Exploration of the decline of the Bathurst caribou herd using a data-driven demographic model.

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Data-driven demographic analysis of Bathurst Caribou herd

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Abstract

The Bathurst barren-ground caribou (*Rangifer tarandus groenlandicus)* in the Northwest Territories of Canada declined from 1986 to 2009. We developed a demographic model that could be objectively fitted to field data to explore the mechanisms for the decline with a focus on the recent accelerated decline. Our modeling indicated that the decline was driven by negative trends in adult female survival rate and trends in reduced calf survival (and/or fecundity). The effect of a constant harvest on the declining herd was one potential cause for the recent accelerated decline in adult survival. The demographic model, that utilized multiple field data sources, detected negative trends in adult female survival that were not detected using standalone analyses of collar-based survival data. The model also 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 a large increase in adult survival and productivity is needed to ensure herd recovery. The methods used in this paper allow objective modelling of caribou demography to inform management based upon all sources of available data.

Introduction

The Bathurst herd of barren-ground caribou (*Rangifer tarandus groenlandicus*) was one of the largest herds of migratory tundra caribou in northern Canada but then declined from an estimated 203,800 (CI=178,197-229,403) breeding females in 1986 to an estimate of 16,604 (CI=12,153-21,056) breeding females in 2009. As well as the statistically significant downward trend in the number of caribou, reduced productivity (calf survival and/or fecundity based upon sex and age composition surveys) and an adult sex ratio biased toward females (Gunn et al. 2005) has suggested a declining herd.

We became interested in further exploring how the measured parameters could interact as mechanisms to explain the decline and advise on management strategies to ensure herd recovery. A variety of models have been previously used to model caribou demography (Fancy et al. 1994; Haskell and Ballard 2007; Jenkins and Barten 2005) based mostly on direct estimates of survival and productivity data from radio-collared individual caribou. The main challenge with fitting demographic models to the Bathurst caribou herd, and, indeed, most barren-ground caribou herds in Canada, is 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. Most information on the demographics of the Bathurst herd came from indirect sources such as late winter and fall calf-cow and related composition surveys, and spring calving ground surveys and composition surveys.

To confront lack of direct demographic rate estimates we adopted a model developed for deer and elk by White and Lubow (2002) that considers multiple data sources for our caribou survey data. The main distinction and advantage of this approach is that both direct and indirect sources demographic information are used to produce model-based estimates of demographic parameters therefore relaxing the need for direct (individual radio-collared-based) estimates. In addition, this approach allows the evaluation of multiple hypothesis regarding temporal variation and trends in herd demographic parameters (Phillips and White 2003; White and Lubow 2002, Lubow and Smith 2004) 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). We furthered this approach to consider demographic stochasticity and used the resulting model to assess the efficiency of field-based measurement of herd demography and as well explore scenarios for potential herd recovery. Our objective 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 using all available data sources.

Methods

We first describe the demographic parameters available for the Bathurst herd and then detail the demographic model that used these parameters.

Estimation of demographic parameters

Adult survival rates

Adult cows in the Bathurst herd have been fitted with satellite or GPS collars since 1996 and the fate of collared caribou was observed or inferred. On average, 12.6 (std. dev=4.5, min=5 max=23) caribou were monitored on a weekly basis. We used the Kaplan Meir method to estimate survival rates of caribou (Pollock et al. 1995) through the assessment of monthly frequencies of collared caribou and associated fates. 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; a requirement for the demographic model used in the analysis. We have no data on adult male survival for the Bathurst herd. We therefore estimated adult male survival based upon assumed sex ratios at birth and observed bull/cow ratios (as discussed later).

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

Fecundity rates

Fecundity was defined as the proportion of adult females calving in a given year. The number of caribou on the calving grounds was estimated from calving ground surveys (as part of population estimate efforts) for 1986, 1990, 1996, 2003, and 2006-2009 (Gunn et al. 2004, Nishi et al 2007). We estimated fecundity as the ratio of the counts of productive females (females observed with calves, with and/or distended udders or with hard antlers as antlers are retained until birth) to total females (including non-productive females without calves, hard antlers and/or distended udders). This estimate applied to the previous year given that females on the calving ground became pregnant in the fall of the previous year and therefore it was the population of females the previous year that most directly applied to the population measured in the subsequent year on the calving ground. A bootstrap procedure (Manly 1997) was used to estimate 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 does not include early neonate mortality or fetal absorption (which is rare). We estimated variance using composition counts from each strata surveyed (Thompson 1992).

Calf survival and adult sex ratios

Late winter sex and age composition surveys to measure calf to cow ratios were conducted from 1985-1995 and 2001-2009 to estimate calf survival through to 9-10 months of age. As distinguishing yearlings from young cows can be unreliable, female yearlings were included in the cow segment. Half of the counts of unknown sex yearlings were also included as female cow segment under the assumption of an even yearling sex ratio (Gunn et al. 2005). Fall composition surveys were also conducted in 2000, 2001, 2004, and 2006-2008 to estimate calf/cow ratios as well as adult sex ratios in 2004 and 2006-08. The sex ratio data were used to further evaluate overall male versus female survival rates; these data were also incorporated into the population model. A bootstrap procedure (Manly 1997) was used to estimate proportions and associated variances with individual groups surveyed as the sample unit.

Estimates of female population from the calving ground surveys

Photographic surveys were conducted on the Bathurst calving grounds in 1986, 1990, 1996, 2003, 2006, and 2009 to estimate the total number of caribou on the calving ground (Gunn et al. 2004, Nishi et al 2007). 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 (Gunn et al. 2004) . This generated the estimate of breeding females.

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 ratio, breeding female population size, and fall sex ratio data. This approach involves first proposing a standard matrix-type model of caribou demography (Figure 1).

This model was based upon a yearly census that occurred each late winter when calves were born (Figure 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 to the next year. Recruitment was defined as fecundity (F_a: the proportion of adult females that successfully give birth with neonatal mortality excluded) 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) which was 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, less than 4% of caribou would survive past their 11th year, 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 the published caribou literature and the satellite-collared cows (1996 to 2007) in the Bathurst and neighbouring herds (Gunn et al. 2001).

The population model was projected from 1985 (the first year of estimated calf/cow ratios) to 2009. The initial population sizes were based on values from the 1986 calving ground survey. As with the 1986 survey, 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 primary emphasis of modelling efforts was exploration of trends in adult female demography given the relative lack of information on bull population size or survival rates.

Predictions of field estimates were generated from the stage-based matrix model. Estimates of late winter calf/cow ratio were estimated as

$N_c S_c^{(t/365)} / (N_f S_f^{(t/365)} + 0.5 N_Y S_Y^{(t/365)})$ where t was the interval from birth of calves to when late winter composition surveys were conducted. As with field measurements, female yearlings were included 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. 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 $\mathrm{N_m\,S_m^{(t/365)}/N_f\,S_f^{(t/365)}}$, 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 to estimate model parameters and test hypotheses about caribou demography

We used White and Lubow's (2002) model 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 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.

The basic objective of modeling was to maximize agreement between field data and model parameters. Therefore, the estimates were iteratively varied (using the SOLVER optimization algorithm in Excel ©) 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. Once the penalty term was minimized, then an AICc score was formulated for the model. Briefly, the AICc 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 AICc score suggests the most parsimonious model which 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 worth considering. In addition, the proportional support of each model, or AICc weight (w_i) was considered in evaluating the support of each model. All parameter estimates were model-averaged using AICc weights to account for model selection uncertainty.

Biologically- based models

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. 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, for caribou, parameters such as fecundity and/or calf survival likely vary over time. Therefore, models that allowed linear and non-linear trends in demographic parameters were evaluated using OLS methods by introduction of linear, quadratic and cubic terms. Survival and fecundity slope terms were logit-transformed (McCullough and Nelder 1989) to ensure that the resulting estimate was on the 0-1 interval.

We separated model building into two 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 could suggest an increase in productivity so we considered models that treated this period separate from previous years. A linear decline in survival was assumed during the productivity model-building phase.

Once a satisfactory productivity model was established we focused on changes in adult female survival. One question was whether the recent (2006-9) 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 cutpoint year therefore simulating a change in overall survival trend. We iteratively searched cutpoints from year 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. Trends in yearling survival and male survival were not considered 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. However, we lacked an adequate sample of field data although field collections 2007-08 did suggest a shift to an older age structure for females (B. Croft unpubl. Data). So we tested this hypothesis by expanding the adult age class up to a maximum age of 15. This age class-maximum age model was then contrasted against the standard stage-based model to see if model fit was significant improved as suggested by overall support from the field data. The initial distribution of age classes was assumed to follow a stable age distribution (Caswell 1989) as determined by initial demographic parameter values, and similar demographic rates were assumed for all age classes. The POP-TOOLS add-on for Excel (Hood 2009) was used 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). The number of each cohort for a given year was estimated as the number of the cohort in the previous year times the corresponding survival rate.

Exploration of the effect of harvest on trends in adult survival

One of the main questions about the Bathurst decline is the changing rates of adult mortality caused by harvest accelerated the herd decline (we did not have measures of predation rates). We were interested in whether harvesting rates were acting as a constant yield with harvesting effort possibly increasing 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 that occurred from 1988-1993 as well as estimates of more recent and unpublished harvest data. Trends in proportional mortality were then compared to estimates of proportional mortality based upon estimates of adult cow survival from the OLS model.

Stochastic model to evaluate demographic scenarios

A stochastic model was used to evaluate various demographic scenarios for the Bathurst herd while accounting for the effects of variation in model parameters (White 2000). The estimates of demographic rates from field data include both biological (also called process variation) and sampling variation. Process variation is 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. We also used random effects models in program MARK (White and Burnham 1999; White et al. 2002) to obtain estimates of process variation for survival rate estimated. We did not have any data to base estimates of variation of adult and yearling survival. We therefore assumed that individual and temporal variation was similar for adult females and males. We also assumed that individual variation in yearlings was similar to calves, but 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 calf survival in caribou. Variance estimates for the OLS model were then calculated by multiplying estimated values by each of the coefficients of variation.

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 then using a logistic transformation to ensure it was within the 0 to 1 interval. Additional individual variation (demographic) in demographic rates was also simulated using the above procedure. Population trends were evaluated using the geometric mean of successive λ ($\lambda=N_{t+1}/N_t$) estimates for simulations run for 20 years. SAS statistical package (SAS Institute 2000) was used for all demographic model simulations.

We first explored overall sensitivity of population trend to individual and temporal variation in model parameters by increasing variation in parameters and observing the resulting change in λ. 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 to provide a common initial basis for comparing simulations.

A critical question 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 segment most directly influences herd productivity. Ranges of adult survival were based upon likely reduction in survival rates due to caribou harvest as estimated as part of deterministic simulations described previously.

Results

OLS deterministic model

Initial model building efforts focused on building a model that described variation in productivity. Trends in calf survival from 1985-2005 were best approximated by a cubic curve whereas trend in fecundity were best approximated by a quadratic curve (Table 1, model 13). The 2006-9 period was modelled by adding additional intercept terms and/or slope terms for calf survival and fecundity. For example, a model with a unique intercept for calf survival allowed calf survival to increase but stay constant over this relatively short time period. Addition of a slope term (denoted by a Δ term in Table 3) allowed the parameter to increase to the intercept term and then change linearly. Trends in calf survival for 2006-9 were best described by an initial intercept term followed by a linear slope terms whereas trends in fecundity were best described by an intercept term only which assumed that fecundity was constant after 2006 (Table 1, Model 1). Models that were less supported assumed trends in both calf survival and fecundity after 2006 (Model 4), trends only in fecundity after 2006 (model 10), or no specific terms for 2006-9 (Model 13).

Once a base productivity model was established 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). Models which assumed different cutpoints (Models 3 ,6 ,7, and 12), or age structure (model 5), or no trends in adult survival (model 8), were less supported. Comparison of penalty terms between the age structure model (model 8) and the corresponding stage-based model (model 1) suggested that the age-structure model did not fit the data as well as the age-structured model except for the adult female survival estimates and breeding cow population estimates. In this case, the age-structure 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.

Model averaged parameter estimates were then used to assess temporal trends in parameters (Figure 2). It can be seen that adult female survival rates declined steadily until 2007 after which the decline accelerated. Calf survival was relatively 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. Productivity, which was the product of fecundity times calf survival, suggested that productivity declined in unison with calf survival, rebounded in 2006 before declining up to 2009.

The model fit all field data reasonably well with model-averaged predictions overlapping confidence intervals from field measurements in most cases (Figures 3 and 4). Model predictions for fall calf-cow ratios paralleled trends in field measurements but were slightly higher for estimates prior to 2005 that was potentially due to the assumption of a 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 (Figure 5).

The adult female survival estimate was within the confidence intervals of point estimates of adult female survival from the Kaplan-Meier model. However, the precision of these estimates was low (as indicated by large confidence intervals) and estimates were only available after 1996. Therefore the model-based estimate is still within the realm of possible field measurements. In comparison, a MARK known fate model using just the data from collared caribou that assumed a linear trend in adult survival was not significantly different than a model that assumed constant survival (χ^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 cohort (yearling to 3 yr olds) decreased until 2006 therefore shifting the overall age structure to older caribou (Figure 6). Increased calf production caused the proportion of younger caribou to increase relative to other classes. Projected proportions for 2009 suggest that the current age structure is dominated by older (10+ year old) and younger (yearling to 3 year old) caribou.

Assessment of the impact of harvest on trends in adult survival

OLS 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% (Figure 2). One potential factor for this decline was potentially constant harvest on the population as it declined. Accurate estimates of recent caribou harvest are unavailable although an annual estimate based on interviews and check stations is in the likely range of 3000 to 5000 cows (Govt. of NWT, unpublished data). The Dogrib Harvest Study (1988-93) for the Bathurst caribou herd assessed mean harvest at 8380 (range: 3855-13107) cows and 7484 (range: 3855-10073) bulls (Table 2).

We contrasted with the change in adult female mortality as estimated by one minus the OLS model averaged survival rate (Figure 7) with proportional harvest mortality for adult cows as estimated by harvest levels divided by OLS population size estimates. From this it can be seen that harvest had relatively little impact on the population until 2000 after which the proportional harvest mortality increased. Harvest rates of 3000, 5000, and 8000 resulted in proportional harvest mortality of 11.6%, 19.3% and 30.9% of the adult cow population at 2009 population size levels. The slope of the proportional harvest mortality curves was roughly parallel to the accelerated OLS survival rate mortality curve after 2007 suggesting 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 5000 could cause the same net change in mortality as estimated by the OLS model. Because harvest levels are uncertain as well as the effects of predation are unknown, it is not possible to conclude that harvest was the principal factor in the later stages of herd decline, however, these results suggest that if harvest rates were additive to predation and other natural sources of mortality, they could potentially cause similar trends as detected in adult survival rates.

Stochastic model results.

Individual (process) variance was low for adult survival compared to fecundity and calf or yearling survival (Table 3). Calf survival had the highest variation over time. The effect of demographic (individual) variance rates on the precision of simulations was negligible given the relatively large population sizes simulated. In general, variation in adult female survival had the greatest influence on estimates as demonstrated by the lower geometric mean of λ when a temporal coefficient of variation of 30% was simulated for each parameter (with no variation in the other parameters) (Table 3).

Scenarios for herd recovery

Results from recovery simulations suggested that the herd would decline unless calf survival was greater than 0.3 regardless of increases in adult female survival (Figure 8). The herd would not increase at any level of calf survival if adult survival stayed at the current 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 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 for the decline of the Bathurst herd are the directional trends in calf survival, fecundity, and adult female survival. The more recent trends of accelerated decline in adult female survival and productivity (Figure 2) is of concern. We demonstrate the potential effect of a relatively constant harvest pressure on a declining population as a potential mechanism for the directional trends in adult survival. However, it is more difficult to determine the causes for reduced productivity unless it is a consequence of predation. If the functional and numerical responses of predation have lagged behind caribou declining abundance, then predation could have a proportionally greater effect.

The large recent decline, directional trends in both survival and productivity, and shifts in age structure, suggest that the current dynamics of the Bathurst herd is highly dynamic. We speculate that depensatory mechanisms (Lierman and Hillborn 2001) and related effects caused by non-stable age distributions (Koons et al. 2006) could potentially be playing an increasing role in herd dynamics as the population declines. The Bathurst herd, as with other caribou herds has shown cyclic fluctuations of abundance (Zalatan et. al. 2006), however, we argue that changes in hunting technology, 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 potentially more difficult to forecast recovery of the herd from its current reduced population size. For example, declines in high density on calving grounds could reduce the effectiveness of predator swamping and calf survival could decline therefore slowing the recovery of the herd.

One challenge of the OLS analysis was that while 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 (Figure 3) due to sample size, and 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 contained information about adult survival. This created a strong covariance between calf survival, fecundity and adult survival that challenged the modelling process. To confront this, we based initial modelling 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 are controlled for 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 rate data.

To some extent, we used a similar approach to (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, they 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 (based upon the OLS model parameter estimates) 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). Therefore, the decline we detected in adult survival suggests that management action is needed to reverse this trend.

Our modelling was also challenged by lack of firm recent estimates of harvest levels. To confront 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. This general result suggests that an annual harvest of approximately 5000 cows on a declining herd could create the observed 19% change in adult survival/mortality. We speculate that if harvesting is acting as a constant yield, the gregarious nature of caribou increases the risk for a relatively sudden change in herd size, as observed in fisheries collapses (Mullon et al. 2005). However, it is difficult to interpret the harvest level without corresponding information on harvest effort. A hidden increase in harvest effort may be the reason why yield appears constant despite a large decrease in abundance and this would be accentuated by the clumped distribution of caribou. However, we cannot conclude that harvest alone was responsible for herd decline given lack of information on predation, as well as the observed variation in productivity that also contributed to reduced overall population vigour. If available, the annual hunter harvest that was standardized for estimated population size could be used to further model potential trends in adult survival

We focused stochastic model simulations on varying levels of survival to further explore how changes in adult survival may affect herd demography and potential recovery. 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 at 0.5. The parameter levels required for recovery are similar to those observed in the Western Arctic herd (Haskell et al 2007) and the Porcupine herd (Fancy et al 1994, Walsh et al. 1995).

The modeling of herd productivity

Our results demonstrate the complexities of interpreting trends in productivity based upon calf-cow ratios and other indirect indicators. Models that suggested increases in fecundity and calf survival after 2006 were most supported (Table 1). Calf survival was especially poor in

2004 and pregnancy rates were also depressed in fall 2004 which resulted in lower estimated fecundity on the calving ground in 2005 (Figure 3) which in turn also influenced calf-cow ratios in the spring of 2006. Possibly the increases in 2006 and 2007 productivity were compensatory as cows who did not calve in 2005 would have been subsequently in better physical condition. This potential mechanism would also explain why increased productivity did not last beyond the immediate 2006-7 time period.

Model estimates also suggest that productivity decreased from 2006-9 (Figure 2) which was due to the influence of the lower calf cow ratios in the fall of 2008 and spring of 2009 (Figures 3 and 4). The decline in productivity (Figure 2) from 2006-9 could also have been due to an age structure that was dominated by younger and older cows (Figure 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 potentially 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 2006-9 as estimated by the model (Figure 2) may seem steeper than suggested by calf-cow ratios (Figures 3 and 4). This is due to the fact that declining adult survival (which affects the denominator of the calf-cow ratio) inflated calf-cow ratios and 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 between 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 partially discussed in Harris et al (2007). The OLS method explicitly models each parameter separately therefore allowing clearer interpretation of trends from field-based calf-cow ratios.

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 late winter 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. 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. The estimates of calf survival from 1995-2005 were less than 0.3 In contrast, the Porcupine herd calf survival rates were above 0.5 (Walsh et al. 1995), which is close to the levels needed for herd recovery (Figure 8). We agree with 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 revealed by sensitivity analyses. Given this, it is essential that productivity is monitored and directional trends in productivity parameters are assessed.

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 6 estimates of female population size over a 20 year period. Given this, more elaborate trends in these parameters were possibly occurring, but not detectable given the sparseness of time series points. 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).

We were unable to model trends or make substantive inference about the male segment of the population. This was due to the fact that the only information we had on the male segment of the population was from 4 bull-cow ratios collected 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) discusses 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. While 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 cutoff 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 cutoff 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. Given this, we cannot conclude that age-structure is irrelevant to the Bathurst caribou. 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. We identify the lack of age-specific information as a short-coming of our analysis as cohort effects in a variable environmental are likely important (Coulson et al. 2001).

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 assumption has been used in other demographic studies of caribou (Fancy et al. 1994; Hewison et al. 2002) 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 fetal sex ratio (Hewison et al. 2002)

Conclusions

In summary, our modeling indicates that the Bathurst herd has declined because of a trend toward reduced calf survival (and/or fecundity) and negative trends in the survival of adult females. Model results demonstrate that directional change in both productivity and survival rate parameters are needed to explain observed trends in the data. Although a reduction in hunting would improve adult survival and may slow the decline, the model indicates that productivity needs to also increase to levels observed prior to 1995. The continued monitoring of productivity is essential in determining if long-term recovery is occurring. 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.

The OLS model approach used in this paper is a useful tool for managers to assist in objective decision making regarding optimal management strategies. For example, OLS model results demonstrate the increased power to detect trends in parameters such as adult survival when all data sources are considered simultaneously. 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. It increases the value of composition surveys by putting them into the context of overall population demography. It also highlights information gaps such as lack of quality adult survival data and corresponding estimates of annual harvest. As more information is gathered the model can be adaptively changed to integrate new information therefore allowing informed management decisions.

Acknowledgements

Adrian D'Hont and Judy Williams (ENR, Govt. of NWT) provided data for satellite collared caribou. We thank Craig Nicolson (University of Massachusetts, Amherst, Massachusetts) for constructive dialogue that aided in model development. We thank Kim Poole

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Table 1: 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 (the number of model and field estimate comparisons used to estimate ΣPen) was 56 for all models. Trends were not modelled in yearling and adult male survival due to lack of corresponding field data for these parameters.

No.	Fecundity[A]	Calf survival[A]	Adult Female Survival	AICc	ΔAICc	w_i	K	ΣPen
1	$F_a+F_a^2+F_{a06}$	$S_c+S_c^2+S_{c06}+\Delta Sc_{06}$	S_a	391.32	0.00	0.46	15	349.3
2	$F_a+F_a^2+F_{a06}$	$S_c+S_c^2+S_{c06}+\Delta Sc_{06}$	S_a+S_{a2007}[B]	391.44	0.12	0.40	16	345.5
3	$F_a+F_a^2+F_{a06}$	$S_c+S_c^2+S_{c06}+\Delta Sc_{06}$	S_a+S_{a2004}	393.42	2.10	0.06	16	347.5
4	$F_a+F_a^2+Fa_{06}+\Delta F_{a06}$	$S_c+S_c^2+S_{c06}+\Delta Sc_{06}$	S_a	393.71	2.40	0.04	16	347.8
5	$F_a+F_a^2+F_{a06}$	$S_c+S_c^2+S_{c06}+\Delta Sc_{06}$	$S_a+S_a^2$	393.93	2.62	0.03	16	348.0
6	$F_a+F_a^2+F_{a06}$	$S_c+S_c^2+S_{c06}+\Delta Sc_{06}$	S_a+S_{a2006}	395.26	3.94	0.01	16	349.3
7	$F_a+F_a^2+F_{a06}$	$S_c+S_c^2+S_{c06}+\Delta Sc_{06}$	S_a+S_{a2000}	398.22	6.90	0.00	17	348.1
8	$F_a+F_a^2+F_{a06}$	$S_c+S_c^2+S_{c06}+\Delta Sc_{06}$	constant	401.46	10.14	0.00	14	363.2
9	AS[C]: $F_a+F_a^2+F_{a06}$	$S_c+S_c^2+S_{c06}+\Delta Sc_{06}$	AS[C]:S_a	403.69	12.37	0.00	15	361.7
10	$F_a+F_a^2+F_{a06}+\Delta Fa_{06}$	$S_c+S_c^2+S_{c06}$	S_a	410.59	19.27	0.00	15	368.6
11	$F_a+F_a^2+F_{a06}$	$S_c+S_c^2+S_{c06}+\Delta$	S_a	410.66	19.34	0.00	14	372.4
12	$F_a+F_a^2+F_{a06}$	$S_c+S_c^2+S_{c06}+\Delta Sc_{06}$	S_a+S_{a2002}	423.78	32.46	0.00	16	377.8
13	$F_a+F_a^2+F_a^3$	$S_c+S_c^2+S_c^3$	S_a	970.17	578.85	0.00	13	935.5
14	constant	constant	constant	1371.78	980.46	0.00	8	1352.7

[A] Only parameters that were varied temporally are shown. Parameters not shown were held constant. Fa_{06} or S_{c06} denote an intercept term that allowed these parameters to change in 2006. A ΔF_{a06} or $+\Delta Sc_{06}$ denote a linear trend in F_a or S_c after 2006.

[B] A year subscript for survival denotes a broken stick model with the breakpoint at the year specified.

[c] AS denotes that an age structure model with a maximum female age of 15

Table 2: Estimates of harvest from Dogrib Harvest Study. Population estimates are based upon model-averaged OLS estimates. The percentage harvest is simply the number harvested divided by the population estimate for bulls and cows respectively. Estimates from the Dogrib Study do not include potential wounding loss

Year	OLS model estimate[1]		Caribou harvested		Proportion of $\hat{N}$	
	$\hat{N}$ bulls	$\hat{N}$ cows	bulls	cows	bulls	cows
1988	105866	234567	4606	3318	4.35%	1.41%
1989	101303	230563	3855	4730	3.81%	2.05%
1990	97736	225611	8970	8450	9.18%	3.75%
1991	94728	219798	10073	11626	10.63%	5.29%
1992	92023	213238	9685	9046	10.52%	4.24%
1993	89301	205878	7712	13107	8.64%	6.37%
Average			7484	8380	8.56%	4.34%

[1] Model-averaged estimates from models in Table 1

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). Also shown is the resulting λ if temporal variation CV=30% for each applicable parameter. Percentile based 95% confidence limits are given in parentheses . The effect of individual variation on λ was negligible.

Parameter	CV (individual)	CV (time)	λ if CV(time)=30%
Adult female survival (S_f)	0.10%	3.15%	0.88 (0.77-0.98)^A
Adult male survival (S_m)	0.10%	3.15%	0.99 (0.98-1.00)
Fecundity (F_a)	8.50%	1.39%	0.98 (0.96-0.99)
Calf survival (S_c)	12.70%	36.79%	0.99 (0.98-1.01)
Yearling survival (S_y)	12.70%	3.15%	0.98 (0.96-0.99)

^{A}λ estimate corresponds to variation in adult female survival

List of figures

Figure 1: Underlying stage matrix life history diagram for the caribou demographic model. This diagram pertains to the female segment of the population. Nodes are population sizes of calves (Nc), yearlings (Ny), and adult females (NF). Each node is connected by survival rates of calves (Sc), yearlings (Sy) and adult females (Sf). Adult females reproduce dependent on fecundity (FA) and whether a pregnant female survives to produce a calf (Sf). The male life history diagram was similar with no reproductive nodes.

Figure 2: Trends in model-averaged estimates of parameter values from models in Table 1 for the Bathurst caribou herd (1985-2009). Productivity as estimated by fecundity times calf survival is given for reference. Adult female survival (Sf), Calf survival (Sc), Fecundity (Fa) and productivity (Fa*Sc) 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..

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

Figure 4: Model-averaged OLS demographic model estimates (Table 1) compared to field estimates for fall survey data for the Bathurst caribou herd (1985-2009). Field estimates have associated confidence intervals.

Figure 5: Model-averaged population estimates for each cohort simulated from OLS deterministic models for the Bathurst caribou herd (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 (1985-2009). Estimates are from the most supported OLS model (Table 1). Caribou aged 4-9 are considered to have the highest level of reproductive output (fecundity and calf survival).

Figure 7: Trends in proportion of adult cows harvested annually as a function of model-averaged estimates of adult cow population size (in units of a thousand) and hypothetical harvest levels for the Bathurst caribou herd (1985-2009). Model-averaged estimates of cow mortality rate (1- cow survival rate) for adult cows (Figure 3) are also shown for reference.

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. Calf survival and female survival was varied whereas yearling survival and adult male survival was held constant at 2009 OLS estimated levels (Figure 2). 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.

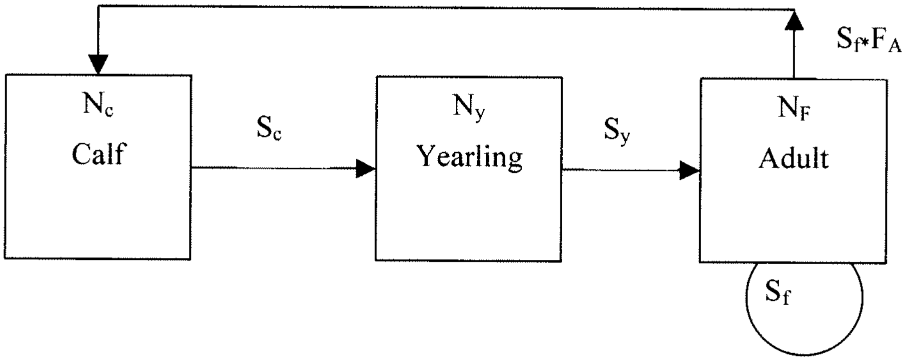


Figure 1

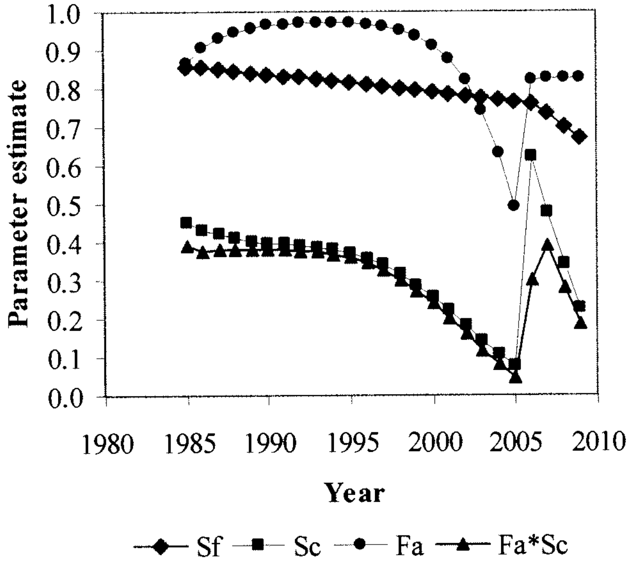

Parameter estimate
1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
1980
1985
1990
1995
2000
2005
2010
Year
Sf
Sc
Fa
Fa*Sc

Figure 2

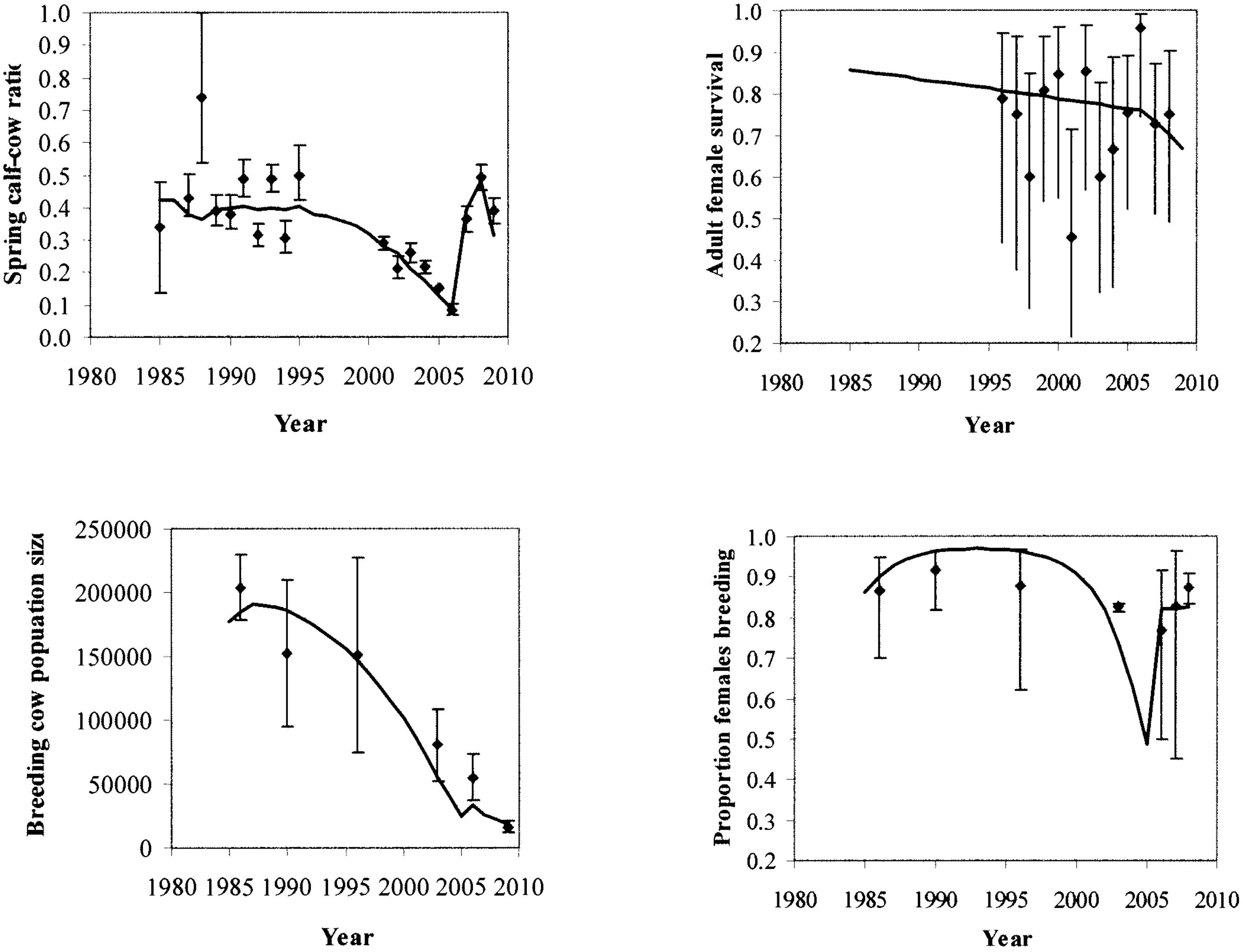

Spring calf-cow ratio
1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
1980 1985 1990 1995 2000 2005 2010
Year
Adult female survival
1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
1980 1985 1990 1995 2000 2005 2010
Year
Breeding cow popuation size
250000
200000
150000
100000
50000
0
1980 1985 1990 1995 2000 2005 2010
Year
Proportion females breeding
1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
1980 1985 1990 1995 2000 2005 2010
Year

Figure 3

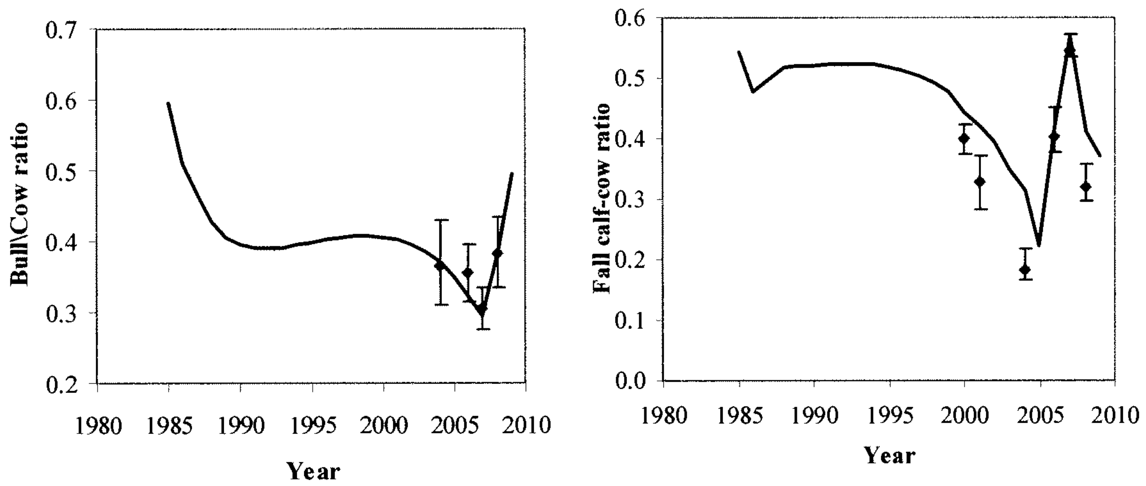
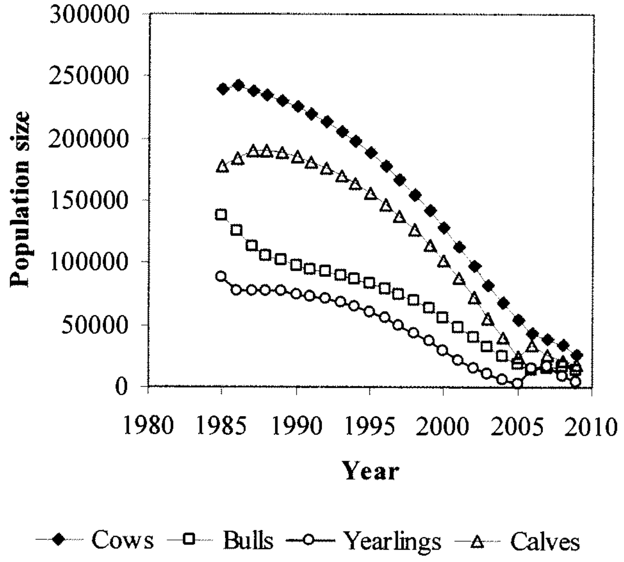

0.7
0.6
0.5
0.4
0.3
0.2
Bull\Cow ratio
1980
1985
1990
1995
2000
2005
2010
Year
0.6
0.5
0.4
0.3
0.2
0.1
0.0
Fall calf-cow ratio
1980
1985
1990
1995
2000
2005
2010
Year

Figure 4.



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742 **Figure 5**

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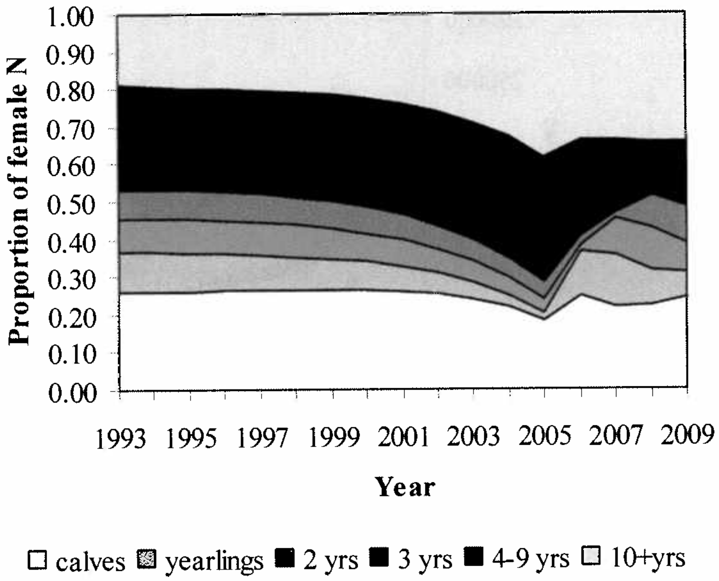
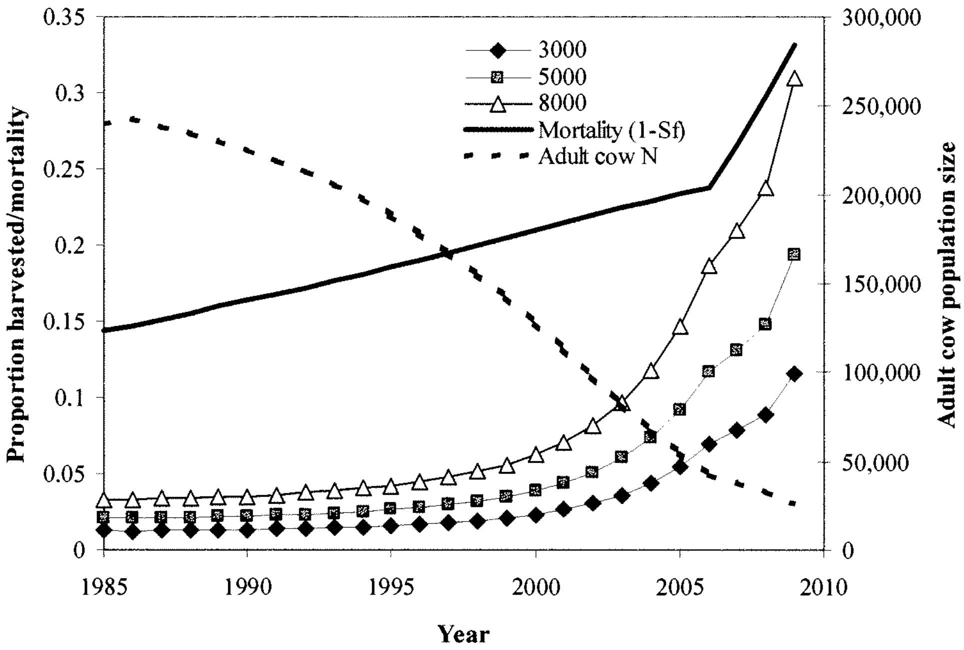

1.00
0.90
0.80
0.70
0.60
0.50
0.40
0.30
0.20
0.10
0.00
Proportion of female N
1993
1995
1997
1999
2001
2003
2005
2007
2009
Year
☐ calves ▨ yearlings ■ 2 yrs ■ 3 yrs ■ 4-9 yrs ☐ 10+yrs

Figure 6



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747 **Figure 7**

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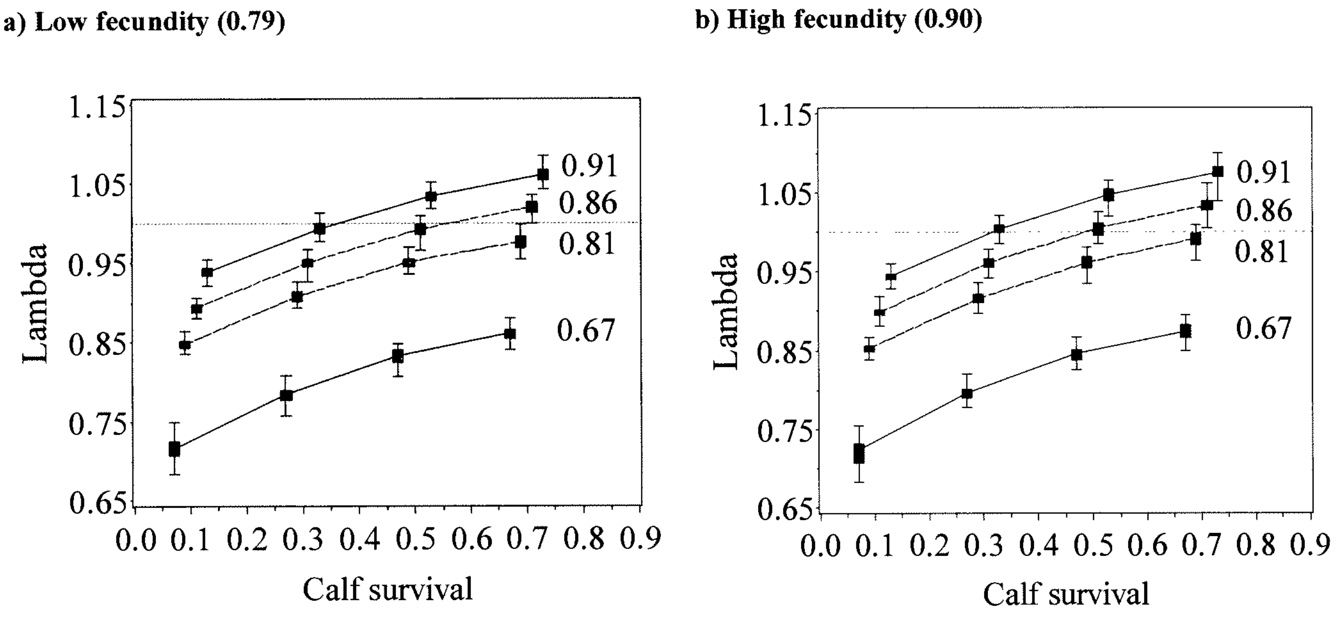

a) Low fecundity (0.79)

b) High fecundity (0.90)

Figure 8