



Research Article

# A Data-Driven Demographic Model to Explore the Decline of the Bathurst Caribou Herd

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**ABSTRACT** The Bathurst herd of barren-ground caribou (*Rangifer tarandus groenlandicus*) in the Canadian central arctic declined from an estimated 203,800 to 16,400 breeding females from 1986 to 2009, with the most rapid decline from 2006 to 2009. A key research and management question was whether the decline was mainly due to decreases in productivity alone or also due to reduced adult female survival. Investigating causes of the decline was hampered by a lack of direct estimates of caribou demographic parameters. We developed a demographic model that could be objectively fitted to field data to explore the mechanisms for the Bathurst decline, with a focus on the recent accelerated decline from 2006 to 2009. Our modeling indicated that the decline was driven by increasing negative trends in adult female and calf survival rates and possibly reduced fecundity. The effect of a constant hunter harvest on the declining herd was one potential cause for the recent accelerated decline in adult survival. The demographic model detected negative trends in adult female survival that were not detected using standalone analyses of collar-based survival data. The model allowed rigorous interpretation of trends in productivity by controlling for the simultaneous influence of trends in adult, calf, and yearling survival and adult fecundity on field-based calf-cow ratios. Stochastic simulations suggested that large increases in adult survival and productivity would be needed for the herd to recover. Our methods enable objective modeling of caribou demography that can assist in caribou management based upon all sources of available data. © 2011 The Wildlife Society.

**KEY WORDS** Bathurst caribou herd, caribou management, demographic model, deterministic model, ordinary least squares, stochastic model, *Rangifer tarandus groenlandicus*.

The Bathurst herd of barren-ground caribou (*Rangifer tarandus groenlandicus*) was one of the largest herds of migratory tundra caribou in northern Canada in the 1980s. Herd size was estimated from the number of breeding females, which declined from 203,800 (95% CI = 178,197–229,403) caribou in 1986 to 55,593 (95% CI = 37,147–74,039) in 2006 and 16,604 (95% CI = 12,153–21,056) in 2009 (Nishi et al. 2007, 2010). Along with the steep decline in the number of caribou, reduced productivity (calf survival or fecundity based upon sex and age composition surveys) and an adult sex ratio biased toward females were consistent with a declining herd (Gunn et al. 2005a, Bergerud et al. 2008). The rate of decline was slow in the 1990s but accelerated as the herd declined. The rapid decline from 2006 to 2009 was of particular concern to wildlife managers, as this herd has been hunted by more Northwest Territories communities than any other, and barren-ground caribou have been a highly valued subsistence and cultural resource for northern

Aboriginal communities for thousands of years (Gordon 2003, 2005). The overall trend in most migratory caribou and reindeer herds across the global north, including Alaska and northern Canada, has been negative, although there are some exceptions where neighboring herds have opposite trends (Vors and Boyce 2009).

Management of the Bathurst caribou herd is through co-management that involves Government of the Northwest Territories, the Tlicho Government and other first nations groups, as well as resident hunters, guide-outfitters, and other stakeholders. In response to observed declines, the Government of Northwest Territories and the Tlicho Government proposed restrictions on harvest, which were discussed during public hearings held by the Wek'eezhii Renewable Resources Board (WRRB) in 2007 and again in 2010. Fundamental to management of the herd and associated hearings was a more solid determination of causes for decline in the Bathurst herd.

One of the main research questions was how demographic parameters such as productivity and adult survival could interact as mechanisms to explain the decline, and what were the corresponding management strategies that could promote herd recovery. A variety of models have been

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previously used to model caribou demography, based mostly on direct estimates of survival and productivity data from intensive studies of radio-collared individual caribou and population surveys (Fancy et al. 1994, Jenkins and Barten 2005, Haskell and Ballard 2007).

The main challenge with fitting demographic models to the Bathurst caribou herd, and, indeed, most barren-ground caribou herds in Canada, was the lack of direct estimates for demographic parameters. For example, although we had direct estimates of survival for adult females from satellite collars, sample size was low, and resulting estimates were imprecise. The range of the Bathurst herd is very large (ca. 350,000 km<sup>2</sup>) and remote, making direct field measurements and study of mortality factors (i.e., predation and hunting) and factors influencing productivity expensive and difficult. Most information on the demography of the Bathurst herd came from indirect sources such as late winter and fall calf-cow and composition surveys and from spring calving ground surveys that estimate breeding female population size.

To confront the lack of direct demographic rate estimates, we adopted a model developed for deer by White and Lubow (2002) that considers multiple sources of field data. The main distinction and advantage of this approach is that both direct and indirect sources of demographic information are used to produce model-based estimates of demographic parameters, relaxing the need for direct (individual radio-collared-based) estimates of survival and productivity. In addition, this approach allows multi-model inference into temporal variation and trends in herd demographic parameters using information theoretic methods of model evaluation (Burnham and Anderson 1998). The flexibility of this approach to accommodate directional trends in parameters was a distinct advantage over other standard population viability analysis (PVA) methods that often assume random or underlying density-dependent relationships but not necessarily directional change in parameters (Boyce 1977, Caswell 1989, Taylor et al. 2003).

Our goal was to describe the demographic mechanisms underlying the decline of the Bathurst herd objectively, using existing field data to allow more informed management of the herd. We furthered the approach of White and Lubow (2002) to accommodate field measurements typical of caribou populations and test caribou-biology-driven hypotheses about trends in adult female survival and productivity. We explored potential biases in calf-cow ratios caused by trends in adult female survival and estimated trends in age structure. We also used the base estimates from the demographic model to explore scenarios for herd recovery using a stochastic model. Our study demonstrates the flexibility of this approach to test a variety of management hypotheses for caribou as well as other wildlife species.

## STUDY AREA

The Bathurst herd of migratory tundra caribou annually moves hundreds of kilometers from wintering ranges below treeline in southern Northwest Territories to calving and summer range on the open tundra near Bathurst Inlet (Gunn et al. 2008). The cumulative annual range is about

350,000 km<sup>2</sup>. Glaciers have largely shaped the landscape, which has esker complexes, boulder moraines, rock outcrops, and numerous lakes. Wintering areas below treeline were composed of Taiga Plains with stunted black spruce (*Picea mariana*) and deciduous vegetation (Ecosystem Classification Group 2009). The climate was semi-arid with annual precipitation of approximately 300 mm, most of which fell as snow. Summers were short and cool with average temperatures of approximately 12 °C, whereas winter temperatures were commonly <−30 °C. Most of the range of the Bathurst herd was only accessible via winter roads or by aircraft.

## METHODS

### Estimation of Demographic Parameters

Adult females in the Bathurst herd have been fitted with satellite or Global Positioning System (GPS) collars since 1996 and the fate of collared caribou was observed or inferred. On average, 12.6 (SD = 4.5, range = 5–23) caribou were monitored on a weekly basis. We used the Kaplan–Meier method to estimate survival rates of caribou (Pollock et al. 1995) through assessment of monthly counts of collared caribou and determination of caribou fates (including hunting and natural death as determined by consecutive stationary locations or confirmed deaths). Some caribou had their collars removed while still alive and we right-censored these records. The Kaplan–Meier is a nonparametric ratio-based survival rate estimation method and, therefore, yearly estimates generated using the Kaplan–Meier model are less likely to be correlated as a result of the estimation procedure. This was a requirement for the demographic model we used in the analysis. No data were available on adult male survival for the Bathurst herd so we based adult male survival estimates upon assumed sex ratios at birth and observed bull-cow ratios as described later.

We also tested for trends in adult female survival using binomial known fate models in Program MARK (White and Burnham 1999) to compare with estimates of adult survival trend from the demographic model. For this, we tested a model that assumed constant survival against a model that assumed yearly linear trends in adult survival. We then assessed significance of the trend model using a likelihood-ratio test (McCullough and Nelder 1989) between the 2 models. We also estimated process variance for female survival using random effects models in Program MARK (White et al. 2002).

We defined fecundity as the proportion of adult females calving in a given year. We estimated the number of caribou on the calving grounds from calving ground composition surveys just after the peak of calving (part of estimating the number of breeding females on the calving grounds) for 1986, 1990, 1996, 2003, and 2006–2009 (Gunn et al. 2005b, Nishi et al. 2010). We estimated fecundity as the ratio of the counts of productive females (females observed with calves, with distended udders, or with hard antlers, as antlers are retained until birth) to total females (including non-productive females without calves, hard antlers, or

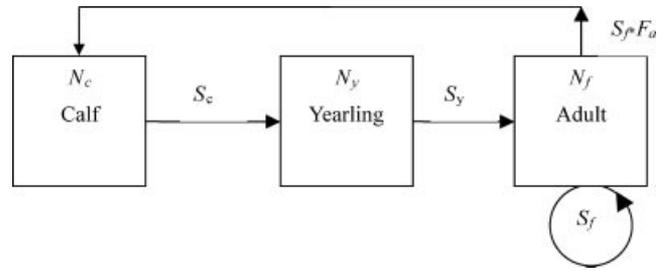
distended udders). This estimate of fecundity applied to the previous year, as females on the calving ground became pregnant in the fall of the previous year. We used a bootstrap procedure (Manly 1997) to estimate robust proportions and associated variances with individual groups surveyed as the sample unit. This measurement of fecundity based upon observation of females on the calving ground did not include early neonate mortality or fetal absorption, which is rare (Thomas and Kiliaan 1998).

We conducted sex and age composition surveys to measure the ratio of calves to adult females (commonly called calf–cow ratios) in late winter from 1985 to 1995 and 2001–2009 to estimate calf survival up to 9–10 months of age. As distinguishing yearlings from young cows can be unreliable, we included female yearlings in the female segment. We included half of the counts of unknown sex yearlings with the adult female segment under the assumption of an even yearling sex ratio (Gunn et al. 2005a). We also conducted fall composition surveys in late October 2000, 2001, 2004, and 2006–2008 to estimate calf–cow ratios as well as adult sex ratios (commonly called bull–cow ratios) in 2004 and 2006–2008 (Adamczewski et al. 2009). The bull–cow ratio data further evaluated overall male versus female survival rates and we also incorporated these data into the population model. We used a bootstrap procedure (Manly 1997) to estimate proportions and associated variances with individual groups surveyed as the sample unit.

Given the large annual ranges and often dispersed distribution of barren-ground caribou, the only viable opportunities to estimate population size are when breeding females are aggregated on distinct calving grounds or during post-calving, when the entire herd may form dense groups of hundreds or thousands as a response to insect harassment. Breeding female caribou from each herd calve gregariously on a calving ground at a predictable location. Photographic surveys in 1986, 1990, 1996, 2003, 2006, and 2009 estimated the total number of caribou on the calving ground. We then corrected the estimates of total caribou for bulls, yearlings, and non-breeding adult females on the calving ground, using data from sex and age composition counts on the calving ground, to estimate breeding females (Gunn et al. 2005b; Nishi et al. 2007, 2010).

### Deterministic Caribou Life History Model

We used a modeling procedure developed by White and Lubow (2002) to fit a demographic matrix model to adult survival, calf–cow ratios, breeding female population size, and fall sex ratio data. This approach involves first proposing a standard stage-based model of caribou demography (Fig. 1). We based the model upon yearly population change, as determined by the population of caribou present immediately after calving that occurred each June (Fig. 1). 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 from the calving ground 1 yr to the calving ground on the following year. We estimated recruitment as fecundity ( $F_a$ ; the proportion of adult females that successfully give birth with neonatal mortality excluded) multiplied by the yearly



**Figure 1.** Underlying stage matrix life history diagram for the Bathurst caribou demographic model for the Bathurst caribou herd, Northwest Territories (1985–2009). This diagram pertains to the female segment of the population. Nodes are population sizes of calves ( $N_c$ ), yearlings ( $N_y$ ), and adult females ( $N_f$ ). Each node is connected by survival rates of calves ( $S_c$ ), yearlings ( $S_y$ ), and adult females ( $S_f$ ). Adult females reproduce dependent on fecundity ( $F_a$ ) and whether a pregnant female survives to produce a calf ( $S_f$ ). The male life history diagram was similar with no reproductive nodes.

adult survival rate ( $S_f$ ). Using this parameterization for recruitment considers 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 on annual censuses, such as those incorporated into the Program RISKMAN (Taylor and Carley 1988, Taylor et al. 2003). As with other caribou demographic studies (Haskell and Ballard 2007, Bergerud et al. 2008), we assumed that yearlings did not breed. We modeled the male population using the same life history model as females (without productivity terms), with the number of male calves determined by recruitment rate multiplied by the sex ratio at birth ( $r$ ) that we assumed to be 1:1. The assumption of an even sex ratio at birth is supported by other demographic studies of caribou (Thomas et al. 1989, Fancy et al. 1994, Haskell and Ballard 2007). The 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, <4% of caribou would survive past their 11th yr, assuming a calf survival rate of 0.34 and adult and yearling survival rates of 0.82.

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 movements of the satellite-collared cows (1996–2007) in the Bathurst and neighboring herds (Ahiak and Bluenose East; Gunn et al. 2008) and more recent analyses of satellite collared caribou data (Adamczewski et al. 2009). Adamczewski et al. (2009) found that of 153 caribou females monitored between 1996 and 2008, only 7 (4.5%) were found on >1 calving ground. Further analyses with multi-strata models (Hestbeck et al. 1991, White et al. 2006) confirmed that rates of immigration or emigration from the Bathurst calving ground were low (<5%) and that immigration rates equaled emigration rates (Adamczewski et al. 2009).

We projected the population model from 1985, the first year of estimated calf–cow surveys. As in the 1986 survey, a bull to cow ratio of 66 males to 100 females based on

estimates from Heard and Williams (1991). This assumption set the initial population size for bulls, using the estimated initial female population size multiplied by the bull–cow ratio. Our primary emphasis in modeling efforts was exploration of trends in adult female demography given the relative lack of information on bull population size or survival rates.

We generated predictions of field estimates from the stage-based matrix model. We estimated late winter calf–cow ratios as:

$$N_c S_c^{(t/365)} / \left( N_f S_f^{(t/365)} + 0.5 N_Y S_Y^{(t/365)} \right),$$

where  $t$  was the number of days from birth of calves to the period (Mar–Apr) when we conducted late winter composition surveys. Using the survey interval ( $t$ ) divided by the number of days in the year (365) scaled annual survival estimates to estimate the proportion of each cohort still alive during the surveys. As with field measurements, we included female yearlings in the denominator of the calf–cow ratio under the assumption of an even sex ratio at birth and equal sex-specific calf and yearling survival rates. We used a similar formula for fall surveys with a different survey interval. Similarly, we derived fall adult sex ratio 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 late winter calving and fall composition surveys. This formula was most useful when sex-specific rates in survival were modeled.

*Ordinary least squares methods.*— We used the modeling methods of White and Lubow (2002) to compare projected population size, late winter calf–cow ratios, fall calf–cow ratios, and bull–cow ratios to estimates from field surveys and parameters that we re-estimated based upon the fit of the model to field survey data. Each model prediction ( $\theta$ ) was compared to a corresponding field estimate  $\hat{\theta}$  using the penalty term ( $\varepsilon^2$ ), where  $\varepsilon^2 = [(\theta - \hat{\theta}) / \text{SE}(\hat{\theta})]^2$ . The penalty term considered the agreement between model predictions ( $\theta$ ) and field estimates ( $\hat{\theta}$ ) in the units of the precision of the field estimate (as estimated by  $\text{SE}(\hat{\theta})$ ). 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.

The basic objective of modeling was to maximize agreement between field data and model parameters. To accomplish this, the parameters were iteratively varied (using the SOLVER optimization algorithm in Excel [Microsoft Corporation, Redmond, WA]) to minimize the sum of penalties for a given set of parameters and model formulation, which is termed the ordinary least squares (OLS) estimator of model parameters. We used the OLS approach to estimate demographic parameters and explore temporal

variation in model parameters. The OLS model estimated all demographic parameters with the exception of initial male population size and sex ratio at birth. We estimated initial male population size as the initial estimated adult female population size multiplied by the assumed bull–cow ratio. Models that allowed linear and nonlinear trends in demographic parameters were evaluated using OLS methods by introduction of linear, quadratic, and cubic terms for demographic parameters. Survival and fecundity intercept and slope terms were logit-transformed (McCullough and Nelder 1989) to ensure that the resulting estimate was in the 0–1 interval.

*Biology-based models.*— Our primary management question was whether the observed declines in population size were most parsimoniously explained by declines in productivity, declines in adult survival, or a combination of the two factors. We therefore separated model building into two 2 phases. First, we constructed a base productivity model that best explained directional trends in productivity caused by changes in calf survival and fecundity. A large increase in calf–cow ratios was observed after 2006, which could suggest an increase in productivity, so we considered models that treated this period separate from previous years. We assumed a linear decline in survival during the productivity model-building phase.

Once we established a satisfactory productivity model we focused on changes in adult female survival. One question was whether the recent (2006–2009) accelerated decrease in population size was caused by an accelerated decline in adult survival. We tested for this using polynomial terms and broken stick survival models. Broken stick survival models assumed an initial linear trend in adult survival but allowed this trend to change at a cut-point year, simulating a change in overall survival trend using a method similar to piecewise regression (Hudson 1966). We iteratively searched for cut-points for each year from 2000 to 2007 to determine if there was a potential change in adult survival trend and if the broken stick model was more supported than other competing adult survival trend models. We did not consider trends in yearling survival and male survival due to lack of corresponding temporal data for these parameters.

We also hypothesized that latent age-structure effects, namely the shifting of age structure to older cohorts due to a series of years with low productivity, and subsequent higher mortality of older caribou, could have accelerated the rate of decline. With the stage-based model we used in the analysis there was no maximum age cut-off, and we did not explicitly consider mortality of older caribou. We tested the hypothesis that mortality of older caribou (>15-yr old) created an accelerated decline by expanding the adult age class up to a maximum age of 15 yr with equal survival rates for all adult age classes. We then contrasted this maximum age model against the standard stage-based model to see if model fit was significantly improved, as suggested by overall support from the field data. We assumed the initial distribution of age classes to follow a stable age distribution (Caswell 1989) as determined by initial demographic

parameter values, and we assumed similar demographic rates for all age classes. We used the POP-TOOLS add-on (Greg Hood, Commonwealth Scientific and Industrial Research Organization, Canberra, Australia; <http://www.cse.csiro.au/poptools/>) for Excel to estimate the stable age distribution from initial parameter values. We also assessed change in age structure by tracking the population size of each cohort of caribou produced since the first year the model was run (1985). We estimated the number of each cohort for a given year as the number of the cohort in the previous year multiplied by the corresponding survival rate.

We used information theoretic methods (Burnham and Anderson 1998), namely the sample-size corrected Akaike Information Criterion ( $AIC_c$ ), to compare competing models. Sample size for  $AIC_c$  calculations was the number of model and field data comparisons we used to estimate penalty terms (White and Lubow 2002). Briefly, the  $AIC_c$  score considers the fit of a model (as indicated by the penalty term) and model complexity (as indicated by the number of parameters). A lower  $AIC_c$  score suggests the most parsimonious model that balances bias (model fit) and precision (model complexity). We also used the difference in  $AIC_c$  values between the most supported model and other models ( $\Delta AIC_c$ ) to evaluate the fit of models when their  $AIC_c$  scores were close. In general, any model with a  $\Delta AIC_c$  score of  $<2$  was worth considering. In addition, we considered the proportional support of each model, or  $AIC_c$  weight ( $w_i$ ), in evaluating the support of each model. We model-averaged all parameter estimates using  $AIC_c$  weights to account for model selection uncertainty (Burnham and Anderson 1998). We evaluated residuals  $[(\hat{\theta}-\theta)/SE(\hat{\theta})]$  of model-averaged estimates compared to field estimates to assess overall model fit. We tested normality of residuals, which would suggest a reasonable fit of the data to the OLS model, using an Anderson–Darling test for normality (Stephens 1974).

*Exploration of the effect of harvest on trends in adult survival.*— One of the main questions about the Bathurst herd's decline was whether the changing rates of adult mortality caused by hunter harvest accelerated the herd decline. We did not have measures of natural mortality rates independent of harvest mortality rates. We were interested in whether harvesting rates were acting as a constant yield due to increased hunting effort as abundance declined. We estimated the proportional mortality caused by hunter harvest using a range of hunter harvest levels divided by the OLS model estimate of adult cow population size. We used a range of hunter harvest levels as estimated by the Dogrib harvest study (Adamczewski et al. 2009) that occurred from 1988 to 1993 as well as estimates of more recent and unpublished harvest data. The Dogrib Harvest study harvest interviewed a sample of hunters monthly for their reports of their wildlife harvests for the previous month. The study then used the methods of Gamble (1984) to estimate annual harvest. More recently, Government of Northwest Territory wildlife officers and biologists worked with 4 Tlicho communities north of Yellowknife to estimate the winter harvest of Bathurst caribou from winter roads, using a combination

of a check-station and interviews with hunters in the communities (Adamczewski et al. 2009). We then compared trends in proportional mortality to estimates of proportional mortality based upon estimates of adult female survival from the OLS model.

### Stochastic Model

We used a stochastic simulation model to evaluate various demographic scenarios for the Bathurst herd while accounting for the effects of variation in model parameters. The estimates of demographic rates from field data include both biological (also called process variation) and sampling variation. Process variation includes demographic, spatial, individual, and temporal variation in rates (White 2000). We used the methods of Burnham et al. (1987) and Thompson et al. (1998) to estimate variance caused by temporal process variation in calf–cow and proportion females pregnant ratios and random effects models in Program MARK (White and Burnham 1999, White et al. 2002) to obtain estimates of temporal process variation for survival rate estimates. We did not have any data on which to base estimates of variation of adult males and yearling survival. We therefore assumed that temporal variation was similar for adult females and males. We also assumed that temporal variation in yearlings was better approximated by variation in adults. The assumption of similar temporal variation in survival rates between yearlings and adults was biologically justified given that yearling survival is usually closer to adult survival than to calf survival in caribou. We then calculated variance estimates for the OLS model by multiplying estimated values by each of the coefficients of variation.

We simulated demographic variation by comparing individual rates to a randomly generated variate based upon a uniform distribution. We simulated individual variation by generating normal random variate centered on the mean parameter value. We simulated temporal variation in demographic rates by picking a random normal variate for each year of simulations and adding it to the mean demographic parameter. We generated parameters on a continuous scale and then logit-transformed it to ensure simulated rates were within the 0–1 interval. We evaluated population trends using the geometric mean of successive population ratio of change ( $\lambda = N_{t+1}/N_t$ ) estimates for simulations run for 20 yr. We used SAS statistical package (SAS Institute, Cary, NC) for all stochastic model simulations.

We first explored overall sensitivity of population trend to individual (which would include spatial variation) and temporal variation in model parameters by increasing variation in parameters and observing the resulting change in  $\lambda$ . We did not simulate any directional trends in parameters. We adjusted adult male and female survival so that the deterministic  $\lambda$  of the population was 1 to provide a common initial basis for comparing simulations.

A critical necessity for herd management is the values of demographic parameters needed for recovery of the Bathurst herd. We therefore ran simulations that considered varying levels of calf survival, adult female survival, and fecundity needed for herd recovery. We focused on variation in adult

female survival rates, as this population segment most directly influences herd productivity (Gaillard et al. 1998). We based ranges of adult survival upon likely reduction in survival rates due to caribou harvest as part of deterministic analyses described previously.

## RESULTS

### Deterministic Model

Our initial model building efforts focused on building a model that described variation in productivity. Trends in calf survival from 1985 to 2005 were best approximated by a cubic curve, whereas trend in fecundity were best approximated by a quadratic curve (Table 1, model 14). We modeled the 2006–2009 period by adding additional intercept terms or slope terms for calf survival and fecundity. For example, a model with a unique intercept for calf survival ( $S_{c06}$ ) allowed calf survival to increase but stay constant over this short time period. Addition of a slope term (denoted by a  $\Delta$  term in Table 1) allowed the parameter to increase to the intercept term and then change linearly. Trends in calf survival for 2006–2009 were best described by an initial intercept term ( $S_{c06}$ ) followed by a linear slope term ( $\Delta S_{c06}$ ), whereas trends in fecundity were best described by an intercept term only ( $F_{a06}$ ), which assumed that fecundity was constant after 2006 (Table 1, model 1). Models that were less supported assumed trends for calf survival and fecundity after 2006 (model 4), trends only in fecundity after 2006 (model 10), or no specific productivity terms for 2006–2009 (models 13 and 14).

Once we established a base productivity model we proposed several candidate models to determine dominant trends in

adult female survival. Of these models, a model that assumed linear trends in adult female survival (model 1), and a broken stick model with cutpoint at 2007, were most supported (model 2) as indicated by  $\Delta AIC_c < 2$ . Models that assumed different cutpoints (models 3, 6, 7, and 12), or a maximum age of 15 yr for females (model 9), or no trends in adult survival (model 8), were less supported. Comparison of parameter-specific penalty terms for the maximum age model (model 9) and the corresponding stage-based model (model 1) suggested that the stage-based model was more supported than the maximum age model except for the adult female survival estimates and breeding cow population estimates. In this case, the maximum age model displayed slightly better fit, however, the difference was only 2.2 and 1.8 penalty units for adult survival and breeding cow population size, respectively.

We then used model-averaged parameter estimates to assess temporal trends in parameters (Fig. 2). Adult female survival rates declined steadily until 2007, after which the decline accelerated. Calf survival was constant until 1995, after which it declined until a rebound after 2006, followed by a decline. Fecundity declined to a low point in 2005 then increased to a constant level. Net productivity, which was the product of fecundity, over-winter survival of adult females, and calf survival, suggested that productivity declined in unison with calf and adult female survival, rebounded in 2006, and then declined until 2009.

The model fit the field data reasonably well with model-averaged predictions overlapping confidence intervals from field measurements in most cases (Figs. 3 and 4). Residuals from model-averaged estimates were normally distributed

**Table 1.** Model selection results from deterministic model of the Bathurst caribou herd, Northwest Territories, Canada, from 1985 to 2009. Sample-size adjusted Akaike Information Criteria ( $AIC_c$ ), difference in  $AIC_c$  between most supported and given model ( $\Delta AIC_c$ ), Akaike weight ( $w_i$ ), the number of parameters ( $K$ ), effective sample size (ESS), and sum of penalties ( $\Sigma Pen$ ) are displayed. Effective sample size (the number of model and field estimate comparisons used to estimate  $\Sigma Pen$ ) was 56 for all models.

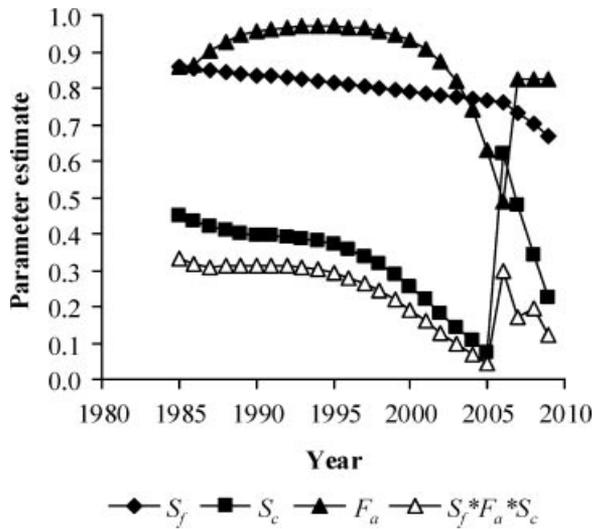
| No. | Model terms (+base model terms <sup>a</sup> ) |                              |                                 | Model selection |                |       |     |              |
|-----|-----------------------------------------------|------------------------------|---------------------------------|-----------------|----------------|-------|-----|--------------|
|     | Fecundity ( $F_a$ )                           | Calf survival ( $S_c$ )      | Adult female survival ( $S_f$ ) | $AIC_c$         | $\Delta AIC_c$ | $w_i$ | $K$ | $\Sigma Pen$ |
| 1   | $F_{a06}^b$                                   | $S_{c06} + \Delta S_{c06}^b$ | $S_f$                           | 391.3           | 0.00           | 0.46  | 15  | 349.3        |
| 2   | $F_{a06}$                                     | $S_{c06} + \Delta S_{c06}$   | $S_f + S_{f2007}^c$             | 391.4           | 0.12           | 0.40  | 16  | 345.5        |
| 3   | $F_{a06}$                                     | $S_{c06} + \Delta S_{c06}$   | $S_f + S_{f2004}$               | 393.4           | 2.10           | 0.06  | 16  | 347.5        |
| 4   | $F_{a06} + \Delta F_{a06}$                    | $S_{c06} + \Delta S_{c06}$   | $S_f$                           | 393.7           | 2.40           | 0.04  | 16  | 347.8        |
| 5   | $F_{a06}$                                     | $S_{c06} + \Delta S_{c06}$   | $S_f + S_f^2$                   | 393.9           | 2.62           | 0.03  | 16  | 348.0        |
| 6   | $F_{a06}$                                     | $S_{c06} + \Delta S_{c06}$   | $S_f + S_{f2006}$               | 395.3           | 3.94           | 0.01  | 16  | 349.3        |
| 7   | $F_{a06}$                                     | $S_{c06} + \Delta S_{c06}$   | $S_f + S_{f2000}$               | 398.2           | 6.90           | 0.00  | 17  | 348.1        |
| 8   | $F_{a06}$                                     | $S_{c06} + \Delta S_{c06}$   | Intercept only                  | 401.5           | 10.14          | 0.00  | 14  | 363.2        |
| 9   | $MA^d: F_{a06}$                               | $S_{c06} + \Delta S_{c06}$   | $MA^d: S_f$                     | 403.7           | 12.37          | 0.00  | 15  | 361.7        |
| 10  | $F_{a06} + \Delta F_{a06}$                    | $S_{c06}$                    | $S_f$                           | 410.6           | 19.27          | 0.00  | 15  | 368.6        |
| 11  | $F_{a06}$                                     | $S_{c06}$                    | $S_f$                           | 410.7           | 19.34          | 0.00  | 14  | 372.4        |
| 12  | $F_{a06}$                                     | $S_{c06} + \Delta S_{c06}$   | $S_f + S_{f2002}$               | 423.8           | 32.46          | 0.00  | 16  | 377.8        |
| 13  | $F_a^3$                                       | Base <sup>a</sup> terms only | $S_f$                           | 970.2           | 578.85         | 0.00  | 13  | 935.5        |
| 14  | Base <sup>a</sup> terms only                  | Base <sup>a</sup> terms only | $S_f$                           | 1,032.9         | 641.63         | 0.00  | 12  | 1,001.7      |
| 15  | Intercept only                                | Intercept only               | Intercept only                  | 1,371.8         | 980.46         | 0.00  | 8   | 1,352.7      |

<sup>a</sup> We used a base model for all models with intercept (yr = 1985) terms for adult female survival ( $S_f$ ), adult male survival ( $S_m$ ), yearling survival ( $S_y$ ), calf survival ( $S_c$ ), adult female fecundity ( $F_a$ ), and initial adult female population size ( $N_f$ ), as well as quadratic terms for trends in fecundity ( $F_a + F_a^2$ ) and cubic terms for trends in calf survival ( $S_c + S_c^2 + S_c^3$ ) from 1985 to 2005. We added additional terms for calf survival and fecundity for 2006–2009 and for overall trends in adult female survival (as noted in the table). We did not model trends in yearling and adult male survival due to lack of corresponding field data for these parameters.

<sup>b</sup>  $F_{a06}$  or  $S_{c06}$  denotes an additional intercept term that allowed fecundity ( $F_a$ ) or calf survival ( $S_c$ ) to change in 2006. A  $\Delta F_{a06}$  or  $\Delta S_{c06}$  term denotes a linear trend term for  $F_a$  or  $S_c$  from 2006 to 2009.

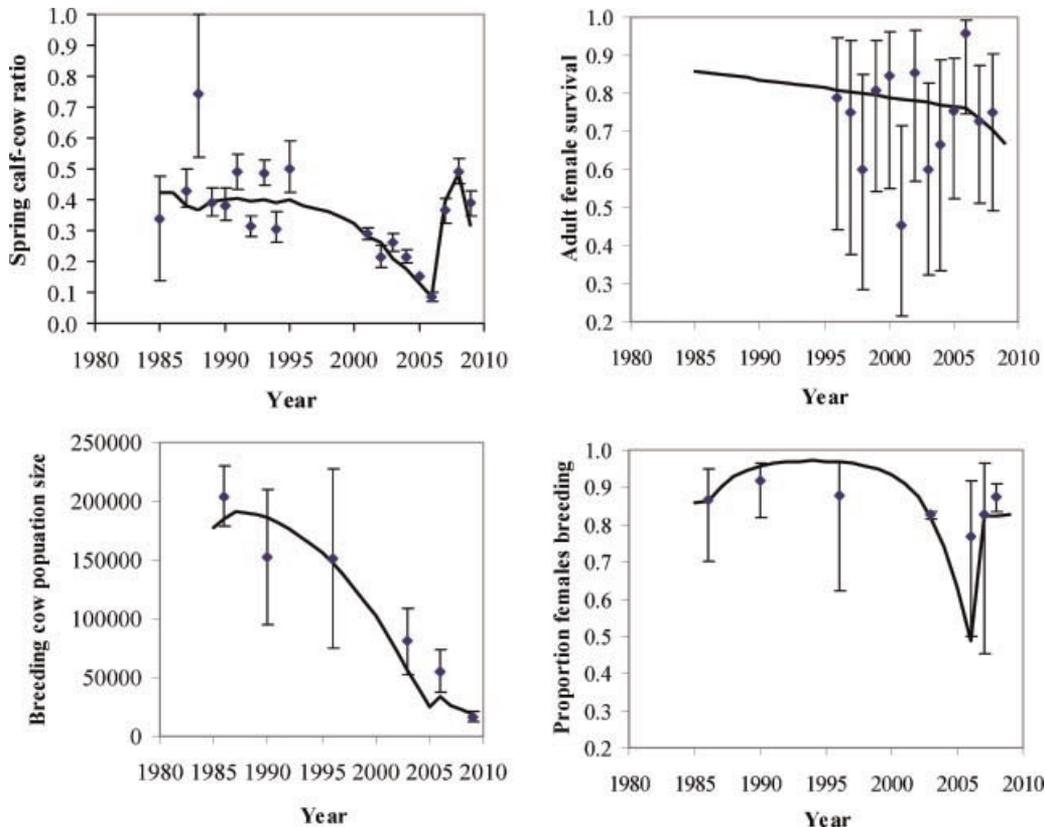
<sup>c</sup> A year subscript for survival denotes a broken stick model with the breakpoint at the year specified.

<sup>d</sup> MA denotes a model with a maximum female age of 15 yr.



**Figure 2.** Trends in model-averaged estimates of parameter values from models in Table 1 for the Bathurst caribou herd, location (1985–2009). We indicate net productivity as estimated by the product of fecundity, adult female, and calf survival for reference. Adult female survival ( $S_f$ ), calf survival ( $S_c$ ), fecundity ( $F_a$ ), and net productivity ( $S_f \times F_a \times S_c$ ) are shown. Adult male survival ( $S_m$ ) was 0.64 and yearling survival ( $S_y$ ) was 0.86 for all years because temporal trends were not simulated in these parameters.

around zero (Anderson–Darling test;  $A^2 = 0.71$ ,  $P = 0.06$ ) with no apparent trends in residuals as a function of year or field data type. Model predictions for fall calf–cow ratios paralleled trends in field measurements but were slightly

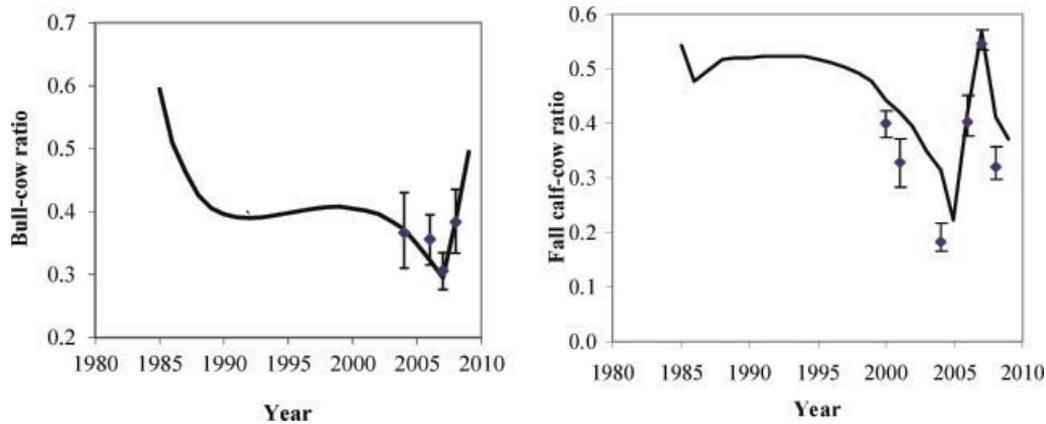


**Figure 3.** Model-averaged demographic model estimates (Table 1) compared to field estimates for late winter calf survival data and adult survival data for the Bathurst caribou herd, Northwest Territories, Canada (1985–2009). Field estimates have associated 95% confidence intervals.

higher for estimates prior to 2005, which was potentially due to the assumption of constant within-year calf and adult survival rates. 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. Model-averaged population estimates suggest declines in all cohorts (Fig. 5).

The adult female survival estimate was within the confidence intervals of point estimates of adult female survival from the Kaplan–Meier model (Fig. 3). However, precision of these estimates was low, as indicated by large confidence intervals, and estimates were only available after 1996. In comparison, a MARK known fate binomial survival model, using just the data from collared caribou, that assumed a linear trend in adult survival, was not different than a model that assumed constant survival ( $\chi^2 = 0.006$ ,  $df = 1$ ,  $P = 0.94$ ). This result further illustrated the lack of precision in adult female survival rates and subsequent low power to detect trends based upon collar data alone.

Reconstructed age classes for the female segment of the population suggest that the proportion of younger cohorts (yearling to 3-yr olds) decreased until 2006, shifting the overall age structure to older caribou (Fig. 6). Increased calf production caused the proportion of younger caribou to increase relative to other classes in the same period (2007–2009). Projected proportions for 2009 suggest that the current age structure has a higher proportion of older ( $\geq 10$ -yr old) and younger (yearling to 3-yr old) caribou than in the 1980s or 1990s.

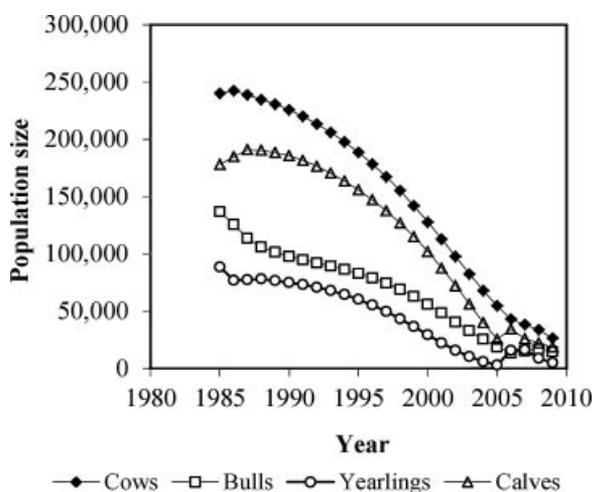


**Figure 4.** Model-averaged demographic model estimates (Table 1) compared to field estimates for fall survey data for the Bathurst caribou herd, Northwest Territories, Canada (1985–2009). Field estimates have associated 95% confidence intervals.

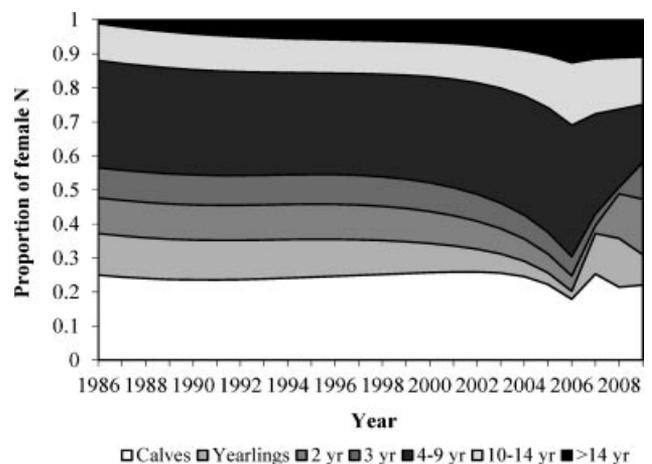
*Impact of harvest on trends in adult survival.*— Ordinary least squares model estimates suggested that adult survival declined from 0.86 in 1985 to 0.76 in 2006, followed by an accelerated decline down to 0.67 in 2009 for a net change of 19% (Fig. 2). One potential cause for the observed decline was a constant harvest on the population as it declined. For the winter of 2008–2009, a total harvest of 2,712 caribou was reported, with a high proportion of these being cows. This total was generally seen as an underestimate, given that some hunters did not report their harvest, the check-station was not always manned, and wounding losses were not accounted for. In addition, there was a limited Aboriginal harvest of mostly bulls in the fall, a limited hunt by resident hunters (<100/yr in recent years), and an average outfitter harvest in the fall of 828.3 bulls (1997–2009; SD = 287.3, range = 223–1,091; Adamczewski et al. 2009). The Dogrib Harvest Study (1988–1993) estimated harvest at 8,380 (range: 3,855–13,107) cows and 7,484 (range: 3,855–10,073) bulls (Table 2). Based on these numbers, we used an estimate of 3,000–5,000 cows and 1,000–

2,000 bulls/yr as the likely range of harvest totals from the Bathurst herd in recent years.

We contrasted the change in adult female mortality as estimated by 1 minus the OLS model averaged survival rate (Fig. 7) with proportional harvest mortality for adult cows as estimated by harvest levels divided by OLS population size estimates. From this we can see that harvest had a limited impact on the population until 2000, after which the proportional harvest mortality increased. Harvest rates of 3,000, 5,000, and 8,000 resulted in proportional harvest mortality of 11.6%, 19.3%, and 30.9% of the adult cow population at 2009 population size. The slope of the proportional harvest mortality curves was roughly parallel to the accelerated OLS survival rate mortality curve after 2007, suggesting that similar rates of change in mortality could be induced by a constant harvest rate at lower population sizes. These results suggest that an average harvest level near 5,000 cows could cause the same net change in mortality as estimated by the OLS model. Because harvest levels have not been documented accurately over time and the effects of predation



**Figure 5.** Model-averaged population estimates for each cohort simulated from ordinary least squares demographic models for the Bathurst caribou herd, Northwest Territories (1985–2009; Table 1).

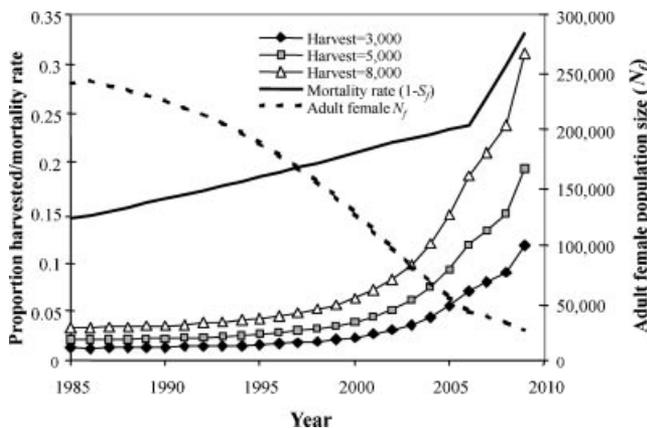


**Figure 6.** Trends in estimated proportion of age classes (females only) based on reconstruction of age classes for the Bathurst caribou herd, Northwest Territories (1985–2009). Estimates are from the most supported ordinary least squares model (Table 1). Caribou aged 4–9 yr are considered to have the highest level of reproductive output (fecundity and calf survival).

**Table 2.** Estimates of harvest from Dogrib Harvest Study for the Bathurst Caribou herd from 1988 to 1993, Northwest Territories, Canada (Adamczewski et al. 2009). Population estimates for bulls and cows are based upon model-averaged ordinary least squares estimates. Percentage harvest is the number of males or females harvested divided by the population estimate for males or females, respectively. Harvest estimates from the Dogrib Study do not include potential wounding loss.

| Year    | OLS model estimate <sup>a</sup> |                   | Caribou harvested |         | Proportion of $\hat{N}$ |             |
|---------|---------------------------------|-------------------|-------------------|---------|-------------------------|-------------|
|         | $\hat{N}$ males                 | $\hat{N}$ females | Males             | Females | Males (%)               | Females (%) |
| 1988    | 105,866                         | 234,567           | 4,606             | 3,318   | 4.35                    | 1.41        |
| 1989    | 101,303                         | 230,563           | 3,855             | 4,730   | 3.81                    | 2.05        |
| 1990    | 97,736                          | 225,611           | 8,970             | 8,450   | 9.18                    | 3.75        |
| 1991    | 94,728                          | 219,798           | 10,073            | 11,626  | 10.63                   | 5.29        |
| 1992    | 92,023                          | 213,238           | 9,685             | 9,046   | 10.52                   | 4.24        |
| 1993    | 89,301                          | 205,878           | 7,712             | 13,107  | 8.64                    | 6.37        |
| Average |                                 |                   | 7,484             | 8,380   | 8.56                    | 4.34        |

<sup>a</sup> Model-averaged estimates from models in Table 1.



**Figure 7.** Trends in proportion of adult females harvested annually as a function of model-averaged estimates of adult females population size (in units of a thousand) and hypothetical harvest levels for the Bathurst caribou herd, Northwest Territories (1985–2009). We also show model-averaged estimates of mortality rate ( $1 - S_f$ ) based on estimates of adult female survival ( $S_f$ ) for adult females (Fig. 3) for reference.

are unknown, it is not possible to conclude definitively that harvest was the principal factor in the later stages of herd decline. However, our results suggest that if harvest rates were additive to predation and other natural sources of mortality, they could potentially cause the trends detected in adult female survival rates.

### Stochastic Simulation Model

Process (temporal) variance was low for adult survival compared to calf or yearling survival (Table 3). Calf survival had the highest temporal variation over time. The effect of individual variation on mean  $\lambda$  estimates from simulations

**Table 3.** Estimates of process (temporal) variation, expressed as coefficient of variation, for input demographic parameters from mark-recapture analysis ( $S_f$ ), and variance component analysis (other parameters) for the Bathurst caribou herd, Northwest Territories, Canada, from 1985 to 2009. Also shown is the resulting population rate of change ( $\lambda$ ) given temporal variation of CV = 30% for each applicable parameter. Percentile based 95% confidence limits [CI ( $\lambda$ )] are also displayed. The effect of individual variation in rates on  $\lambda$  was negligible.

| Parameter                       | CV (time) (%) | $\lambda$ If CV (time) = 30% | CI ( $\lambda$ ) |
|---------------------------------|---------------|------------------------------|------------------|
| Adult female survival ( $S_f$ ) | 3.15          | 0.88 <sup>a</sup>            | 0.77–0.98        |
| Adult male survival ( $S_m$ )   | 3.15          | 0.99                         | 0.98–1.00        |
| Fecundity ( $F_a$ )             | 1.39          | 0.98                         | 0.96–0.99        |
| Calf survival ( $S_c$ )         | 36.79         | 0.99                         | 0.98–1.01        |
| Yearling survival ( $S_y$ )     | 3.15          | 0.98                         | 0.96–0.99        |

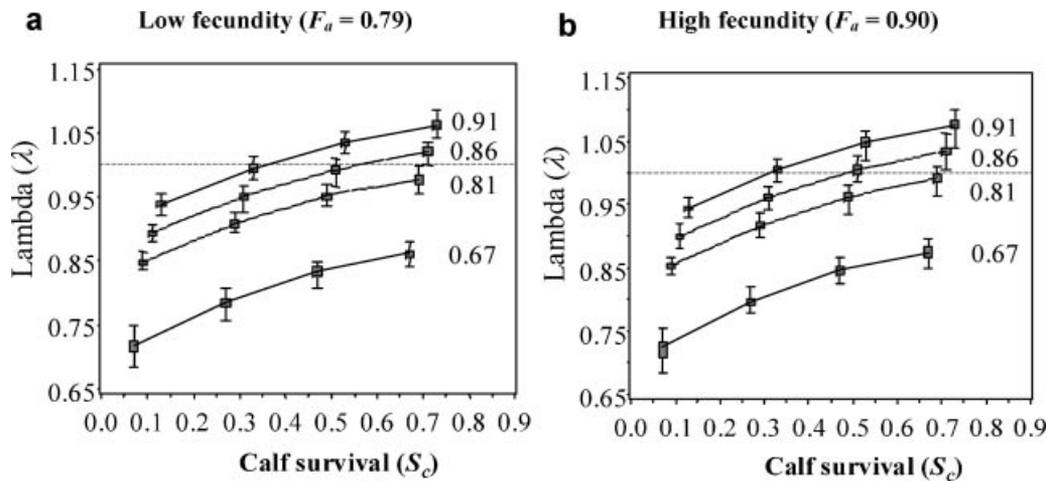
<sup>a</sup>  $\lambda$  Estimate corresponds to variation in adult female survival ( $S_f$ ).

was negligible given the relatively large population sizes we simulated. In general, temporal variation in adult female survival had the greatest influence on estimates, as demonstrated by the lower geometric mean of  $\lambda$  when we simulated a temporal coefficient of variation of 30% for each parameter, with no variation in the other parameters (Table 3).

Results from recovery simulations suggested that the herd would decline unless calf survival was  $>0.3$  regardless of increases in adult female survival (Fig. 8). The herd would not increase at any level of calf survival if adult survival stayed at the 2009 OLS estimate of 0.67. An increase in adult female survival to 0.86, which is the estimated 1985 level, would allow the herd to stabilize with calf survival levels of 0.53 (low adult fecundity,  $F_a$ ) to 0.50 (high  $F_a$ ). An increase in adult female survival to 0.91 would allow the herd to stabilize with calf survival values of 0.32 (high  $F_a$ ) to 0.35 (low  $F_a$ ).

## DISCUSSION

Our modeling suggests that the demographic mechanisms causing the decline of the Bathurst herd were the directional trends in calf survival, fecundity, and adult female survival. The more recent trends of accelerated decline between 2006 and 2009 in adult female survival and productivity (Fig. 2) is a major concern to wildlife managers, as the herd cannot stabilize or recover if these rates, particularly low cow survival persist. We demonstrated the potential effect of a constant harvest pressure on a declining population as a potential mechanism for the directional trends in adult survival. It is more difficult to determine the causes for reduced productivity that could have been due to environmental con-



**Figure 8.** Geometric mean of the ratio of successive population sizes ( $\lambda = N_{t+1}/N_t$ ) in simulations with low (a) and high (b) fecundity. We varied calf survival and female survival, whereas we held yearling survival and adult male survival constant at 2009 ordinary least squares estimated levels (Fig. 2). We staggered calf survival values for easy interpretation. Bottom and top of the boxes around each point represent the 25th and 75th percentiles of estimates, respectively. Vertical lines represent the entire range of  $\lambda$  estimates. Note the vertical line of 1.0, which is the point of population stability ( $\lambda = 1$ ).

ditions as well as predation. If the functional and numerical responses of predation have lagged behind caribou declining abundance, then predation could have a proportionally greater effect. The indices of wolf populations that were available (den surveys and aerial sightings; Adamczewski et al. 2009) did not allow modeling or estimation of wolf-caribou functional response curves to further explore the effect of predation.

The large recent decline, directional trends in both survival and productivity, and shifts in age structure suggest that the current population ecology of the Bathurst herd is highly dynamic. We speculate that compensatory mechanisms and related effects caused by non-stable age distributions could have played an increasing role in herd dynamics as the population declined (Lierman and Hillborn 2001, Koons et al. 2006). The Bathurst herd, like other caribou herds, has shown cyclic fluctuations of abundance (Zalatan et al. 2006). However, changes in hunting technology and increased access, habitat change due to a greater human presence including mines and other developments, and change in range conditions caused by fluctuations in climate make it more difficult to forecast recovery of the herd. It is possible to add environmental, anthropogenic, and other temporal covariates to the OLS model to further explore the effects of the environment and other factors on demography, which is a topic of ongoing research.

One challenge of the OLS analysis was that although adult survival was one of the driving parameters of overall dynamics as shown by sensitivity analyses (Table 3), we had the least amount of precise information about adult female survival (Fig. 3) due to sample size and we had only limited information on factors affecting adult survival such as harvest and predation. In contrast, the most precise and frequent information about the herd came from calf-cow ratios that are not direct estimates of survival, but still depend partly on adult survival. Therefore, calf-cow ratios influenced adult survival estimates which created a covariance between estimated productivity and adult survival. To confront this covariance,

we based initial modeling efforts on determining the best model for productivity and then tested models for adult survival. This approach was similar to an analysis of covariance (Milliken and Johnson 2002) where background covariates were controlled to allow assessment of variables that are of most biological interest. In doing this, we detected a decreasing trend in adult survival that was not detectable by stand-alone analysis of the imprecise collar-based survival data.

We used an approach similar to that of Haskell and Ballard (2007) for the Western Arctic caribou herd, as we also used a deterministic model to develop a stochastic model to explore observed trends in population size. However, Haskell and Ballard (2007) used subjective methods to fit their model to observed data. For example, Haskell and Ballard (2007) subjectively adjusted parameters to allow fit of the model to observed population trajectories. In contrast, 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.

### Effects of Change in Adult Survival and Hunting

Our modeling, specifically the elasticity analysis and stochastic simulations, suggest that trends in herd size are very sensitive to changes in adult survival. This general trait has been found in other large herbivores using matrix model methods (Gaillard et al. 1998) and in other barren-ground caribou herds (e.g. Porcupine herd: Fancy et al. 1994; George River herd: Crete et al. 1996; Western Arctic herd: Haskell and Ballard 2007). Simulations suggested that an increase in survival rate to 1985 levels (a net change of 19%) could potentially aid in recovery if calf survival was approximately 0.5. The parameter levels required for recovery are similar to those observed in the Western Arctic herd (Haskell and

Ballard 2007) and the Porcupine herd (Fancy et al. 1994, Walsh et al. 1995).

Our modeling was also challenged by limited data on harvest levels over time. To deal with this we considered a range of likely levels of harvest and compared these to the change in mortality for adult cows as estimated by adult survival rates. Comparison of proportional adult female mortality caused by harvest with change in adult female mortality rates suggests that an annual harvest of approximately 5,000 cows from a declining Bathurst herd could have created the observed 19% change in adult survival or mortality. We speculate that if harvesting is acting as a constant yield, the gregarious nature of caribou increases the risk for a sudden change in herd size, as observed in fisheries collapses (Mullon et al. 2005). Aboriginal cultures in northern Canada have experienced periodic times of scarcity in caribou previously (e.g., Zalatan et al. 2006). However, caribou at those times likely were more remote, as barren-ground caribou herds pull back to smaller core ranges at low numbers (Bergerud et al. 2008). Changes in hunting technology such as snowmobiles and aircraft to access herds, and access to wintering areas from winter roads, has increased hunting efficiency so that it was possible to harvest the Bathurst herd at a proportionally high level with little increase in effort as it declined. However, we cannot conclude that harvest alone was responsible for the herd's decline, given limited information on predation, as well as the observed variation in productivity that also contributed to a declining trend.

### Modeling Herd Productivity

Our results demonstrate the complexities of interpreting trends in productivity based on calf–cow ratios and other indirect indicators. Model estimates suggest that productivity decreased from 2006 to 2009 (Fig. 2) due to the influence of the lower calf cow ratios in fall of 2008 and spring of 2009 (Figs. 3 and 4). The decline in productivity (Fig. 2) from 2006 to 2009 could also have been due to an age structure dominated by younger and older cows (Fig. 6) that had lower fecundity and potentially lower calf survival rates (Thomas and Kiliaan 1998) when compared to middle-aged caribou in the population. This shift in age structure could in part explain the variation in productivity such as lower 2008 fall calf–cow ratios that suggests low recruitment. The rate of decrease in calf survival from 2006 to 2009 as estimated by the model (Fig. 2) may seem steeper than suggested by calf–cow ratios (Figs. 3 and 4), because declining adult survival (which affects the denominator of the calf–cow ratio) inflated calf–cow ratios. Therefore, both productivity and calf survival had to decline more steeply for the model to produce calf–cow ratios that corresponded to field estimates. The calf cow ratio also included female yearlings in the denominator and was therefore influenced by the survival and relative proportion of female yearlings in the population. For example, the higher proportion of yearlings in 2007 likely reduced calf–cow ratios. This example further illustrates the covariance among calf survival, fecundity, adult female survival, and yearling survival that can complicate interpretation

of age ratios, especially when there are directional trends in any of the parameters as noted by Harris et al. (2007). The OLS method explicitly models each parameter separately, thus allowing clearer interpretation of trends from field-based calf–cow ratios.

Although we cannot separate the effect of changes in fecundity from those of calf survival, the OLS model considered what combination of trends in parameters would best fit observed differences between fall and late winter calf/cow ratios, which would mainly be due to calf survival over winter. The OLS model also used information about trends in adult fecundity from calving ground composition counts. Thus, joint modeling of fecundity and calf survival trends was still reasonable given the constraints of field data. 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. A cow is likely to maintain her protein reserves even at the expense of lactation (Gerhart et al. 1997), which argues for fecundity being less variable than calf survival. The estimates of calf survival from 1995 to 2005 were  $<0.30$ . In contrast, the Porcupine herd calf survival rates were  $>0.50$  (Walsh et al. 1995), which is close to the levels needed for herd recovery (Fig. 8). We agree with Gaillard et al. (1998) and Coulson et al. (2005), who suggested that, although herbivore populations can tolerate random variation in calf survival, continuously reduced recruitment and calf survival may have a larger influence on population trajectories than revealed by sensitivity analyses. Thus, it is essential that productivity is monitored and directional trends in productivity parameters are assessed.

### Strengths and Weaknesses of OLS Model Fitting and the Demographic Model

The OLS method of model fitting is simple compared to the large array of procedures that are currently available (Williams et al. 2002, Buckland et al. 2004). The intuitiveness of penalties based upon units of error used in model fitting makes this modeling method more understandable by managers and stakeholders who have minimal statistical background. This reduces the black box aspect of the modeling process increasing understanding and buy-in to model findings by stakeholders in the caribou management process. However, the OLS method does make simplifying assumptions such as 0 covariance between field measurements and normally distributed statistical errors in estimates (White and Lubow 2002). We attempted to use independent field measurements to minimize any covariance between input model parameters, but the modeling process created covariance in estimated parameters. More complex procedures that allow more elaborate modeling of multiple data sources with consideration of covariance's, such as SAS PROC MODEL (SAS Institute 2009) are available, but these procedures do not allow for missing yearly data (White and Lubow 2002), which was prevalent in our data set. We also considered the approach of Lubow and Smith (2004), however, sparseness and prevalence of missing data, lack of age class-specific population sizes, and issues with binomial likelihoods from

staggered-entry Kaplan–Meier survival estimates with censored observations (White and Lubow 2002) precluded this more elaborate approach.

Limitations on demographic data should be considered when interpreting results from our modeling. For example, we had only 6 estimates of female population size over a 20-yr period. Given this, finer-scale trends in these parameters may be occurring, but not detectable, given the sparseness of the population estimates. We were unable to model trends or make substantive inference about the male segment of the population because the only information we had on the male segment of the population was from 4 bull–cow ratios collected annually after 2004. We emphasize that our lack of investigation of the male segment does not imply that males do not influence population dynamics. For example, Mysterud et al. (2002) discussed effects of skewed sex ratios on timing of calving, calf survival, and other factors.

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. Although this was a simplification, we argue that a simpler model was most appropriate given the sparseness of data on the strength or weakness of individual cohorts and age-specific demographic rates. We tested a model that had more detailed age structure, including a maximum age cut-off and found that it was less supported than the simpler stage-based model. However, the main difference between our age-structure model and the stage-based model was the maximum age cut-off for the age-structure model. We did not have any data to estimate age-specific survival or pregnancy rate parameters to better inform the age-structure model. We cannot draw clear conclusions about the effects of age structure on the Bathurst decline; however, in other herds, age structure changes were shown to be significant contributors to declines (Eberhardt and Pitcher 1992). Data from hunter collections, although limited by sample sizes, also suggested a slight shift to older aged caribou (B. Croft, Government of Northwest Territories, unpublished data). In fact, the age-structure model did show slightly better fit in terms of population estimates and survival rates; however, this was offset by reduced fit to other field estimates resulting in lower overall support for the age-structure model.

## MANAGEMENT IMPLICATIONS

Results of our demographic model were used to inform management proposals and public hearings for the Bathurst herd, with emphasis on potential demographic reasons for its decline and scenarios for herd recovery. One principal message was that the observed demographic trends in the data could be explained by reduced productivity combined with a constant harvest rate on the decline caribou population. The modeling also raised the possibility that the Bathurst herd might decline further even with no harvest, as shown by low productivity parameters in recent years. In addition, the herd had almost no chance of stabilizing or recovering with any substantial continuing harvest of breed-

ing females. And finally, there was recognition that there was uncertainty around survey results and around modeling outcomes and that there were multiple factors acting on caribou that were beyond human control. Any management program for the Bathurst caribou herd would have to be flexible and adaptive, hence capable of being adjusted as additional information became available (Walters 1986, Williams et al. 2002).

The stochastic demographic model is currently being used to further refine future management scenarios. The OLS-based stochastic model allows us to assess the relative risk of population decline given observed levels of productivity and harvest. Currently, strategies such as bull-dominated harvest are being recommended to allow some aboriginal harvest while minimizing risk of continued decline. An emphasis for current management is the reporting of all harvest levels which will allow partitioning of harvest versus predation and other causes of natural mortality through inclusion of harvest levels in the OLS model.

The OLS model approach we used is a useful tool for managers of caribou or other wildlife to assist in objective decision making regarding adaptive management strategies even when direct demographic data is not available. The OLS model and associated information theoretic 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. The value of composition surveys is increased by putting them into the context of overall population demography. As more information is gathered, the model can be adaptively updated to integrate new information therefore allowing informed management decisions.

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