Changes in landscape composition influence the decline of a threatened woodland caribou population

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Summary

1. Large-scale habitat loss is frequently identified with loss of biodiversity, but examples of the direct effect of habitat alterations on changes in vital rates remain rare. Quantifying and understanding the relationship between habitat composition and changes in vital rates, however, is essential for the development of effective conservation strategies.

2. It has been suggested that the decline of woodland caribou *Rangifer tarandus caribou* populations in North America is precipitated by timber harvesting that creates landscapes of early seral forests. Such habitat changes have altered the predator–prey system resulting in asymmetric predation, where predators are maintained by alternative prey (i.e. apparent competition). However, a direct link between habitat condition and caribou population declines has not been documented.

3. We estimated survival probabilities for the threatened arboreal lichen-feeding ecotype of woodland caribou in British Columbia, Canada, at two different spatial scales. At the broader scale, observed variation in adult female survival rates among 10 distinct populations (range = 0·67–0·93) was best explained by variation in the amount of early seral stands within population ranges and population density. At the finer scale, home ranges of caribou killed by predators had lower proportions of old forest and more mid-aged forest as compared with multi-annual home ranges where caribou were alive.

4. These results are consistent with predictions from the apparent competition hypothesis and quantify direct fitness consequences for caribou following habitat alterations. We conclude that apparent competition can cause rapid population declines and even extinction where changes in species composition occur following large scale habitat change.

Key-words: apparent competition, caribou, extirpation, habitat loss, population dynamics, predation, survival analysis.

Introduction

Habitat loss is a major cause of extinction (Caughley 1994; Sih, Jonsson & Luikart 2000; Fahrig 2003).

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The effect of habitat loss has been particularly well documented in the decline of species associated with late-successional forests such as the northern spotted owl *Strix occidentalis caurina* (Merriam) in western North America (e.g. Franklin *et al.* 2000; Noon & Blakesley 2006). Although maintaining old forests in protected areas will help conserve many species, protected areas are generally too small for wide-ranging and migratory species (Carroll, Noss & Paquet 2001;

Berger 2004), and land-management decisions made outside protected areas usually determine their fate. Natural resources, and in particular old forests, are of great economic importance and thus the trade-off between conservation and economic value is the basis for many land-use decisions. Quantifying the relationship and understanding the mechanism between habitat composition and changes in vital rates for the species of concern is therefore required to make appropriate decisions.

The relationship between habitat composition and vital rates of wide-ranging species has rarely been quantified due to the challenge of conducting large-scale manipulative research. However, vital rates influencing population viability vary spatially and an inductive comparison among populations can be insightful. At relatively fine scales, such comparisons among population units have been successful in linking variation in vital rates to habitat conditions (e.g. Coulson *et al.* 1999; Franklin *et al.* 2000; Pettorelli *et al.* 2005).

The obligate arboreal lichen-feeding ecotype of woodland caribou *Rangifer tarandus caribou* (Gmelin) (referred to throughout the manuscript by their local name of 'mountain caribou') in British Columbia, Canada, is a wide-ranging species that is dependent on attributes of old forests for several life-history requirements, including the arboreal lichen they eat during winter (Rominger, Robins & Evans 1996; Terry, McLellan & Watts 2000). Over the past decade, the abundance of these caribou has declined by approximately 8% per year across their distribution with individual populations decreasing at up to 20% per year (Wittmer *et al.* 2005a). By 2004, the remaining caribou were fragmented into 18 largely isolated populations varying in size from < 10 to > 400 individuals and totalling < 1600 individuals. As a consequence of the increased risk associated with small, declining and fragmented populations, mountain caribou are categorized as 'threatened' with extinction in Canada (COSEWIC 2002) and 'endangered' in the USA (US Fish and Wildlife Service 1994).

It has been suggested that the decline of woodland caribou across North America, including that of mountain caribou, has been precipitated by timber harvesting that creates landscapes of early seral stage vegetative communities (Rettie & Messier 1998; Schaefer 2003; Wittmer *et al.* 2005a). These early successional communities resulted in population increases of other ungulates such as moose *Alces alces* (Linnaeus) (Rempel *et al.* 1997), which in turn support higher densities of predators (Schwartz & Franzmann 1991; Ballard *et al.* 2000). This relationship has led to the hypothesis that the decline of woodland caribou is based on an indirect interaction between caribou and landscape composition through other prey species and their shared predators (Bergerud & Elliot 1986; Seip 1992; Wittmer, Sinclair & McLellan 2005b). Such an indirect interaction between prey populations is commonly referred to as apparent competition (Holt

& Lawton 1994). While studies generally show that predation is the primary cause of adult mortality in woodland caribou (Stuart-Smith *et al.* 1997; Rettie & Messier 1998; Wittmer *et al.* 2005a), the relationship between habitat composition, caribou vital rates and population decline consistent with the apparent competition hypothesis has not been quantified.

Adult female survival is the parameter that most strongly influences population declines of mountain caribou (Wittmer *et al.* 2005a). In this paper we evaluate the importance of several environmental factors, including those consistent with the apparent competition hypothesis, on the survival of adult female caribou. Our analysis covers two spatial scales. At the broader, population scale, we consider the variability of habitat composition among caribou populations. At the finer, home range scale, we consider the variability of habitat composition among the home ranges of caribou killed by predators. Our analyses highlight the importance of quantifying the relationship between vital rates and limiting factors causing population decline and should support land-use decisions for effective mountain caribou conservation, particularly outside of protected areas.

Methods

STUDY AREA

Mountain caribou are the southernmost remaining caribou in North America. Their distribution currently covers > 50 000 km^2 from just south of the Canada/USA border at 49°N latitude to north-east of Prince George, British Columbia, Canada, at approximately 55°N latitude (Fig. 1). Topography is variable across the distribution of caribou with elevation ranging from 400 m to > 3500 m. The climate is influenced by Pacific air masses resulting in high annual precipitation, most of which falls as snow during winter. Owing to wet conditions and infrequent wildfires, forests in the study area are naturally dominated by old stands (Meidinger & Pojar 1991) that are subject to different intensities of forest harvesting. Wittmer *et al.* (2005a) provide a detailed description of the vegetative communities across the range of mountain caribou in British Columbia.

Mountain caribou in southern British Columbia are part of a multiprey, multipredator system. The distribution of other species is determined by topography, climate and habitat characteristics. In general, mountain goats *Oreamnos americanus* (de Blainville) and mule deer *Odocoileus hemionus* (Rafinesque) are found across the distribution of caribou populations. Moose are also found across the distribution of the caribou populations, but densities are greater in the northern and central portions. Although some moose were present in portions of the study area, their numbers and distribution have greatly expanded since the early 1900s (Spalding 1990). Elk *Cervus elaphus* (Linnaeus) and white-tailed deer *Odocoileus virginianus* (Zimmermann) are more abundant in southern areas, and their distribution has
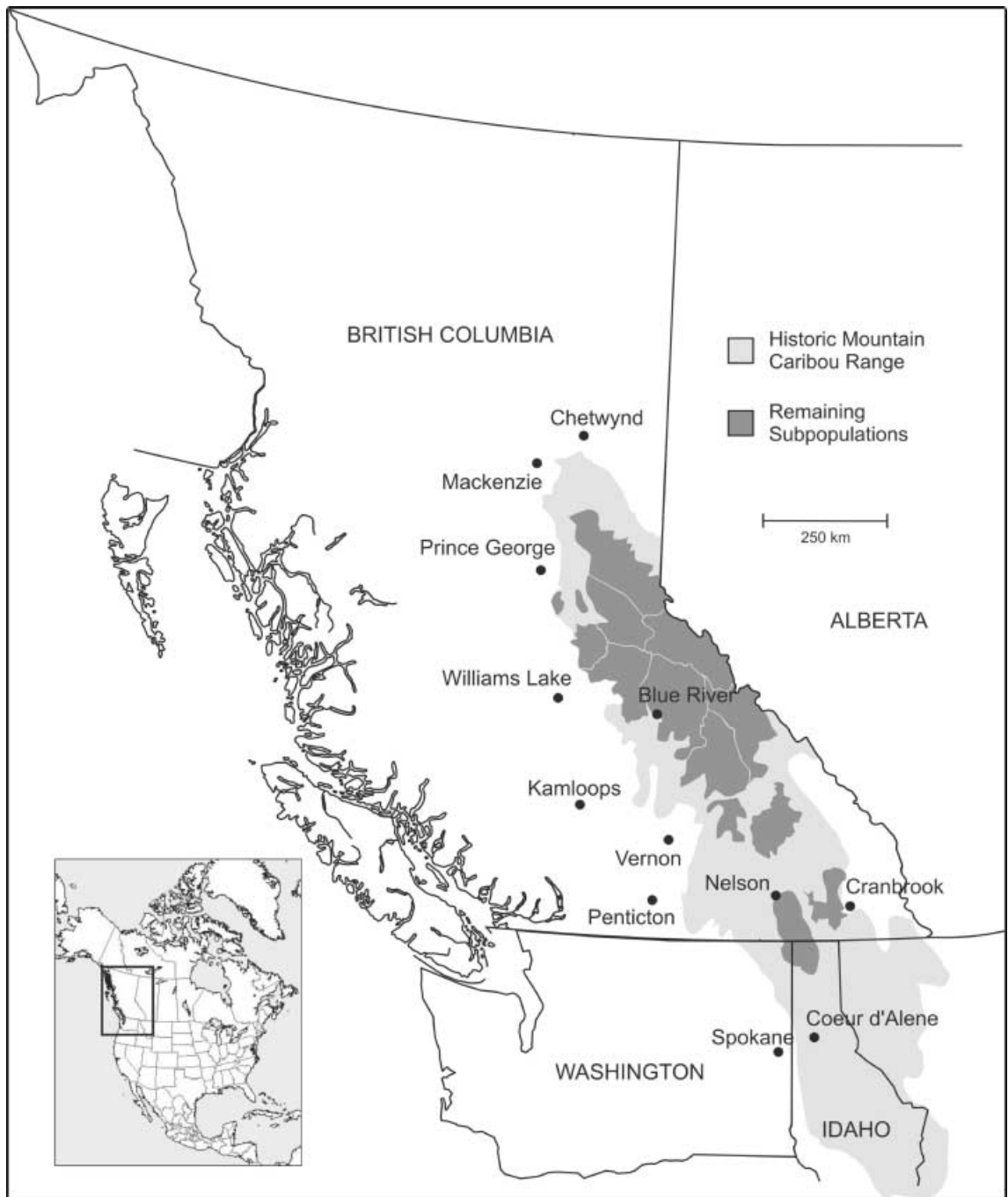
Fig. 1. Approximate current and historic range of mountain caribou in British Columbia, Canada.

also increased over the past several decades (Shackleton 1999). Common predators across the distribution of caribou include grizzly bears *Ursus arctos* (Linnaeus), black bears *Ursus americanus* (Pallas) and wolverine *Gulo gulo* (Linnaeus), whereas wolves *Canis lupus* (Linnaeus) are more abundant in the north and cougar *Puma concolor* (Linnaeus) are more abundant in the south.

CARIBOU CAPTURE AND MONITORING

From 1984 to 2004, we captured 338 adult (≥ 2 years) female caribou and fitted them with mortality motion-sensitive radiotelemetry collars to obtain location and survival data. Capture and marking procedures are described by Wittmer *et al.* (2005a). Caribou were relocated from fixed-wing aircraft at 1–2-week intervals. Locations were plotted on aerial photographs or topographic maps and coordinates of each animal were recorded to the nearest 100 m. Individual caribou were on average relocated 53·08 (± 44·56) times and were monitored for up to 10 consecutive years (mean = 2·72 ± 1·10 years).

When the signal from a motion-sensitive radio-collar indicated a stationary collar, the site was investigated as soon as possible to confirm whether the caribou had died or dropped its collar. A total of

141 female caribou were found to have died and 68% of mortalities with known cause were attributed to predation (Wittmer *et al*. 2005a).

COVARIATES WITH SURVIVAL

Wittmer *et al*. (2005a) estimated adult survival rates of female mountain caribou in our study area using a staggered entry Kaplan–Meier procedure (Pollock *et al*. 1989). They found large variation in annual survival rates among populations (range = 0·55–0·96) and demonstrated that the variation in female survival was largely responsible for the observed variation in population growth rates (λ) (range = 0·82–1·03). We evaluated covariates potentially affecting adult survival at two scales: within distinct populations and within individual home ranges.

Habitat covariates

We selected habitat covariates based on the hypothesis that caribou population declines are related to the conversion of old forests to young forests (Rettie & Messier 1998). At both spatial scales, we estimated the proportion of forests within different age classes and that of nonforested habitat above the treeline (Table 1). In addition to age, the configuration of forest stands may also be important for caribou, particularly where forests have become increasingly fragmented through harvest. Within mountain caribou range, most forest harvesting has occurred over the past 30–40 years and has targeted old stands. Therefore, we restricted our estimates of fragmentation indices to forest stands of age 1–40 years and age > 140 years. Forest stands that are 40–100 years predominantly originated from wildfires, although the proportion of these fires that were naturally ignited or were set by early settlers and mineral prospectors is not known. We extracted all habitat covariates from 1 : 20 000 digital forest inventory planning files (Resource Inventory Branch 1995) rasterized to 250 m resolution. Forest age data were updated to the year 2000 and are assumed to reflect forest composition over the sampling period.

Climate covariates

In contrast to other woodland caribou in North America, mountain caribou depend almost exclusively on long-strand arboreal lichen during winter (*Bryoria* spp. and *Alectoria sarmentosa*) (Rominger & Oldemeyer 1989; Rominger *et al*. 1996; Terry *et al*. 2000). The deep snow pack of generally 1–5 m in the study area buries all terrestrial food but caribou walk on top of the deep snow to access lichen in the forest canopy. Arboreal lichen does not grow lower on trees than the maximum snow accumulation, so large interannual variation in snowpack may result in too little snow accumulation in some years for caribou to reach lichen in the lower canopy (Goward 1998).

We explored the effects of among-year variability in snow depth on survival, using variation in annual snow depth as an indicator of winter severity. This approach is consistent with an among-year study approach of climatic variation described by Rotenberry & Wiens (1991). The height of snow (cm) was measured on the first day of each month from January to April at measurement stations maintained by the Ministry of Sustainable Resource Management (2004). Measurement stations ranged in elevation from 1520 m to 2010 m and we assumed that snow data were representative of conditions experienced by caribou in distinct populations on high elevation late winter ranges. For each caribou population, we then calculated the average yearly snow accumulation during this period (i.e. late winter). Finally, we calculated the coefficient of variation (Zar 1999) in snow accumulation among years.

Population density

The decline of caribou in our area has been correlated with population density, with smaller populations declining at faster rates than larger ones (Wittmer *et al*. 2005b). The inverse density dependence or Allee effect has been hypothesized to be a consequence of high predation rates where caribou are secondary prey to a predator population that relies on other primary prey. We evaluated the relationship between population density

Table 1. Covariates used to explain variability in survival of female adult mountain caribou at both the population and home range scales in British Columbia, Canada

Covariates	Definition
Amount of habitat	Proportion of early seral forest habitat age 1–40 years (FOR1-40)
	Proportion of mid-seral forest habitat age 40–100 years (FOR40-100)
	Proportion of mid-seral forest habitat age 100–140 years (FOR100-140)
	Proportion of late-seral forest habitat age > 140 years (FOR140)
	Proportion of nonforested (alpine) habitat (NONFOR)
Distribution of habitat	Edge density around forest habitat age 1–40 years (ED1-40)
	Mean patch size forest habitat age 1–40 years (MPS1-40)
	Mean patch size forest habitat age > 140 years (MPS140)
Climate variable*	Coefficient of variation average yearly snow accumulation (Jan–Apr) (SNOW)
Population density*	Population density within population range (DEN)

*Population scale only.

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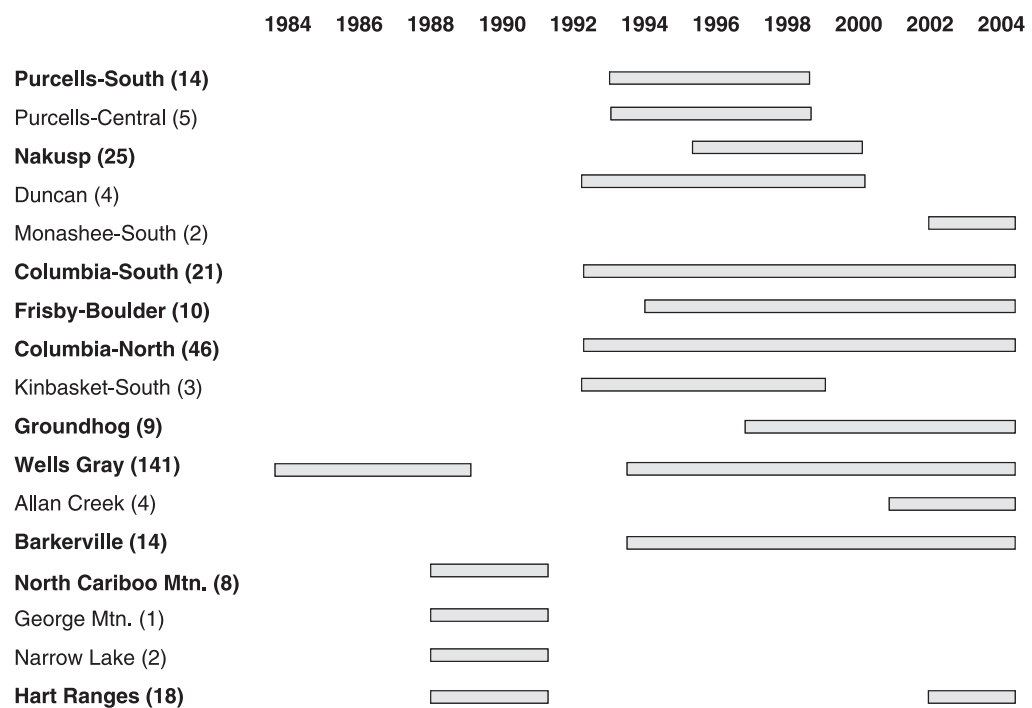Ecology*, **76**,
568–579

Fig. 2. Temporal distribution of telemetry data of mountain caribou by identified population (number of collared females) in British Columbia, Canada.

and adult female survival, using density estimates derived by dividing each current population estimate by its associated range size.

MODELLING THE EFFECTS OF COVARIATES ON ADULT SURVIVAL

Population scale

At the population scale, we estimated annual adult survival probabilities (ϕ) using known-fate mark–recapture models in program MARK (White & Burnham 1999). We estimated annual survival for a year that began on 21 May, the approximate start of the calving season (Wittmer *et al*. 2005a). As caribou were captured in March, this approach likely eliminated potential effects of mortalities associated with capture. Individuals were recorded as alive or dead within the year, with multiple resightings of individuals equating to single encounters. To reduce the effects of small sample sizes (*sensu* Wittmer *et al*. 2005a), we only included populations monitored for at least three complete years with at least four caribou collared at the start of each year (Fig. 2). A total of 67 years from 10 of the identified populations met these requirements.

At the population scale, covariates with survival rates were based on habitat parameters measured within the range of each distinct population. We used range boundaries of populations delineated using a 95% adaptive kernel density estimator where locations of all radio-collared individuals from each distinct population had been pooled (Table 2) (Wittmer *et al*.

Table 2. Areas used in summarizing covariates at the population and home range scales for mountain caribou in British Columbia, Canada

Population	Population range (km²)*	Summer (km²)	Winter (km²)
Purcells-South	771	63	53
Purcells-Central		53	57
Nakusp	2340	51	56
Duncan		46	35
Monashee-South		38	64
Columbia-South	1761	42	59
Frisby-Boulder	613	46	81
Columbia-North	4526	53	79
Kinbasket-South		22	37
Groundhog	1277	41	87
Wells Gray	8141	86	200
Allan Creek		57	61
Barkerville	742	74	51
North Cariboo Mtn.	1779	65	66
George Mtn.		17	92
Narrow Lake		14	63
Hart Ranges	3890	31	49

*From Wittmer *et al*. (2005a).

2005a). For each population, we attached covariates associated with the population range.

We initially considered five basic survival models. The first model assumed survival of adult females to be constant over both time and populations ϕ (.). The second model assumed time dependency in adult survival ϕ (t), while the third considered variation in survival among populations ϕ (g). The fourth model considered additive effects between year and population

ϕ $_{(t+g)}$, and the fifth model considered an interaction between time and population ϕ $_{(t \times g)}$. The fully saturated model ϕ $_{(t \times g)}$ executed with a deviance of 0 indicating good model fit. We thus did not adjust ĉ to account for possible model overdispersion (Cooch & White 2001).

We pooled data from multiple samples resulting in different numbers of females collared over time and population. To eliminate effects due to sampling variance, we therefore decomposed variance components of the best initial model ϕ $_{(g)}$ following guidelines described by White, Burnham & Anderson (2001). Underlying process variance can be estimated in MARK using 'shrunk' estimates ($\tilde{S}$) where confidence intervals are based on corrected estimates. These corrected estimates ensured that only process variance was included in our survival probabilities.

We then developed a set of 14 a priori candidate models that incorporated the variation in female survival probabilities as a function of the environmental covariates (see Table S1 in Supplementary materials for list of candidate models). Covariates were inspected for collinearity (see Table S2 in Supplementary materials for a list of correlation coefficients) and bivariate correlations were all ≤ 0·75 within candidate models. We compared models using ΔAIC_c (Akaike's Information Criterion corrected for small sample size bias) and considered models within < 4 AIC_c of the top model (Burnham & Anderson 2002). All covariates were standardized prior to the analysis following guidelines outlined by Cooch & White (2001). We also performed a principal components analysis (PCA) to attempt and reduce the number of covariates tested. The first two components of the PCA explained 50·73% and 22·97% of the variation (see Table S3 in Supplementary materials for loadings of covariates), however, including the first two components as covariates did not improve model fit.

To investigate the relationships among survival probabilities and covariates, we constrained survival probabilities as linear functions of covariates, where the design matrix was linked to the model parameters by the logit link function (White & Burnham 1999). To directly evaluate the relationship between covariates and real estimates of survival we thus had to back transform covariates as:

$$\text{logit } \phi = \alpha_0 + \beta_1(X') \qquad \text{eqn 1}$$

and

$$\phi = \frac{\exp(\alpha_0 + \beta_1(X'))}{1 + \exp(X')} \qquad \text{eqn 2}$$

where α_0 is the intercept and β_1 is the slope of the standardized covariate X'.

Home range scale

We evaluated whether the likelihood of caribou dying from predation can be explained by factors that vary at

the scale of an individuals' home range. Because location sample sizes for some caribou were not sufficient to determine a home range before they died, we did not use animal-specific home range delineations. Instead, we first estimated the mean minimum convex polygon (MCP) home range size for each population using animals that did have sufficient data. Estimates were based on summer (11 June–21 October) or winter (22 October–23 April) seasons, defined using dates that reflect seasonal elevational migrations of mountain caribou in the Columbia Mountains (Apps *et al.* 2001). For each individual and year, we then calculated the mean positional coordinate for both seasons, regardless of sample size. By splitting the data seasonally, we expected to avoid estimating home range centres that fell within zones of migration between sometimes disjunct winter and summer ranges. Around each estimated seasonal home range centroid, we applied a circular buffer equivalent to the average population-specific home range size (Table 2). We then extracted covariate attributes and averaged them between seasons and among years for each animal. Combining seasonal ranges into multi-annual home ranges in this way was necessary to ensure that our samples were independent. We restricted the number of covariates to the ones that potentially varied among home ranges within populations (i.e. we excluded snow and population density).

Using logistic regression in SAS 9·1, we evaluated whether home range characteristics where individuals had been killed by a predator ($n = 59$) were different from characteristics associated with multi-annual home ranges where individuals had been alive ($n = 301$). Survival was modelled as a linear function of the covariates with the dichotomous dependent variable 'status' (dead or alive). We developed 16 a priori candidate models (see Table S4 in Supplementary materials for list of candidate models) and models were ranked based on AIC. Covariates were again inspected for collinearity (see Table S5 in Supplementary materials for a list of correlation coefficients) and bivariate correlations were all ≤ 0·70 within candidate models.

Results

POPULATION SCALE

Our results strongly support models considering population effects (Table 3). Corrected survival estimates of ϕ $_{(g)}$ for distinct populations vary between 0·67 in the Purcells–South population and 0·93 in the Hart Ranges population (Table 4). Model fit is improved by including covariates. Specifically, caribou survival generally declines among populations with increasing proportions of early and mid-seral forest stands (FOR1-40, FOR40-100). Higher survival is primarily explained by increasing proportions of old forests (FOR140) and nonforested habitat (NONFOR), and increasing population density (DEN). Models that

Table 3. Initial models and top models ($\Delta AIC_c < 4$) of female survival fitted to data from 10 distinct populations of mountain caribou in British Columbia, Canada; β ($\pm$ SE) of standardized covariates, number of model parameters (k), Akaike's information criterion (AIC_c) adjusted for small sample size bias, AIC_c differences (Δ), AIC_c weights (ω) and model deviance (see Table 1 for definition of covariates)

Parameters	Intercept ($\pm$ SE) + β ($\pm$ SE)	k	AIC_c	ΔAIC_c	AIC_c ω	Deviance
Initial models						
ϕ (g)		10	728·05	10·46	0·01	85·26
ϕ (.)		1	731·63	14·05	0·00	107·10
ϕ (gxt)		55	740·31	22·73	0·00	0·00
ϕ (t+g)		27	743·50	25·91	0·00	65·13
ϕ (t)		19	746·11	28·52	0·00	84·66
Models with covariates						
ϕ FOR1-40 + DEN	1·65(0·13) − 0·40(0·12) + 0·46(0·20)	3	717·59	0	0·48	89·03
ϕ FOR40-100	1·63(0·10) − 0·53(0·14)	2	720·20	2·61	0·13	93·66
ϕ FOR1-40 + FOR40-100	1·56(0·11) − 0·21(0·18) − 0·35(0·20)	3	720·80	3·21	0·10	92·24
ϕ FOR140 + NONFOR	1·57(0·10) + 0·49(0·14) + 0·43(0·14)	3	721·06	3·48	0·09	92·51

Table 4. Estimates of female adult survival rates of mountain caribou populations in British Columbia, Canada

Population	Survival estimates*	Corrected survival estimates†
Purcells-South	0·55 ± 0·10	0·67 ± 0·14
Nakusp	0·85 ± 0·04	0·85 ± 0·04
Columbia-South	0·85 ± 0·04	0·86 ± 0·03
Frisby-Boulder	0·90 ± 0·10	0·90 ± 0·05
Columbia-North	0·81 ± 0·03	0·81 ± 0·03
Groundhog	0·78 ± 0·10	0·79 ± 0·07
Wells Gray	0·84 ± 0·02	0·85 ± 0·02
Barkerville	0·88 ± 0·06	0·88 ± 0·04
North Cariboo Mtn	0·91 ± 0·04	0·90 ± 0·05
Hart Ranges	0·96 ± 0·03	0·93 ± 0·03

*From Wittmer *et al.* (2005a).
†Survival estimates corrected for process variation using program MARK.

include habitat amount consistently perform better than models that include habitat configuration.

The four candidate models with ΔAIC_c values < 4 (Table 3), account for 0·80 of the sum of AIC_c weights. The top ranked model (ϕ FOR1-40 + DEN) is 3·69 times more likely to be the best model than the second ranked model (ϕ FOR40-100). The best model includes both a negative relationship between caribou survival and proportion of young forests 1–40 years (FOR1-40) (Fig. 3a) as well as a positive relationship with population density (DEN). Correlation between independent variables in the best model was low (i.e. 0·13). Despite substantial model selection uncertainty, several effects are consistent across top models. In particular, the proportion of early and mid-seral forest is a main effect in three of the top four models. Of the top models, those that include young forest (FOR1-40) sum to a greater AIC_c weight (0·58) than those that include other covariates.

A *post hoc* analysis showed that a model constraining survival probabilities only as a function of young forests once the proportion of FOR1-40 increases above a threshold (i.e. 0·08, 0·09 or 0·10) could further improve model fit. In the best threshold model (i.e. $\phi = 1·91(\pm 0·12) − 0·59(\pm 0·17) \times FOR1-40 + 0·42(\pm 0·21 \times DEN$; $AIC_c = 717·38$, $\Delta AIC = −0·21$), survival is constrained as a function of young forests only in populations where the proportion of FOR1-40 within population ranges exceeds 0·09 (Fig. 3b). Below this threshold, survival is only constrained by population density resulting in estimates of survival probabilities of 0·83, 0·87 and 0·95 when density is kept constant at the minimum, mean and maximum of observed population densities, respectively.

HOME RANGE SCALE

Our results consistently support models considering the proportion of old forests (Table 5). Top models indicate that caribou are more often killed by predators in home ranges with low old forest (FOR140) composition. Increased vulnerability to predation is also explained by increasing proportions of mid-seral forest stands (FOR40-100 & FOR100-140) and decreasing proportions of nonforested (NONFOR) habitat. With the exception of FOR140, however, effects of all other covariates in the top model set are questionable because their confidence limits overlap zero. Models that include habitat amount are consistently better supported by the data than those that include habitat configuration.

The six candidate models with ΔAIC values < 4 account for 0·91 of the sum of AIC weights (Table 5). The best model of caribou survival includes a positive relationship with forests aged > 140 years (FOR140) and a negative relationship with forests aged 40–100 years (FOR40-100). The best model, however, performs only 1·26 times better than the second-ranked model that includes only old forests (FOR140). Despite substantial model selection uncertainty, the proportion of old forests (FOR140) is included in all six top models (sum AIC weights = 0·91), while mid-aged forest (FOR40-100) was the second-most predictive variable (sum AIC weights = 0·24).
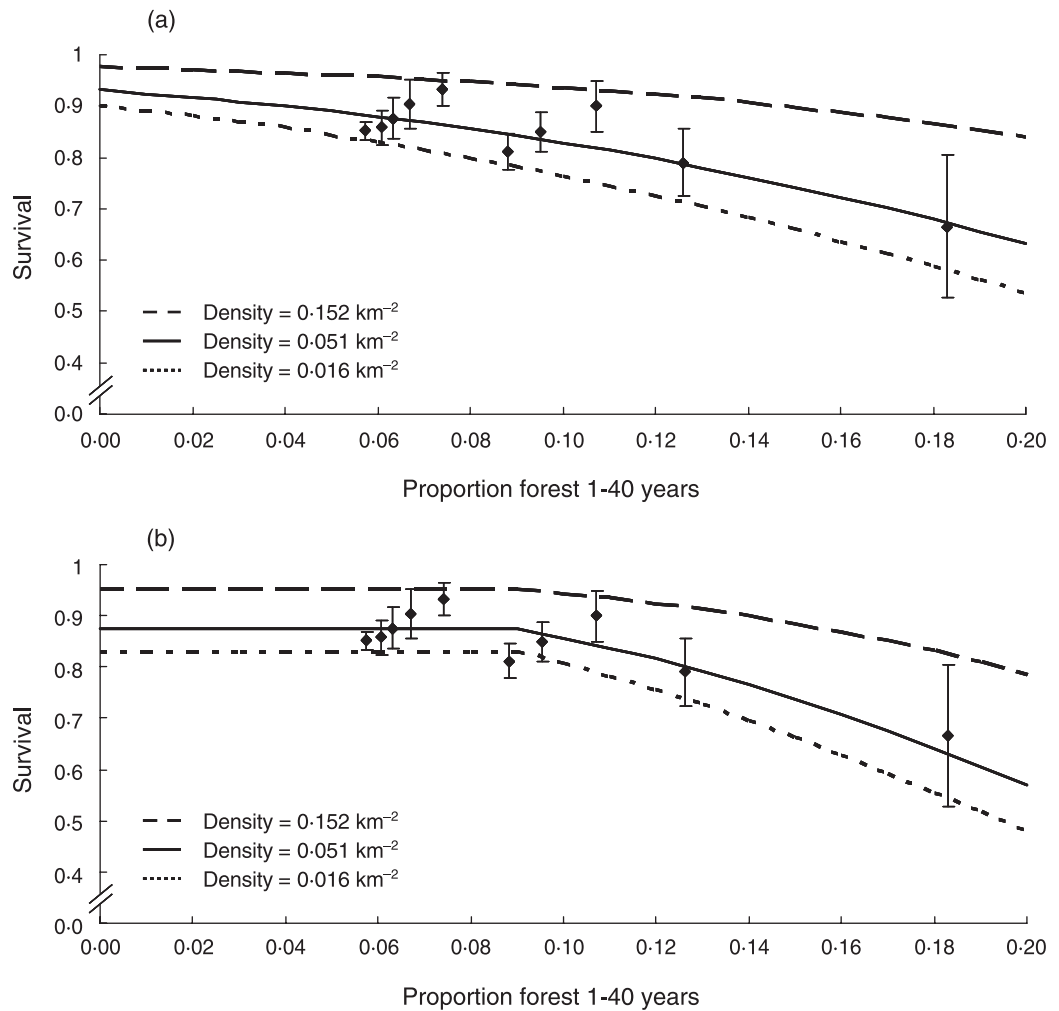
Fig. 3. Correlation between proportion of forest 1–40 years and female adult survival rates of mountain caribou in British Columbia, Canada. The lines indicate goodness-of-fit curves from (a) the best *a priori* survival model (i.e. $\phi = 1.65(\pm 0.13) - 0.40(\pm 0.12) \times FOR1\text{-}40 + 0.46(\pm 0.20) \times DEN$), and (b) the best threshold survival model (i.e. $\phi = 1.91(\pm 0.12) - 0.59(\pm 0.17) \times FOR1\text{-}40 + 0.42(\pm 0.21) \times DEN$), back-transformed to real survival estimates using eqns 1 and 2. Density kept constant at minimum (0·016 per km²), mean (0·051 per km²) and maximum (0·152 per km²) of the observed densities. Data points show population specific survival estimates (± SE) corrected for process variation (Table 4).

Table 5. Top models (ΔAIC < 4) of female caribou dying from predation fitted to data from 338 female mountain caribou in British Columbia, Canada; β (± SE) of covariates, number of model parameters (k), Akaike's information criterion (AIC), AIC differences (Δ), and AIC weights (ω) (see Table 1 for definition of covariates)

Model	Intercept (± SE) + β (± SE)	k	AIC	ΔAIC	AIC ω
FOR140 − FOR40-100	0·68(0·54) − 0·03(0·01) + 0·03(0·02)	3	314·45	0·00	0·24
FOR140	0·23(0·46) − 0·03(0·01)	2	314·94	0·49	0·19
FOR140 − FOR100-140	0·50(0·49) − 0·03(0·01) + 0·04(0·03)	3	315·05	0·59	0·18
FOR140 + NONFOR	0·50(0·72) − 0·04(0·01) − 0·01(0·01)	3	315·37	0·91	0·15
FOR140 + MPS140	0·24(0·46) − 0·03(0·01) − 0·00(0·16)	3	316·77	2·32	0·08
FOR140 + FOR1-40	0·23(0·47) − 0·03(0·01) − 0·00(0·02)	3	316·94	2·49	0·07

Discussion

Our objective was to examine the importance of several environmental variables at two spatial scales that may affect vital rates and thus precipitate population declines of a threatened large herbivore. We focused our analyses on factors influencing adult female survival because

variation in rates of decline among caribou populations was best explained by differences in this parameter (Wittmer *et al.* 2005a). At both spatial scales, forest age class distribution was the best predictor of adult female survival.

At the population scale, variation in adult survival was influenced by the proportion of early and mid-seral

forests within population ranges with survival being lower where younger forests are more common. This result is consistent with the conclusions of Wittmer *et al.* (2005b) who found the proximate cause of mountain caribou decline to be predation in the form of apparent competition rather than food regulation or predation-sensitive foraging. Forests in early seral stages due to recent timber harvest or wildfire are preferred habitat for alternate ungulate prey such as moose (Schwartz & Franzmann 1991; Rempel *et al.* 1997) that have expanded in distribution and number over the past several decades in our study area (Spalding 1990). Similarly, white-tailed deer populations may also increase following anthropogenic habitat modifications (Roseberry & Woolf 1998) and have recently expanded their distribution within our study area (Shackleton 1999). Forests in mid-seral stages do not support ideal habitat conditions for either caribou or alternate prey species. However, higher proportions of these forests reflect drier portions of our study area with a relatively frequent fire history across the broader ecosystem and more abundant alternative prey and predators over longer periods of time. Because the amount of early and mid-seral forests within population ranges were highly correlated, it is difficult to clearly differentiate between their respective effects.

At the home range scale, caribou were more likely to be killed by predators if they had a relatively small proportion of old forest in their range. This result supports suggestions by James & Stuart-Smith (2000) that caribou population declines may be precipitated by increased predator abundance and efficiency following a reduction and fragmentation of older forests due to forest harvesting or wildfire as well as increased roading in conjunction with forest harvesting. This result also suggests that resource selection at small spatial scales may influence fitness of individual caribou (McLoughlin, Dunford & Boutin 2005).

Conducting similar analyses but at different spatial scales may provide opposing results and suggest the influence of different mechanisms (Wiens 1989). In the case of mountain caribou, however, features affecting their persistence remain similar across scales. These caribou currently persist in the portion of their historic distribution with wetter climatic conditions with relatively deep snow, infrequent fire history and consequently, more old and less mid-seral forests than where they have been extirpated (Apps & McLellan 2006). Accordingly, we found that adult female survival was lowest in populations associated with a higher proportion of young and mid-seral forests. At the home range scale, females were killed by predators more frequently in landscapes with relatively low old forest composition. These results suggest that without additional management of predators and alternative prey, mountain caribou populations can only remain viable in landscapes where early seral forests are rare and where old forests are common in their home ranges.

Our analysis has also evaluated the relative influence of landscape patterns vs. overall habitat amount (Boutin & Hebert 2002). At both spatial scales, we found greater support for variables reflecting habitat amount than habitat configuration. This result is consistent with other studies that compared relative effects of these factors (Fahrig 2003) and is expected in landscapes with high proportions of suitable habitat (Andren 1994). Although forest managers often focus on minimizing habitat fragmentation, our results suggest that overall habitat amount is more important to adult female survival at broader scales. At finer spatial scales, however, the distribution of old forest edge may influence caribou vulnerability to some predators (Apps *et al.* 2006).

Survival rates can be influenced by the age structure of the population, both in the absence of predators and where predation is a significant cause of mortality (e.g. Gaillard *et al.* 2000; Festa-Bianchet, Gaillard & Cote 2003). Variation in age structure among populations of mountain caribou may thus have contributed to the observed variation in survival among populations. We were unable to test the effect of age because accurate estimates were unavailable for the living sample.

Of particular importance to conservation, we found an additive effect between early seral forest stands and population density. At low population densities, caribou had lower survival probabilities in areas with greater amounts of young forests. The additive effect between low population density and young forests suggests that caribou are vulnerable to predation and continued population decline even at very low densities. This result supports the prediction of Wittmer *et al.* (2005b) (based on the same data set), that caribou population declines are likely to continue even as populations reach very low densities because caribou have become secondary prey to predators whose populations are responding to increasing alternate ungulate prey species. In such a system, the secondary prey species may be extirpated where they fail to spatially or temporally separate themselves from alternate prey species and their predators (Holt & Lawton 1994; Roemer, Donlan & Courchamp 2002). The apparent resilience of caribou survival when the proportion of young forests within population ranges is at very low levels further suggests that changes in the predator–prey system may occur at a specific threshold. Such a threshold may be explained by a population response from other ungulate species and their predators, resulting in unsustainable predation on caribou.

Predation strongly influences ungulate population dynamics (e.g. Messier 1991; Sinclair, Mduma & Brashares 2003; Owen-Smith, Mason & Ogutu 2005) particularly when the relative availability of prey species changes. Increasingly, the observed extinction processes of many species have been linked to anthropogenic changes in species composition, particularly following the introduction of exotics (Sinclair *et al.* 1998; Roemer *et al.* 2002). Asymmetric predation by means of apparent competition, where predators are

maintained by the more common, often exotic alternative prey, has been identified as the underlying mechanism causing the decline and extinction of native species. The importance of apparent competition resulting from shifts in the abundance and distribution of native species following anthropogenic habitat modifications and possibly climate change in the absence of exotic species has largely been overlooked (but see Sweitzer, Jenkins & Berger 1997; Robinson, Wielgus & Gwilliam 2002). Caribou in this study are part of a complex multipredator, multiprey system where the distribution and abundance of alternative ungulate prey populations have increased in response to habitat modifications and likely climate change (Spalding 1990; Shackleton 1999). Our results suggest that even without the introduction of exotics, apparent competition can cause rapid population declines and extirpation where prey availability has increased. Conserving a species that is in rapid decline and nearing extinction due to apparent competition in a system of indigenous species is a significant challenge for managers (Courchamp, Woodroffe & Roemer 2003). Management options required to maintain such a species include continuous predator management or a temporary reduction of predators combined with a continuous reduction in their primary prey either by hunting or by allowing vegetative conditions to gradually return to where they are less favourable to the primary prey.

Acknowledgements

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Supplementary material

The following supplementary material is available for this article.

Table S1. List of *a priori* candidate models at the population scale used to evaluate the importance of covariates for survival of female mountain caribou in British Columbia, Canada.

Table S2. Correlation coefficients of covariates used to model survival probabilities of adult female mountain caribou in British Columbia, Canada.

Table S3. Loadings of first and second principal components based on parameters measured within 10 distinct population ranges of mountain caribou in British Columbia, Canada.

Table S4. List of *a priori* candidate models at the home range scale used to evaluate the importance of habitat covariates on the probability that caribou were killed by predation.

Table S5. Correlation coefficients of habitat covariates used to model probabilities of caribou dying from predation.

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