland caribou (Stuart-Smith et al., 1997; Rettie and Messier, 1998; Schaefer et al., 1999; Wittmer et al., 2007); however, this does not preclude 100% of individuals surviving in any given year by chance alone (see above). Because we do not know reproductive rates of young mountain caribou, uncertainty regarding the proportion of 2-year old animals giving birth (0, 0.2, and 0.8) were explored to evaluate the sensitivity of model predictions to age of first reproduction.

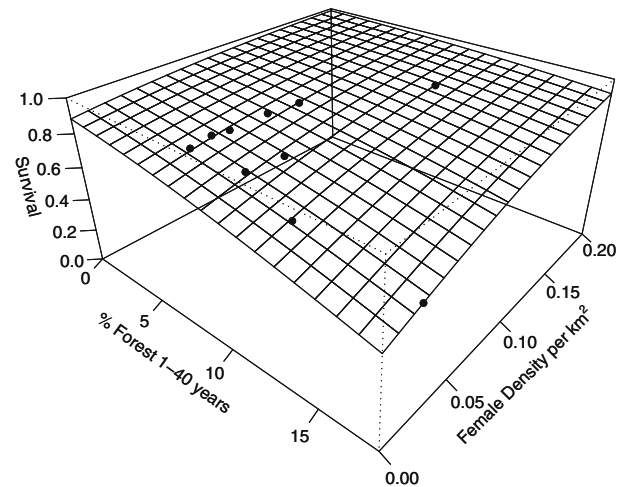


Fig. 2. Relationship between survival of adult females, percentage of young forest age 1–40 years and female density for 10 populations of mountain caribou in British Columbia (population-specific survival estimates shown in graph).

2.4.2. Alternative models

Wittmer et al. (2007) found that variation in adult female survival rates was best explained by a model that considered both the effects of the amount of young (i.e., <40 years) forests within the range of distinct caribou populations and population density. Results from this model indicated that survival decreased with increasing percentage of young forest and declining population density (i.e., positive density dependence) (logit $\phi = 2.036 (\pm 0.346) - 0.1032 (\pm 0.031) * (\text{FOR1-40}) + 11.109 (\pm 4.952) * (\text{density})$) (Fig. 2) (Wittmer et al., 2007). Standard errors of the slope and intercept for the derived parameters were estimated using the delta method (Cox, 1998) thus eliminating sampling variance from our estimates of survival. From this relationship we then estimated the effect of density on survival by standardizing the effect of forest age to: (i) the minimum percentage (5.74%; $S_{t,t+1} = 1.042 (\pm 0.040) + 0.049 (\pm 0.022) * \ln(\text{density}_t)$); (ii) the mean percentage (9.22%; $S_{t,t+1} = 1.051 (\pm 0.055) + 0.064 (\pm 0.031) * \ln(\text{density}_t)$); (iii) the maximum percentage (18.29%; $S_{t,t+1} = 1.051 (\pm 0.115) + 0.112 (\pm 0.064) * \ln(\text{density}_t)$) of forest age 1–40 years currently observed in population ranges of caribou in our study. In all three alternative models, female survival rates were updated at each time step using values from the regression between population density and survival rates.

For each population time to extinction and the resulting cumulative probability distributions of years to extinction were determined from 10,000 simulations. A maximum time horizon of 200 years was used for all simulations. Although a maximum of 200 years is somewhat arbitrary, it is a reasonable time horizon to explore factors impacting population persistence in the short term given current knowledge of population demography and facilitates the visual comparison of differences between populations. Population parameters were updated at the beginning of each calving season and time to extinction was determined when $N_t = 0$.

3. Results

3.1. Initial models

Using current estimates of vital rates and the amount of forest <40 years of age remaining static and excluding potential effects of positive density dependence, three populations (Purcells-South, Columbia-North, Groundhog) had high probabilities (>0.95) of

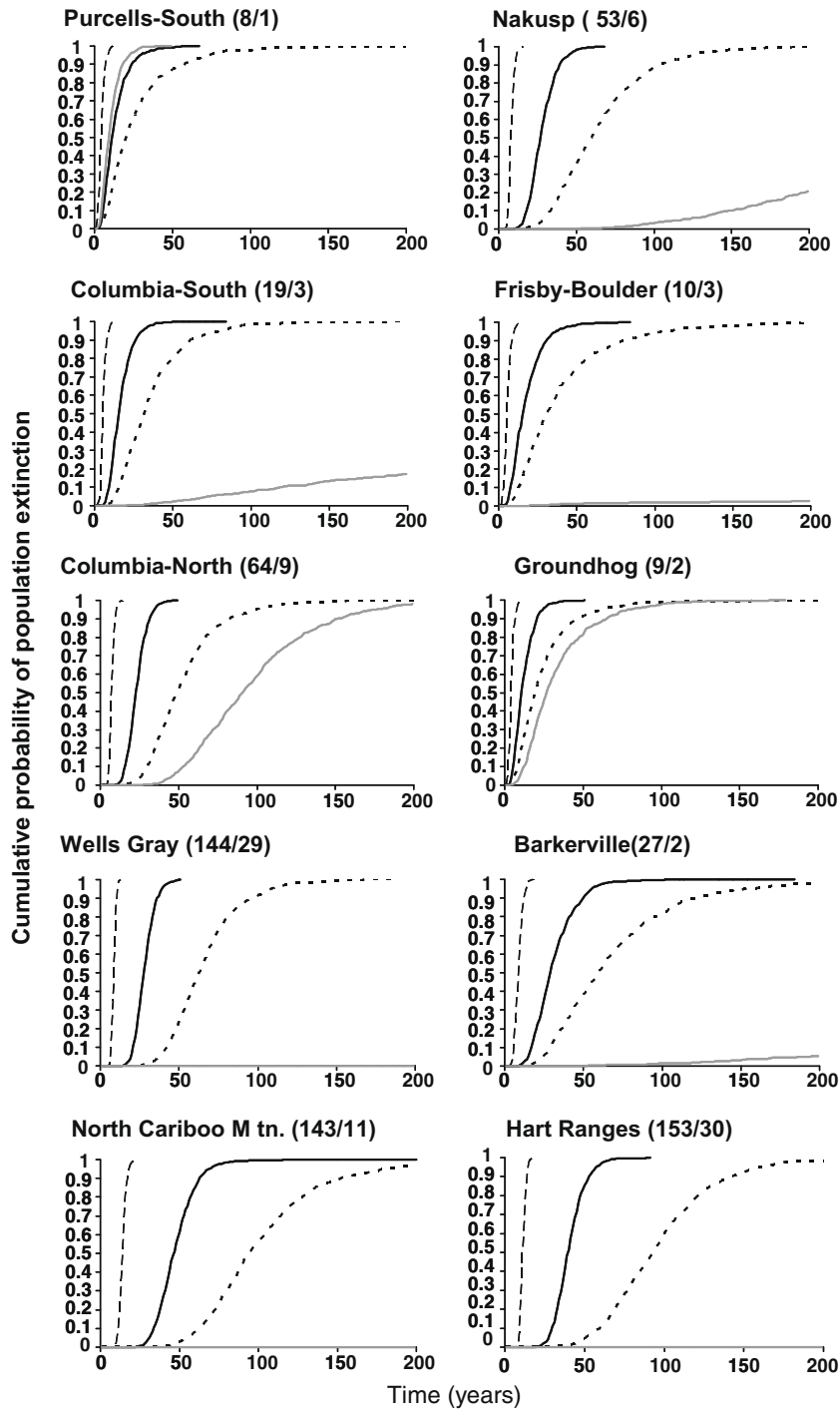


Fig. 3. Cumulative probability of population extinction for 10 populations of mountain caribou in British Columbia assuming: (a) constancy in demographic parameters (—) and (b) as a function of both, variation in percentages of forest 1–40 years (5.74% (---), 9.22% (—), and 18.29% (···)) within population ranges and population density. Populations are ordered south to north (initial number of females/female calves).

extinction within the 200 year time horizon (Fig. 3). The Purcells-South and the Groundhog populations had extinction probabilities of 1.0 within 50 and 188 years, respectively. Four more populations had low cumulative extinction probabilities of <0.2. Assuming constancy in vital rates, the three populations with the largest initial population sizes (Wells Gray, North Cariboo Mtn., Hart Ranges) did not appear to be at risk of extinction within the time frame of this analysis. Extinction probabilities generally declined when we increased the proportion of 2-year old animals giving birth. Extinction probabilities, however, were not substantially affected

by uncertainties in age of first reproduction (Table 2). In only one population (Columbia North) did mean extinction probabilities from the three different scenarios differ by more than 5 years.

3.2. Alternative models

When the survival of adult females depended on habitat condition and population density, all 10 populations had high probabilities (>0.95) of extinction within the 200-year time horizon (Fig. 3). Differences in extinction probabilities between the two alternative

Table 2

Mean time to extinction of 10 populations of mountain caribou with varying proportions of 2-year olds (p_2) giving birth.

Population	$p_2 = 0$	$p_2 = 0.2$	$p_2 = 0.8$
Purcells-South	10	10	10
Nakusp	200	200	200
Columbia-South	200	200	200
Frisby-Boulder	200	200	200
Columbia-North	82	96	147
Groundhog	27	28	32
Wells Gray	200	200	200
Barkerville	200	200	200
North Cariboo Mtn.	200	200	200
Hart Ranges	200	200	200

scenarios were largest in populations with high initial numbers of females (Wells Gray, North Cariboo Mtn. and Hart Ranges) that were not considered at risk of extinction when assuming constancy in survival rates. Time to extinction probabilities for all populations depended on the amount of young forest within population ranges (Fig. 3). Increases in the amount of young forests resulted in faster extinction rates in all populations. In only one population (Purcells-South) did extinction probabilities under the initial scenario exceed extinction probabilities under the alternate scenarios, which was likely an artifact of the modeling, because initial survival rates for this population were below the estimates drawn from the regression used in the alternative models (i.e., Fig. 2).

4. Discussion

Our results suggest that PVA models that fail to incorporate the effects of anticipated changes in vital rates with either deteriorating environmental conditions and/or an Allee effect will lead to overly optimistic assessments of the probability of population persistence in endangered species. Our initial models predict that while some (but not all) small populations of mountain caribou will soon become extinct, most should persist for the 200-year time frame we considered. These outcomes were derived from models that included demographic stochasticity and were otherwise based on estimates of population parameters derived from a large sample (>350 collared individuals) monitored over an unusually long time frame (up to 20 years) for an endangered species. Results from these initial models are in sharp contrast to predictions derived from models that incorporated the potential effects of increasing proportions of young forests and population density. Both habitat conditions and population density were in the top model explaining variation in female adult survival in mountain caribou across their distribution (Wittmer et al., 2007), the vital rate considered most crucial for the long-term persistence of long-lived species such as caribou (Gaillard et al., 2000). Under these more likely scenarios, all populations, including the largest, are predicted to decline to extinction within 200 years.

Like most studies on endangered species, limitations in available data may have affected our ability to accurately estimate extinction probabilities. For example, vital rates in cervids are known to vary substantially with age (Gaillard et al., 2003). Reliably estimating the age of caribou relies on extracting a tooth. Because this procedure is not acceptable for an endangered ungulate, we were unable to evaluate the effect of age structure on the viability of populations. Additionally, some population parameters could only be estimated with substantial uncertainty. We dealt with the uncertainty in parameter estimates in two ways. First, when possible, we used parameter estimates that had been selected from a set of competing models using Akaike's Information Criterion (AIC) (Burnham and Anderson, 2002). This process allowed models for survival of adult caribou to be selected based

on the optimal compromise between bias and precision (Wittmer et al., 2007). Second, we quantified the sensitivity of model predictions to uncertainty in parameter estimates using sensitivity analyses (Morris and Doak, 2002). Results from our sensitivity analyses showed that uncertainty in parameter estimates were unlikely to significantly change model predictions because at the very low population sizes we observed in our study, demographic stochasticity is expected to overwhelm the effects of uncertainty in parameter estimates (Caughley, 1994). Thus, while extinction probabilities may vary substantially for distinct populations because of uncertainty associated with parameter estimates, trends and management implications likely remain the same.

Because mountain caribou have existed in this ecosystem for centuries, the pessimistic results of the PVA that incorporate habitat deterioration and density may not appear realistic. Historic information, however, suggests a long-term decline from high numbers a century ago. For example, Spalding (2000) and McLellan (2009) report observations of >100 individuals in a group as well as a few groups of >1000 individuals from early in the 1900s, whereas the largest of the 5565 groups seen by biologists in the past 20 years was 62 animals (McLellan, 2009). The distribution of mountain caribou has also contracted. Historically, caribou were observed 170 km further west and 300 km further south than today (Apps and McLellan, 2006; McLellan, 2009). Additionally, recent surveys indicated that two populations (George Mountain and Purcells-Central) have become extinct since 2004 and two additional populations now have <10 animals (Hatter, 2006; c.f. from Wittmer et al., 2005b). Natural recovery of these newly extirpated populations by immigration is unlikely as natal and reproductive dispersal of mountain caribou is limited (Van Oort et al., unpublished). Thus, the historic and recent trends suggest that our estimates of high extinction probabilities for mountain caribou may be realistic.

The differences in time to extinction suggested by the alternative models have important implications for caribou management and land-use decisions. Extinction probabilities appear strongly influenced by changes to the forest age structure, particularly if these changes result in increasing numbers of predators and other prey species. Furthermore, this impact is exacerbated if the relative impact of predation is stronger at low caribou densities (depensatory mortality) (Dale et al., 1994; McLellan et al., in press). This result is of particular concern. It suggests the number of populations potentially becoming extirpated is greater than would be assessed in the absence of this effect and the time until extirpation (the period over which management has to act) is shorter.

Forestry is the dominant land-use activity across and beyond the range of mountain caribou in British Columbia (Fenger, 1996) and forest management actions influence the persistence of caribou populations by altering the amount of early seral forests. In addition to this effect, climate change may also influence the amount of early seral forests through increased insect outbreaks and wildfires. Land-use plans across the distribution of mountain caribou in British Columbia now include the protection of >2,000,000 ha of forested land to help maintain mountain caribou (B.C. Ministry of Environment, 2009). These protected forests are undoubtedly important for the conservation of many other species as well as caribou, but if caribou are extirpated, the immediate impetus for their protection is lost and their future uncertain. Because current forest age structure is unlikely to change fast enough to lead to reduced alternate prey and predators before caribou populations become extinct, careful consideration should also be given to alternate management strategies such as predator-prey management (Wittmer et al., 2005b; Raffel et al., 2008). Given the high probability of extinction in distinct populations, such management should be implemented immediately. Unfortunately, our analysis does neither determine threshold proportions of young forests

where caribou can coexist with alternate prey species and their predators nor does it determine the total size of managed areas required to effectively reduce the impact of large, wide-ranging predator species. Setting such thresholds requires a better understanding of the ecology of caribou in multiprey, multipredator systems and their response to habitat change.

An important consideration for population augmentation, a practice often used to recover species like mountain caribou (Compton et al., 1995), is the potential impact of reducing the source population (Caughley and Gunn, 1996). Since all populations of mountain caribou are considered at risk of extinction when assuming positive density dependence, source populations for planned future augmentations (Hatter et al., 2002) should not be from any mountain caribou populations. Alternate model results suggest that such augmentation may potentially have unexpected negative impacts on source populations by increasing female mortality through reduced density.

Incorporating uncertainty is the most challenging component of PVA modeling. Recognized sources of uncertainty in PVA modeling include: (a) the inability to predict stochasticity inherent to the particular system (demographic, environmental and genetic stochasticity); (b) uncertainty in parameter estimates such as survival and reproduction; (c) uncertainty in predicting future changes in model parameters (e.g., Morris and Doak, 2002; Regan et al., 2002; Cariboni et al., 2007). While demographic and environmental stochasticity have been a mainstay of PVA modeling since its inception (Shaffer, 1981) and incorporated into all commonly used PVA packages (e.g., Lacy, 2000) dealing with the effects of uncertainty in current estimates of vital rates and the potential mechanisms which give rise to such rates remains inconsistent. The most commonly used approach to deal with uncertainty in estimates of vital rates is to quantify the sensitivity of model predictions to uncertainty in parameters estimates. Such sensitivity analyses allow managers to identify and rank influential parameters, evaluate potential effects of different management scenarios and ultimately to prioritize research and data collection (Morris and Doak, 2002; Reed et al., 2002; Naujokaitis-Lewis et al., 2009). Our results suggest that incorporating anticipated future changes in parameters with environmental conditions and population density are also essential and can strongly alter the conclusions drawn from a PVA.

While it is widely recognized that reliable estimates of population persistence depend on our understanding of the effects of population density, few studies have considered these effects using empirical data (Henle et al., 2004). In particular, there is a growing body of literature suggesting that the decline of populations at low densities may be non-linear (i.e., accelerated at low densities) (reviewed in Fagan and Holmes, 2006) including for caribou (Dale et al., 1994; Wittmer et al., 2005a). The most common method used to simulate the effects of negative changes in demographic parameters at low population densities is to apply a quasi-extinction level where, at some low population size, the population is considered extinct (Morris and Doak, 2002). The influence of quasi-extinction levels on persistence time depends on both the initial population size and the population growth rate. Extinction thresholds should always be considered in PVA modeling if populations start from very low numbers and exhibit low population growth rates (Henle et al., 2004). Due to a lack of data, however, quasi-extinction levels are frequently estimated and thus can only approximate population dynamics at low population densities. The positive density dependence in adult female survival that is suggested in our data differs from an extinction threshold in that it is based on empirical observations of survival rates across a range of population densities and habitat conditions. Contrary to a quasi-extinction threshold, larger populations were more affected by the positive density-dependent effects than smaller populations because in the initial models larger populations generally

had higher survival rates than smaller populations. This shows that merely accounting for positive density dependence in PVA is of limited use for the development of effective recovery strategies if the underlying mechanism remains unknown.

Efforts to counteract declines of endangered species require addressing both proximate and ultimate causes of decline (Sinclair and Byrom, 2006). Incorporating anticipated future changes in vital rates with environmental conditions and population density into our PVA helped propose appropriate recovery strategies for endangered mountain caribou. In particular, our results suggest that immediate habitat protection and restoration is required to avoid potentially accelerated rates of decline of mountain caribou at low densities and these actions have begun (B.C. Ministry of Environment, 2009). Results from our PVA have also shown that many mountain caribou populations are likely to be extirpated without immediate management of the predator–prey system that appears to be the proximate cause of their decline (Seip, 1992; Wittmer et al., 2005a, 2005b, 2007) and some action has been initiated (B.C. Ministry of Environment, 2009). These results highlight the potential benefits of PVA modeling for the development of effective management strategies.

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