EXPLORING POSSIBLE MECHANISMS FOR THE DECLINE OF THE BATHURST HERD OF BARREN-GROUND CARIBOU USING DEMOGRAPHIC MODELING

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ABSTRACT

The Bathurst herd of barren-ground caribou (*Rangifer tarandus groenlandicus)* declined between 1986 and 2006 at a mean annual rate of about 5% (Gunn at al. 2005a). We use a demographic model to explore possible mechanisms that were responsible for this decline. The modeling exercise had three components. First, we compiled demographic data from previous research on the Bathurst herd and other migratory tundra caribou herds. Second, we developed a population model that could be objectively fitted to the field data. Third, we undertook further demographic analysis using results of the initial population model to investigate effects of harvesting and potential scenarios for herd recovery. The field data most supported a model with calf survival and fecundity declining while adult male and female survival was constant. However, low sample sizes of collared caribou reduced survival estimate precision therefore reducing the power to detect trends in survival. Elasticity analysis suggested that the population could tolerate a larger degree of variation in productivity compared to adult survival. The model with declining calf survival and fecundity was then used to explore potential effects of harvest and herd recovery. We simulated potential increases in adult survival rates due to reduced hunting (with productivity constant). The model predicted that the population would still decline unless the adult survival rate was increased by more than 7.5%, suggesting that herd productivity (calf survival and fecundity) must increase for population recovery to occur. We ran simulations using 2007 parameter estimates of fecundity or calf survival and found that the herd would still decline unless calf survival increased to levels (i.e. 0.5 to 0.6). The principal challenge for our modeling was objectively determining plausible demographic model parameters and model formulations given the relatively few field measurements of demographic rates. Our modeling indicated that the Bathurst herd declined because of a trend toward reduced calf survival (and/or fecundity), which was likely exacerbated by reduced survival of adult females. Although a reduction in hunting would improve adult survival, our modeling suggested the herd will not be able to recover until calf survival improves. In addition, our results highlight the need for continuous monitoring of population parameters such as adult survival and productivity.

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INTRODUCTION

The Bathurst herd of barren-ground caribou (*Rangifer tarandus groenlandicus*) declined between 1986 and 2006 at an average annual rate of about 5% (Gunn at al. 2005a). As well as the statistically significant downward trend in the number of caribou, we have also documented a reduction in herd productivity (calf survival and/or fecundity based upon composition surveys) and an adult sex ratio biased toward females (Gunn et al. 2005b). A necessary step to managing a declining caribou herd is to understand the mechanisms for the decline. An instructive approach to exploring the factors involved in a decline, and their interactions, is to use demographic modeling (Caswell 1989). As a first step, modeling allows us to explore what demographic mechanisms are involved in the decline – for example is it adult mortality, reduced calf survival, or a combination of the two?

This paper is also in part a response to the 2004 Bathurst herd co-management plan developed by the Bathurst Caribou Management Planning Committee (BCMPC) (www.nwtwildlife.com). The plan includes management action 1.2.4 to develop a computer model "to predict the impact of harvesting activity on the herd and identify appropriate harvest levels". We restricted our approach to looking at how relatively low levels of harvesting could affect the recovery of the Bathurst herd.

We report here on deterministic and stochastic explorative modeling conducted to explore factors causing the decline and explore the impact of harvesting. The modeling was explorative and, given limitations of the data, we were not modeling to predict the absolute effects of specific management actions. We are also only modeling the mechanisms – the changes in demographic rates - rather than the causes of the changes in those rates. We lack data on the potential causes such as predation rates or the availability of forage.

METHODS

The modeling had three components. The first component was to compile data from previous analyses. In some cases, such as adult survival, we analyzed those data further to assess the assumptions of the demographic models used in the analysis. Additionally, we compiled demographic estimates from other migratory barren-ground caribou herds for comparison with the Bathurst herd. The second component was to develop a population model that could be fitted to multiple sources of field data. This model allowed testing of hypotheses about caribou demography and further estimation of demographic parameters. The third component involved demographic analysis using results of the population model and associated parameter estimates to investigate aspects of harvesting and recovery of the herd.

Estimation of demographic parameters

Much of the estimation of demographic parameters for the Bathurst herd has been undertaken in previous analyses. For this exercise we furthered those analyses to meet the requirements of a population model.

Adult survival rates: We updated our previous survival analyses of the satellite-collared cows (Boulanger et al. 2003) to include data up to the 2006/07 winter (i.e. October 2006 to April 2007). This data set was used to test for temporal and seasonal trends in survival rates using the binomial known fate models in program MARK (White and Burnham 1999).

One of the critical assumptions of the commonly used Population Viability Analyses (PVA) models is that the population parameters do not vary over time. We used random effects models in program MARK (White and Burnham 1999, White et al. 2002) to estimate process variance from the time series of adult survival rate estimates from the Bathurst herd from 1996 to 2007. Process variance is the biological variation in survival rates over time. Survival rate estimates from field data include both sampling and process variance and therefore overestimate the process variance that is of most biological interest. Use of parameter estimates with sampling variance included can potentially bias PVA model predictions (White 2000). Random effects models assume that yearly survival rates are a random sample of survival rates with a given variance. They provide survival rates with potentially lower variances (by fitting simpler models to the data) as well as estimates of process variance. Boulanger et al. (2003) provide more details on this satellite-collared cow data set.

One issue with temporal survival rate estimates from program MARK is that the error estimates are correlated, since they are estimated using the same model. This can create bias issues with the Ordinary Least Squares (OLS) (White and Lubow 2002) models, which we used for the population modeling. Boulanger et al. (2003) also estimated survival rates using the Kaplan-Meier (Pollock et al. 1995) model. The Kaplan-Meier is a non-parametric ratio-based survival rate estimation method and therefore yearly estimates generated using the Kaplan-Meir model are less likely to be correlated as a result of the modeling procedure. We therefore used the Kaplan-Meier estimates for the OLS model but used MARK to explore temporal trends in survival rates.

We have no data on adult male survival for the Bathurst herd. We therefore estimated adult male survival based upon sex ratios at birth and observed bull/cow ratios (as discussed later).

Fecundity rates: Fecundity was measured as the proportion of adult females breeding in a given year. The number of caribou on the calving grounds was estimated from calving ground surveys (as part of population estimate efforts) from 1986, 1990, 1996, 2003, and 2006 (Gunn et al. 2005a, J. Nishi, In prep). However, these estimates included yearlings, young bulls, and non-breeding cows that were on the calving grounds. Therefore the data from these surveys were further analyzed to estimate the proportion of pregnant females or females with calves compared to the number of females observed during composition counts (i.e. including barren cows). The methodology for these surveys changed, which prevented the use of jackknife or bootstrap methods to estimate variance from the earlier surveys. Instead, we estimated variance using composition counts from each strata surveyed (Thompson 1992). This method ensured comparability of variance estimates from all surveys.

We also used fecundity rates measured from corpus lutea in the Beverly herd (Don Thomas, CWS, unpublished data) and estimates from collared cows in the Porcupine herd (Fancy et al. 1994) to compare with field-based estimates. Estimates of fecundity were also estimated as part of the modeling procedure (described later).

Calf survival rates and adult sex ratios: Composition surveys to measure calf to cow ratios were conducted from 1985-1995 and 2001-2006 to estimate calf survival through to 9-10 months of age. Analyses of spring calf/cow ratios suggest that calf survival as an index for recruitment to the herd has declined, particularly from

2001 to 2004 (Gunn et al. 2005b). Spring calf/cow ratios combine both female productivity (i.e. fecundity) and calf survival, as spring surveys occur almost a year after the birth of caribou. Gunn et al. (2005b) assumed estimates of adult survival and female fecundity to estimate calf survival from calf/cow ratios. However, from a demographic model standpoint, calf survival estimates using this method are correlated with other adult survival and fecundity. This creates potential bias due to non-independence of demographic parameters. We therefore mainly used calf/cow ratios for the population model rather than calf survival rates derived from calf/cow ratios and fecundity rates.

Fall composition surveys were also conducted in 2000, 2001, 2004, and 2006. These surveys provided estimates of calf/cow ratios as well as adult sex ratios. The sex ratio data were used to further evaluate overall male versus female survival rates; these data were also incorporated into the population model. Only sex ratios from the 2004 and 2006 surveys were used in the model because the surveys in fall 2000 and 2001 were not considered to be representative of the herd (Gunn et al. 2005b).

Estimates of female population from the calving ground surveys

Photographic surveys were conducted on the Bathurst calving grounds in 1986, 1990, 1996, 2003, and 2006 to estimate the total number of cows and the number of breeding females in the herd (Gunn et al. 2005a, J. Nishi in prep.). For the population model we were mainly interested in the estimated total number of females in the herd rather than the estimate of the number of breeding females. Estimation of breeding females involved estimation of the number of females not breeding in a given year and was therefore partially correlated with estimates of female fecundity, which was another model parameter. Estimation of total herd size depends on assumed sex ratio in the herd (Heard 1985). We were interested in using field measurements for model fitting that had the least amount of subjective assumptions. Therefore, we used total female population size for model fitting. We reduced estimates of total females for the proportion of bulls and yearlings on the calving ground using data from composition counts on the calving ground (Gunn et al. 2005a). For this, the total number of caribou observed on the calving ground was multiplied by one minus the proportion of bulls and male yearlings observed on the calving ground to estimate total number of female caribou. For this calculation, we assumed that half of the yearlings observed were male.

Inference from other studies As noted above, there are no direct measures of calf or yearling survival for the Bathurst herd. We therefore considered demographic parameters from studies of the Porcupine herd (Fancy et al. 1989, Fancy et al. 1994, Walsh et al. 1995) (Table 1). Fecundity was estimated at 0.76 (SE=0.49) (Don Thomas, pers. comm.), from calving ground survey composition counts and by placental ovarian scars from the Beverly caribou herd. These parameters were not used directly in modeling, but were considered when evaluating the biological feasibility of parameters estimated from the model we developed.

Table 1: Estimates of demographic rates for Porcupine caribou herds

Parameter	Estimate	SE	CV	Period
Survival				
Adult survival	0.83	0.04	0.05	1989-1992
Yearling survival	0.93	0.17	0.18	1989-1992
Calf survival	0.56	0.06	0.11	1989-1992
	0.71	0.03		2001-2
Fecundity				
Ovarian scars	0.82	0.05	0.06	1989-1992

Deterministic caribou life history model

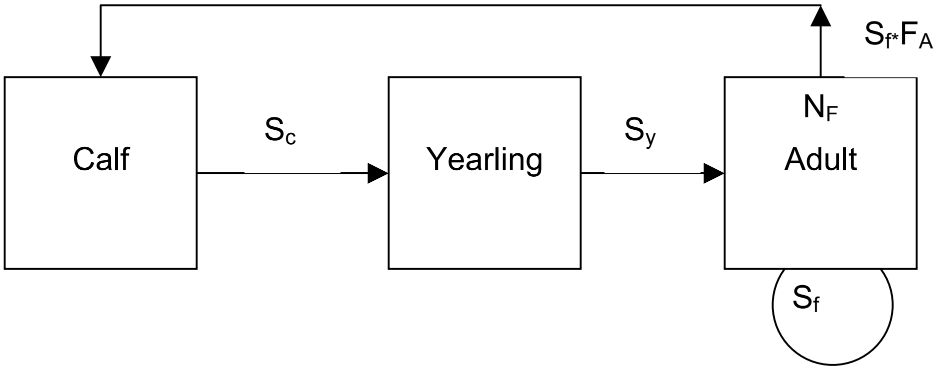
We initially used a deterministic model to explore caribou demography in which population parameters had no biological or environmental variance. Most demographic parameters were not directly measured or estimated. For example, only adult female survival had been estimated. This is in contrast to calf survival, adult male survival, and yearling survival, which were either not estimated or were indirectly estimated from sex and age composition surveys. Given this, standard PVA model methods (which require firm parameter estimates) were inappropriate. In addition, we suspected that recruitment varied over time, which violated the assumption of temporal invariance of parameters needed for standard matrix model projection. However, it was still possible to infer the demography of caribou through the modeling of indirect demographic data. For example, a time series of calf/cow ratios, adult survival estimates, and breeding cow population estimates did exist for the Bathurst herd.

We used a modeling procedure developed by White and Lubow (2002) to fit a demographic matrix model to adult survival, calf/cow ratio, female population size, and fall sex ratio data. This approach involves first proposing a standard matrix-type model of caribou demography with a number of parameters (Table 2).

Table 2: Demographic model parameters

Parameter	symbol
S_f	Adult female survival
S_m	Adult male survival
S_y	Yearling survival (sexes pooled)
S_c	Calf survival
F_a	Adult female fecundity
N_f	Population size females
N_m	Population size males
r	Sex ratio at birth (assumed to be 1:1)

The female portion of the model is summarized below. This model was based upon a yearly census that occurred each spring when calves were born.



We defined survival rates for calves (S_c), yearlings (S_y) and adults (S_f and S_m) as the probability that a cohort would survive to the next year. Recruitment was defined as fecundity (F_a-the proportion of adult females that give birth) times the yearly survival rate (S_f). Using this parameterization for recruitment takes into account that some females that were pregnant in a given year would not survive. This parameterization is equivalent to that used in life-table models based upon annual censuses (Taylor and Carley 1988), such as those incorporated into the program RISKMAN (Taylor et al. 2003). We assumed that yearlings did not breed. The male population was modeled using the same life history model as females (without productivity terms), with the number of male calves determined by recruitment rate times the sex ratio at birth (r). This model assumes that immigration or emigration into the Bathurst herd does not occur or that emigration balances immigration so that there is no net movement to or from the herd. This assumption is based on the published caribou literature and the satellite-collared cows (1996 to 2007) in the Bathurst and neighbouring herds (Gunn et al. 2001, Gunn et al. In prep.)

The population model was projected from 1985 (the first year of estimated calf/cow ratios) to 2007. The initial population sizes were based on values from the 1986 calving ground census. As with the 1986 census, a bull to cow ratio of 66 males to 100 females was assumed based upon estimates of sex ratio from Heard and Williams (1991). This assumption was used to set the initial population size for bulls, using the estimated initial female population size times the bull/cow ratio. The sex ratio at birth was assumed to be 1:1. This assumption is supported by other demographic studies of caribou (Thomas et al 1989 Fancy et al 1994, Haskell and Ballard 2007).

Predictions of field estimates were generated from the stage-based matrix model. Estimates of spring calf/cow ratio were estimated as $F_a S_c^{(t/365)} / S_f^{(t/365)}$ where *t* was the interval from birth of calves to when spring composition surveys were conducted. A similar formula was used for fall surveys with a different survey interval. Using the survey interval scaled survival estimates to the duration between birth and surveys. Similarly, fall sex ratio was derived from the model as $N_m S_m^{(t/365)} / N_f S_f^{(t/365)}$, which estimated the number of caribou in the herd while accounting for caribou mortality between spring calving and fall composition surveys. This formula was most useful when sex-specific rates in survival were modeled.

The stage-based model does not make assumptions regarding maximal life span of caribou. However, multiplying successive survival rates can approximate the proportion of caribou surviving to later cohorts. Using this approximation, less than 5% of caribou would survive past their 11th year, assuming a calf survival rate of 0.34 and adult survival rate of 0.82. These survival rates are within the range of values recorded for barren-ground caribou (for example Miller 1974, Thomas 1998).

Ordinary Least Squares methods to estimate model parameters and test hypotheses about caribou demography

The main distinction and advantage of White and Lubow's (2002) model is that projected population size, spring calf/cow ratios, fall calf/cow ratios, and bull/cow ratios can be compared to estimates from field surveys and parameters re-estimated based upon the fit of the model to field survey data. Each model prediction (θ) was compared to a corresponding field estimate $\hat{\theta}$ using the following penalty term (ε).

$$\varepsilon = [(\theta - \hat{\theta}) / \mathrm{SE}(\hat{\theta})]^2$$

The penalty term basically considered the agreement between model predictions (θ) and field estimates ($\hat{\theta}$) in the context of the precision of the field estimate (as estimated by SE ($\hat{\theta}$)). For example, a large difference between a model prediction and a field estimate might not result in a large penalty if the standard error of the field estimate was large. White and Lubow (2002) further showed that the penalty terms were proportional to the log-likelihood of the model and therefore could be used instead of log-likelihood values to assess model fit. For example, a large penalty or log-likelihood would suggest poor model fit. This allowed evaluation of the fit of a set of parameters and model formulations.

Both parameter estimates and model formulation influence the fit of the model. The basic objective of modeling was to maximize agreement between field data and model parameters. Therefore, the estimates were iteratively varied (using an optimization algorithm) to minimize the sum of penalties for a given set of parameters and model formulation. This type of estimator is termed the Ordinary Least Squares (OLS) estimator of model parameters. Once the penalty term was minimized then an AICc score was formulated for the model. Briefly, the AICc score basically considers the fit of a model (as indicated by the penalty term) and model complexity (as indicated by the number of parameters). A lower AICc score suggests the most parsimonious model that balances bias (model fit) and precision (model complexity) (Burnham and Anderson 1998). The difference in AICc values between the most supported model and other models (ΔAICc) was also used to evaluate the fit of models when their AICc scores were close. In general, any model with a ΔAICc score of less than 2 was worthy of consideration. In addition, the proportional support of each model, or AICc weight (w_i) was considered in evaluating the support of each model.

The OLS approach was used to estimate demographic parameters and explore temporal variation in model parameters. The OLS model estimated all the parameters in Table 2 with the exception of initial male population size and sex ratio at birth. Initial male population size was estimated as the initial estimated adult female population size times the assumed bull/cow ratio. Most standard matrix models assume demographic parameters do not change over time. However, it is more likely that for caribou, parameters such as fecundity and/or calf survival vary over time. Therefore, models that allowed linear and non-linear trends in demographic parameters were proposed and evaluated using OLS methods by introduction of trend parameters. Non-linear trends were estimated using polynomial (i.e., quadratic and cubic) terms.

We also considered the density dependent equation of Smith and Slatkin (1973) to model non-linear trends. This equation assumes that vital rates are constant until an inflection point (I) that is determined by population size (N). The equation is $X'_{ij}=x_{ij}/(1+(N/I)^{b})$ where x_{ij} is the density independent parameter value, X'ij is the density dependent parameter value, N is population size, I is the inflection point, and *b* is the slope of the function (Haskell and Ballard 2007). This is a very general equation for density dependence; it allows vital rates to change as a function of population density but does not assume an inherent carrying capacity.

This approach provided further inference on forms of demographic variation in caribou that were most supported by the field data. For example, this model attempted to answer the question “Were observed changes in field estimates brought upon by temporal changes in demographic parameters, or could the observed data result from temporally constant demographic parameters?” In addition, it was possible to constrain parameters to mimic biological relationships. For example, yearling survival was constrained to be less than adult survival in simulations.

Deterministic matrix models to evaluate elasticity of life history parameters

We used a stage-based matrix model (Caswell 1989) for the female segment of the population to evaluate the elasticity of life history parameters. Elasticity is the proportional change in λ (population rate of change; N_{t+1}/N_t)) caused by a percentage change in a given parameter. Elasticities are useful for comparisons as the elasticities of all parameters in a matrix model add up to 1, therefore allowing direct comparison of parameters. In addition, λ (as determined by the dominant eigenvalue of the matrix model) was estimated. We used parameter values estimated from field data, other studies, and the OLS model results. We used the PopTools (Hood 2003) program for elasticity calculations.

Stochastic model to evaluate demographic scenarios

Deterministic models are useful to evaluate the relative contribution of demographic parameters to population rates of change. However, it is important to consider the variance of parameters when evaluating actual rates of increase. We used a stochastic model to evaluate various demographic scenarios for the Bathurst herd. The stochastic model's formulation was based on the most supported OLS deterministic model.

We programmed this model in SAS (SAS Institute 2000) rather than using existing software packages such as VORTEX (Miller and Lacy 2005) or RISKMAN (Taylor et al. 2003), because we wished to have more flexibility in modeling demographic parameters than these packages offered. For example, these packages do not allow the direct modeling of temporal trends in demographic rates as was detected for the Bathurst herd using the OLS model (discussed later).

The stochastic model simulated various forms of stochasticity. Demographic stochasticity, or individual variation in demographic rates was simulated by comparing individual rates to a randomly generated variate based upon a uniform distribution. Temporal variation in demographic rates was simulated by picking a random normal variate and then using a logistic transformation to ensure it was within the 0 to 1 interval. This process is the method in which confidence intervals are generated for survival probabilities. Additional individual variation (demographic) in demographic rates was also simulated using the above procedure.

Estimates of demographic rates from field data include both biological (termed process variation) and sampling variation. Process variation encompasses both demographic and temporal variation in rates. We used the methods of Burnham et al. (1987) and Thompson et al. (1998) to estimate the proportion of variance caused by biological and sampling variation. This involved analyzing the time series data of calf/cow ratios (for calf survival variance) and proportion females breeding during population surveys (for fecundity variance). We assumed that variance in the calf/cow ratios would be roughly similar to the degree of variance in calf survival rates. The procedure involved estimating weighted means and variances for yearly estimates (since it could not be assumed that variance from yearly surveys were equal) and then iteratively solving for the most likely temporal variance from the time series. The outputs of this analysis were coefficients of variation of estimates based upon temporal and sampling variation (Table 3). Variance estimates for the OLS model were then calculated by multiplying estimated values by each of the coefficients of variation.

Table 3: Estimates of temporal and individual (demographic) variation, expressed as coefficient of variation (CV) for input demographic parameters from mark-recapture analysis (Sa), and variance components analysis (other parameters).

Parameter	CV (individual)	CV (time)
Adult survival (S_f and S_m)	0.10%	3.15%
Fecundity (F_a)	8.40%	3.29%
Calf survival (S_c)	12.70%	36.79%
Yearling survival (S_y)	12.70%	3.15%

A key point is that precise estimates of future population trajectories for the Bathurst herd are not possible from this model given lack of data on parameter values and their associated variance. Instead, this model was used to explore the relative sensitivity of Bathurst herd demography to various scenarios.

The effect of variation in calf survival, fecundity and adult survival on population trend

One apparent trend in calf/cow ratios is the large degree of yearly variation in estimated productivity of the Bathurst caribou herd (Gunn et al 2005b). This variation could be due to variation in fecundity and/or calf survival, as well as sampling variation. Heterogeneity in demographic rates can generally result in lower rates of population growth (Conner and White 1999, White 2000), however, it is difficult to know how variation in different demographic parameters might affect overall trends. For this reason, we conducted simulations where we increased proportional variation in demographic rates and then assessed overall population trend. This simulation basically complemented deterministic elasticity analyses by evaluating the effect of stochastic variation on demographic parameters.

The effect of hunting on survival rates of females and resulting population trends

Hunters annually harvest caribou from the Bathurst herd but reporting harvest levels is only mandatory for outfitter–guided hunting and voluntary for residents. , The aboriginal harvest is largely unrecorded. Thus, estimates of the actual number of caribou harvested are limited. Some data are available from a harvest study conducted in 1988-93 (The Dogrib Harvest Study, GNWT unpublished data). In addition, the proportion of collared female caribou that were shot also provides information on the effect of harvest on female survival rates. We used these two sources of information to define a plausible range of reduction of survival rates for female caribou caused by hunting. The proportion of the adult population harvested was estimated from the harvest study by taking the number of reported harvested caribou and dividing by estimated population size from the OLS model for the years of the harvest study. In addition, survival analyses were conducted with and without harvested caribou. The survival estimates were then compared to determine the approximate reduction in survival rates caused by hunting. These estimates were used to simulate the potential change in overall population trend caused by varying proportional reduction in survival rate caused by hunting.

Potential scenarios for herd recovery

We used results from the OLS model to explore potential recovery scenarios for the herd based upon historic estimates of demographic parameters. A main objective of the OLS model was to detect likely trends in parameters over time. If this was successful, it was also possible to estimate starting (1985) and ending parameter values (2007) for the model. We used these values to estimate the required levels of female survival, calf survival, and fecundity that would produce an increase in herd population size. We focused on the adult female segment of the population since this segment most directly influences herd productivity.

RESULTS

Adult female survival rate estimation

Model selection results from the MARK known fate models suggested that adult female survival rates were relatively constant (Table 4). A linear trend (S(T)) and seasonal (S(season)) model were marginally supported by the data also as determined by delta AICc values of less than 2.

Table 4: Program MARK model selection for adult female survival rate

Model	AICc	ΔAICc	w_i	K	Deviance
constant	302.7	0.00	0.47	1	13.79
trend	304.2	1.54	0.22	2	13.31
season	304.6	1.86	0.19	2	13.63
season + trend	306.1	3.46	0.08	3	13.20
season + quadratic trend	307.8	5.07	0.04	4	12.77
year-specific	315.2	12.49	0.00	11	5.65
season*year	333.4	30.70	0.00	22	0.00

Random effects models were run for data series to estimate mean survival rate and variance components (Figure 1). The mean survival rate from the random effects intercept model was 0.81 (SE=0.029, CI=0.76 to 0.86). This estimate was similar to the constant survival (S(.)) model, but the variance was lower as process variance had been removed from sampling variance. A plot of year X season survival rates also does not suggest a dominant trend in survival rates over time. The yellow line in Figure 1 is survival rate estimates for each year and season. The mean random effects survival rate estimate is given as the red line. The random effects intercept model estimate (assuming a constant survival rate over time) is given as a blue line. Both the year and season survival rate and random effects model lines fluctuate randomly around the random effects intercept model estimate. This result suggests that adult female survival rates were relatively constant for the time period that collaring had occurred.

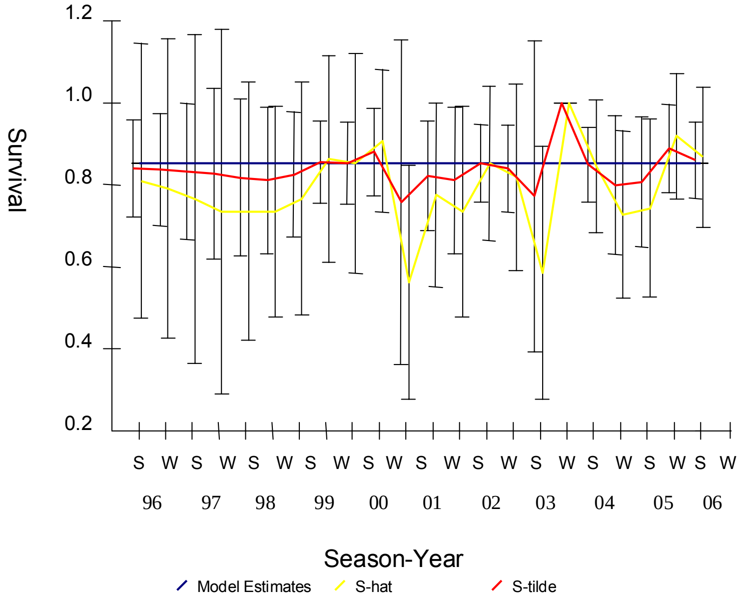


Figure 1: Model based estimates (S-hat), random effects estimates (S-tilde), and intercept model estimates (model estimates) of adult female survival for the Bathurst caribou herd 1996-2007.

Ordinary Least Squares Population model

We ran various forms of the OLS model that each made specific assumptions about trends in demography of the Bathurst herd (Table 5). The most supported model assumed a quadratic trend in calf survival (Table 5, model 1) and a linear trend in adult fecundity. This model held the weight of support as indicated by an AICc weight score of 0.85. The density dependent calf survival model was not supported. As discussed later, given the parameterization of the model and available data it was difficult to completely separate the effects of decreasing calf survival and adult fecundity given that the two values were confounded in terms of observed calf/cow ratios. Models with trends in adult survival were not supported (Models 5, 9, 13 and15). This result was also apparent in MARK analysis of female survival data alone (Table 4). A model with all parameters constant (model 14) was not supported.

Table 5: AICc model selection results from OLS deterministic caribou model. Sample-size adjusted Akaike Information Criteria (AICc), difference in AICc between most supported and given model (ΔAICc), Akaike weight (w_i), the number of parameters (K), effective sample size (ESS), and sum of penalties (ΣPen) are displayed. Effective sample size is the number of model and field data comparisons used to estimate penalties.

No	Model[A]	AICc	ΔAICc	w_i	K	ESS	ΣPen
1	S_c, S_c^2, F_a	628.7	0.00	0.85	9	44	605.4
2	S_c, S_c^2	632.2	3.53	0.15	8	44	612.1
3	den dep S_c[B]	638.5	9.82	0.01	8	44	618.4
4	S_c, F_a	657.4	28.76	0.00	8	44	637.3
5	S_c, S_c^2, F_a, and S_f	681.4	52.72	0.00	12	44	647.3
6	S_c	683.8	55.09	0.00	7	44	666.7
7	S_c, S_c^2,F_a,F_a^2	696.7	68.03	0.00	12	44	662.6
8	S_c,S_c^2,S_c^3	709.7	81.05	0.00	9	44	686.4
9	S_c,S_f,F_a	756.7	128.01	0.00	11	44	726.4
10	F_a	821.1	192.45	0.00	7	44	804.0
11	F_a,F_a^2	1027.1	398.46	0.00	9	44	1003.8
12	F_a,F_a^2,F_a^3	1030.5	401.83	0.00	10	44	1003.8
13	S_f	1156.1	527.38	0.00	7	44	1138.9
14	all constant	1249.5	620.79	0.00	6	44	1235.2
15	S_f,S_f^2	1321.8	693.13	0.00	10	44	1295.1
16	S_m	1331.5	702.85	0.00	7	44	1314.4
17	S_c, F_a,F_a^2	1847.7	1218.99	0.00	11	44	1817.4
18	den dep F_a	1397.6	768.89	0.00	8	44	1377.5

[A] Only parameters that were varied temporally are shown. Other parameters were held constant

[B] The density-dependent model of Smith and Slatkin (1973) was used to allow temporal variation of this parameter

Estimates from the most supported OLS model suggest a decline in fecundity and initial stable to increasing calf survival followed by a decline in calf survival after 1991 (Figure 2).

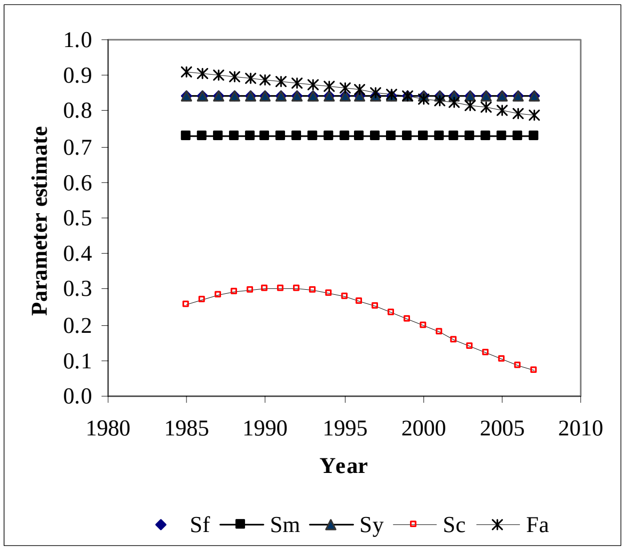


Figure 2: Trends in parameter values for most supported OLS model (Table 5, Model 1).

Initial (1985) estimates of parameters from each of the models are given in Table 6. Female survival estimate from the OLS model (0.842) was higher than that estimated from collared cow data 0.81 (SE=0.029, CI=0.76 to 0.86), but still within the confidence limits of field estimates. Male survival was lower (0.730) than female survival (0.842) in all of the models.

Table 6: Initial (1985) model parameter estimates from OLS models from Table 5.

No.	Model	S_f	F_a	S_m	S_y	S_c
1	S_c, S_c^2, F_a	0.842	0.913	0.730	0.842	0.259
2	S_c, S_c^2	0.839	0.818	0.727	0.839	0.279
3	den dep S_c	0.840	0.819	0.731	0.840	0.401
4	S_c, F_a	0.843	0.999	0.733	0.843	0.343
5	S_c, S_c^2, F_a, and S_a	0.710	0.931	0.783	0.710	0.169
6	S_c	0.836	0.819	0.731	0.836	0.499
7	S_c, S_c^2,F_a,F_a^2	0.823	0.975	0.713	0.823	0.139
8	S_c,S_c^2,S_c^3	0.818	0.820	0.708	0.818	0.211
9	S_c,S_f,F_a	0.713	1.000	0.780	0.713	0.385
10	F_a	0.857	1.000	0.738	0.857	0.183
11	F_a,F_a^2	0.848	1.000	0.718	0.848	0.115
12	F_a,F_a^2,F_a^3	0.848	1.000	0.718	0.848	0.115
13	S_f	0.564	0.818	0.824	0.564	0.180
14	all constant	0.870	0.818	0.770	0.870	0.163
15	S_f,S_f^2	0.546	0.818	0.237	0.546	0.039
16	S_m	0.845	0.820	0.771	0.845	0.158
17	S_c, F_a,F_a^2	0.818	0.999	0.707	0.818	0.386
18	den dep F_a	0.910	0.988	0.819	0.910	0.205

Figures 3 and 4 show model predictions compared to field data for the most supported OLS model. The model fit all field data reasonably well with model predictions overlapping confidence intervals from field measurements in most cases. Model predictions were extrapolations of actual field trends for some relationships such as bull/cow ratio and adult survival, as those parameters were not measured in the 1980s or early 1990s. The adult female survival estimate is slightly higher than point estimates of adult female survival from the Kaplan-Meier model. However, the precision of these estimates is low (as indexed by large confidence intervals) and estimates are only available after 1996. Therefore the model-based estimate is still within the realm of possible field measurements.

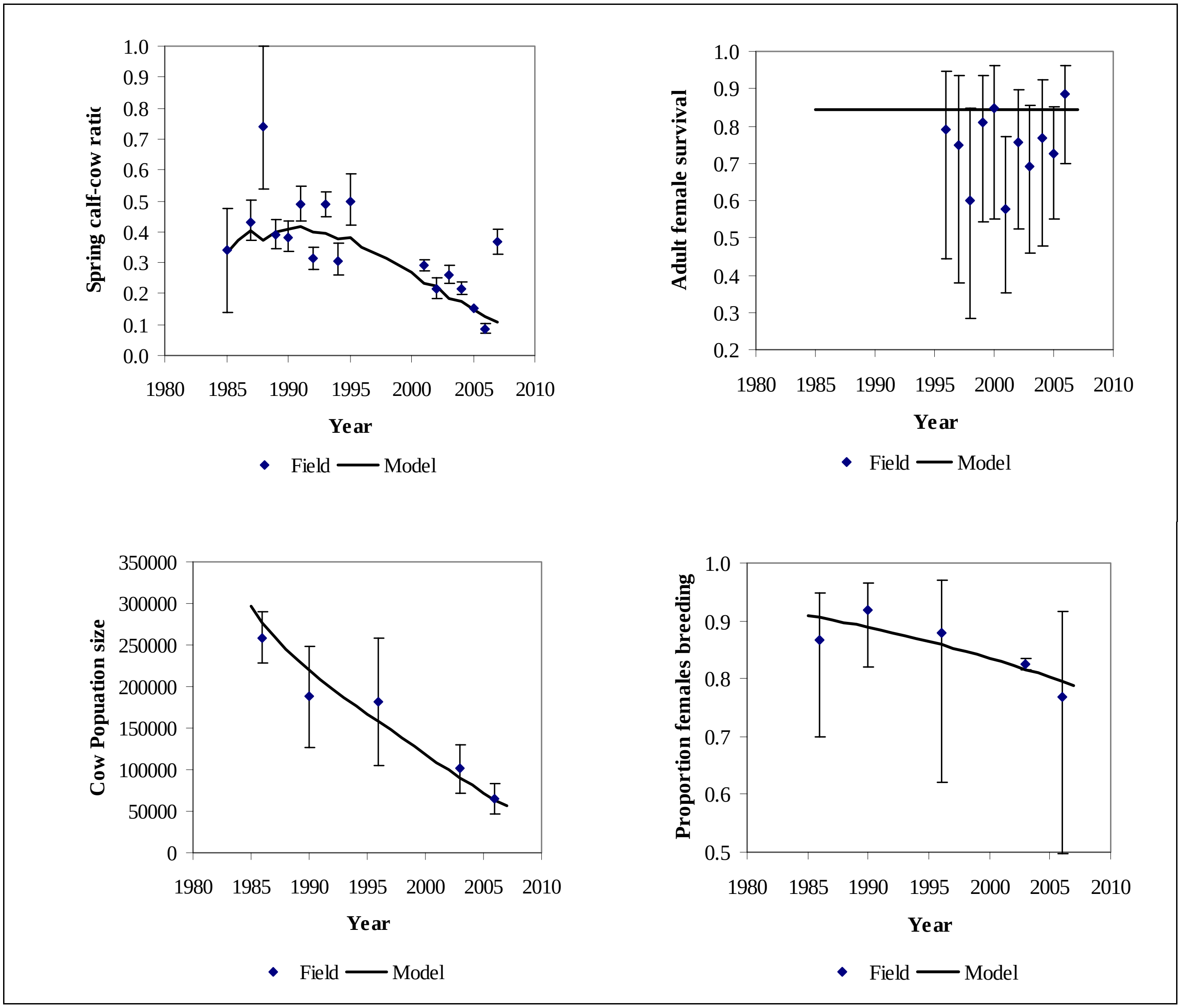


Figure 3: OLS demographic model estimates compared to field estimates for spring survey data and adult survival data. Estimates are for the most supported OLS model (Table 5, model 1). Field estimates have associated 95% confidence intervals.

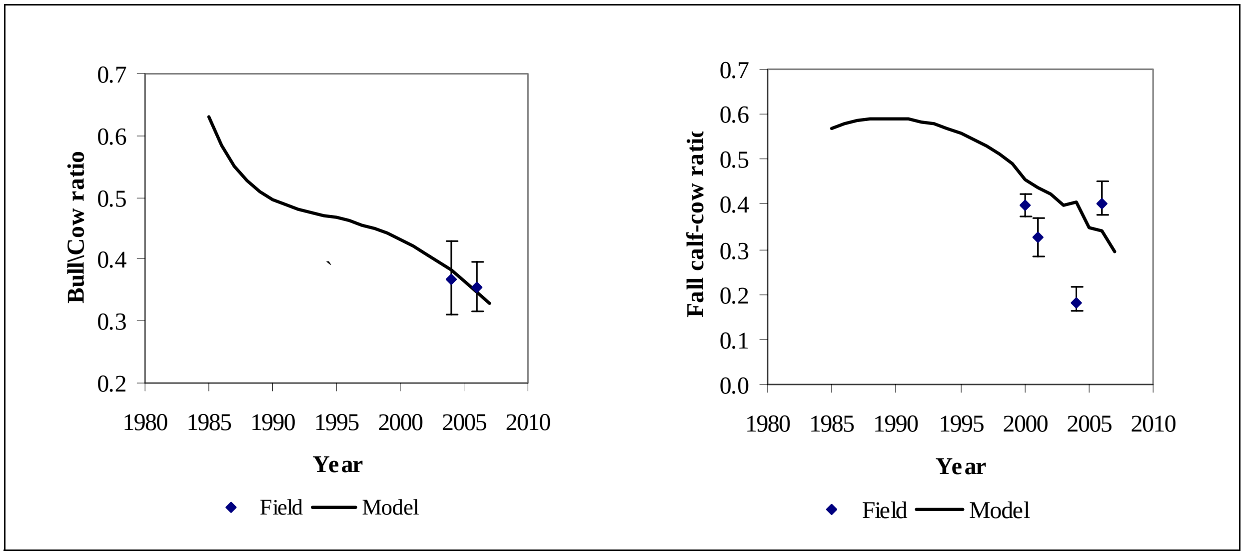


Figure 4: OLS demographic model estimates compared to field estimates for fall survey data. Estimates are from the most supported OLS model. Field estimates have associated confidence intervals.

The decline of bull/cow ratio over time (due to lower model-based estimates of adult survival rates (Figure 4)) is contingent on the initial assumption that the bull/cow ratio was 66/100 in 1985 (Heard 1985) and the initial 1:1 sex ratio at birth. We ran the model with different assumed initial bull/cow ratios and found that the overall effect on male survival was negligible. For example, if the initial bull/cow ratio was 0.35, 0.66 (ratio used) or 0.8 the resulting male survival estimate from the most supported OLS model was 0.730, 0.730, and 0.729, respectively. This may seem counterintuitive, however, the main contribution of the assumed initial bull/cow ratio was the setting of initial bull population size and therefore the impact of this assumption is not large. Bull/cow ratio was mainly influenced by the assumed initial birth sex ratio in the model and differential adult survival. If mortality were equal between sexes, then the bull/cow ratio would be the same as the sex ratio at birth. The lower observed bull/cow ratios of 0.36 and 0.35 observed in 2004 and 2006 suggest that mortality is higher in male caribou, and as a result 0LS male survival estimates are lower than those for females.

The model fit the spring calf/cow ratio data well, except for 2007 where the field observation was considerably higher than model predictions (Figure 3). In addition, estimates from 1988 were much higher than predicted by the model. The influence of these two points was not great enough to significantly influence model fit. For example, a cubic calf survival model was tested with the data that could have resulted in calf/cow ratios increasing to meet the 2007 observation. However, this model was less supported than the quadratic calf survival model. We used the 2007 estimate of calf survival to explore potential scenarios for herd recovery.

Simulated population trajectories for the most supported OLS model suggest declines in all cohorts (Figure 5).

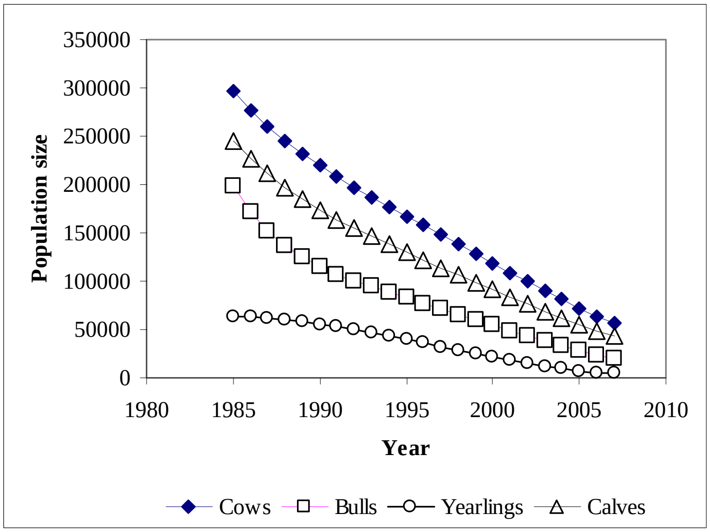


Figure 5: Estimated population size for caribou cohorts from the most support OLS model.

Elasticity analyses

We used deterministic elasticity analyses to estimate the influence of model parameters on population trends. We restricted the analyses to females because females contribute directly to population growth. Elasticities of parameters across a range of OLS model values are given in Table 7. We modeled productivity as the product of adult female survival and fecundity (as described earlier). High and low calf survival (S_c) and fecundity (F_a) values were taken from the initial and endpoint values of the most supported OLS models (Table 6). OLS estimates of fecundity were multiplied by 0.5 (assuming an even sex ratio at birth) as we were analyzing only the female portion of the population. Adult female survival had the highest degree of influence on population trend as indicated by a high average elasticity of 75.7%. Yearling survival, calf survival, and adult fecundity had equal influence to each other, but together contributed only 24.3% to the total elasticity. This suggests that caribou populations can tolerate a large degree of variance in productivity and survival rates of calves and yearlings. This topic was explored further in stochastic simulations, below.

Table 7: Elasticity analysis of model parameters for the female segment of the population. Scenarios based on OLS model estimates and an "Estimated" scenario based on field and estimates from other studies. Fecundity (F_a) is half of the value used for the male and female model assuming a 1:1 sex ratio at birth.

Scenario	**Parameters**				**Model Results**				
					λ	Elasticity			
	S_f	S_y	S_c	F_a		S_f	S_y	S_c	S_f*F_a
High S_c	0.842	0.842	0.500	0.410	0.99	65.4%	11.5%	11.5%	11.5%
Low S_c	0.842	0.842	0.110	0.410	0.88	87.3%	4.2%	4.2%	4.2%
High F_a	0.842	0.842	0.259	0.450	0.94	74.9%	8.4%	8.4%	8.4%
Low F_a	0.842	0.842	0.259	0.390	0.93	77.1%	7.6%	7.6%	7.6%
High S_f	0.900	0.842	0.259	0.450	0.99	76.9%	7.7%	7.7%	7.7%
Low S_f	0.810	0.842	0.259	0.450	0.91	73.6%	8.8%	8.8%	8.8%
estimated	0.842	0.842	0.259	0.450	0.94	74.9%	8.4%	8.4%	8.4%
average						75.7%	8.1%	8.1%	8.1%

Stochastic simulations

We used a stochastic model to further explore resulting population trends if random variation was allowed in demographic rates. This allowed us to explore the effects of environmental variation, such as a late spring, under the assumption that any trend in environmental variation would influence trends in calf survival and fecundity (the most supported OLS model).

Sensitivity to variance in demographic rates

For this analysis, the 1985 parameter values for most supported OLS model were used (Table 5, Model 1). No temporal trends in parameters were simulated. In addition, we adjusted adult male and female survival so that the deterministic λ of the population was 1. This provided a common initial basis for comparing simulations. Temporal variance in parameters was then simulated for one parameter, while allowing no variance in the other parameters. Variances, as indexed by a coefficient of variation up to 0.3, were simulated. Individual demographic variance in rates was also initially simulated, with similar results to temporal variation simulations. The effect of demographic (individual) variance rates on the precision of simulations was negligible given the relatively large population sizes simulated. In general, variance in calf survival and fecundity had less influence on overall population trend. In contrast, variance in adult female survival caused more substantive negative population trends (Figure 6).

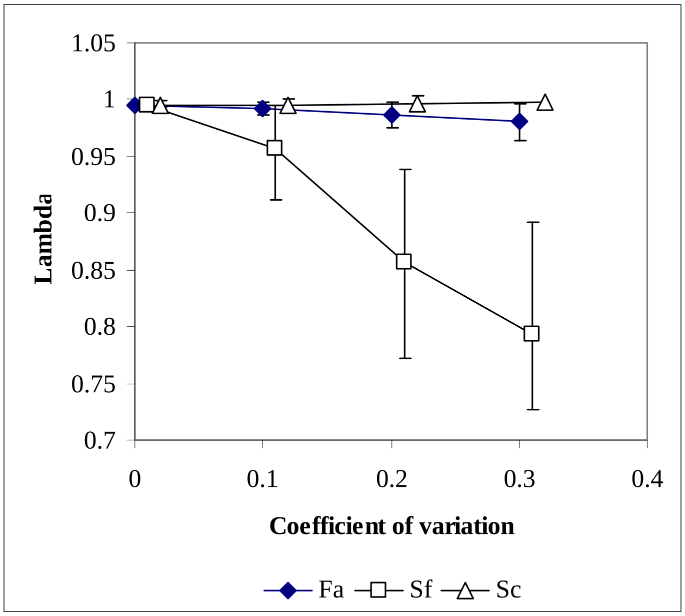


Figure 6: Geometric mean estimates of trend from simulations as a function of variation in parameters as indexed by coefficient of variation (CV).

These results can be viewed in terms of population trajectories of females with a CV equal to 0.3 for all parameters (Figure 7). Variation in calf survival does not influence trajectories substantially compared to variation in adult female survival. Fecundity has a moderate effect on herd trajectory.

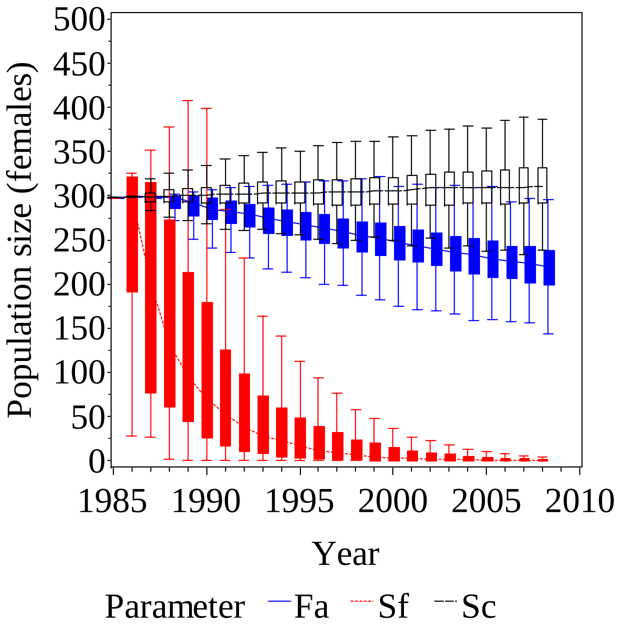


Figure 7: The effect of temporal variation in demographic parameters. Temporal variation (coefficient of variation=0.3) was simulated for adult female fecundity (F_a), adult female survival (S_f) and calf survival (S_c), while no variation was simulated in the other parameters. The bottom and top of the boxes around each point represent the 25th and 75th percentiles of estimates. The lines represent the entire range of estimates.

Hunting

Comparison of Kaplan-Meier survival rate estimates with and without hunting suggested a slight increase in adult female survival rates of 3% without hunting (Table 8). This can be interpreted to mean that on average there would be 3 more adult female caribou out of 100 not killed per year in the absence of hunting. We assumed that hunters would neither select for or against collared cows, as the collars are relatively inconspicuous.

Table 8: Summary statistics and survival rates for adult female collared caribou with hunting mortalities included and excluded

Year	Collared caribou mean	 std	Mortalities shot	 total	Survival Hunt	 SE	 No hunt	 SE
1996	8.9	1.1	0	2	0.79	0.13	0.79	0.13
1997	6.7	0.7	0	2	0.75	0.15	0.75	0.15
1998	13.6	5.8	1	5	0.60	0.16	0.64	0.17
1999	13.8	0.9	0	3	0.81	0.10	0.81	0.10
2000	13.3	2.2	0	2	0.85	0.10	0.85	0.10
2001	16.3	3.5	1	8	0.58	0.11	0.63	0.11
2002	17.1	3.3	0	5	0.76	0.10	0.76	0.10
2003	16.5	2.7	2	6	0.69	0.11	0.78	0.10
2004	14.0	6.4	1	3	0.77	0.12	0.85	0.10
2005	28.2	2.9	0	9	0.73	0.08	0.73	0.08
2006	21.2	2.7	2	3	0.89	0.06	0.95	0.05
Geometric mean					0.74		0.77	

We compared estimates of population size for cows and bulls from the most supported OLS model to estimates of harvested caribou from the Dogrib Study. These estimates were then used to obtain another estimate of the proportion of caribou harvested (Table 9). This is similar to gain in survival rate, since each estimates the proportion of caribou that would not have been killed if there were no harvest. In this case the proportion was 4.07% for cows and 6.65% for bulls. In other words, an average of 4.07 and 6.65 caribou out of 100 were removed from the population by hunting. The highest proportion of harvest was for bulls in 1992 when 9.2% of the population was harvested. We note that these figures are for reported harvest and do not include potential mortalities due to wounding loss. There were no estimates of wounding loss from the Dogrib Harvest study.

Table 9: Estimated proportion of bulls and cows removed from using OLS model population size and estimates of harvest from the Dogrib Harvest Study.

Year	OLS model estimate[1]		Caribou harvested		Proportion of N	
	N bulls	N cows	bulls	cows	bulls	cows
1988	139836	244937	4606	3318	3.3%	1.4%
1989	128523	231470	3855	4730	3.0%	2.0%
1990	119350	219210	8970	8450	7.5%	3.9%
1991	111642	207872	10073	11626	9.0%	5.6%
1992	104890	197200	9685	9046	9.2%	4.6%
1993	98729	186991	7712	13107	7.8%	7.0%
Average			7484	8380	6.65%	4.07%

[1] Most supported OLS model (Table 5, model 1) used for population estimates.

It is difficult to evaluate how much survival might increase in the absence of hunting for 1985-2007. We therefore ran simulations for a 0%, 5% and 7.5% increase in adult female and adult male survival rates to cover the most likely range of values. The most supported OLS model with trends in calf survival and fecundity was used for simulations (Table 5, model 1). The simulated adult survival rates for the 0%, 5% and 7.5% scenarios were 0.842, 0.884, 0.905 and 0.729, 0.766, 0784 for females and males, respectively. The 0% simulation used survival rates from the OLS model with no adjustment therefore corresponding to a scenario with hunting. The 5% and 7.5% simulations corresponded to potential scenarios in which survival rate was increased due to no hunting mortality.

Evaluation of adult female population trajectories suggests that the population would still decline unless survival rate increased by at least 7.5% (Figure 8). In contrast, declines in the male component of the population would still occur regardless of the scenario. This result was due to the lower estimated OLS model survival rate for males. The 0% scenario closely matches estimated female population size, which makes sense given that this scenario was based on the most supported OLS model parameters.

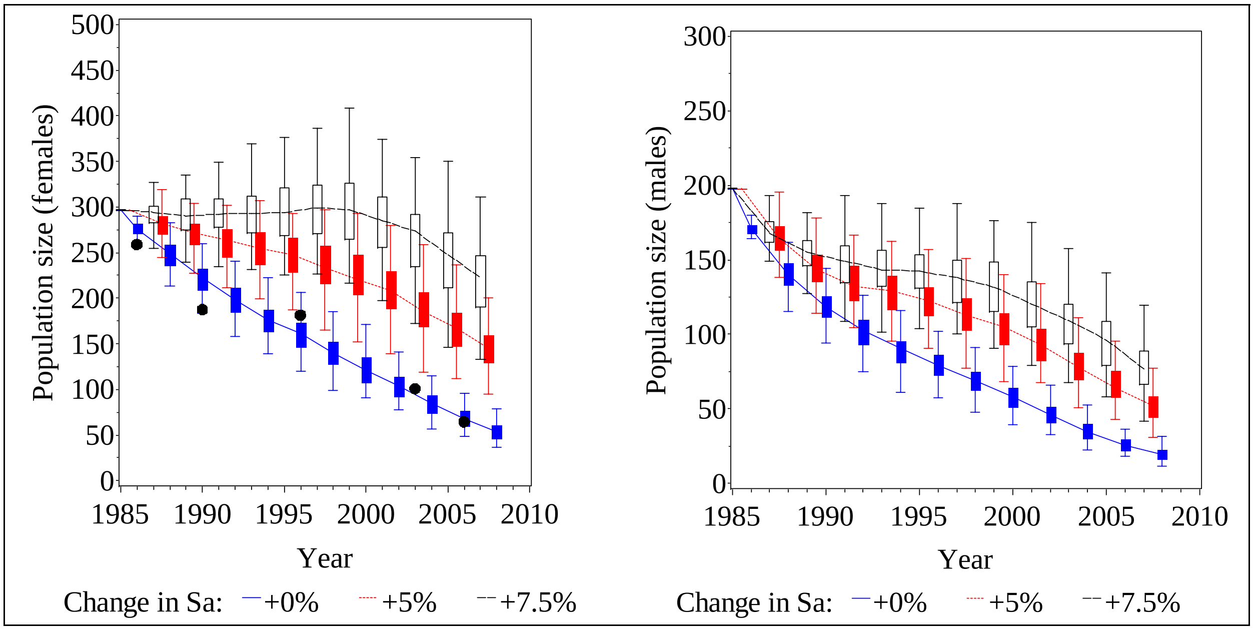


Figure 8: Population size of females and males (X 1000) as a function of varying levels of adult survival (S_a). The black dots correspond to empirical estimates of female population size from spring calving ground surveys. The bottom and top of the boxes around each point represent the 25th and 75th percentiles of estimates. The lines represent the entire range of estimates.

Overall population size of the herd still declined regardless of scenario, however, the decline was initially moderate with the +7.5% scenario (Figure 9). This suggests that increases in calf survival and other parameters were needed in addition to increases in adult survival to stabilize herd population trajectories.

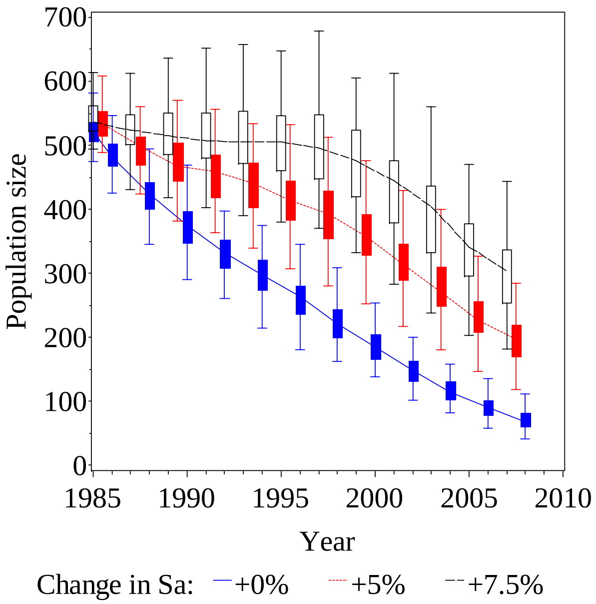


Figure 9: Population size of entire herd (excluding calves) (X 1000) as a function of varying levels of adult male and female survival. The bottom and top of the boxes around each point represent the 25th and 75th percentiles of estimates. The lines represent the entire range of estimates.

Scenarios for herd recovery

We used the stochastic model to explore scenarios in which a recovery might occur. The OLS model results suggested that decreasing calf survival was one of the primary drivers of change in herd size (as also suggested by declining calf/cow ratios but reasonably stable adult survival). The OLS model produced estimates of population parameters and population indicators for 2007. The question becomes, to what level would parameters need to be increased to cause the herd to stabilize or recover?

We ran simulations with demographic parameters at estimated 2007 levels (Table 5, model 1) to explore potential recovery scenarios. We did not simulate trends in calf survival or fecundity. Instead, we simulated the full range of calf survival estimates observed from the OLS model as well as calf survival estimates of Gunn et al. (2005b). We also simulated increases in adult survival of 0%, 2.5% and 7.5%. Finally, we ran simulations at low and high fecundity levels. We mainly focused on the female segment of the population as this segment has the greatest impact on overall herd productivity.

Results from simulations suggested that the herd would decline unless calf survival was greater than 0.33 regardless of increases in adult female survival (Figure 10). Calf survival would have to be 0.55 to 0.62 to allow the herd to stabilize (as indicated by a geometric mean λ of 1) with no change in adult survival at high and low fecundity levels. An increase in adult female survival of 5% would allow the herd to stabilize with calf survival levels of 0.39 (high F_a) to 0.43 (low F_a). An increase in adult female survival of 7.5% would allow the herd to stabilize with calf survival values of 0.33 (high F_a) to 0.37 (low F_a).

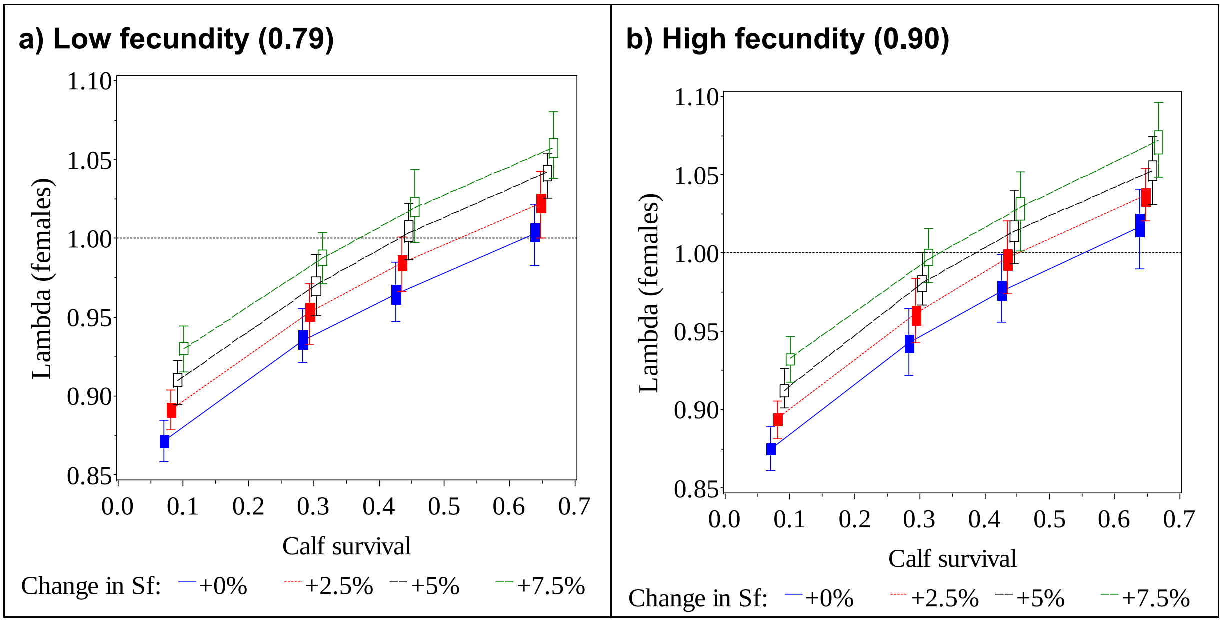


Figure 10: Geometric mean of the ratio of successive population sizes ($\lambda=N_{t+1}/N_t$) in simulations with OLS parameters at 2007 levels at low (a) and High (b) fecundity. Calf survival and female survival was varied. The calf survival values were staggered for easy interpretation. The bottom and top of the boxes around each point represent the 25th and 75th percentiles of estimates. The vertical lines represent the entire range of λ estimates.

The general correspondence between calf/cow ratios and calf survival can be seen in Figure 11. Basically, regardless of the level of fecundity, the observed calf/cow ratios in the period of 1985 to 1995 correspond to calf survival levels of 0.28 or above. Calf/cow ratios that occurred in 2002 and later correspond to lower calf survival values.

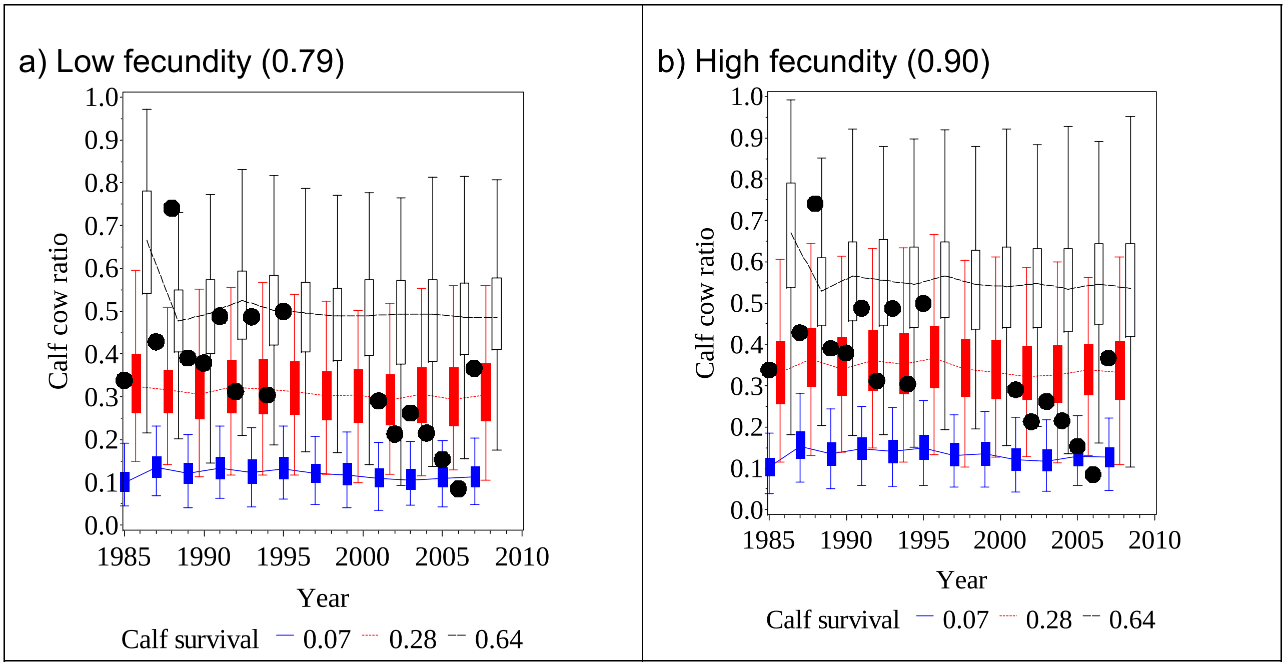


Figure 11: Calf/cow ratios as a function of varying levels of calf survival. Adult female survival was held at OLS estimate (0.842) and fecundity levels of 0.79 (a) and 0.90 (b) were simulated. The black dots correspond to empirical estimates of calf cow ratios from spring composition counts. The bottom and top of the boxes around each point represent the 25th and 75th percentiles of estimates. The vertical lines represent the entire range of estimates.

DISCUSSION

The OLS approach that we use to model Bathurst demography was designed to provide managers with a deductive and objective tool to explore demography of ungulate populations (White and Lubow 2002, Phillips and White 2003). The OLS model and associated AIC_c model selection optimizes model fit and complexity to the amount of information that is available, therefore grounding the complexity of models by the constraints of field data. Model results suggest that reduced trends in calf survival and/or fecundity were principal driving forces in the decline of the Bathurst caribou herd, and that an increase in calf survival is essential for herd recovery. This general finding parallels Gaillard et al. (2000) and Coulson et al. (2005), who suggested that while herbivore populations can tolerate random variation in calf survival, continuously reduced recruitment and calf survival may have a larger influence on population trajectories than reflected by deterministic sensitivity analysis.

Effects of change in adult survival and hunting

Lower levels of precision and missing survival data from 1986-1995 limited the power to detect trends in adult female survival using program MARK and the OLS model. However, our modeling, specifically the elasticity analysis (based upon the OLS model parameter estimates) and stochastic simulations, suggest that herd growth is very sensitive to changes in adult survival and therefore the Bathurst caribou herd cannot tolerate reduction in adult survival. This general finding is relevant across all potential values of adult survival. This general trait has been found in other large herbivores using matrix model methods (Gaillard et al. 1998). An additional possible mechanism for the decline of the Bathurst herd was revealed by the stochastic simulations, which suggest that small changes in adult survival have a large influence on herd population trajectories.

The hunting simulations assumed a constant rate of hunting for the entire time period (1985-2007). The only hunting data available was from the Dogrib study (1988-93) and therefore it is difficult to evaluate this assumption. Hunting varies among years depending on the proximity of caribou to the communities and winter roads. In addition, the effect of wounding loss is not estimated by harvest statistics. It is for these reasons that we ran simulations across a full range of hunting-related mortality given the relative uncertainty in the exact effect of hunting on adult survival.

The factors initiating a decline, the factors maintaining or accelerating a decline, and the factors initiating and maintaining a recovery are not necessarily mirror images of each other. Although our modeling does not specifically identify hunting as a factor in the decline, hunting contributed to adult mortality. Hunting is one of the few factors that lend themselves to management, hence our exploration of the influence of reduced levels of hunting on recovery of the Bathurst herd. However, it is difficult to evaluate the plausibility of the recovery simulations based on reduced levels of hunting given that recovery simulations require a change in calf survival as well as adult survival. Additionally, data are unavailable to model hunting relative to predation or other causes of death for adult caribou. Therefore, we cannot fully determine the impact of hunting on herd trajectories relative to other mortality sources such as predation.

Potential causes of observed trends

Diagnosing the reasons for the trend in reduced calf survival and/or female fecundity requires as a first step, determining any trends in the environment, especially on the post-calving and summer ranges, as the reduction in calf survival is higher during the summer (Gunn et. 2005b). Other analyses have identified two trends in environmental factors on the post calving and summer ranges. First, the number of days when warble fly and mosquito insect harassment was greater for 1982-2005 compared to 1957-1981 (Gunn and Lee In Press.) based on an index derived from the daily weather records for the area. Second, the amount of human activity has increased on the post calving and summer ranges with the construction of four diamond mines and heightened mineral exploration activity. We have no direct measures of if or how these two environmental changes could reduce calf survival. The link between severe insect harassment and caribou behaviour and condition, however, has been documented elsewhere (Russell et al. 1993, Hagemoen and Reimers 2002, Weladji et al. 2003). Caribou responses to the diamond mines include changes in distribution (Boulanger et al. 2004). However, how those changes relate, if at all, to caribou calf survival is uncertain given our current state of knowledge. No data have been collected on predation rates on Bathurst caribou, and therefore the effects of predation on calf survival are not known.

The OLS approach compared to other approaches

The principal challenge for our modeling was to objectively determine plausible demographic model parameters and model formulations given the sparseness of measured demographic rates. The OLS model approach used is a way to consider multiple sources of data to aid in formulating biologically supported demographic models. Furthermore, it allowed the exploration of trends in demographic rates as suggested by field-based measurements. One of the main advantages of the OLS method is that it allows the use of data even if data points are missing. Through AICc model selection, the appropriate model is chosen with explicit consideration of the data limitations. This keeps the conclusions of the demographic modeling consistent with the available demographic data. One limitation of the OLS model is that covariances between estimated parameters are assumed to be zero. More complex procedures that allow more elaborate modeling of multiple data sources, such as SAS PROC MODEL (SAS Institute 2000) are available, however these procedures do not allow for missing data (White and Lubow 2002).

The approach we used is similar to demographic models used on the Western Arctic caribou herd (Haskell and Ballard 2007). Both approaches used a deterministic model to develop a stochastic model as a means of exploring observed trends in population size. However, Haskell and Ballard (2007) used more subjective methods to fit their model to observed data. For example, they subjectively adjusted parameters to allow fit of the model to observed population trajectories. We used an objective optimization procedure (the OLS approach) that also adjusted parameters (such as adult survival) by simultaneously considering the fit of model-based estimates to field-based estimates (as determined by the difference between model and field estimates scaled by estimate precision). We also tested for density dependence, but used AICc methods to evaluate the relative support of density dependent models to more general polynomial models. Both our study and the study of Haskell and Ballard (2007) suggested that adult female survival must be higher than that estimated from radio collars to fit observed trajectories. However, we suggest that this is a matter of estimate precision rather than bias of adult survival rate estimates from collars. For example, the OLS estimate of female survival (0.842) overlaps the confidence interval of random effects model survival rates ($\hat{S}$= 0.81 SE=0.029, CI=0.76 to 0.86) from program MARK. We have tested for the immediate effects of collaring on caribou survival in previous analyses and have found no effect on survival (Boulanger 2003). The main limitation of adult survival estimates is that the number of females collared is small compared to overall herd size. Small sample sizes of collars basically result in less precise estimates of survival. Unlike Haskell and Ballard (2007), we did not have enough data on predator populations to test for the affect of predation on caribou survival.

Assumptions and limitations of the demographic model

Limitations on demographic data should be considered when interpreting results from our modeling. For example, we had only four estimates for the proportion of breeding females and female population size. Given this, more elaborate trends in these parameters were possibly occurring, but not detectable given the sparseness of time series points.

The stage-based demographic model used for the OLS procedure made some simplifying assumptions. It assumed equal demographic rates for each stage. For example, all adult female caribou, regardless of age, had similar survival rates and fecundity rates. While this was a simplification, we argue that a simpler model was most appropriate given the sparseness of data on caribou age classes and age-specific demographic rates. As discussed earlier, senescence was controlled by survival rates with less than 5% of caribou surviving past their 11th year, assuming a calf survival rate of 0.34 and adult survival rate of 0.842.

We assumed a 1:1 sex ratio for calves at birth given the lack of data on sex ratios at birth for calves in the Bathurst herd. This general assumption has been used in other demographic studies of caribou (Fancy et al. 1994, Haskell and Ballard, 2007). Some studies suggest that the sex ratio of caribou at birth may be influenced by maternal age. For example, Thomas et al. (1989) suggested that younger female caribou are more likely to produce females whereas older females are more likely to produce males (although the overall sex ratio (across age classes) was close to 1:1). However, a recent review did not find that maternal age influenced foetal sex ratio (Hewison et al. 2002).

Sex ratio, in the context of the demographic model, is closely linked to recruitment. Namely, a sex ratio that is skewed towards females could boost overall productivity of the herd, therefore partially offsetting lower survival rates. However, at the current time, there is no empirical evidence to suggest that the sex ratio at birth of the Bathurst caribou herd differs on average from 1:1.

A stable age distribution was assumed for simulations. Again, this assumption was a necessity given the lack of age-specific data. However, recent research suggests that perturbations that cause changes in age-structure (and a non-stationary age distribution) can result in predictions different than deterministic models suggest (Koons et al. 2006). Also, we used polynomial terms to model non-linear trends in vital rates such as calf survival. Using this approach constrains the model to only be relevant for the time series that was used with the model. We suggest that higher order polynomials (such as cubic or higher order polynomial terms) be used to allow vital rates such as calf survival to change direction (i.e. recover) for future model runs. For example, a cubic model could suggest that calf survival was stable, decreased, and then increased over time. This model was not supported with the current analysis; however, it may be more supported if higher calf/cow ratios are observed in future surveys. Thus caution is necessary and any absolute predictions of population trajectories should be interpreted with these limitations in mind.

The modeling of herd productivity

Although we cannot separate the effects of changes in fecundity from calf survival, the OLS model considered what combination of trends in parameters would best fit observed differences between fall and spring calf/cow ratios (that would mainly be due to calf survival). It also used information about trends in adult fecundity from calving ground composition counts. Therefore, the joint modeling of fecundity and calf survival trends was still reasonable given the constraints of field data available. Calf survival and fecundity are likely correlated. For example, fecundity is influenced by female nutrition, and female nutrition also affects calf condition (through lactation), which in turn influences calf survival. Research elsewhere also suggests that a cow is likely to maintain her protein reserves even at the expense of lactation (Russell and White 2000), which argues for fecundity being less variable than calf survival. Our results support this; the estimated trend in calf survival suggests that it decreased the most after 1995 compared to a constant decrease in fecundity. We note that calf survival was very low during surveys conducted in 2001-2005 with OLS estimates of less than 0.2, which is similar to the estimates of Gunn et al. (2005b). In contrast, the Porcupine herd calf survival rates were above 0.5 (Table 1), which is close to the levels needed for herd recovery (Figures 10-11). This further supports the hypothesis that low productivity and recruitment (potentially combined with lower adult survival) have primarily driven the decline of the Bathurst herd.

Density dependence and carrying capacity

Detection of density dependence was difficult given that the population estimates declined approximately linearly over time, confounding population size and year of study. The density dependent models were not supported by the data (Table 5) for any of the demographic rates. Density dependence is highly unlikely for adult female survival, but possible for calf survival and fecundity (Gaillard et al. 1998). Manseau et al. (1996) reported marked changes in vegetation on the summer range of the George River caribou herd, which coincided with a decline in herd size and condition of the caribou. However, Manseau et al. (1996) did not demonstrate either the absence of other environmental trends or that forage abundance was insufficient. We have no evidence, such as a visible change in shrub communities on the summer range, that would suggest the density of caribou had increased to where their foraging was affecting the plants.

By modeling trends in demographic rates it is possible to model the effects of environmental trends or, for example, trends in carrying capacity. For instance, it might be argued that carrying capacity was decreasing over the course of the time period that the herd was monitored, either related to density of caribou or increasing summer temperatures. One potential result of this would be reduced female condition resulting in reduced calf survival and fecundity. This type of hypothetical scenario was introduced in the OLS modeling procedure through the modeling of trends in demographic rates. We also note that it is possible to introduce environmental covariates (using hypothetical relationships between herd demographic parameters and environmental parameters) to the OLS procedure to test whether these covariates are associated with population trends. For example, future revisions to the modeling could include examining the effects of trends in summer weather on calf survival.

The effects of reduced male survival and skewed adult sex ratios

Although the OLS model results suggest reduced survival for males, and we acknowledge it as a concern, we lack the data to explore the consequences of this further. Although male caribou can breed more than one cow (polygamy), recent experience with other polygamous large herbivores suggests the need for caution when the sex ratio becomes skewed strongly to females (Mysterud et al. 2002). Although we know from other herbivores that excessive harvesting of prime males can, in extreme cases, lead to population declines we do not know at what levels the risks increase for caribou. The mechanisms for population declines in other species with a sex ratio strongly biased toward females include breeding by young bulls, which causes delayed conception, later calving, and lower birth weights and lower survival (Mysterud et al. 2002). Holand et al. (2003) used an experimental approach to investigate the consequences of a very skewed sex ratio (8-14 bulls: 100 cows) in reindeer. Calving was later with the skewed ratio and the age of the bulls did not affect the date of calving. Synchrony of births and calf birth weight increased with the higher sex ratio. Although the reindeer were in a large enclosure, the number of animals was low which introduces a note of caution in extrapolating these results to free-ranging caribou.

CONCLUSIONS

The OLS modeling emphasizes the need for adequate monitoring data. This is also called for in the Bathurst co-management plan. Monitoring should include both direct and indirect measurements of herd survival and productivity. The use of multiple sources of data results in a population model that is grounded in field-based measurements.

In summary, our modeling indicates that the Bathurst herd has declined because of a trend toward reduced calf survival (and/or fecundity) and likely reduced survival of adult females. Although a reduction in hunting would improve adult survival and may slow the decline, the model indicates that the herd will likely not recover until calf survival improves. Concerns, which our modeling could not address, include the causes of the low calf survival (and or fecundity) and the role that the sex ratio biased toward females play in the decline.

RECOMMENDATIONS

1. Model results suggest that trends in calf survival and/or adult fecundity are associated with observed declining population trajectories. We suggest that spring composition surveys (calf/cow ratios) are continued to obtain valuable information on trends in herd productivity. Given more data, future OLS models can be run to further explore the relationship between herd productivity and overall population trajectories.
2. One component of productivity that was difficult to model was adult fecundity, given that it is confounded with calf survival in spring calf/cow ratio counts. Therefore, further direct inference of this parameter using composition surveys on calving grounds, hunter-based observations of pregnancy or other approaches such as ovary scar counts would be useful in determining the role of female fecundity in overall herd productivity.
3. Estimation of adult female survival rates is limited to small sample sizes of collared females compared to overall herd population size. Despite this, it is useful to continue monitoring adult female survival using collar data.
4. Better estimates of harvest levels are needed to determine trends in numbers of caribou harvested relative to estimated population size.
5. OLS model results suggest reduced survival for males. However, this result is mainly based on observed sex ratios during recent fall composition counts. Knowledge of male survival (via sex ratios) is useful for determining male survival relative to female survival. In addition, fall calf/cow ratios provide a secondary

estimate of calf survival and herd productivity, which can be used to estimate calf survival if a composition survey is also conducted during the following spring.

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APPENDIX 1 SUMMARY OF FIELD DATA USED TO FIT OLS MODEL

Year	Calf-cow ratios				Adult female survival		Calving ground surveys				Adult sex ratio	
	Spring		Fall				Total females		Pr. Females breeding		Fall surveys	
	Estimate	SE	Estimate	SE	S_f	SE	$\hat{N}$	SE	Estimate	SE	Estimate	SE
1985	0.34	0.10										
1986							259136	15707.9	0.87	0.06		
1987	0.43	0.03										
1988	0.74	0.12										
1989	0.39	0.02										
1990	0.38	0.03					187780	31282	0.92	0.04		
1991	0.49	0.03										
1992	0.31	0.02										
1993	0.49	0.02										
1994	0.30	0.03										
1995	0.50	0.04										
1996					0.79	0.13	181572	39072	0.88	0.09		
1997					0.75	0.15						
1998					0.60	0.16						
1999					0.81	0.10						
2000			0.40	0.01	0.85	0.10						
2001	0.29	0.01	0.33	0.02	0.58	0.11						
2002	0.21	0.02			0.76	0.10						
2003	0.26	0.01			0.69	0.11	100867	14665	0.83	0.01		
2004	0.22	0.01	0.18	0.02	0.77	0.12					0.37	0.03
2005	0.15	0.01			0.73	0.08						
2006	0.09	0.01	0.40	0.02	0.89	0.06	64579	9511.6	0.77	0.11	0.36	0.02
2007	0.34	0.10	0.40	0.01	0.79	0.13						