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Projection of Woodland Caribou Populations in Newfoundland

An application of Leslie-Matrix population models to predict the future of Newfoundland Caribou Herds (2010-2035)

Shawn F. Morrison, Jackie N. Weir, Shane P. Mahoney, & J. Glenn Luther

Technical Bulletin No. 003

March 2012

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This report is a progress report on continuing research. Information may be refined at a later date. Please cite the report as:

Morrison, S. F., Weir, J. N., Mahoney, S. P. and Luther, J.G. 2012. Projection of woodland caribou populations in Newfoundland: An application of Leslie – Matrix population models to predict future of Newfoundland caribou herds (2010 – 2035). Technical Bulletin No. 003. Sustainable Development and Strategic Science, Department of Environment and Conservation, Government of Newfoundland and Labrador. St. John's, NL, Canada.

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PROJECTION OF WOODLAND CARIBOU POPULATIONS IN NEWFOUNDLAND

An Application of Leslie-Matrix Population Models to Predict the Future of Newfoundland Caribou Herds (2010-2035)

Technical Bulletin No. 003

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Executive Summary

1. The woodland caribou population on the island of Newfoundland has declined by more than 60% since the mid-1990's. Several individual herds have declined more than 90%. Overall, these declines have created a concern for the future status of caribou in Newfoundland.

2. A five-year *Caribou Strategy* was launched in 2008 by the Government of Newfoundland and Labrador to conduct an ecosystem-level analysis of caribou population dynamics. Research activities included investigations into caribou demography, morphology, predator-prey dynamics, spatio-temporal habitat use patterns, and human dimensions.

3. This report describes efforts to use mathematical models (matrix projection models) to assess the likely future status of caribou populations in Newfoundland. The models considered a) the island-wide population, and b) individual herds, using long-term demographic data.

4. Radio-telemetry data and aerial surveys indicated that annual calf survival in the past decade was dramatically lower than in previous decades, while most other age classes have remained relatively stable. Poor calf survival has resulted in:
    i. a numerical decline in the caribou population, and
    ii. a steadily aging breeding population that is not being replaced, also known as the "*Demographic Wave*" issue.

5. The models developed in this report considered a range of scenarios related to calf survival including the continuation of low survival rates, as well as a return to pre-decline levels of survival.

6. Herd age classification data, and model projections indicate that the "*Demographic Wave*" has largely passed through the herd by 2011. This suggests the age structure of the population is likely not a concern with respect to population trajectories, assuming that adult reproductive ability is independent of age.

7. The models indicate that a continuation of low calf survival into the future (i.e., the *status quo*) would result in a further 90% decline in the Newfoundland population over the next 25 years. Similar patterns were observed for individual herds.

8. However, if annual calf survival increases to between 40 and 55%, there exists a strong likelihood that the population decline will be halted or reversed. These rates have been observed previously in Newfoundland calves and are therefore within the realm of possibility as a management objective.

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1. Introduction

A fundamental objective of ecology is to determine the factors influencing species abundance (Krebs 2001). Management and conservation efforts also require an estimation of the probable fate of a given population under various natural or imposed scenarios (i.e. a forecast). These objectives are particularly important for species that may be declining in abundance and require management interventions such as woodland caribou (*Rangifer tarandus caribou*). Declines in woodland caribou abundance have occurred throughout North America (Bergerud 1974, Gray 1999, Vors et al. 2007, Vors and Boyce 2009) to the extent that the Boreal Population is now federally listed as *Threatened* and the Atlantic-Gaspésie population is listed as *Endangered* (COSEWIC 2002).

Woodland caribou on insular Newfoundland have been monitored by the Government of Newfoundland and Labrador since the 1950s. In 1996, the *Caribou Data Synthesis* was established to compile all available demographic and morphological data on caribou across Newfoundland. The evaluation of this database has revealed that caribou abundance increased from the 1950s to a peak of >90,000 caribou by the late-1990s. However, since the peak, caribou numbers have declined by more than 60%, with some individual herds declining by 90% (Norman et al. 2006, Mahoney and Weir 2009). These declines were accompanied by dramatic declines in calf survival, increased adult age, increasingly biased sex ratios, and reductions in adult body size. The Newfoundland population was last assessed by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) in 2002 at which time it was classified as *Not at Risk*, the only population of caribou in North America with that designation (COSEWIC 2002). Given the declines in abundance and the accompanying demographic and morphological changes that occurred after the 2002 assessment, the Newfoundland population is approaching the criteria for an *At Risk* classification during its next COSEWIC assessment (scheduled to begin in 2012).

In addition to concerns over the current population decline, poor calf survival raised a concern that the breeding segment of the population (i.e., adult females) was not being replaced. If the mean age of adult females gradually increased due to poor recruitment, the age structure would be composed of increasingly older females over time. As these cohorts age, without replacement by younger individuals, it will create a wave-like pattern, i.e., a "*Demographic Wave*". The combination of poor calf survival and increasing female age created a concern that the breeding segment of the population would die-off over time without being replaced by younger individuals, leading to an enhanced rate of population decline.

In 2008 the Government of Newfoundland and Labrador initiated a five-year research effort known as the *Caribou Strategy* to address the recent declines in caribou abundance and develop an appropriate management plan. The *Caribou Strategy* investigates predator-prey dynamics, habitat use, and socio-economic issues related to caribou in Newfoundland. An important component of the Strategy involves the development of population projection models to forecast future population abundance.

This report describes a series of matrix population models (Caswell 2001) developed to determine the likely future population abundance and age structure of caribou across Newfoundland (herds pooled) and for all major herds individually (see Figure 1 for map of herd ranges). The models were parameterized using data compiled by the Department of Environment and Conservation, and considered a number of factors believed to be important for the future of caribou in Newfoundland including 1) calf survival, 2) productivity, 3) adult survival, and 4) age of breeding females.

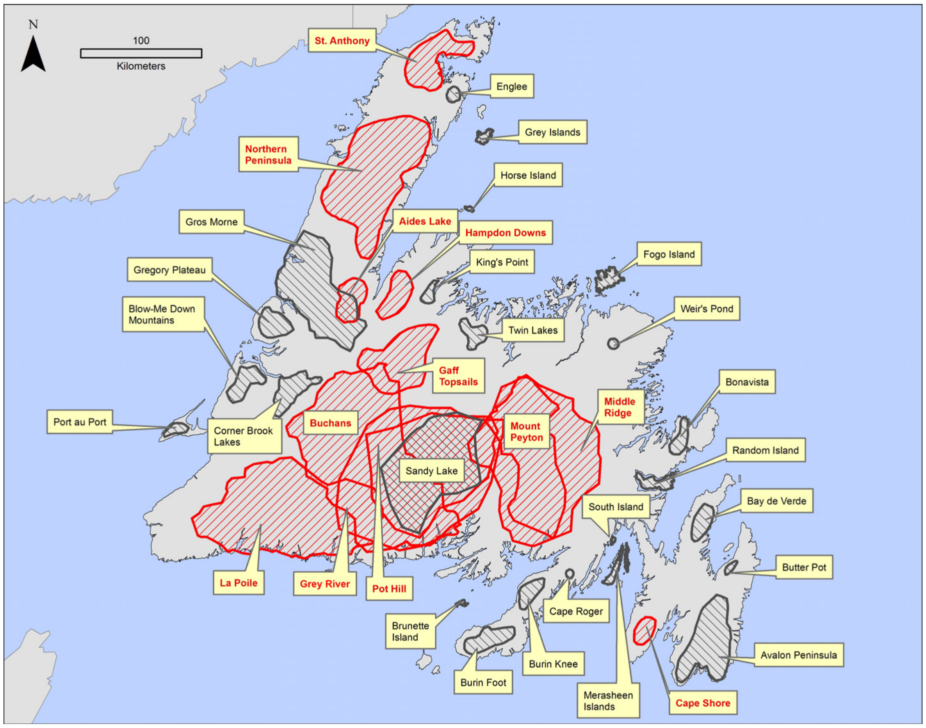

Figure 1: Locations and names of individual caribou herds in Newfoundland. Red text indicates the major caribou herds considered in this report. Most other herds are introduced populations and/or are very low in numbers and unhunted.

The objective for each model was to investigate the future (2010-2035) population size and age structure of caribou under two scenarios: 1) a continuation of poor calf survival, and 2) improved calf survival. Recent research indicated the proximate cause of low calf survival was due to predation (Mahoney and Weir 2009, Trindade et al. 2011). The scenarios investigated how calf survival may limit population growth and the extent to which improvement in calf survival would alter the current population declines. The model was also validated using data from 2003-2010 to determine the extent to which model projections reflected "known" population abundance estimates during that period. Similarity between model projections and known estimates would increase confidence that the model was accurately capturing the population dynamics of the herd.

Model projections also considered the "*Demographic Wave*" issue and determined the effect of this pattern on future population abundance. The 2010-2035 time-frame (a 25 year span) was selected as it is consistent with that being considered for management plans for the insular Newfoundland populations currently under development (Mahoney, pers. comm. 2010).

1.1 Excel Spreadsheet

The model presented in this report is available as an Excel spreadsheet. The spreadsheet was developed to allow 'what-if' scenarios to be considered, and to allow the model to be accessible to as many people as possible without the need for specialized software. The Excel sheet also shows all calculations and uses a series of charts and figures to illustrate the consequences of modifying various aspects of the model.

All vital rates (productivity and survival) may be independently modified for all ages. It also allows for scenarios that include different starting conditions such as initial age structure and population size.

2. Model Development

2.1. Sources of Data

Demographic data and trend analysis were provided by the Department of Environment and Conservation and were collected during the course of other research activities on Newfoundland caribou. The methods used to calculate survival and reproduction estimates are provided below in Sections 2.3 and 2.4, respectively. Summarized demographic data used in this report are given in Table 1.

The herds examined in this report were Insular Newfoundland (herds pooled), Adies Lake, Buchans, Cape Shore, Gaff Topsails, Grey River, Hampden Downs, La Poile, Middle Ridge, Mount Peyton, Northern Peninsula, Pot Hill, and St. Anthony (Figure 1).

2.2. Matrix Population Model

Population projections were based on standard Leslie matrix population models that followed a birth-pulse post-breeding census design (Caswell 2001). This matrix modeling approach allowed for the inclusion of age-specific life-history information such as reproduction and survival. The matrix model developed in this study tracked caribou from birth to age 13+ years (Figure 2), which is well suited to the objective of this study to track each age group through time. This age-specific approach allows the "*Demographic Wave*" created by an aging adult female population with minimal recruitment, to be tracked through time.

The models used in this report followed the methodology described by Caswell (2001). Population models, such as those developed and analyzed in this study, allow for projections to be made regarding the fate of each caribou herd. The projections made by this type of analysis address how the population would behave '*if the present conditions were to be maintained indefinitely*' (Caswell 2001). Keyfitz (1972) suggested that this is one of the most powerful techniques to study the current condition of a population because it addresses the consequences of current conditions on population dynamics.

$$\begin{bmatrix}
F_{calf} & F_1 & F_2 & F_3 & F_4 & F_5 & F_6 & F_7 & F_8 & F_9 & F_{10} & F_{11} & F_{12} & F_{13} \\
S_{calf} & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & S_1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & S_2 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & S_3 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & S_4 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & S_5 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & S_6 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & S_7 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & S_8 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & S_9 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & S_{10} & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & S_{11} & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & S_{12} & S_{13+}
\end{bmatrix}$$

Figure 2: Structure of the age-classified matrix population model. Fertilities are along the top row for each age, where F_x is the fertility for age 'x'. Survivals are along the sub-diagonal where S_x is the survival of age 'x'. Fertilities were the product of productivity, birth sex ratio, and survival.

2.2.1. RATIONALE FOR SINGLE SEX MODEL

Matrix population models typically are based on female life history patterns (Caswell 2001). The exclusion of males is based on the assumption that males are not limiting in the population. If males are limiting, such as in the cases of extremely skewed sex ratios, then it may be useful to explicitly include males in the models. Males may affect population dynamics in several ways including reproduction (productivity), and calf survival.

Because sex ratios have become increasingly male-biased across Newfoundland (Mahoney and Weir 2009), these possibilities were examined using data from all major herds. Regression analysis indicated there was no relationship between productivity and the percentage of stags in the herd during the previous fall (S. Morrison, unpublished report), supporting the use of a single-sex model. Similarly, no relationship was found between calf survival and the percentage stags in the previous fall (S. Morrison, unpublished report), again supporting the use of a female-based model.

2.3. Survival Estimation

Adult female survival rates were estimated based on radio-telemetry data from collars deployed on adult female caribou on the South Coast and Northern Peninsula regions of the island of Newfoundland between 2004 and 2009. Data from collars deployed on South Coast caribou were used to estimate survival rates for La Poile, Buchans, Grey River, Gaff Topsails and Pot Hill herds. Data from collars deployed on Northern Peninsula caribou were used to estimate survival rates for Northern Peninsula, St. Anthony, Hampden Downs and Adies Lake herds. The average rate for data from all collared animals was used to estimate survival rates for Middle

Ridge (2007 and 2008), and Mount Peyton. The 2009 Middle Ridge adult survival rate was derived from radio collars deployed on the Middle Ridge caribou during spring 2009. Calculation of annual survival rates followed Heisey and Fuller (1985).

Survival estimates for calves and yearlings were based on herd classification data. Calf survival rates were calculated from iterative spring and fall composition surveys according to:

$$\text{Calf Mortality} = 1 - \frac{\text{Calves per 100 does (fall)}}{\text{Productivity (spring)}}$$

Although this estimate is more accurately described as the rate of survival to six months of age, we used this estimate as a proxy for annual calf survival. We made this assumption because 1) fall herd composition surveys were conducted during a time when all age and sex classes of caribou are together and thus, provide the best estimate of age and sex composition of the herd, b) overwinter mortality was minimal (Trindade et al. 2011), and c) more data were available from fall herd composition surveys relative to winter surveys.

2.4. Reproduction

Reproduction can be measured in at least two ways. First, reproduction could be estimated as the number of calves seen per 100 females during aerial surveys in the spring or early summer (i.e., immediately following parturition). These estimates are then used to calculate the number of calves per female. The other method is to use productivity data that is defined as the proportion of adult females that exhibited signs of breeding (distended udders, presence of a calf, etc.):

$$\text{Productivity} = \frac{\text{\# Breeding Females}}{\text{Total Number of Females}}$$

Previous discussions with staff from Department of Environment and Conservation determined that productivity data is the preferred measure of reproduction as calves per 100 does underestimates productivity due to calf loss which may occur prior to visual classification and late calving which may not occur until after visual classification, and thus productivity was used in the modeling approach in this report.

All females ≥ 2 years old were assumed to be reproductively mature (Adams and Dale 1998), and to have equal productivity. In addition, productivity calculated during classifications included adults ≥ 2 years of age. The sex ratio at birth was assumed to be 1 male:1 female. Adult female fertility (F) was calculated according to Caswell (2001) and included female survival (S), productivity, and the sex ratio of calves at birth. There is some evidence that the birth sex ratio of some caribou herds is slightly biased towards males (Bergerud et al. 2008), but in the absence of herd-specific data, a 50:50 ratio was used. Therefore, the fertility of adult females (F_3) was calculated as follows (based on an 81.3% survival (S_3), 81.6 productivity, and a 50:50 sex ratio at birth):

$$F_3 = \frac{S_3 \cdot \text{Productivity}}{\text{SexRatio}} = \frac{0.813 \cdot 0.816}{0.5} = 0.3317 \text{ female calves per year}$$

3. Model Projection and Analysis

3.1. Time Periods & Model Starting Conditions

Vital rates (survival and productivity) for caribou were based on all available data for the appropriate time frame (Table 1). The initial age structure for both time periods was based on jawbone data submitted by hunters, and the starting population size was assumed to be the same as the latest census or population estimate for that herd, following an adjustment to include calves. That is, the post-calving population was the sum of the pre-calving census plus the expected number of calves based on known productivity for that year. Adult survival was assumed to be independent of age. An exception to this assumption was the survival of 13+ age individuals was assumed to be 50% of that for younger age classes to ensure a realistic maximum age.

The insular Newfoundland model was applied to two time periods. The first period, 2003-2010, was selected to 1) determine the extent to which the projection model tracked known population estimates, and 2) to investigate the *Demographic Wave* issue and determine whether it remained a cause for concern. The second time period, 2010 to 2035, was selected to investigate 1) population size projections assuming the current demographic conditions remain constant and (2) the extent to which improving calf survival may affect the age structure and population trajectory over the next 25 years. For the 2010-2035 period, calf survival was varied between 0.15 and 0.65 in 0.05 increments. The mean calf survival prior to the population decline (pre-decline: 1970-1989) was also included as a scenario ($S_{calf} = 0.487$). The objective of these scenarios was to explore a range of calf survival rates and determine the rate at which population decline was halted and/or reversed.

Individual herds were projected from 2010-2035 and considered the effects of 1) continued low calf survival, and 2) a return to historical calf survival rates (i.e., observed during the increase phase of the population).

Productivity and cow and calf survival estimates for the 2003-2010 scenario were based on data averaged from 2003-2005; estimates for the 2010-2035 scenario were based on a 3-year mean using data from 2008-2010 (Table 1). If data were missing for a particular herd for any one of the three years, we used the mean of the latest available three years (since 2006) for that herd to estimate the missing value. If data were missing for all years for any particular parameter for a particular herd, we used the mean estimate for all herds combined (i.e., the insular Newfoundland mean). Calf survival estimates for the ‘pre-decline’ period were based on mean data from 1970-1989, a period of high population growth (Table 1).

Table 1: Mean productivity and survival of female caribou adults and calves for insular Newfoundland (herds pooled) and individual herds. 'Recent' estimates of calf survival were based on average data from 2003-2005 for the 2003-10 simulation and average 2008-2010 for the 2010-2035 simulations. Calf survival estimates for the 'pre-decline' period were based on average data from 1970-1989, a period of high population growth. The island-wide mean was used when data were unavailable for individual herds.

Herd	Productivity	Cow Survival	Calf Survival ('Recent')	Calf Survival ('Pre-Decline')
Insular Nfld (2003-2010)	0.7548	0.8432	0.1883	---
Insular Nfld (2010-2035)	0.7832	0.8926	0.2197	0.487
Adies Lake	0.7832	0.9189	0.1315	0.462
Buchans	0.8014	0.8736	0.2469	0.575
Cape Shore	0.6835	0.8926	0.4303	0.553
Gaff Topsails	0.8482	0.8736	0.2763	0.492
Grey River	0.7832	0.8736	0.1608	0.376
Hampden Downs	0.6842	0.9189	0.1772	0.613
La Poile	0.8063	0.8736	0.1482	0.471
Middle Ridge	0.8639	0.8742	0.146	0.494
Mount Peyton	0.7409	0.8742	0.2765	0.435
Northern Peninsula	0.7247	0.9189	0.1808	0.463
Pot Hill	0.8291	0.8736	0.1530	0.695
St. Anthony	0.7247	0.9189	0.3807	0.462

3.2. Population Growth Rate, λ, and 95% Confidence Intervals

The population growth rate, known as λ (lambda), may be calculated as the ratio between population abundance (*N)* in year *t+1* to the population abundance in the previous year *t*. Lambda may also be calculated directly from the matrix, as it is the dominant eigenvalue of the matrix (Caswell 2001). Regardless of the method used, populations are declining when $\lambda<1$, remain stable when $\lambda=1$, and are increasing when $\lambda>1$.

Each of the vital rates was associated with some uncertainty (variation) and it was therefore important to estimate the effects of this variance on the population growth rate. The series approximation method, also known as the 'delta' method, was used to calculate standard errors and 95% confidence intervals (CIs) for λ. This procedure incorporates the variance within all vital rates, weighted by the sensitivity of λ to each vital rate, to estimate the variance associated with λ (Caswell 2001). This method has been used to estimate the 95% CIs around λ for a several wildlife species including black bears (Hebblewhite et al. 2003), the Northern Spotted Owl (Lande 1988), and a variety of others (Sæther and Bakke 2000).

3.3. Sensitivity and Elasticity Analysis

Sensitivity and elasticity analysis was used to determine how the population growth rate (λ) would respond to changes in vital rates (e.g., fertility and survival) (Caswell 2000, 2001). Sensitivity refers to the change in λ resulting from a change in matrix elements (i.e., the vital rates) and elasticity refers to the proportional response of λ to a proportional change in a matrix element (Caswell 2000, 2001).

Sensitivities and elasticities are additive (Caswell 2001: p. 244). For example, the total sensitivity (or elasticity) of λ to survival, with all age classes pooled, can be estimated by summing the survival sensitivities (or elasticities) of each age-class. Note that sensitivities and elasticities should not be added to each other. The calculation and interpretation of sensitivity and elasticity analysis is explained in Appendix A.

4. Results & Discussion

4.1. Period: 2003 – 2010, Insular Newfoundland (herds pooled)

Calf survival and subsequent recruitment likely began declining in the mid-1990s in tandem with the overall population trend. This is similar to patterns reported elsewhere in which juvenile survival is often one of the first vital rates to decline as a result of increasing population density (Eberhardt 1985). Calf survival was calculated using estimates from 2003-2005 to present to reflect that dramatic drop in calf survival.

The model indicates a continued decline in the insular Newfoundland population if the vital rates do not improve relative those observed from 2003-2005. Model results showed a decline from approximately 103,900 caribou (post-breeding) in 2003 to 40, 000 caribou by 2010 (again, post breeding), with an overall population growth rate of λ = 0.844 (95% CI: 0.820-0.869). Field surveys show that the trajectory of the population continued to decline during this period in a manner very similar to that projected by the matrix model (Figure 3). Thus, we were encouraged that the model was capturing the known trend of declining abundance in this population.

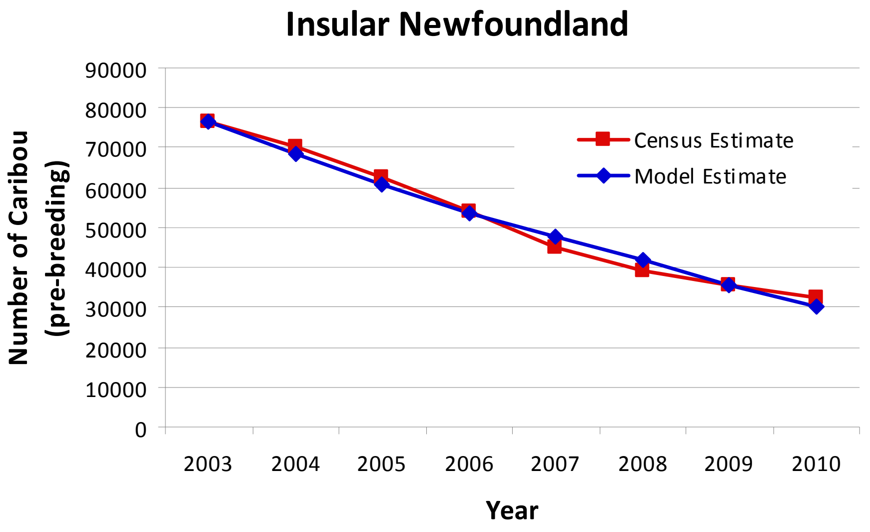

Figure 3: Comparison of population abundance derived from aerial census estimates and the matrix model. Population abundances were expressed in pre-breeding numbers for the sake of comparison. Model estimates discussed in the text are based on the post-breeding population and are therefore larger than illustrated here.

Furthermore, the model also clearly illustrated the trend of aging adult females with minimal recruitment of calves into the herd. Productivity estimates showed that calves were being produced at expected rates (i.e., productivity was within the normal range and did not appear to be declining), however low calf survival meant that very few calves survived to become yearlings or older age classes. This meant that the mortality of adults was not being balanced by the recruitment of younger animals.

The "*Demographic Wave*" can be clearly seen progressing through the population from 2003 to 2010 (Figure 4). Based on the results of the matrix models, we conclude that the "*Demographic Wave*" has largely finished passing through the herd by 2010 or 2011. Therefore, population decline should not be further exacerbated by a rapid drop in adult female survival. Following the passing of the demographic wave, the age distribution becomes more evenly distributed. If the model were to be projected forward for a longer period of time, the herd would eventually reach a stable age distribution (Figure 5). In the case of the insular Newfoundland herd, the age class distribution expected in 2035 is more heavily weighted toward younger aged individuals than observed in recent hunter jawbone returns (Figure 5). This is clearly different than the age distribution observed from 2003-2010 that was more heavily weighted toward older age classes due to poor calf survival and recruitment (Figure 4).

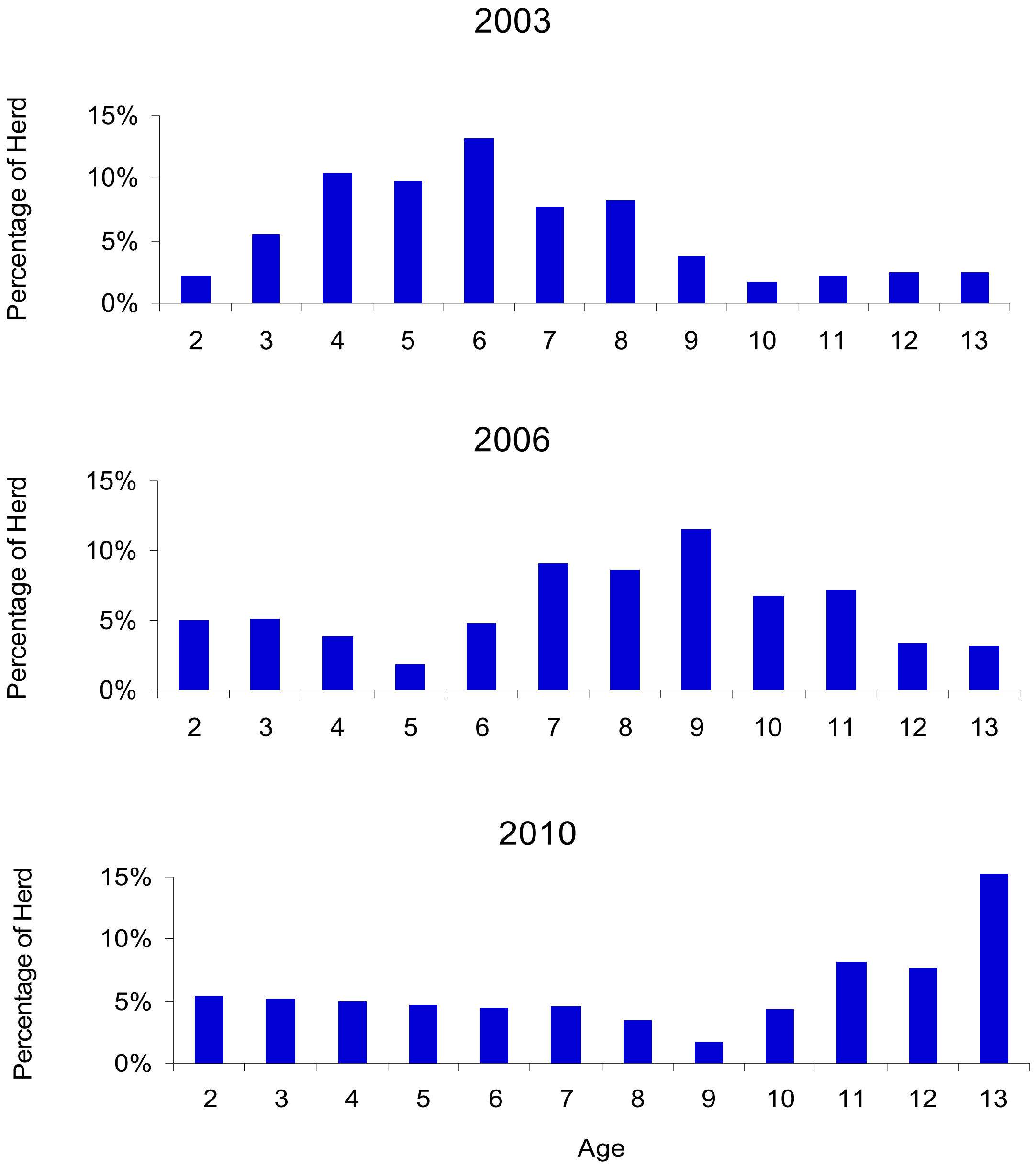

Figure 4: Age structure of caribou 2+ years old based on a Leslie matrix model parameterized with data from 2003-2005. Distribution shows that the "demographic wave" is largely passed through the population by 2010.

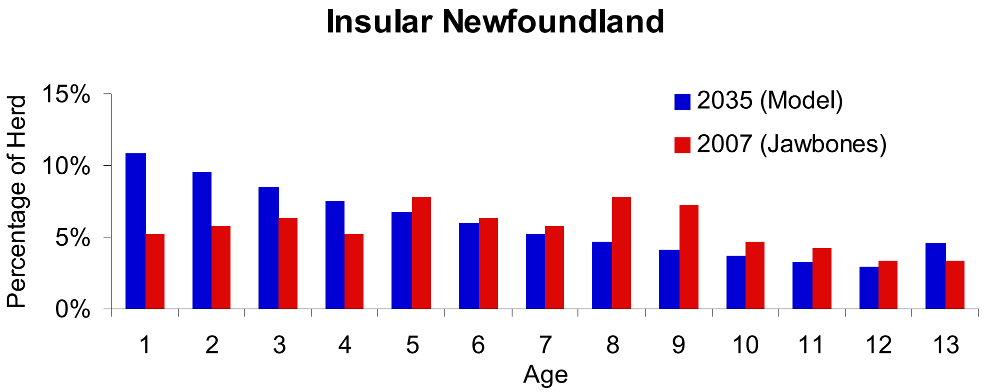

Figure 5: Age distribution of Newfoundland caribou based on a) hunter-submitted jawbones in 2007, and b) model-projected age structure in 2035 using calf survival set at 48.7%.

4.2. Period: 2010 – 2035

4.2.1. INSULAR NEWFOUNDLAND (HERDS POOLED)

The first scenario for the island-wide population projection considered the continued effects of low calf survival ($S_{calf} = 0.219$). Under this status-quo scenario, the herd declined by >90% from a post-calving population estimate of 53,181 individuals to 5074 individuals by 2035 (Figure 6). The population growth rate during the period was $\lambda = 0.91$ (95% CI: 0.874 - 0.942). Clearly, if calf survival remains at current levels, the island-wide population will continue to decline and the potential for population persistence is poor.

A second scenario for the island-wide population projection involved a return to historical (i.e., pre-decline) levels of calf survival ($S_{calf} = 0.487$), while holding productivity and adult survival constant at current rates. The primary result of improved calf survival was a stable or growing caribou population from 2010-2035 (Figure 6). The model projected a modest growth from a post-calving population of 53,181 caribou in 2010 to 58,460 caribou by 2035 ($\lambda = 1.01$ (95% CI: 0.98 - 1.04). Confidence intervals around this result indicate the growth rate cannot be distinguishable from a stabilized population (Figure 7).

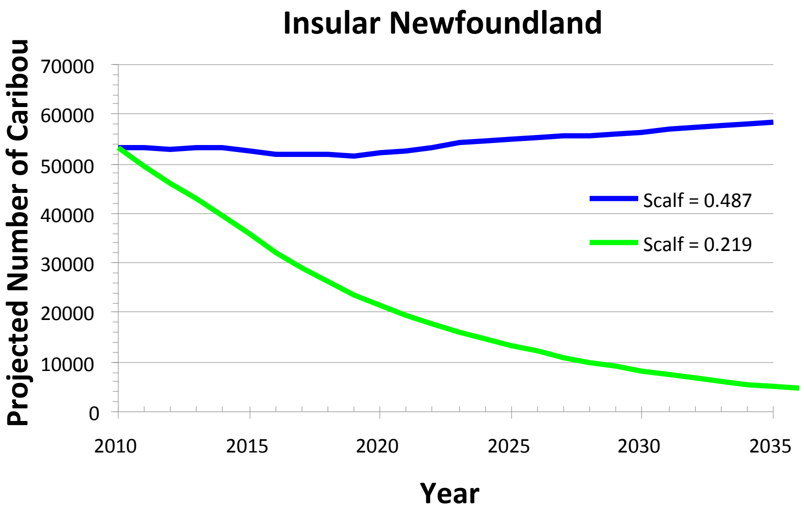

Figure 6: Projected population size for Insular Newfoundland caribou based on matrix population models. Two scenarios were considered: 1) Calf survival remaining at recent levels (S_{calf} = 0.219), and 2) returning to pre-decline levels (S_{calf} = 0.487). The projected number of caribou reflects post-calving population size and thus is larger than pre-calving census estimates.

The effect of calf survival on population growth and decline was further examined to determine the rate at which population stability and/or growth could be achieved. For example, could population stability be reached at calf survival levels lower than those observed in the pre-decline phase? To address this issue, the model was repeatedly rerun using a series of calf survival values from 0.15 to 0.65. The results indicated population declines could be halted when calf survival was between 0.40 and 0.55 (Figure 7). That is, the 95% confidence intervals around λ included the possibility that the herd may stabilize (i.e., $\lambda = 1.0$). A return to pre-decline levels for calf survival (i.e., $S_{calf} = 0.487$) would produce a stable, or potentially growing, caribou population. The population began to increase when calf survival exceeded $S_{calf} > 0.55$. That is, the 95% CI no longer included $\lambda = 1$).

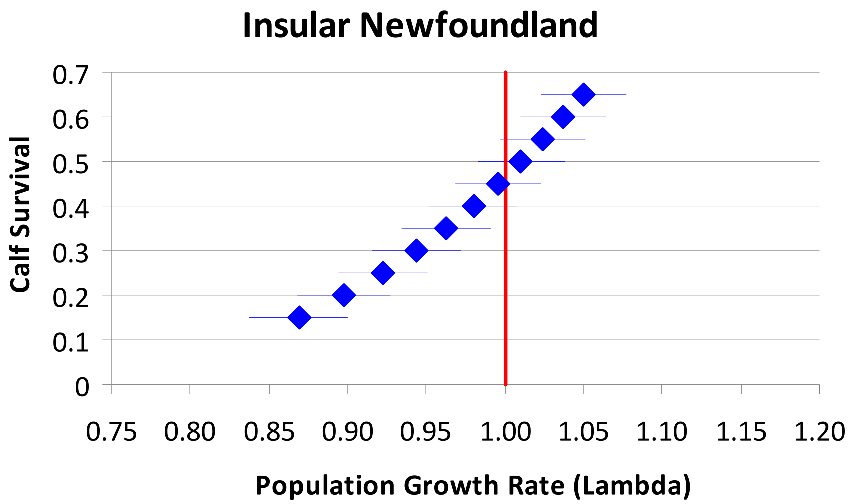

Figure 7: Relationship between calf survival and population growth rate (λ ± 95% CI) for the insular Newfoundland caribou herd from 2010-2035. The red vertical line indicates population stability.

4.2.2. Individual Herds

Models for individual herds revealed similar patterns when calf survival rates were returned to historical levels. In most individual herds, a return to historical levels was sufficient to return to a status of population growth (Appendix B). For all herds, the scenario that assumed calf survival rates did not improve beyond those observed in the 2008-2010 period resulted in continued population declines (Appendix B).

4.2.3. Sensitivity and Elasticity Analysis

Calf survival has declined dramatically for most Newfoundland herds and the decline appears to be associated with the recent declines in population density (Trindade et al. 2011). Calf survival declined faster than other vital rates, consistent with a density-dependent response in which younger age classes are negatively affected prior to older age classes (Eberhardt 1985, Gaillard et al. 2000). Given that other vital rates have not sharply declined it is natural to conclude that the population growth rate must be most sensitive to calf survival.

However, the results of the sensitivity and elasticity analysis indicated that the population growth rate was most affected by adult female survival (

Table 2). That is, a change in adult female survival would have a greater effect on the growth or decline of a population than changes in any other vital rate.

See Appendix A for additional discussion on interpreting sensitivities and elasticities.

Table 2: Sensitivities and elasticities of the population growth rate to changes in vital rates for the period 2010-2035 (using calf survival = 48.7%).

Vital rate	2010-2035	
	Sensitivity	Elasticity
Productivity	0.36	0.14
Calf Survival	0.29	0.14
Yearling Survival	0.16	0.14
2-year-old Survival	0.16	0.14
Adult Survival	0.65	0.59

This result is consistent with results reported for other large mammals. An extensive review of large mammal life histories by Gaillard et al. (2000) clearly showed that:

> *"…the population growth rate of large herbivores is much more sensitive to a given relative variation in adult survival than to the same relative variation in any other fitness component.*" – Gaillard et al. (2000).

In addition, the sensitivity of the population growth rate to adult survival is often 2-3 times larger than to the survival of younger age classes or to reproduction (Nelson and Peek 1982, Escos et al. 1994, Gaillard et al. 2000, Heppell et al. 2000, Gaillard and Yoccoz 2003).

In general, the survival of younger age classes is more variable than for older age classes (Gaillard et al. 1998), but has lower sensitivity/elasticity than observed for adult survival (low variation but high sensitivity/elasticity) (Gaillard et al. 2000). These results support the "Canalization Hypothesis" that suggests that vital rates that have the greatest effect on the population growth rate should be canalized against environmental variation (Gaillard and Yoccoz 2003). That is, these traits are hypothesized to have been under selection pressures against variability relative to younger age classes. Adult females will limit variation in survival by altering their reproduction during unfavorable environmental conditions, resulting in greater variability in reproduction and the survival of younger age classes such as calves – in effect, they trade reproduction for survival (Gaillard and Yoccoz 2003).

Therefore, the results obtained in the present analysis fit well with established life-history theory for large mammals: adult female survival was less variable yet showed the greatest effect in the population growth rate relative to younger age classes. Calf survival, on the other hand, had greater variability but had a lesser effect on the population growth rate.

From a management perspective, it would be quite difficult to increase adult female survival given that it has remained relatively high (i.e., no indication of a declining trend), and minimally variable, despite its relatively large effect on growth rate. On the other hand, increasing calf survival maybe more tractable despite it relatively smaller effect on population growth rate as indicated by sensitivities. It is not inconceivable that calf survival could be increased several-fold whereas that the same increase would be impossible for adult females.

Therefore, the management path that seems to make the most sense would be to take actions that increase calf survival. Other management actions that would positively affect other aspects of caribou life history and demography would also assist in halting and reversing the observed declines. However, these actions must occur along with improved calf survival to effectively assist in the recovery of caribou populations in Newfoundland.

4.3 Comparison with Other Woodland Caribou Populations

The Newfoundland woodland caribou population is declining, following a trend similar to many caribou populations across their circumpolar range (Thomas and Gray 2002, Vors and Boyce 2009). Predation has been identified as the proximate cause for most caribou deaths (Thomas and Gray 2002, Bergerud et al. 2008). However, predation rates are significantly influenced by ultimate causes such as anthropogenic changes to the landscape (habitat loss, degradation, fragmentation), disturbance (e.g., logging activities, construction, traffic, low-flying aircraft), hunting, parasites, and weather/climate (Farnell and Gardner 2002, Thomas and Gray 2002). Interactions among factors are common (e.g., Hegel et al. 2010) resulting in complex reasons for observed patterns of population dynamics and demographics.

Current demographic trends in Newfoundland are consistent with previous research, in that declines in herd size have been paralleled by reduced calf survival whereas adult survival has remained relatively high and stable (McLoughlin et al. 2003, Chisana Caribou Recovery Team 2010). As with most large ungulates, caribou survival rates are age-specific with older animals having higher annual survival than younger animals (Caughley 1966, 1977). Calves typically have the lowest survival rates of all age classes due to their vulnerability to predators (Bergerud and Elliot 1986, Bergerud 2000, Mahoney and Virgl 2003), adverse climate conditions (Hegel et al. 2010), foraging conditions (Rettie and Messier 1998, Lenart et al. 2002, Thomas and Gray 2002, Mahoney and Virgl 2003), and the quality of calving areas (Mahoney and Virgl 2003). Calf survival fluctuates more than adult survival from one year to the next and this pattern is a common feature of large ungulate population dynamics (Gaillard et al. 1998). Thus, caribou population dynamics, like that of other ungulates, is often driven by variation in the survival of calves rather than adults (Bergerud 1971, Bergerud et al. 1983, Adams et al. 1995).

An understanding of calf mortality is therefore essential for understanding caribou population dynamics. Caribou calf mortality is generally highest during the first few weeks of life, both within Newfoundland and in other parts of Canada, and predation seems to be the major proximate cause (Bergerud 1971, Stuart-Smith et al. 1997, Mahoney and Virgl 2003, Mahoney and Weir 2009, Trindade et al. 2011). Calves are generally an easier target for predators than adults, and weak or sick calves probably more so (Bergerud 1971). It appears that most calves that are fit enough and have sufficient parental care to survive through the fall are likely to survive until the next growing season (Bergerud 1971, Mahoney and Virgl 2003, Mahoney and Weir 2009, Trindade et al. 2011).

The models developed in this report indicated that a calf survival rate of 40-55% was required for the decline to be halted. This range of survival is consistent with the estimated 42% calf survival required for population stability in other woodland caribou populations (Yukon Renewable Resources 1996), and is within the range of survivals observed during the rapid growth-phase of the Newfoundland population.

At present, calf survival and recruitment in Newfoundland caribou is extremely low, and predation seems to be a major driving force (Schaefer and Mahoney 2007, Trindade et al. 2011). However, the Newfoundland pattern does not appear to be an isolated case for caribou populations (Chisana Caribou Recovery Team 2010). For example, calf survival in the Gaspésie population was only 10% from 1987-1992, with most deaths a result of predation (mainly black bears and coyotes) (RENEW 1993, 1994, Crete and Desrosiers 1995). Predator control, combined with restrictions on human access, allowed calf survival to improve (RENEW 1994). Similarly, calf recruitment in the Chisana population (Yukon & Alaska) was 6-14 calves/100 does during a population decline, predation was the primary cause for the 80% decline in abundance between 1989 and 2000 (Farnell and Gardner 2002). In this population, pregnant cows were captured and placed in a predator-proof enclosure. Cows and calves were held for several weeks post-partum to ensure calves escaped the period of greatest predation risk, and achieved higher rates of annual survival (Chisana Caribou Recovery Team 2010).

In both case studies above, limiting predation rates had a positive effect on calf survival. Note, however, that reducing predation rates in both case studies addressed the *proximate* cause of low calf survival and not the *ultimate* cause. In other words, there was likely an underlying cause to explain *why* neonatal calves became more susceptible to predation relative to previous years.

Nevertheless, improvement of calf survival will be a key component towards halting the decline of Newfoundland caribou observed in recent years. It is possible that calf survival may rebound without management intervention. However, if it does not, aggressive predator management intervention may be required to increase calf survival in order to maintain a viable population of woodland caribou in Newfoundland.

4.4 Next Steps

Leslie-matrix models are only one of the many population modeling approaches that could be used to forecast the future of Newfoundland caribou. Our next step is to use Population Viability Analysis (PVA). PVA is widely used in conservation biology and wildlife management to evaluate threats faced by species, the probability of extinction or decline, and the chances for recovery based on alternative management options (Boyce 1992, Akçakaya and Sjögren-Gulve 2000, Brook et al. 2000). This approach has been used to determine the fate of numerous taxa including avian, mammalian, reptilian, and fish species (Brook et al. 2000). Furthermore, PVA has been used extensively to assess potential threats and to model the fate of caribou in North America (see recent examples in Hatter et al. 2004, Wittmer 2004, Decesare et al. 2010, Wittmer et al. 2010).

We will use PVA to project the probable fate of several major caribou herds on the island of Newfoundland, in order to (1) project population size with current demographic conditions, and (2) assess the likely impact of two potential management actions (elimination of legal harvest and improvement of calf survival, potentially via predator manipulation exercises) on these projected trends.

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Appendix A: Calculation and interpretation of sensitivity and elasticity analysis

The sensitivity of the population growth rate (λ) to various vital rates is often of interest to those investigating the population dynamics of a species. For a Leslie matrix model, such as the one used in this study, the sensitivity of λ to a vital rate is calculated as follows:

$$\text{Sensitivity} = \frac{\partial \lambda}{\partial a_{ij}},$$

where $\frac{\partial \lambda}{\partial a_{ij}}$ indicates the change in λ as a result of a change in a_{ij} which is the matrix element in the ith row and jth column of the projection matrix.

If the population growth rate was plotted against the range of possible values for a vital rate the sensitivity of λ to that vital rate would be equal to the slope of the line. Although this seems to be a basic calculation, difficulties arise in interpreting sensitivities because the relationship between λ and the vital rate is not necessarily linear. Therefore, the sensitivity of λ to the vital rate may vary depending on the value of the vital rate.

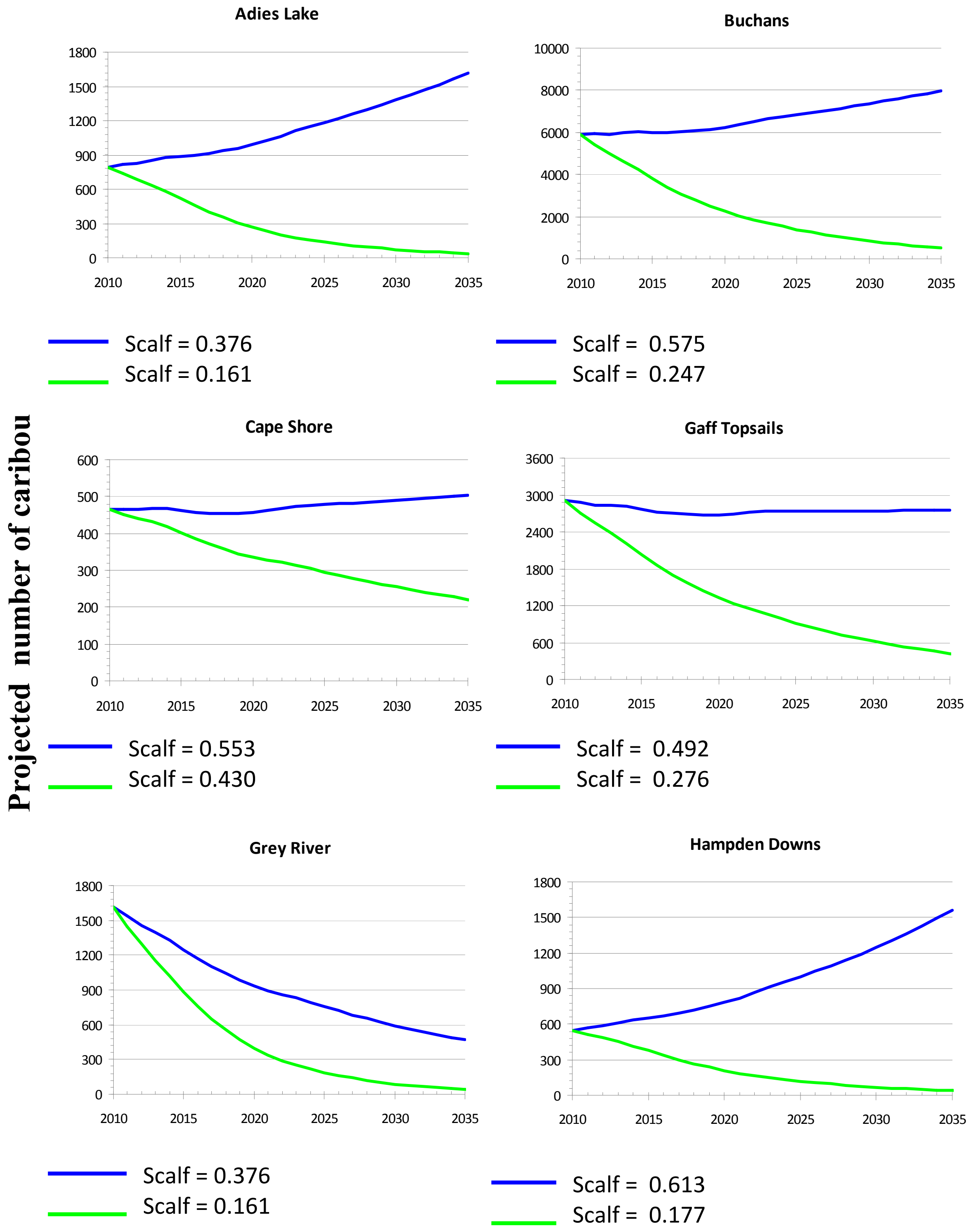
Example of Interpreting Sensitivities (taken from Morris and Doak (2002), page 329)
In the Morris and Doak (2002) example, juvenile survival was very low (0.136) and the population growth rate was $\lambda = 0.989$. The sensitivity of λ to juvenile survival was 0.580. If juvenile survival was somehow increased to 0.70 (say through a management action), then the new estimate of λ would be calculated as the current growth rate (0.989) plus the change in juvenile survival (0.70 – 0.136) times the sensitivity (0.58). This produces a new population growth rate of 1.21. However, the authors cautioned that this new value for λ may differ from the λ obtained by updating the matrix with the new value because of the non-linearity of sensitivities. Therefore, sensitivities must be interpreted cautiously.

Comparison of sensitivities also may be difficult because vital rates are measured on different scales. For example, survival can vary only between 0 and 1, whereas fertilities can vary between 0 and a much higher upper limit (for many species). For caribou, both survival and fertilities typically are bounded between 0 and 1 so this is less of an issue. Nevertheless, it is useful to re-express the sensitivities on a common scale to facilitate comparison among different types of vital rates. The rescaled values are called elasticities. Elasticities represent *proportional* changes in λ for a *proportional* change in a_{ij} and are calculated as:

$$\text{Elasticity} = \frac{a_{ij}}{\lambda} \frac{\partial \lambda}{\partial a_{ij}}.$$

Two vital rates with the same elasticity value mean that the same *proportional* change in the vital rate would have the same equal *proportional* change in the population growth rate.

Appendix B: Projections of population size for individual caribou herds using the Leslie-Matrix model.



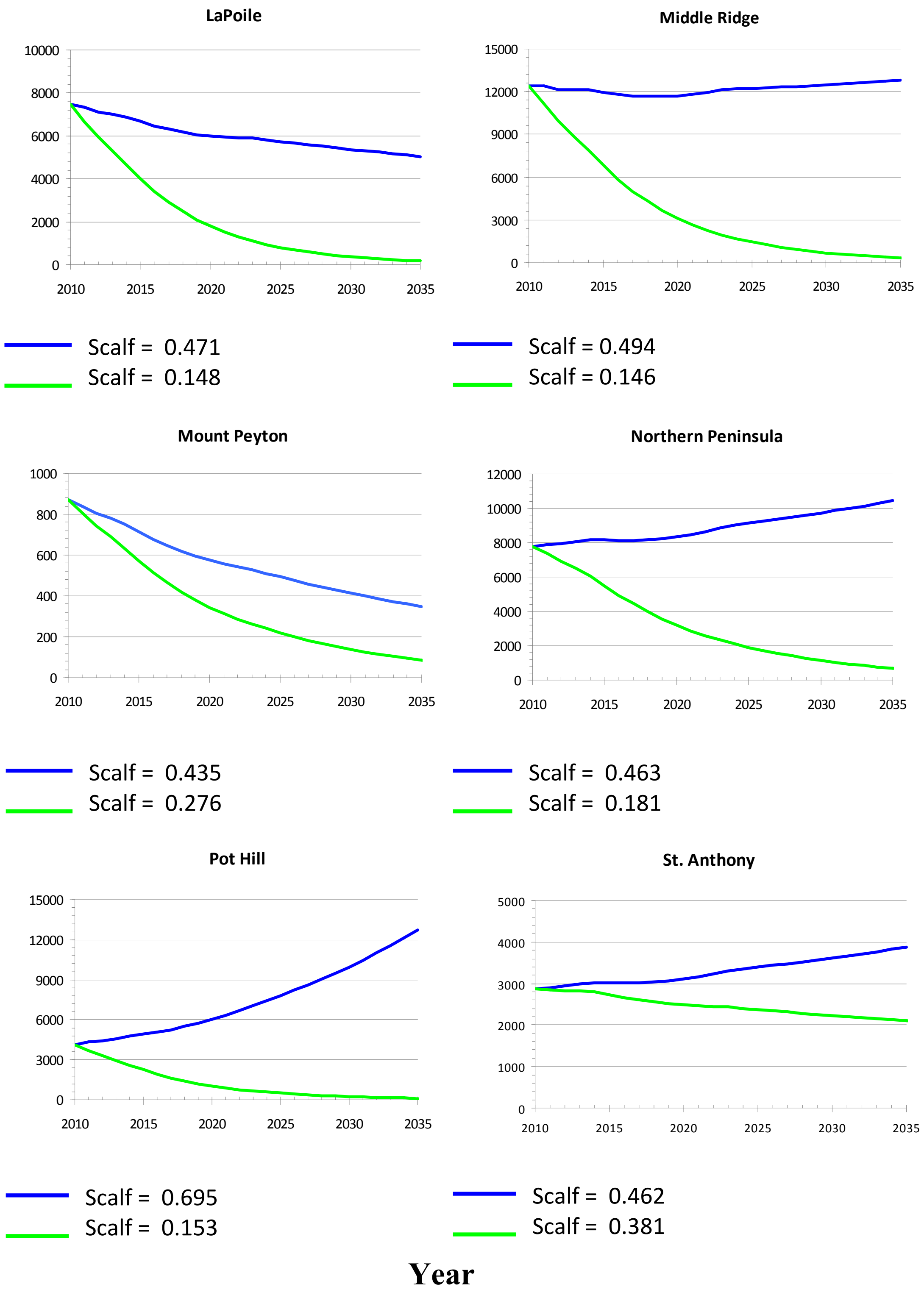


Figure 8: Projected population size for 12 insular Newfoundland woodland caribou herds based on Leslie-matrix population models. Two scenarios were considered: current conditions (green line) and improved calf survival (average 1980-1989 pre-decline rates; blue line).

Newfoundland Labrador
Environment and Conservation

Technical Bulletin No. 003

March 2012