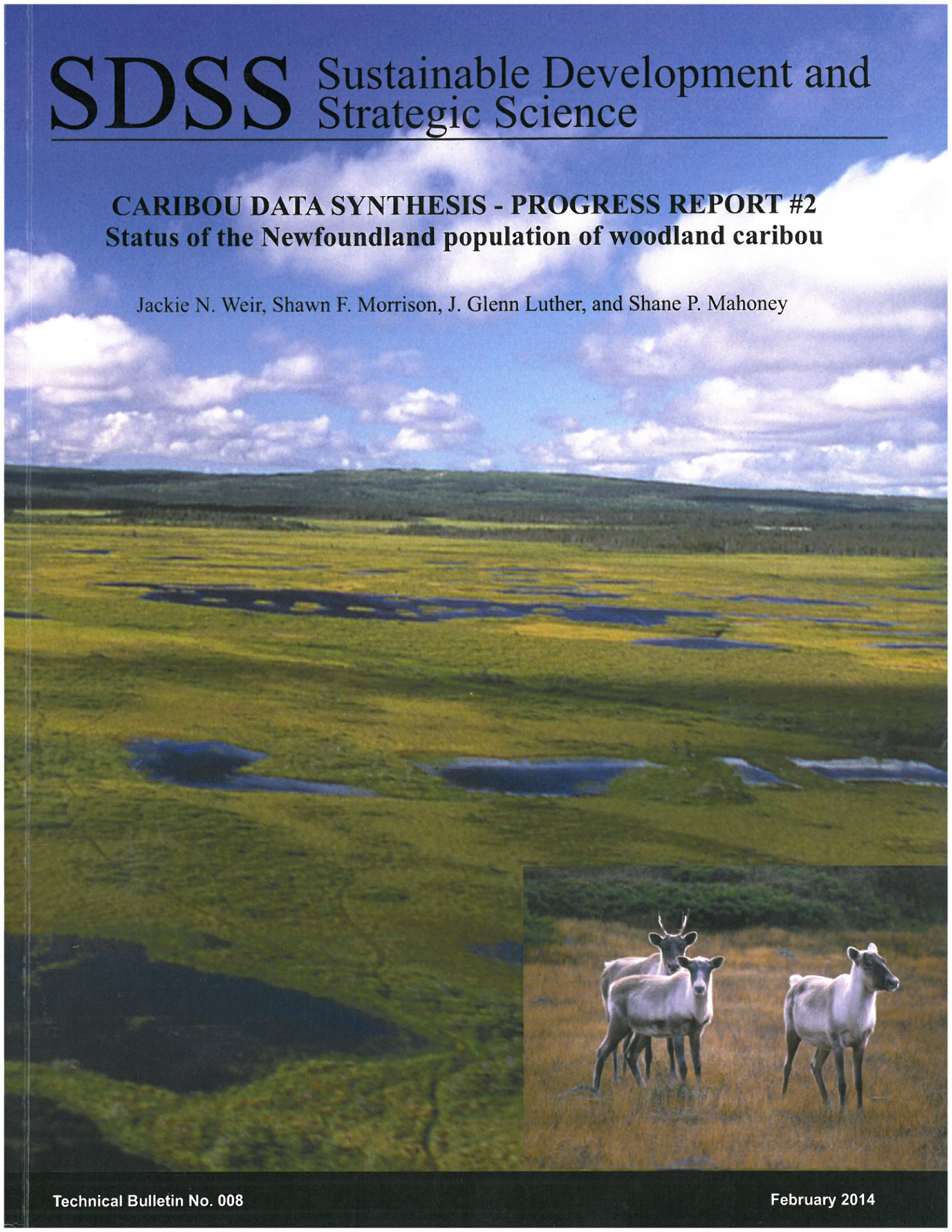


SDSS Sustainable Development and Strategic Science

CARIBOU DATA SYNTHESIS - PROGRESS REPORT #2 **Status of the Newfoundland population of woodland caribou**

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CARIBOU DATA SYNTHESIS – PROGRESS REPORT #2

Status of the Newfoundland population of woodland caribou

Technical Bulletin 008

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EXECUTIVE SUMMARY

After its long period of increase through the latter part of the twentieth century, the Newfoundland caribou commenced a rapid decline beginning in about 1996 and has continued to decline, through at a much reduced pace, ever since. In recent years calf survival has improved and, in combination with reduced hunting pressure, has led to a substantial improvement in herd prospects but insufficient as of yet to stabilize population decline. Positive growth cannot be expected until calf survival increases to 40-45%.

Predation accounts for the vast majority of calf mortality and high calf mortality is considered the most important proximate (immediate) cause of the population decline. Predation rates and the number of predator species increased over time with the arrival of the Eastern coyotes in the 1980's and the phenomenon of bald eagle predation on caribou calves first noted in the 1990's. Currently, black bear and coyote predation are the most predominant causes of calf death and the high rates of calf mortality have severely restricted herd recruitment rates. The decline in recruitment rate has slowed but at its current average level of ~ 11% recruitment remains insufficient to enable any population increase.

Hunting pressure, while conceded to be additive to natural mortality, is not believed to have initiated the caribou population decline. Nevertheless, until licenses were adjusted downwards, approximately 8 years after the population peaked in 1996, the proportion of the population harvested increased for several years after the decline began. These high rates of harvest (particularly for males) certainly exacerbated the rate of decline and the sex ratio distortion in the population.

Concurrent with the population decline, other demographic traits in addition to poor calf survival were noted: 1) the mean age of caribou increased from the 1980s to the early 2000s but declined thereafter; 2) the survival of older age classes (i.e. not calves) has remained high and constant throughout the period of study; 3) the percentage of males in the adult population, reduced to very low numbers by early 2000s, increased since 2006 likely because of changes in hunting quotas; 4) productivity declined since the 1970s and 1980s, but this reduction was not consistent across the island, nor were the declines significant enough to explain the synchronous and drastic decline in caribou numbers; 5) the birth weight of calves declined in the 1980s and 1990s, but increased since the early 2000s (heavier calves have a higher probability of survival); 6) adult body size (based on jawbones and antlers) decreased in the 1980s but both increased since the mid-2000s to pre-decline levels; 7) caribou born in the early 2000s experienced accelerated tooth wear when compared with caribou born in previous decades, possibly indicating that these caribou fed on rougher, low quality forage in poor quality habitats; 8) caribou food habits changed over the past 20 years showing reduced use of lichen, a preferred food, and increased use of moss and horsetails, both poor quality forage; and 9) caribou changed their habitat use patterns, site fidelity, and timing of migration as the population rose and fell. These changes together strongly suggest forage reduction, as a consequence of high numbers of caribou in the late 1990s, may have ultimately led to the population decline.

Thus, the best-supported hypothesis to explain the observed trends in the Newfoundland caribou population involves the influence of density dependence. Data on calf survival, reproductive

rates, recruitment, spatial use and habitat selection, and morphology all support this hypothesis. Specifically, while predation was the proximate (or immediate) cause of low calf survival, the ultimate (or underlying) cause of the decline was density-dependent forage limitation, induced by high caribou numbers, that led to smaller calves and increased vulnerability to predation.

The Newfoundland caribou population has exhibited a 66% decline in numbers. Based on trends in demography, morphology, space use and behaviour we are cautiously optimistic that a halt to the decline is likely. However, rates of calf mortality remain high, predation remains the predominate cause of death, and the island-wide population continues to decline, though at a much reduced rate. Predator manipulation experiments do suggest that improvements to calf survival can be achieved through intensive lethal removal of primary predators, but this management approach would appear feasible only in rather restricted areas.



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PURPOSE

The intent of this document is:

1. To provide an update on the analytical findings of the Caribou Data Synthesis.
2. To provide our current interpretation of long-term patterns in Newfoundland caribou demographics, morphology, and space use with particular emphasis on new data gathered since the initiation of the *Newfoundland Caribou Strategy* in 2008.
3. To provide our current understanding of the cause of the current population decline.

It is important to note that our research on caribou and their interaction with predators and habitat is ongoing. As such, figures, analyses, predictions, and interpretations are updated as new data become available.

INTRODUCTION

The Newfoundland and Labrador government has invested heavily in caribou research and monitoring on the island of Newfoundland. This investment was spurred by the value of caribou to citizens of the province and by the government's commitment to knowledge-based management of wildlife resources. While scientific surveys and studies (such as those evaluating the influence of various development activities on caribou) began in the 1950s and have expanded in recent years, no comprehensive organization and interpretation of these data existed prior to the mid-1990s.

The Caribou Data Synthesis was initiated in 1996 and involved a systematic compilation and evaluation of all data available for insular woodland caribou (Mahoney 2000). The Synthesis resulted in organized, error-checked, long-term data series on population abundance, demographics, distribution, movement, mortality, food habits, body condition, morphology, and hunter trends, extending back to the 1960s. Based on this information, Mahoney and Weir (2009) provided a comprehensive summary and interpretation of the population dynamics of Newfoundland caribou from 1960 through to 2007 culminating in several firm conclusions:

- The Newfoundland caribou population experienced rapid growth from the 1970s to the mid-1990s after which the population declined drastically (~60%) by the mid-2000s. The rapidity of the decline was evidenced in all herds.
- Calf recruitment to the population, based upon annual herd composition surveys, declined from 25% to 30% in the 1980s to less than 10% in most herds in the early 2000s.
- From 2003 to 2007, over 80% of radio-collared calves died during the first 6 months of life primarily because of predation.
- Calf production (birth rate) declined for some herds since the 1980s but the magnitude and direction of trends in productivity were not consistent across herds.

- Mean adult survival did not change throughout the pre-decline and decline phases (mean ~ 86%), but mean calf survival decreased to <10% in the early 2000s from a pre-decline mean of 66%.
- The proportion of adult males declined significantly beginning in the late 1980s, likely a result of Newfoundland's male-biased harvest regulations.
- As a result of low recruitment of new animals due to high calf mortality, the mean age of the adult caribou population increased significantly.
- Male antler size, calf birth weight, and adult female jawbone size declined significantly.
- Hunter success rate decreased from 80%–85% in the late 1980s to less than 60% in 2005 and resulted in harvest quota restrictions.
- Both recreational human disturbance and industrial development was intensively studied and confirm caribou avoidance responses, in some cases to negatively affect caribou vigour and, potentially, survival.
- Analysis of island-wide compilations of historical weather data and long-term climatic changes indicated that climate may be contributing to changes in caribou body size.

Collectively, these trends indicated a critical situation for Newfoundland caribou leaving no doubt that a protracted and steep decline in numbers was continuing but without a clear conclusion as to how this decrease in numbers was caused or how it might be reversed. Therefore, in 2008, the Government of Newfoundland and Labrador announced a 5-year, \$15.3 million research and management program to address this worsening problem. This *Newfoundland Caribou Strategy* furthered and significantly expanded ongoing caribou population monitoring and research, explicitly incorporated predator ecology research and population monitoring, and emphasized habitat mapping. The program included a controlled experimental approach to reducing predation pressure on calves to further determine the role of predators and the feasibility of direct predator management as a tool for caribou conservation. In addition, efforts continued to examine nonpredation factors of the population decline and incorporated data collection specifically to examine caribou–predator–habitat interactions. One additional emphasis was to ensure integration of the vast historical database (the Synthesis effort) with the new research findings of the Caribou Strategy itself.

The goal of this report is then to provide an update on the Caribou Data Synthesis effort by incorporating the data collected as part of the Caribou Strategy in an effort to update and refine our understanding of the population dynamics of Newfoundland caribou. We focused predominately on perceived changes in trends or indices since 2008 but interpret these data in the context of existing long-term demographic, morphological, and space-use trends. Furthermore, we also provide a more fulsome view of the significance and taxonomic relationships of Newfoundland caribou and provide our best understanding of the cause of the current population decline.

NEWFOUNDLAND CARIBOU DESCRIPTION AND SIGNIFICANCE

Taxonomy and Significance

The species *Rangifer tarandus* includes all caribou and reindeer populations across North America, Europe, and Asia. However, there is substantial variation in the morphology and behaviour within this species resulting in numerous efforts to classify various populations into a varying number of subspecies. A review of *R. tarandus* taxonomy was recently compiled to facilitate conservation efforts (COSEWIC 2011), and only a cursory overview is provided here.

Rangifer tarandus currently contains four recognized extant subspecies within North America based on skull measurements, pelage, antler shape, and hoof morphology (Banfield 1961): *R. t. caribou* (woodland caribou), *R. t. pearyi* (Peary caribou), *R. t. groenlandicus* (Greenland caribou), and *R. t. granti* (barren-ground caribou). However, additional research on morphology, behaviour, and genetic variation since Banfield's (1961) classification strongly suggests a revision of subspecies definitions is warranted (e.g., Courtois *et al.* 2003a; Cronin *et al.* 2005; Geist 2007; Couturier *et al.* 2010; COSEWIC 2011). To further complicate the taxonomic issue, *Rangifer* subspecies also have been classified according to “ecotype”, which represent populations that experience similar environmental conditions and have similar morphological, behavioural, and demographic characteristics (Banfield 1961; Courtois *et al.* 2003b; Cronin *et al.* 2005; Couturier *et al.* 2010).

All caribou herds in Newfoundland are considered woodland caribou (*R. t. caribou*). Prior to Banfield's (1961) revision, Newfoundland caribou were considered a distinct subspecies: *R. t. terraenovae*. Recently, Geist (2007) challenged Banfield's (1961) classification and argued that caribou in Newfoundland are “totally different” from other *R. t. caribou* populations and may constitute its own subspecies (Geist 1998). Newfoundland caribou have several haplotypes not found in other *Rangifer* populations (Cronin *et al.* 2005). Within Newfoundland, and with the exception of the Avalon herd, there is little evidence of genetic structure based on mtDNA evidence (Wilkerson 2010).

Based on a review of phylogenetics, genetic diversity, morphology, movements and behaviour, distribution, and discreteness, the Newfoundland population is considered a “Designatable Unit” (DU5) by COSEWIC (2011). A classification as a distinct DU means that the Newfoundland caribou represent a “...discrete and evolutionarily significant unit of the taxonomic species, where 'significant' means that the unit is important to the evolutionary legacy of the species as a whole and if lost would likely not be replaced through natural dispersion.” (COSEWIC 2009). The Newfoundland population has very likely evolved behavioural and morphological adaptations to facilitate their isolated existence on an island that has formed a significant barrier to immigration and emigration, as well as providing a complex landscape of considerable ecological variability. Thus, regardless of any current taxonomic categorization we may accept that the insular Newfoundland caribou represent a unique assemblage within this broader North American caribou lineage. Caribou also represent the only indigenous ungulate in Newfoundland and have enormous cultural, social, and economic importance to local residents and have long been a source of great interest to nonresident sportsmen and recreationists.

The Newfoundland population is separated from the nearest *Rangifer* population (in Labrador) by a 15 km span of ocean known as the Strait of Belle Isle. There are no documented movements of caribou across this water body in either direction. Therefore, one may conclude that the Newfoundland population is unlikely to be rescued by immigration from neighbouring *Rangifer* populations in Labrador.

Newfoundland Caribou Range, Dispersal, and Migration

Caribou are located throughout most of the island (Figure 1), although there is substantial seasonal variation in their distribution (e.g., calving versus noncalving periods; Figure 2). Newfoundland caribou use a variety of habitat types (forests, barrens, and wetlands; Figure 3) and most large herds move to and aggregate on specific calving grounds on an annual basis, though some smaller herds typically use a “dispersed” strategy for calving. While some herds do not migrate (Mahoney and Virgl 2003) in the true sense of the term, others move and disperse within more limited ranges (Mahoney and Schaefer 2002a).

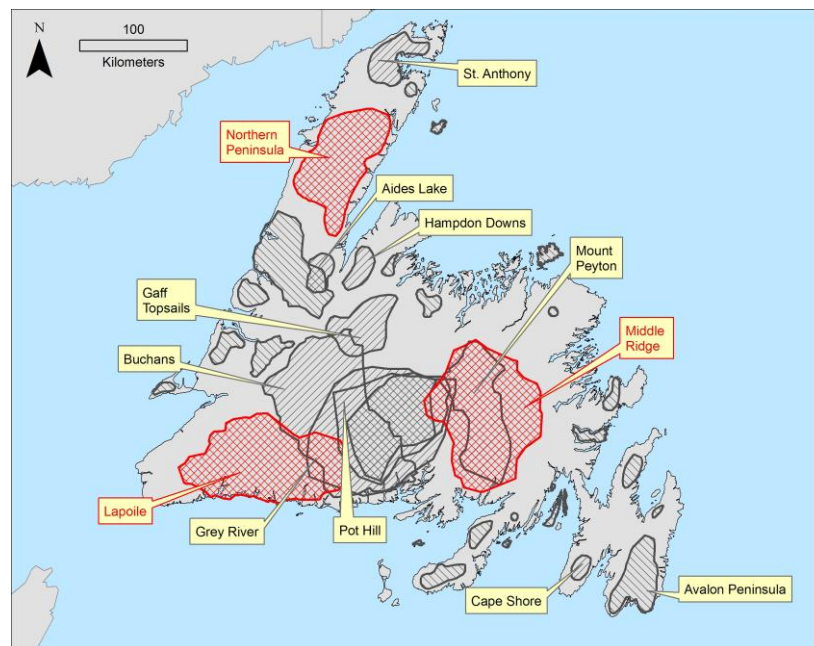


Figure 1: Annual ranges of Newfoundland woodland caribou herds. Individual herds were identified by their traditional calving grounds. Herd ranges identified in red were the main focus of the 2008–2013 Caribou Strategy.

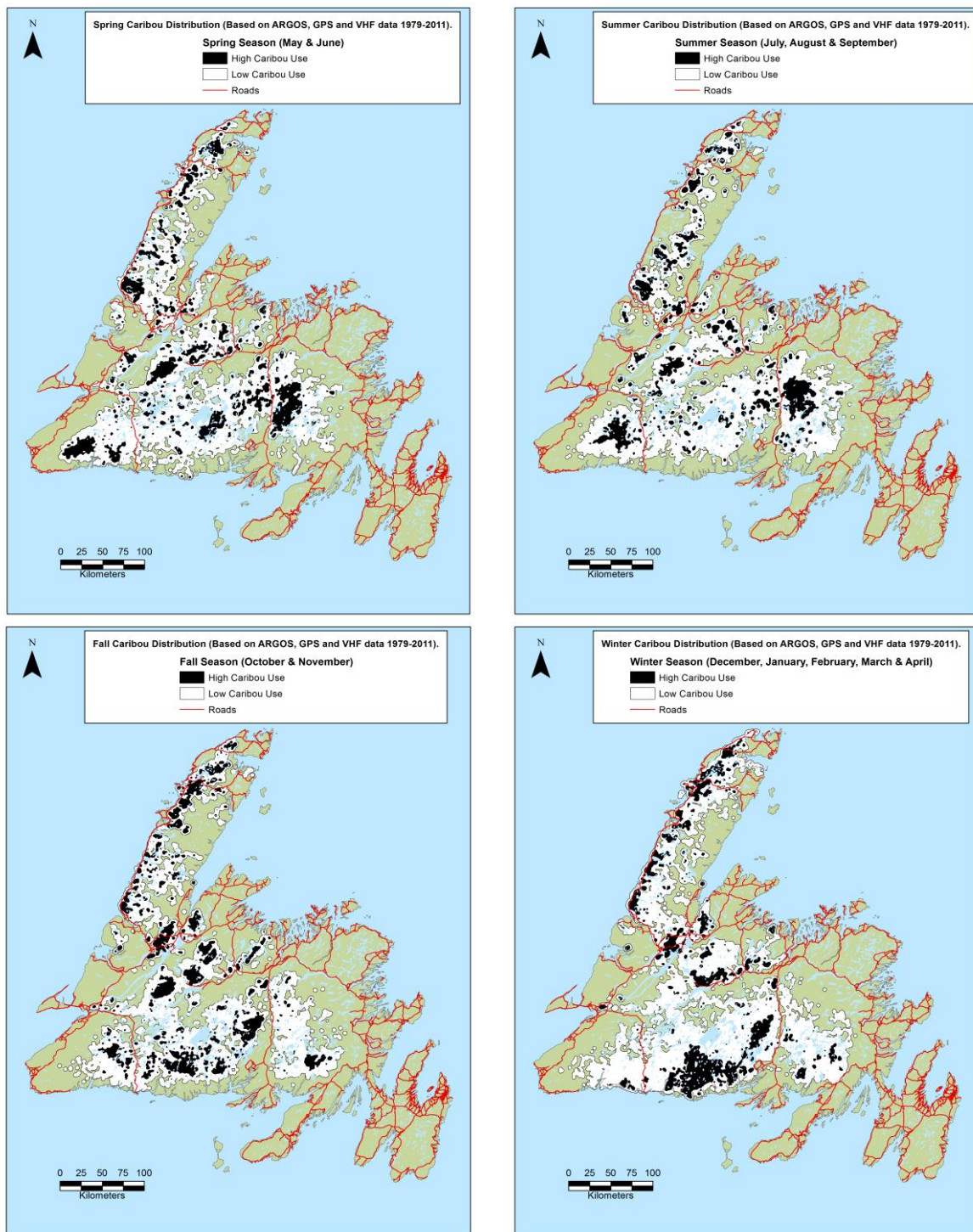


Figure 2: Seasonal distribution of collared woodland caribou in Newfoundland, 1979–2011. While involving most, not all herds contained collared individuals and thus population distribution is not fully described by these figures. Top left: spring distribution; top right: summer distribution; bottom left: fall distribution; and bottom right: winter distribution.



Figure 3: Typical Newfoundland caribou habitat.

Similar Species — Moose

Moose (*Alces alces*), the only other large ungulate in Newfoundland, is currently more common than caribou. Moose are not native to Newfoundland; the current population is descended from two introductions: (1) two moose (one male and one female) transplanted in 1878 and (2) four individuals (two males and two females) transplanted in 1904 (Pimlott 1953; Broders *et al.* 1999). Since 1904, the Newfoundland moose population grew to approximately 150,000 individuals by 1997 (Broders *et al.* 1999; McLaren *et al.* 2004) and declined to about 125,000 individuals by 2004 (McLaren *et al.* 2004); the 2012 population estimate was approximately 114,000 individuals (NL Department of Environment and Conservation).

Moose currently occupy all ecoregions in Newfoundland and generally select forested areas as primary habitat (McLaren *et al.* 2004). While caribou in Newfoundland use a variety of habitat types (forests, barrens, and wetlands; Figure 3), they are far less dependent upon forested landscapes and occupy mostly open barrens, bogs, and fens. Moose and caribou do not appear to compete for resources in Newfoundland (McLaren *et al.* 2004).

POPULATION SIZE AND TRENDS

Abundance

Population abundance was assessed on a herd basis across Newfoundland intermittently from 1960 to 2013, following systematic strip, random block, or mark–recapture census procedures (Mahoney *et al.* 1998; Mahoney 2000). With regard to the latter method, a comparative evaluation (Mahoney *et al.* 1998) indicated no substantial differences in estimates among fixed-wing, helicopter, and ground resighting surveys. Changes in population growth determined from these aerial surveys were consistent with estimates from survival–recruitment schedules (Mahoney and Schaefer 2002b; SDSS, unpublished data), providing support for the population trajectories presented here.

The Newfoundland caribou population abundance was based on the pooled estimates for individual herds. However, abundance estimates were not available for all years for most herds so estimates for missing years were interpolated (Mahoney *et al.* 2011). Population viability analysis (PVA; Vortex v. 9.99b; Lacy 1993) was used to estimate abundance for herds not recently surveyed. Census estimates did not control for the geographic area occupied by a herd, and therefore, estimates of true density (animals per area) were not presented; consequently, the text refers exclusively to caribou abundance when referencing caribou numbers.

The Newfoundland population of has experienced both a dramatic increase and decline since the 1960s (Figure 4). Caribou abundance was relatively low throughout the 1960s, slowly increased in the 1970s and then more rapidly in the 1980s before peaking in the mid-1990s. Notably, between 1975 and 1996, island-wide caribou abundance quadrupled (from ~23,000 to 94,000 individuals). Following the peak of 94,000 animals in 1996, the caribou population declined rapidly to 32,000 by 2013. This represents a 66% decline in 17 years. Similar patterns were observed for most individual herds.

While the Newfoundland caribou population continues to decline, the rate of decline has slowed in recent years. From 2000 to 2006, the population declined at an average of 9% per annum. Since 2007 the rate has slowed to an average of 5% per annum. The reduction in the rate of decline is likely due to slight improvements in observed calf survival since 2007 (see below) and to the reduction of hunting pressure on adult caribou since 2004 (see below).

The rapidity and magnitude of the recent decline is of concern from a sustainable management and conservation perspective, but is not unique in the population history of Newfoundland caribou. We reconstructed population trends for Newfoundland caribou since the late 1880s using written sources for the bulk of the historical (pre-1950s) data including (1) published material by early explorers, hunters, and travellers in the province, (2) scientific articles, and (3) Government of Newfoundland and Labrador documents such as the Annual Reports from the Game and Inland Fisheries Board and the Department of Natural Resources. Records indicated there were large numbers of caribou in Newfoundland in the late 1800s (probably in excess of 100,000 animals) and these numbers declined dramatically around the turn of the last century. Furthermore, anecdotal evidence suggests that the dramatic decline was preceded by a reduction

in animal stature (body weight and antler size). Caribou populations remained low until the 1960s despite the disappearance of the wolf, the absence of coyotes, and closed hunting seasons.

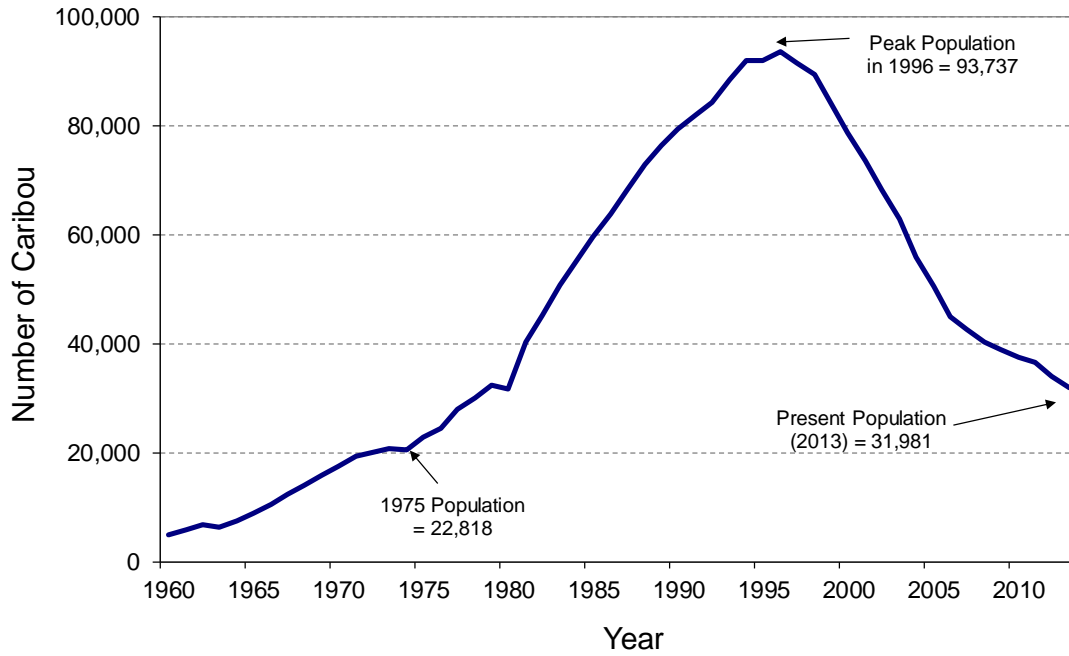


Figure 4: Estimated abundance of the Newfoundland population of woodland caribou, 1960–2013. Estimates were derived from aerial surveys across multiple herds and PVA. Surveys were not conducted on all herds annually and intervening years were interpolated.



Age

An essential component of any ungulate management program is monitoring population age structure, which strongly influences changes in population size (Fiesta-Bianchet *et al.* 2003; Gordon *et al.* 2004). Further, density-dependent and density-independent effects can vary substantially across age classes where variation in resource abundance or stochastic events such as inclement weather (Gaillard *et al.* 1998, 2000; Gordon *et al.* 2004) can differentially influence a population dependent upon its age structure at any given point in time.

We investigated trends in the age structure of Newfoundland caribou by analyzing tooth cementum age. Caribou hunters voluntarily submitted jawbones from harvested caribou. Teeth were removed from the jawbones and used to estimate the age of the individual through standard tooth cementum analysis (Matson’s Laboratory LLC, Milltown, Mont.). The mean age of caribou across Newfoundland steadily increased from 1980 to the mid-2000s, and this pattern holds true for both male and female caribou (Figure 5). The average age of female caribou increased from 3.8 years in 1980 to about 6.9 years by 2005. The average age of males similarly increased, however, at a slower rate than females, from approximately 4.2 years in 1980 to 6.0 years by 2003. The mean age of males and females then declined and by 2009 the mean age approximated the mean age of harvested caribou in the 1990s (Figure 5).

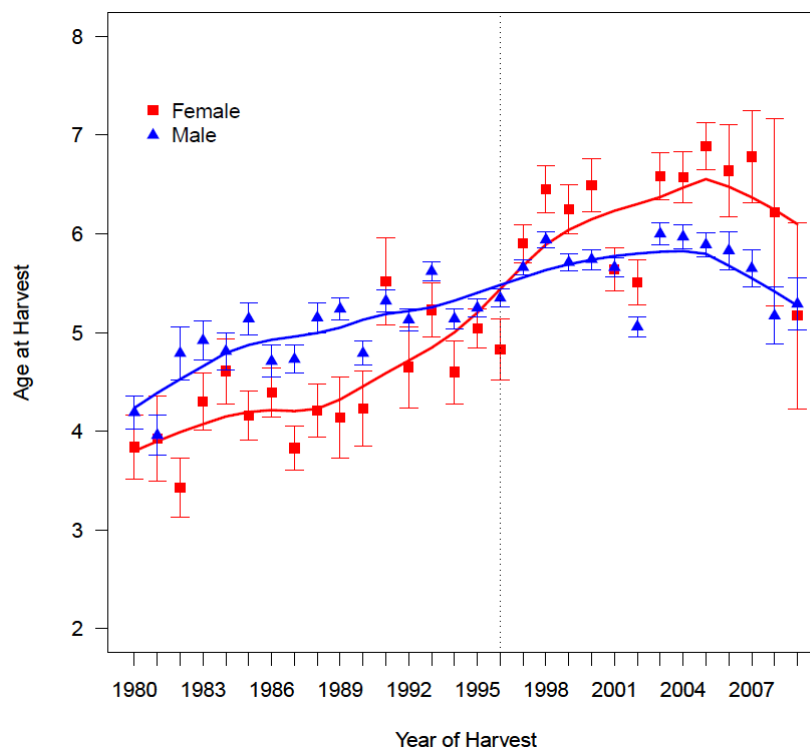


Figure 5: Age (mean \pm SE) of harvested Newfoundland caribou, 1980–2009. Solid lines are loess smoothing curves used to illustrate trends. The vertical dotted line indicates when population abundance was at its peak.

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. To test this hypothesis, we constructed a Leslie matrix population model that assessed the effect of this “Demographic Wave” on future population abundance (Morrison *et al.* 2012). Based on the results of the matrix models (Figure 6), we concluded that the “Demographic Wave” had largely passed through the population by 2010 or 2011. Therefore, population decline should not be expected to be further exacerbated by a rapid drop in adult female survival (Morrison *et al.* 2012).

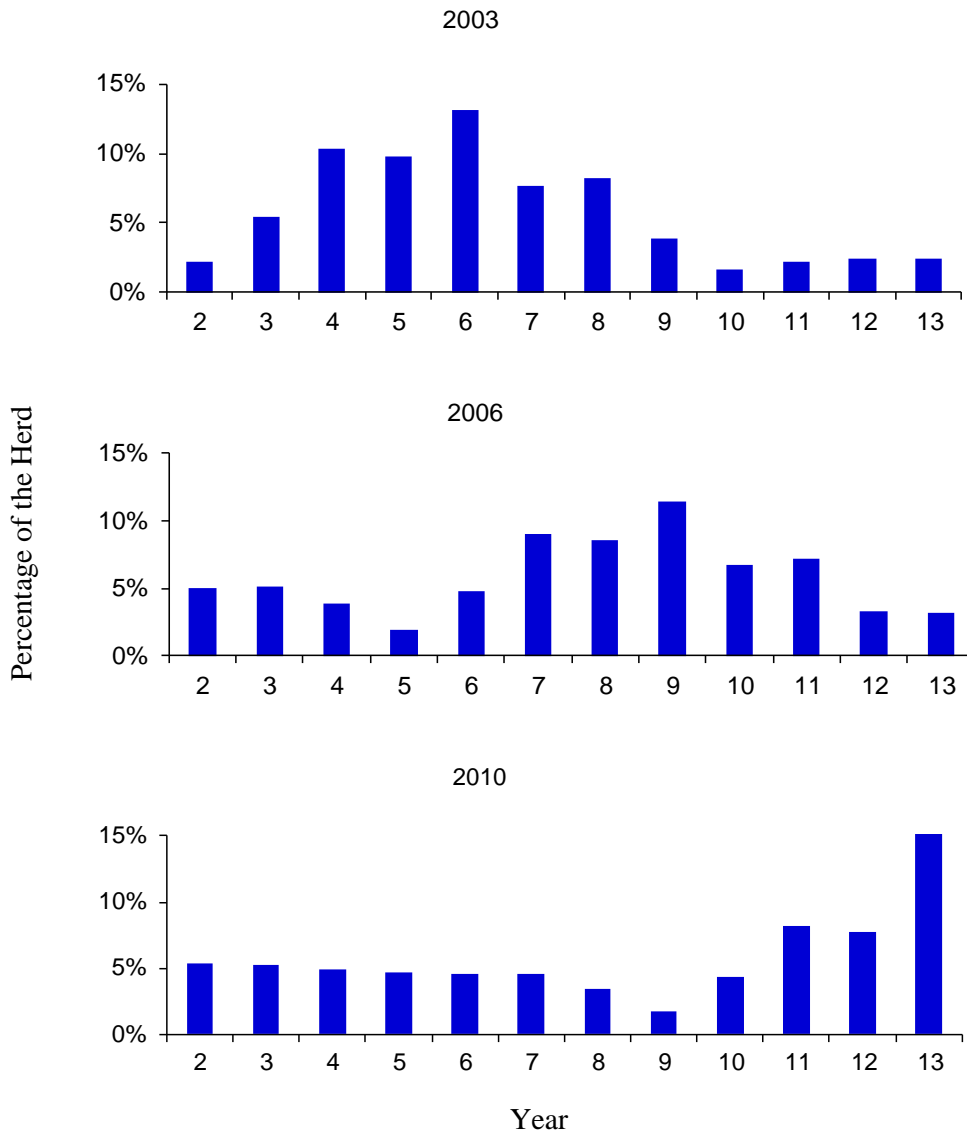


Figure 6: Age structure of caribou 2+ years old based on a Leslie matrix model parameterized with Newfoundland caribou data from 2003 to 2005 (Morrison *et al.* 2012). The distribution shows that the “Demographic Wave” had largely passed through the population by 2010.

Survival and Cause of Death

Survival of caribou is a key component of population growth and decline. If survival is too low to adequately counter-balance death or emigration then population declines are inevitable. Conversely, high rates of survival coupled with high rates of reproduction can produce rapid population growth. As with most large mammals, the survival of caribou varies according to age with older animals having higher (and less variable) annual rates of survival than juveniles (Caughley 1966, 1977; Gaillard *et al.* 1998).



For this reason, significant research effort has been directed towards monitoring the survival and cause-specific mortality of Newfoundland caribou. Specifically, calves and adult caribou (from multiple herds) were live-captured, collared (VHF, GPS, or Argos), and monitored from 1979 to 1997 and 2003 to 2012. Collared calves that survived beyond the first year of life were monitored for the duration of the collar-life (up to 3 years) and provided sex-specific estimates of survival for yearling and 2-year-old caribou. A standardized field investigation of the

caribou remains and the mortality site was conducted, when possible, to determine the cause of death (see detail in Mahoney *et al.* 1990; Trindade *et al.* 2011; Lewis and Mahoney 2014).

Adult caribou were captured using a net gun or darted and chemically immobilized. Collars were fitted and standard body measurements were taken. The monitoring schedule of adults varied depending on season, budget, and research questions. For this reason, data on cause of death were not always available. Neonate calves were spotted from helicopters and captured (at generally less than 5 days of age in late May – early June) without the use of drugs or nets. An expandable VHF radio-collar and ear-tags were attached and standard body measurements were taken. Calves were released immediately after processing and were observed to ensure they had rebonded with their mothers. Generally, calves were monitored daily during the first week postcapture, every 2–4 days for the following 5–6 weeks, and then every 5–10 days until August. Monitoring was typically conducted on a bi-weekly or monthly basis after August (Mahoney *et al.* 1990; Trindade *et al.* 2011; Lewis and Mahoney 2014).

We estimated annual rates of survival for all cohorts using the Heisey–Fuller method (Heisey and Fuller 1985). Because rates of calf mortality were not constant throughout the year, we also estimated calf survival during the first 6 months of life (birth to fall) using nest survival models in Program MARK (White and Burnham 1999). We compared trends in calf survival based on radio-telemetry with trends in calf survival estimated from herd composition data.

The annual survival of adults, 2-year-olds, and yearlings was relatively high and constant from 1979 to 2012, while annual calf survival declined dramatically over this time period (Figure 7A–7D). Most calf deaths occurred in the first 8–12 weeks of life (Mahoney and Weir 2009; Trindade *et al.* 2011; Lewis and Mahoney 2014). Overwinter survival of calves was high and generally comparable with that of adults, yearlings, and 2-year-olds (Mahoney and Weir 2009; Trindade *et al.* 2011; Lewis and Mahoney 2014) indicating that survival to 6 months of age was the major impediment to calf survival.

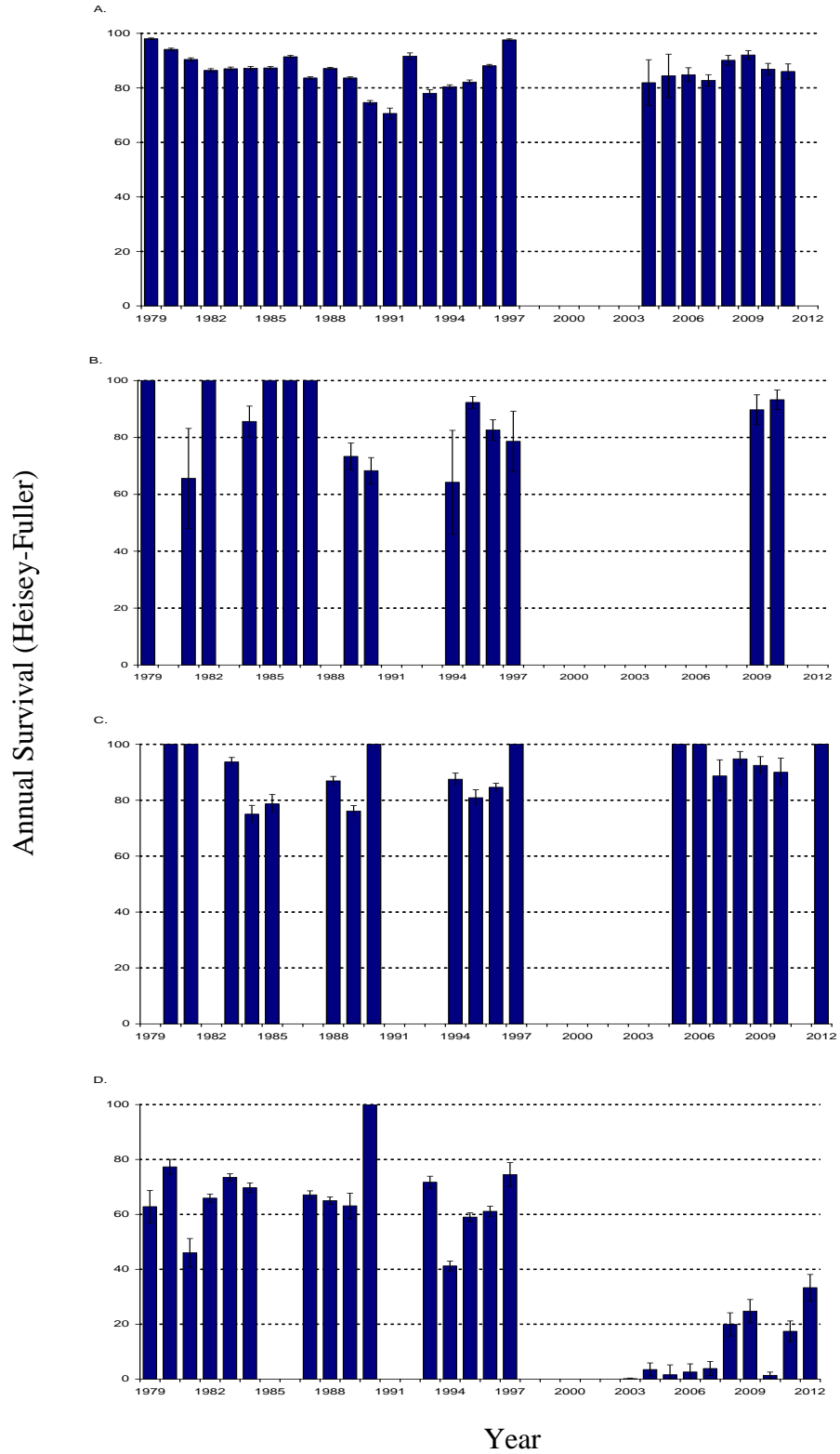


Figure 7: Annual survival (Heisey–Fuller) estimates for A) adult females, B) 2-year-olds, C) yearlings, and D) calves based on radio-telemetry data, 1979–2012. Sample sizes (number of years, number of individuals per year, and individual herds) varied over time.

Although calf survival estimates derived from radio-telemetry were generally higher than those based on herd composition surveys, the pattern of dramatic decline observed in the early 2000s was consistent across the two independent estimation methods (Figure 8). Calf survival in the 1980s and 1990s ranged from 41% to 84% for the first 6 months of life before declining to 7% in 2003 (MARK estimates; Figure 8). Calf survival has increased since 2007 (Figure 7D and Figure 8) and is approaching rates required for population stability (40%–45%; Morrison *et al.* 2012; Randell *et al.* 2012). Survival estimates based on herd composition surveys were more conservative and do not support the magnitude of increase shown by telemetry data (Figure 8). The discrepancy between the two estimation methods requires further examination; caution should be taken when using current rates of calf survival as an indication of population recovery.

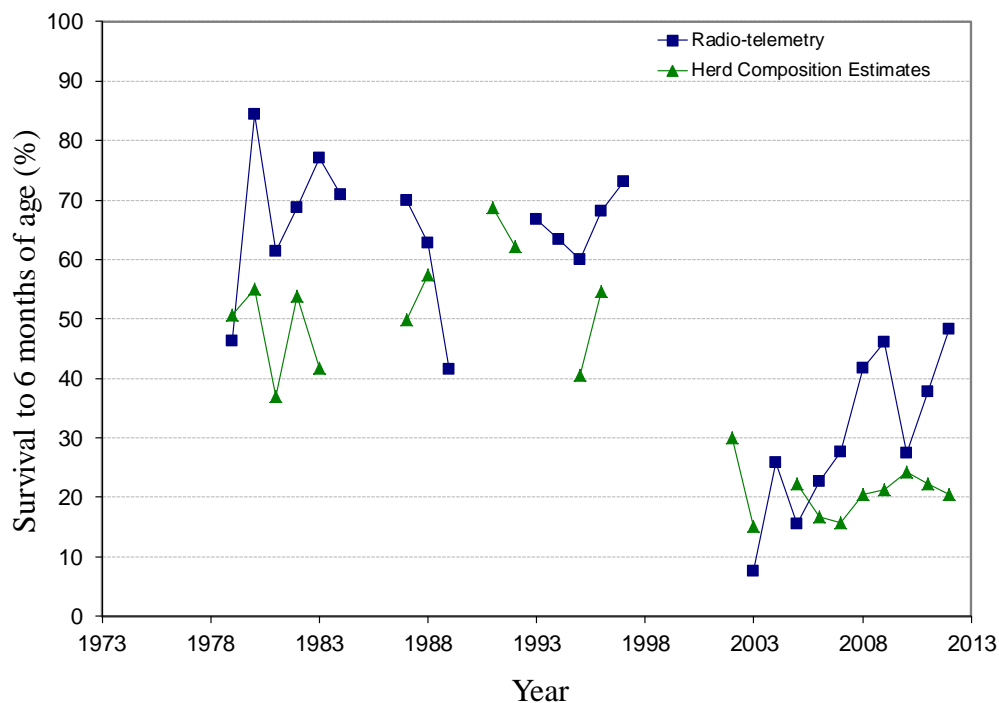


Figure 8: Survival of Newfoundland caribou calves (1979–2012) based on herd composition surveys (green) and radio-telemetry data (blue). Survival from herd composition surveys was calculated as the ratio of calves per 100 adult females in fall and productivity in the previous spring.

Because the survival of adults, 2-year-olds, and yearlings was relatively high and constant over time (Figure 7) and because information on cause of death for these cohorts was limited, we focused on cause of death for calves only in this report (see Lewis and Mahoney 2014 for fate of older age classes).

During both time periods, predation was the dominant source of mortality for calves; unknown and other causes of death represented relatively small amounts of calf mortality (Figure 9). However, the percentage of mortalities due to predation and the number and diversity of predator species increased over time (Figure 9). From 1979 to 1997, predation accounted for 59.2% of all calf deaths ($n = 147$). Of those calves killed by predators, black bear (69.0% of all predation-related deaths), lynx (21.8%), fox (2.3%), bald eagle (1.1%), coyote (1.1%), and unknown

predators (4.7%) were the responsible species. From 2003 to 2012, predation increased and accounted for 88.7% of all deaths ($n = 444$), the diversity of predator species increased, and the species-specific percentages were markedly different from the 1979–1997 period. In particular, the pattern changed from being dominated by black bears to being more evenly split between coyotes and black bears (35.0% and 34.0% of all predation-related deaths, respectively), and predation by lynx (5.5%), eagles (4.6%), and unknown predators (20.9%) increased relative to the 1979-1997 period (Figure 9).

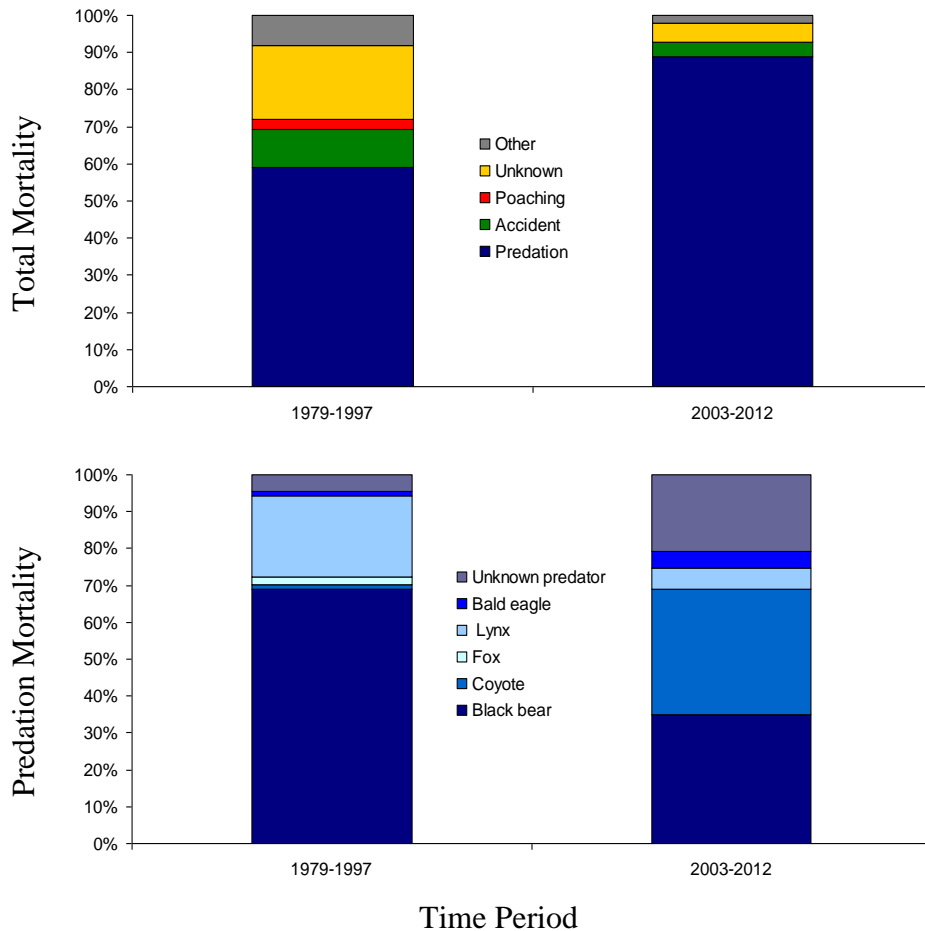


Figure 9: Causes of calf mortality (top) and causes of predation mortality (bottom) in Newfoundland caribou across two time periods. Sample sizes (number of years, number of individuals per year, and individual herds monitored) varied over time.

Sex and Age Composition

Herd composition surveys provide information on the sex and age percentages in a herd and are fundamental for the management of caribou. Demographic parameters, such as recruitment, productivity, and adult sex ratios, provide insight into trends that may be occurring in a population or herd and add important context to the numerical changes that may be observed (e.g., population increase or decline). Therefore, herd composition surveys are a critical

component of caribou population monitoring because the data provided assists managers in identifying issues that may need to be addressed through proscriptive actions.

Composition surveys were generally conducted from the ground or utilizing aircrafts during three key time periods throughout the year (spring calving, fall, and late winter). From data collected on age and sex composition, it was possible to estimate vital rates such as recruitment (the number of calves per 100 adult females, the percentage of the herd that were calves), adult sex ratio (the percentage of the adult population represented by stags), productivity (the proportion of female caribou that gave birth to a calf), and calf survival. Annual estimates for the Newfoundland population were calculated as the mean of estimates available for individual herds.

Recruitment

The number of calves in the Newfoundland caribou population during fall declined between 1966 and 2012 (Figure 10). The decline was most apparent following the mid-1990s and coincided with the decline in calf survival as measured by telemetry data (Figure 7 and Figure 8) and the overall population decline (Figure 4). In the years prior to the decline (1966–1997), recruitment averaged 40.8 calves per 100 adult females; after 1997 the average ratio dropped to 16.3 calves per 100 females (Figure 10). This pattern is also apparent in recruitment data collected during the winter and across individual herds (SDSS, unpublished data). Data since 2004 (Figure 10) suggest the decline in recruitment rate has halted, but recruitment has remained low.

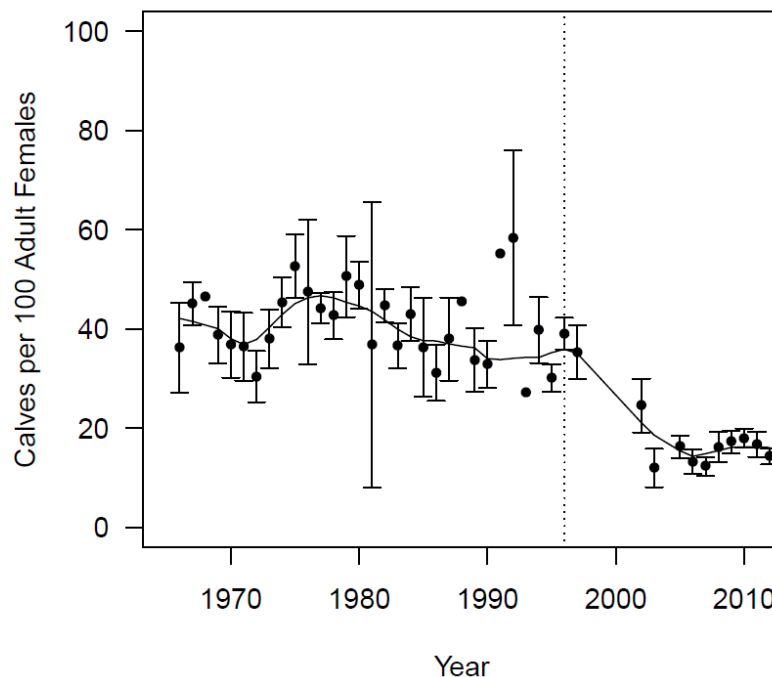


Figure 10: Recruitment (# calves / 100 adult females, mean \pm SE) of Newfoundland caribou calves during fall, 1966–2012. The solid line is a loess smoothing curve used to illustrate trend. Each annual estimate was the mean of estimates for individual herds. The vertical dotted line indicates when population abundance was at its peak.

Adult Sex Ratio

The adult sex ratio of caribou across Newfoundland was skewed towards females (Figure 11). In general, the percentage of males in the adult population has rarely exceeded 40% since data collection began in the 1960s. The fall sex ratio has steadily declined from 35.5% in the 1970s to 23.1% in the years following 2000, suggesting that adult male survival has decreased relative to adult females (Figure 11). This decline was likely a consequence of the high rate of male harvest that occurred for several years after the population decline began (see below). Since 2006, the decline in sex ratio appears to have ameliorated and may be reversing, possibly because of a change in quota allocation (reduced total allocations and reduced proportion of male only licences relative to either sex licence).

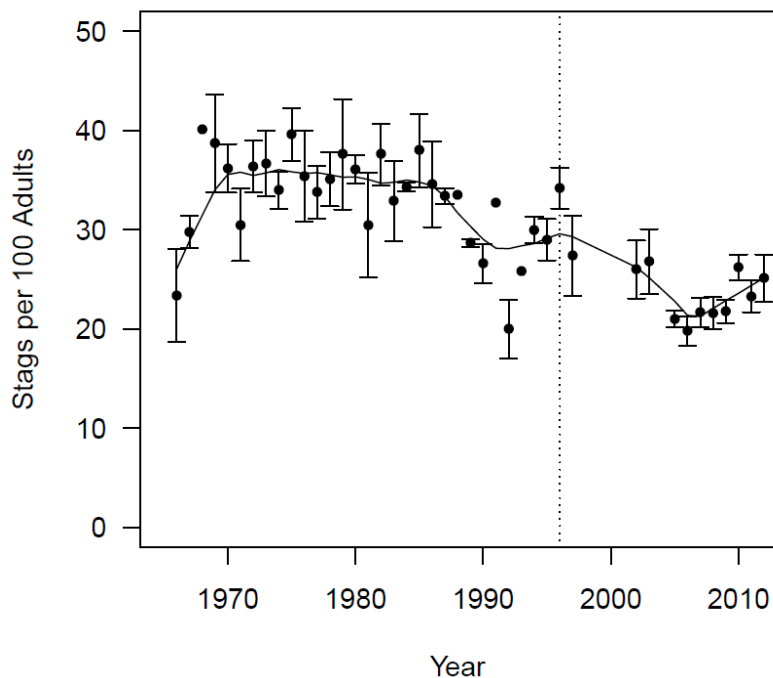


Figure 11: Adult sex ratio (# of stags / 100 adult caribou, mean \pm SE) of Newfoundland caribou during fall, 1966–2012. The solid line is a loess smoothing curve used to illustrate trend. Each annual estimate was the mean of estimates for individual herds. The vertical dotted line indicates when population abundance was at its peak.

Productivity



Productivity is the proportion of parous female caribou (females that produced a calf) in the population and indicates the reproductive output of the population. The productivity of the Newfoundland population ranged between 70% and 100% from 1960 to 2012, with most years falling between 70% and 90% (Figure 12). The data showed slight decline over time (slope = -0.20 ± 0.08 , $F_{1,31} = 6.80$, $P = 0.014$) but no dramatic changes such as those observed for abundance (Figure 4), age (Figure 5),

calf survival (Figure 8), recruitment (Figure 10), and adult sex ratios (Figure 11).

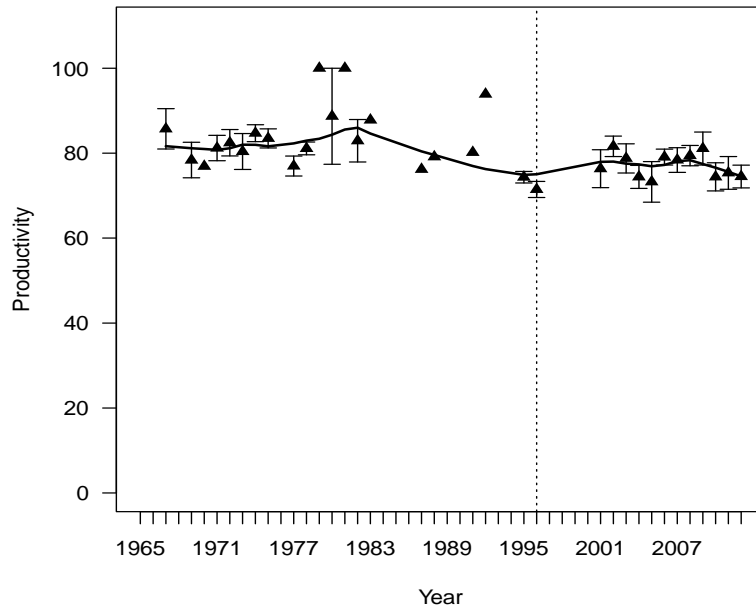


Figure 12: Productivity (mean \pm SE) of Newfoundland caribou in June, 1966-2012. The solid line is a loess smoothing curve used to illustrate trend. Each annual productivity estimate was the mean of estimates for individual herds. The vertical dotted line indicates when population abundance was at its peak.

Morphology: Calf Weight, Jawbones, Antlers, and Tooth Wear

One method to assess the health or condition of caribou is to measure morphological indices such as body size and weight. Not only can individuals be compared within a population, but the health of animals in a population can be monitored over time (Veeroja *et al.* 2008). Any changes in body size or stature may reflect an improvement or decline in the condition of the herd, which may reflect changes in competition for food, predation pressure, or environmental conditions (Skogland 1983; Veeroja *et al.* 2008; Mahoney *et al.* 2011).

Calf Weight



Calf weight at birth correlates with calf survival, with heavier calves typically having higher survival rates than lighter calves (Bergerud *et al.* 2008; Lewis and Mahoney 2014), presumably because heavier calves are more robust and therefore better able to avoid being captured and killed and/or are more resilient with respect to the influence of weather and disease.

Weights in Newfoundland were collected from neonatal calves (usually captured within 5 days of birth) as part of a larger study of caribou population dynamics. Overall, calf weight declined from the 1970s to the 1990s before increasing after 2003 (Figure 13). Female weight was typically the same or lower

than male weight. When statistically analyzed according to sex and decade of birth (i.e., a two-way ANOVA), calf weight varied by sex ($F_{1,1300} = 24.2, P < 0.001$) and decade ($F_{3,1300} = 10.1, P < 0.001$). The sex–decade interaction was not significant ($F_{3,1300} = 0.19, P = 0.902$), suggesting sexes responded in a similar manner through time.

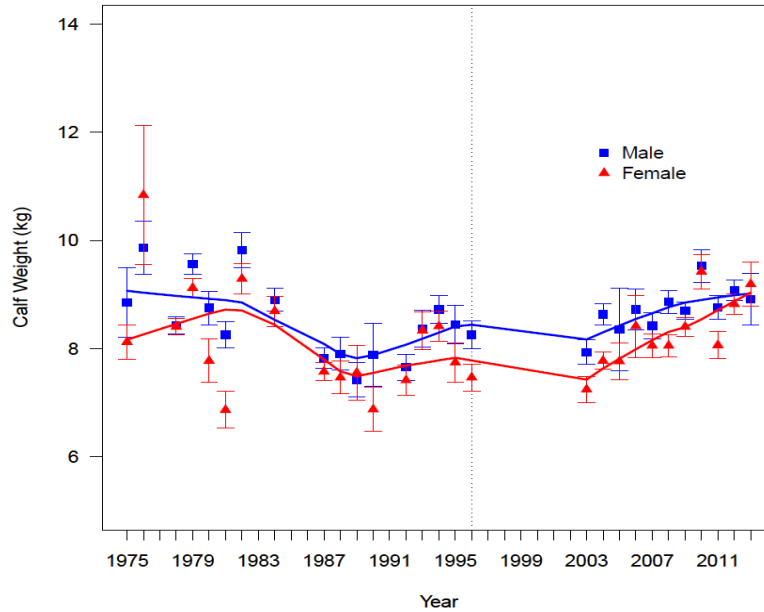


Figure 13: Male (blue) and female (red) calf weight (mean ± SE) at capture, 1975–2013. The solid line is a loess smoothing curve used to illustrate trend. The vertical dotted line indicates when population abundance was at its peak.

Jawbones and Antlers

Skeletal measurements can be used as indicators of overall body size for whole animals (Peters 1983) when whole animals are unavailable. Furthermore, because skeletal measurements are resistant to seasonal variability in resource availability, they are useful for examining long-term trends in body size (Høye and Forchhammer 2006; Mahoney *et al.* 2011). Jawbone size, for example, is strongly correlated with body mass (Veeroja *et al.* 2008) and is frequently used as an estimate of condition for ungulates (e.g., Høye and Forchhammer 2006).



Photo credit: NL Wildlife Division

Jawbones from harvested caribou were measured for total mandible length, molar row length, and diastema width (Banfield 1961; Bergerud 1964) and antlers for the number of points. The age of each caribou was determined by standard tooth cementum analysis. Annual jawbone size was statistically corrected for age by using the residuals from a Gompertz growth curve model fitted to the data for each sex independently.

Jawbone size varied substantially from 1980 to 2009 for both male and female caribou (Figure 14). For females, jawbone length increased in the late 1980s before rapidly declining into the

1990s. Following the initiation of the population decline in 1996, female jawbones appear to increase in size and returned to levels previously observed in the late 1980s (Figure 14). For males, jawbone size was relatively constant from 1980 to approximately 2000 at which point they increased in size similar to the trend observed for females (Figure 14).

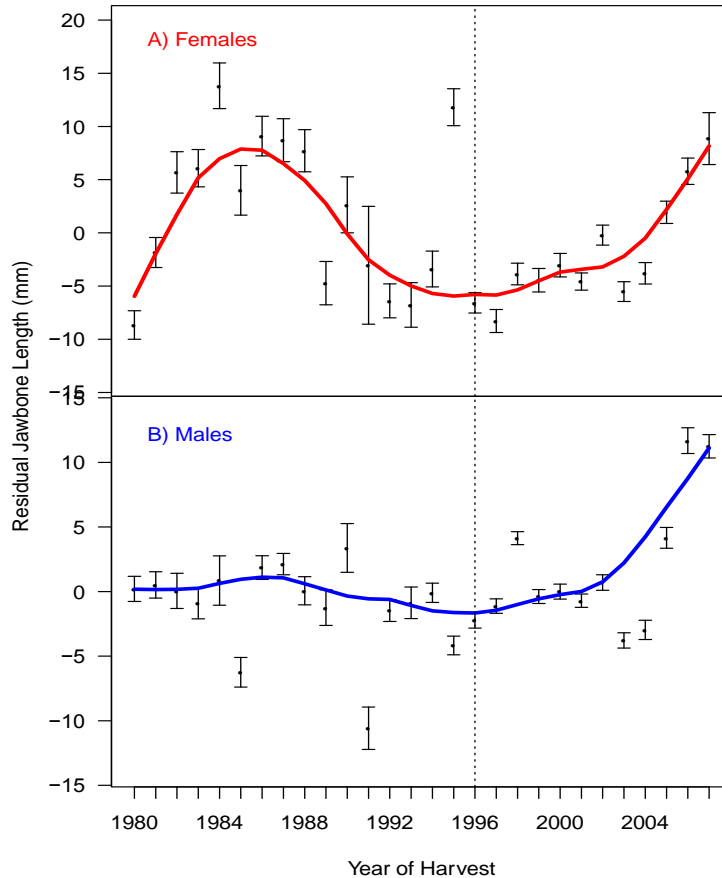


Figure 14: Jawbone size (mean residual \pm SE) for A) female and B) male Newfoundland caribou, 1980–2007, based on residuals from Gompertz growth equations (analysis not shown). Loess smoothing curves are provided to indicate trend in residuals. The vertical dotted line indicates when population abundance was at its peak.

Similar to jawbone size, male antler size (measured as the number of antler points for males 5+ years of age) varied through time (Figure 15). The number of antler points decreased steadily from 1986 to 2003. Similar to the trends observed in jawbones, the number of antler points began increasing in 2003.

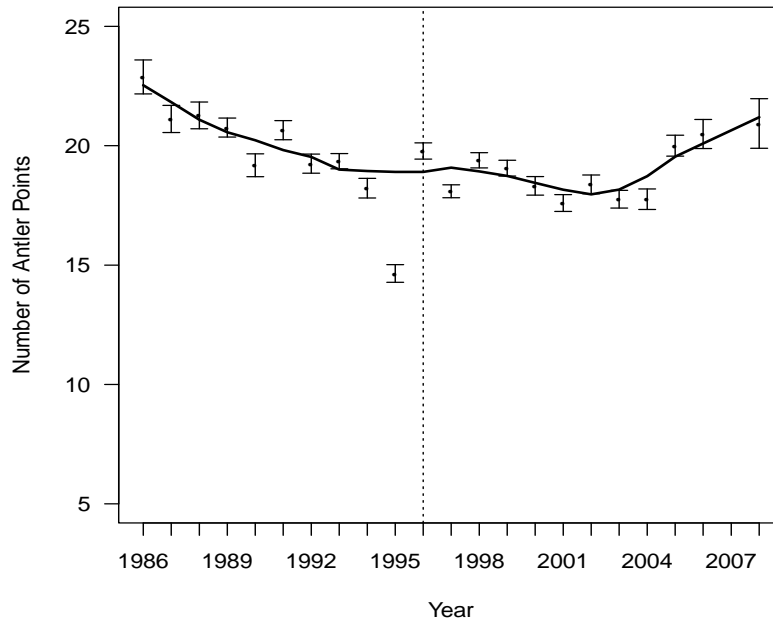


Figure 15: Number of antler points (\pm SE) on adult (5+ years) male caribou harvested in Newfoundland, 1986–2008. A loess smoothing curve was used to indicate trend. The vertical dotted line indicates when population abundance was at its peak.

Tooth Wear

Examination of tooth wear pattern in ungulate jawbones can provide information on the nutritional status of ungulates and the availability of high quality forage (Nussey et al. 2007). Individuals living in poor quality habitats may experience accelerated rates of tooth wear because they consume, large quantities of rougher, low quality forage (Kojola *et al.* 1998). Furthermore, high population densities may lead to a rapid depletion of good quality forage or lead to forage being cropped close to the ground, and feeding individuals may ingest more soil particles, leading to accelerated tooth wear (Skogland 1988; Loe *et al.* 2003).

Caribou jawbones were measured for precise age and tooth wear. Patterns of tooth wear were classified into age categories and provided a second assessment of caribou age. We used a one-way ANOVA design to compare the actual age of jawbones (i.e., cementum age) between decades of birth for each tooth wear assessment class (i.e., 2, 3, 4–6, 7–9, and 10+ years). For brevity, only results for the 4–6 year wear class are presented here. Tooth wear class and cementum age corresponded well in the 1970s, 1980s, and 1990s, but not for caribou born after 2000 (Figure 16). That is, prior to the 2000s, caribou identified as 4–6 years old based on tooth wear were confirmed to be correctly aged based on cementum analysis. However, the mean tooth cementum age of caribou born between 2000 and 2005 was significantly lower than the age classification identified by tooth wear (i.e., their teeth were worn more than expected based on cementum age). This pattern indicated caribou teeth were wearing more quickly than observed in previous decades — a potential indicator of poor forage quality. Similar patterns were observed for caribou assigned to other wear age classes (Luther and Smith 2010).

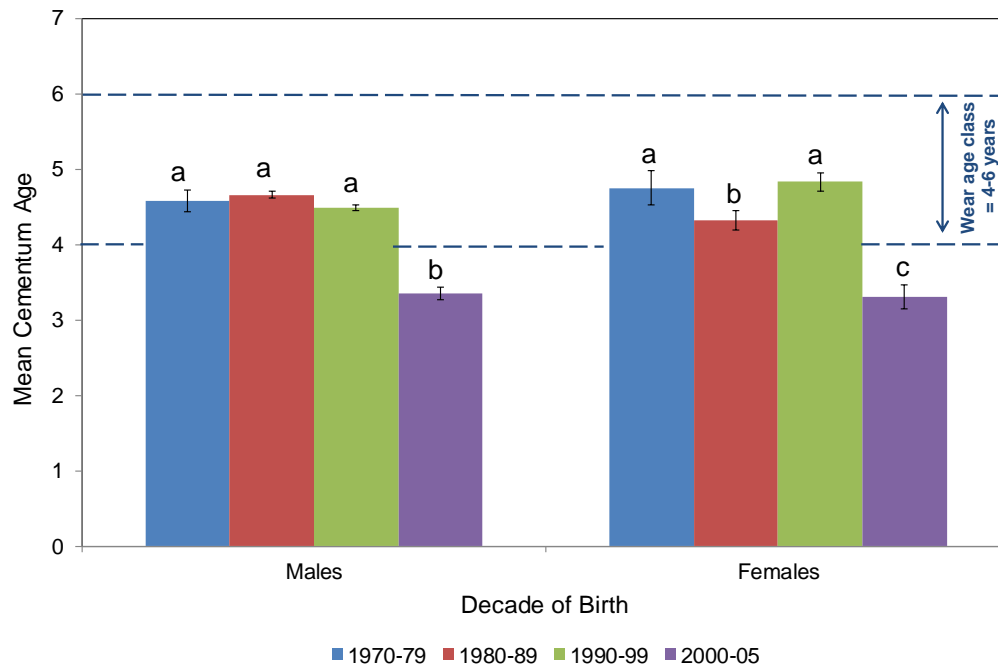


Figure 16: Cementum age (mean \pm SE) of male and female caribou classified as 4–6 years of age by tooth wear assessment (1970–2005). Data were stratified and compared between decades of birth. Statistically significant differences in cementum age between decades are indicated by letters above bars. Other tooth wear classes were also compared (i.e., 2, 3, 7–9, and 10+ years) but data are not shown.

Predictive Population Modelling

The probable future status of the Newfoundland caribou population was assessed by two modelling methods (Morrison *et al.* 2012; Randell *et al.* 2012). Both methods were parameterized using available field data, and both explored the population-level consequences of several scenarios that reflected possible management interventions or plausible changes in caribou vital rates. Models were density independent, meaning that they did not explore the effects of density on population abundance, and were projected into the future. Because both modelling approaches led to similar population projections, we provided a summary of only one approach: PVA (Randell *et al.* 2012). For more information on the second modelling approach, Leslie matrix, refer to Morrison *et al.* (2012).

A PVA was conducted using the software package Vortex (v. 9.99b; Lacy 1993; Lacy *et al.* 2003), and parameter estimates were based on means for the last 3 years of available data. Projections were made from 2011 to 2030. The scenarios differed dramatically in outcome. Under current demographic conditions (*Scenario 1*), the insular Newfoundland caribou population size was projected to decline between 2011 and 2030 (Figure 17) at an average rate of 5.1% per year ($\lambda = 0.949 \pm 0.012$). With the elimination of legal harvest (*Scenario 2*), the population size also declined, albeit at a slower rate (3.5% per year; $\lambda = 0.965 \pm 0.012$). However, even under continued harvest, increased rates of calf survival (*Scenario 3*) resulted in an increase in population size from approximately 36,200 in 2011 to approximately 65,300

caribou by 2030. In that scenario, population size increased at an average annual rate of 2.9% per year ($\lambda = 1.029 \pm 0.013$). Improved calf survival coupled with the elimination of harvest (Scenario 4) resulted in 3.6% growth per year ($\lambda = 1.036 \pm 0.013$) and resulted in a 2030 population of 73,000 animals. The probability of extinction by 2030 for the whole Newfoundland population was zero for all four scenarios.

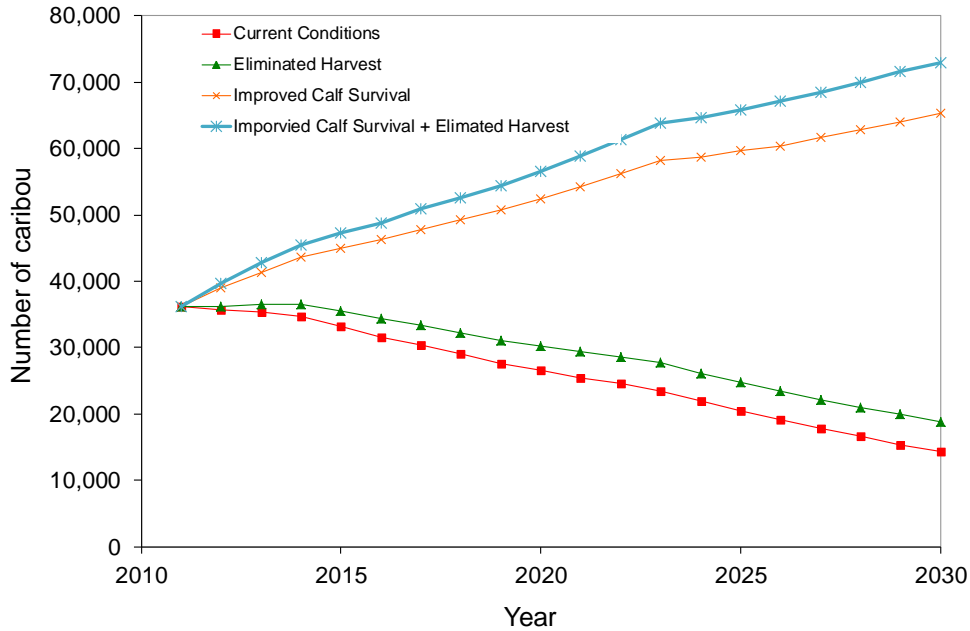


Figure 17: Projected population size of the Newfoundland caribou population, 2011–2030, based upon PVA using four scenarios (current conditions, elimination of hunting, improved calf survival, and both elimination of hunting and improved calf survival).

The effect of calf survival on population growth and decline was further examined to determine the rate at which population stability and/or a return to growth could be achieved. To address this issue, the PVA 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 annual calf survival was between 0.40 and 0.45 (Figure 18). The population began to increase when calf survival exceeded 0.45.

Overall, the projected PVA modelled rate of decline (under current conditions) was consistent with recent population censuses that have indicated continued decline in the Newfoundland population (Figure 4). Furthermore, assuming that current rates of productivity, adult survival, and harvest remain constant, the PVA models indicated that minimum calf survival rates between 40% and 45% were required to attain population stability. These projected rates of calf survival are comparable with calf survival observed during a period of rapid population growth for Newfoundland caribou (Figure 7). Both these findings suggest the PVA models are consistent with observed trends and provide reliable projections of likely population trends.

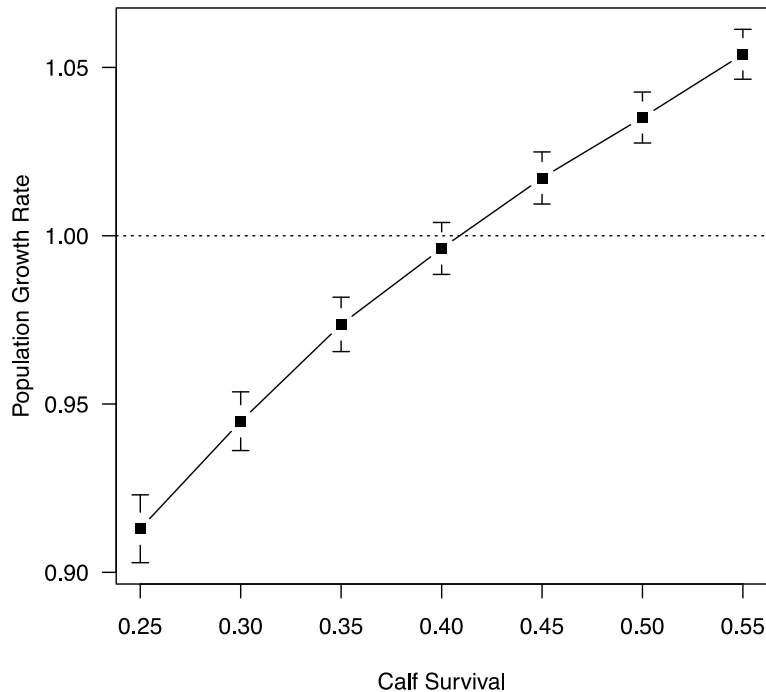


Figure 18: Expected population growth rate ($\lambda \pm 95\%$ CI) of the Newfoundland caribou population for varying levels of calf survival. The horizontal dotted line indicates population stability (i.e., $\lambda = 1.0$).

Caribou Spatial Dynamics and Demography

The abundance and distribution of plants and animals is intricately linked. Positive relationships between abundance and range size are widespread and exhibited by a range of species including caribou (Schaefer and Mahoney 2003; Bergerud et al. 2008). Schaefer and Mahoney (2013) tested the link between demography and spatial ecology of Newfoundland caribou. They analyzed site fidelity, degree of movements, and timing of migration based upon observations of nearly 700 radio-tracked females from five herds, coincident with their numeric growth (1980s and 1990s) and decline (2000s).

Site Fidelity

Female caribou displayed a distinct seasonal rhythm of site fidelity — a tendency to return to calving and especially postcalving locations from the previous year. This pattern was remarkably consistent across herds and may be related to postpartum security for females and calves. Furthermore, the strength of summer site fidelity appeared linked to numerical change (Figure 19). Across decades, fidelity was weakest at high population densities, perhaps reflecting heightened competition for summer foods. In contrast, females were much less philopatric during winter when



individuals were typically 30–40 km away from their previous year’s location. The predictability of philopatric behaviour suggests its utility in habitat and environmental assessments.

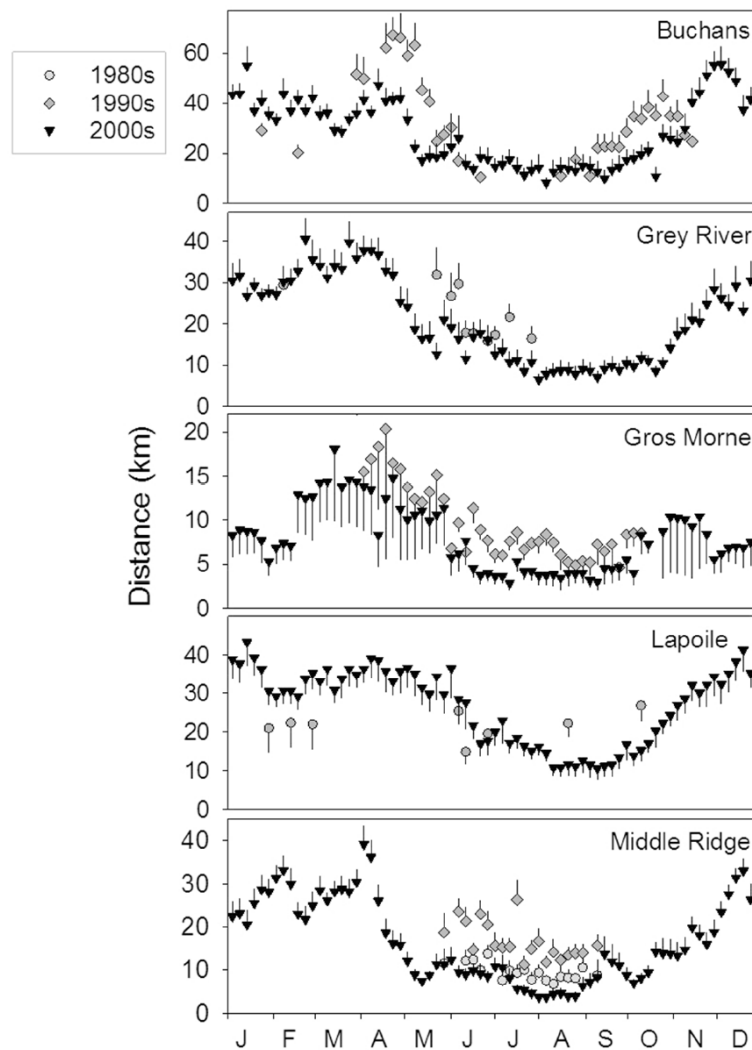


Figure 19: Site fidelity of female caribou from five Newfoundland herds expressed as distance between consecutive-year locations of individuals. Data were stratified by decade representing periods of population growth (1980s and 1990s) and decline (2000s). Means \pm SE are displayed. Graph taken from Schaefer and Mahoney (2013).

Movement and Timing of Migration

Movement is central to the ecology of caribou and for migratory herds, may reflect changes in demography. Changes in movement may reflect population limiting factors and trends in population growth (Messier *et al.* 1988; Schaefer and Wilson 2002). Schaefer and Mahoney (2013) reported, with the exception of the Middle Ridge herd, adult female caribou showed reductions in movement in the 2000s compared with earlier decades, but there were no clear differences (for two herds) between the 1980s and 1990s. Reduced movements in the 2000s may indicate that forage conditions may have improved in the 2000s and that caribou did not have to

move as much to find food. The magnitude of change between earlier decades and the 2000s was variable among herds and pronounced for the Grey River herd. The reason for differences among herds was unclear, but may be related to the sporadic telemetry observations reported for some herds.

Schaefer and Mahoney (2013) also found that the timing of movements appeared linked to the rise and fall in Newfoundland caribou numbers. For example, during an era of sustained population growth the Buchans herd's (1957–1997) spring migration to calving and summer range became progressively delayed, while fall migration occurred earlier — a change of 2 months occupancy across 4 decades (Mahoney and Schaefer 2002a). Schaefer and Mahoney (2013) reported a reversal of this long-term trend (Figure 20) in the 2000s. Compared with the 1990s, the Buchans herd migrated 3 weeks earlier in spring and 2 week later in autumn. These caribou are now spending roughly 5 weeks longer per year on their calving and summer range than a decade ago. Decreased time on the summer range in the 1990s suggested that summer forage may have been limited and competition higher when the population was nearing peak numbers. With the rapid decline in numbers, competition has been reduced and summer forage may no longer be limiting. Patterns in adult and calf morphology support this hypothesis — decreased size during the 1990s and increased size in recent years.

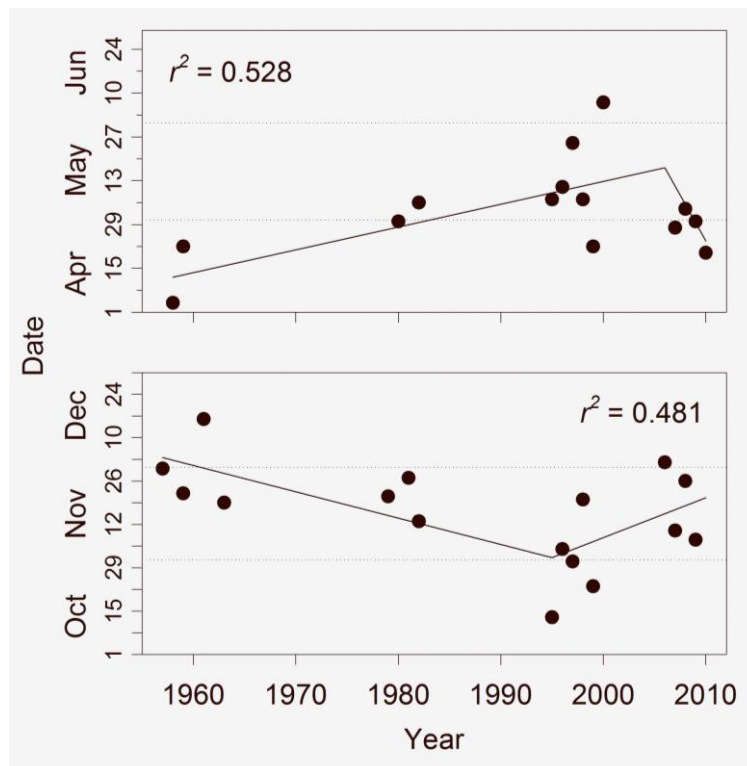


Figure 20: Timing of peak spring and autumn migration by Buchans caribou, 1957-2010. Observations, 1957–2000, are from Mahoney and Schaefer (2002); and observations, 2004–2010, are from Schaefer and Mahoney (2013). Lines of best fit and coefficients of determination were determined from two-segment regressions.

THREATS AND LIMITING FACTORS

Density Dependence

Density dependence has been implicated in the decline of vigour and abundance, as well as changes in spatial ecology, of Newfoundland caribou, including changes in their morphology (Mahoney *et al.* 2011), calf survival (Norman and Mahoney 2007; Mahoney and Weir 2009), decreased calf birth weights, habitat use (Schaefer and Mahoney 2013), the partial disintegration of herd structure and loss of calving site fidelity (Mahoney 2000; Bridges *et al.* 2004, 2006; Schaefer and Mahoney 2013), and changes to the timing of annual migrations (Mahoney and Schaefer 2002a; Schaefer and Mahoney 2013). Overall, the mechanism underlying the density-dependent responses is likely related to competition for forage resources or degradation of habitat due to overgrazing (Mahoney *et al.* 2011; Schaefer and Mahoney 2013). Recent changes observed in the diet of Newfoundland caribou, including an increased presence of moss and other low quality plant species and a decrease in lichen content (SDSS, unpublished data), and premature tooth wear of prime age and older caribou support the hypothesis of habitat quality driven nutritional stress issuing density-dependent responses in the population. Furthermore, in the early 2000s, female caribou with calves reduced vigilance in favour of foraging intensity during spring and summer despite the high risk of predation to calves (Soulliere 2008). Based on the published literature reviewed, this behaviour is unexpected (Soulliere 2008) and also indicates summer forage limitation and provides a possible link between declining forage resources and increasing juvenile mortality.

These changes to morphology, demographics, and behaviour correspond well with the observed changes in population abundance. Indeed, consistent with density-dependent responses, many of these characteristics have improved recently as the population has become less abundant. However, these positive changes are still too preliminary to be a definite indication of population recovery. Overall, the Newfoundland population continues to decline, albeit at a slower rate. While density-dependent processes may have ultimately caused or influenced the population decline, predation remains an important limiting factor to recovery.

Predation

Predation in the first 2–3 months of a calf’s life is the single most important proximate cause of mortality for Newfoundland caribou calves. Predation as the dominant proximate cause of caribou mortality is a common occurrence for caribou (Bergerud and Elliot 1986; Rettie and Messier 1998; McLoughlin *et al.* 2003; Wittmer *et al.* 2005; Bergerud 2007). However, there are important differences between insular Newfoundland and other areas, and the contribution and number of different predators has changed over the 30+ years it has been studied in insular Newfoundland. Unlike many jurisdictions, black bears were, in general, the dominant predators across this time series. There is some variation among herds, but black bears are always a significant factor (Trindade *et al.* 2011;



Lewis and Mahoney 2014). In other parts of North America, other predators, such as wolves and grizzly bears, take more caribou than black bears (Guistine *et al.* 2006).

A major change in the ecology of insular Newfoundland has been the arrival of the coyote, sometime in the 1980s. Calf mortality increased as the coyote population expanded, which is similar to other areas where coyotes are recent arrivals (Crête and Desrosiers 1995). However, it is not clear to what degree coyote predation is additive or compensatory, and therefore, it is difficult to determine the exact contribution of the arrival of coyotes to the caribou population decline. It is clear that coyote predation beyond the first 6 months of a calf's life is minimal (Mahoney and Weir 2009; Lewis and Mahoney 2014).

Currently, lynx appear to be a minor predator of caribou but previously lynx were thought to be the main predator of caribou calves (Bergerud 1971, 1983; Mahoney *et al.* 1990). Lewis and Mahoney (2014) offered possible explanations for this discrepancy. First, other predators may have played a more important role than previously reported by Bergerud (1971, 1983) who did not have the benefit of radio-telemetry. Second, the arrival of coyotes may have altered the availability of caribou for the other predators through exploitation and/or interference competition. Third, predation may



be proportional to predator species abundance in a given study area and abundance likely varies across the landscape and over time. Regardless, provincial trapping records for lynx show no relationship with caribou calf survival since 1990 (NL Department of Environment and Conservation). Eagles are a minor predator and their influence on these trends was minimal. The increased predation on calves by eagles recorded since 2003, and during the population decrease, was perhaps due to small calf sizes and increased periods of vulnerability or to decreased availability of coastal food.

Although predation is the main proximate factor influencing calf survival, limited forage conditions (as a result of competition, degradation, or phenology) ultimately may have predisposed calves to higher predation rates because of smaller sizes at birth and a lower ability to escape predators (Bergerud 1971; Bergerud *et al.* 2008) or adult nutritional stress may have resulted in reduced maternal care and defence. Schaefer and Mahoney (2013) reported that competition for summer forage may have recently declined as a result of reduced population abundance and surmised that recent increases in calf survival (Figure 7 and Figure 8) may be a consequence of this pattern.

PVA modelling indicated that a decrease in calf mortality would allow the population to grow. Given most calf mortality was due to predation, we hypothesized a reduction in calf predation would allow calf survival rates to increase and therefore allow the population to increase. SDSS conducted a predator manipulation experiment which consisted of diversionary feeding of bears and coyotes (2010, 2011) and lethal removal of coyotes (2012, 2013) in the southern Middle Ridge calving area; other Caribou Strategy study areas were used as experimental controls (see Gullage *et al.* 2014 for full details).

Diversionsary feeding began prior to calving season (mid-May) and continued until late July, when caribou typically leave the calving grounds. During the first year, bakery waste was placed on a grid in an attempt to divert bears from predateding on caribou calves; in 2011 beaver carcasses were added to the same area in an attempt to divert bears and coyotes. Bakery waste was consumed in vast quantities by bears and was moderately successful in changing patterns of bear movements, but coyotes were not attracted to either bait type. Diversionsary feeding improved calf survival although the effect was modest. Lethal removal of coyotes, by snaring, began several weeks prior to the calving season in 2012 and 2013 and continued for 4-6 weeks. Sixteen (16) and 24 coyotes were removed in 2012 and 2013 respectively, and calf survival improved significantly. Predator manipulation shows promise as a means to improve caribou calf survival; however, because of the economical and logistical challenges, its application will only be feasible in rather restricted areas.



Hunting

Newfoundland caribou are harvested by resident and nonresident hunters. The majority of harvested animals are taken by residents for meat, and a smaller proportion are harvested by nonresidents as part of a “trophy” hunt (Mahoney *et al.* 2011). Most harvested caribou are male likely contributing to the female-dominated sex ratio (Figure 10) observed in this population (i.e., males experience greater overall mortality and are therefore less represented in the total population). Management quotas for caribou were based on population assessments and hunter success rates; quotas were increased or decreased depending on recent population trends and/or hunter success in the previous years.

Hunter success rates decreased dramatically in concert with the population decline from approximately 80% in the late 1990s to a low of 60% in 2005. Interestingly, the success rate has increased since 2006 despite continued population decline (Figure 21). This observed increase in hunter success may reflect less competition for animal harvest because quotas were reduced. Alternatively (or additionally), greater hunter success at reduced animal density may suggest caribou alter their space-use patterns as a function of population densities or perhaps hunters are less selective because they have learned that harvest opportunities may be scarce. While further investigation is needed to understand this pattern, this finding does suggest managers should use caution when using the hunter success rate index to adjust hunting quotas.

On average, 3.8% of the Newfoundland caribou population was harvested annually from 1966 to 2012 (Figure 22). However, harvest intensity varied dramatically during the period of increase and decline in population abundance. Licence sales increased steadily until 2004 resulting in an 8-year lag from the population peak to quota reduction that resulted in the highest rates of harvest (5.9%–7.6% from 1999 to 2005) during the period of rapid population decline (Figure 21). Of note, the overall rate of harvest peaked at greater than 12% for some individual herds and greater than 18% when considering only the adult male segment of the population.

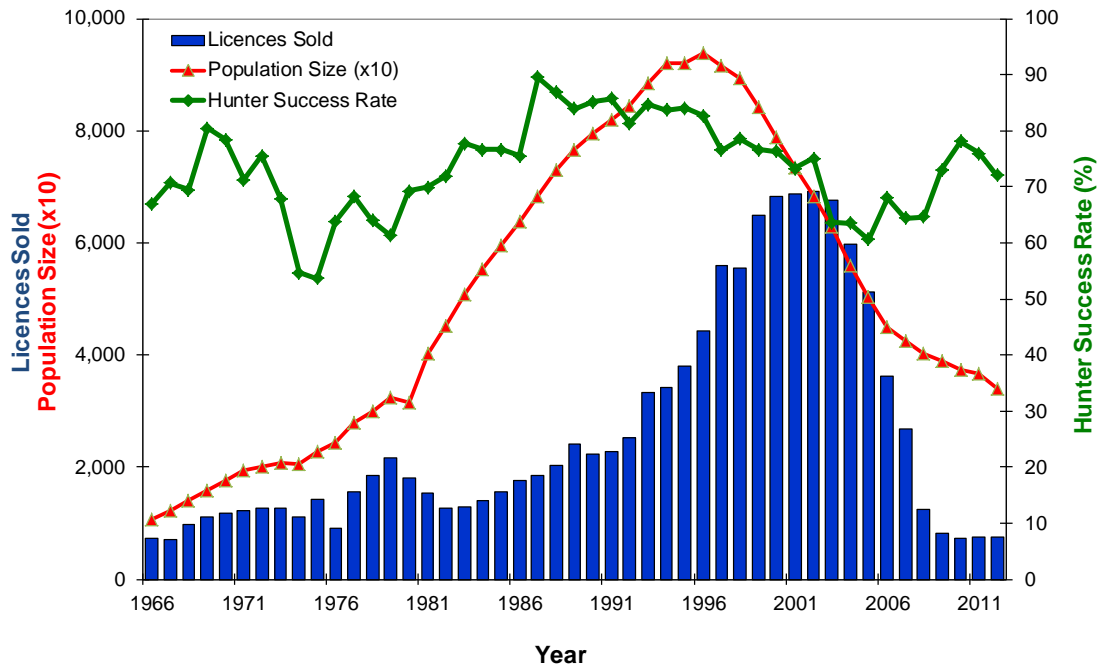


Figure 21: Number of licences sold, hunter success rate (%), and population abundance of Newfoundland caribou, 1966–2012.

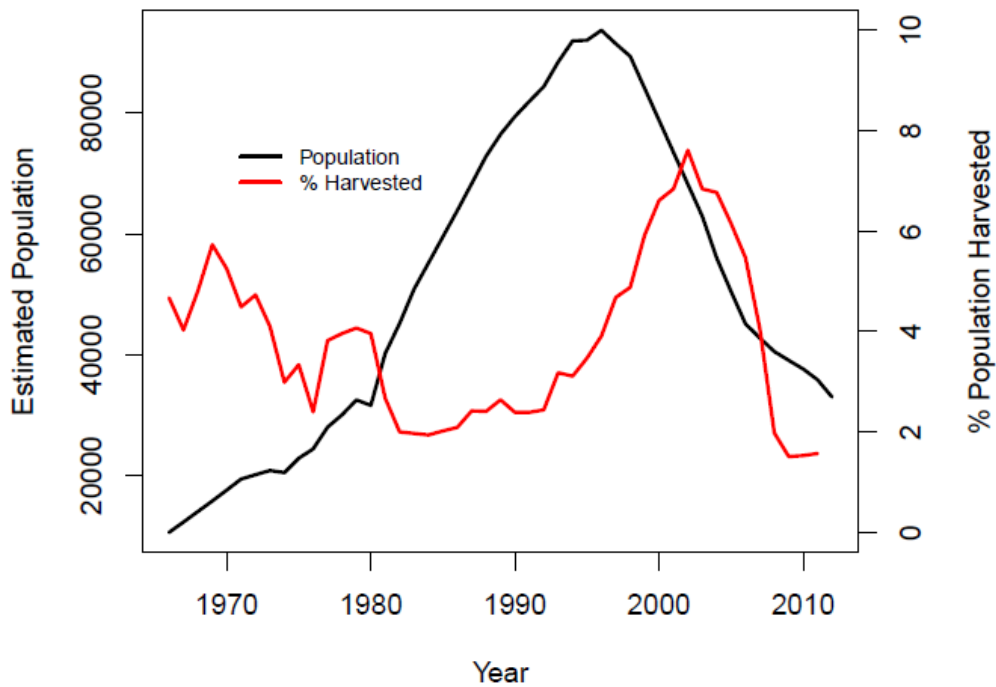


Figure 22: Newfoundland caribou population abundance and the percentage of the population harvested, 1966–2012.

These findings do not imply that hunting was the cause of the Newfoundland caribou population decline, but they do suggest that the rate of decline was exacerbated by high rates of harvest in the early years of the population downturn. If all hunting had ceased in 1996, population models suggested the Newfoundland population would have continued to increase in 1997 and 1998 and the 2012 population would have been approximately 59,000 (1.8 times larger than the 2012 population estimate of 33,000 caribou) (Figure 23). Currently, approximately 2% of the Newfoundland population is harvested annually. While predictive models suggested that the closure of all hunting would not be sufficient on its own to halt or reverse the population decline, the recovery predicted (using PVA) with improved rates of calf survival could be enhanced if hunting was eliminated for some period of time (scenario 4, Figure 17).

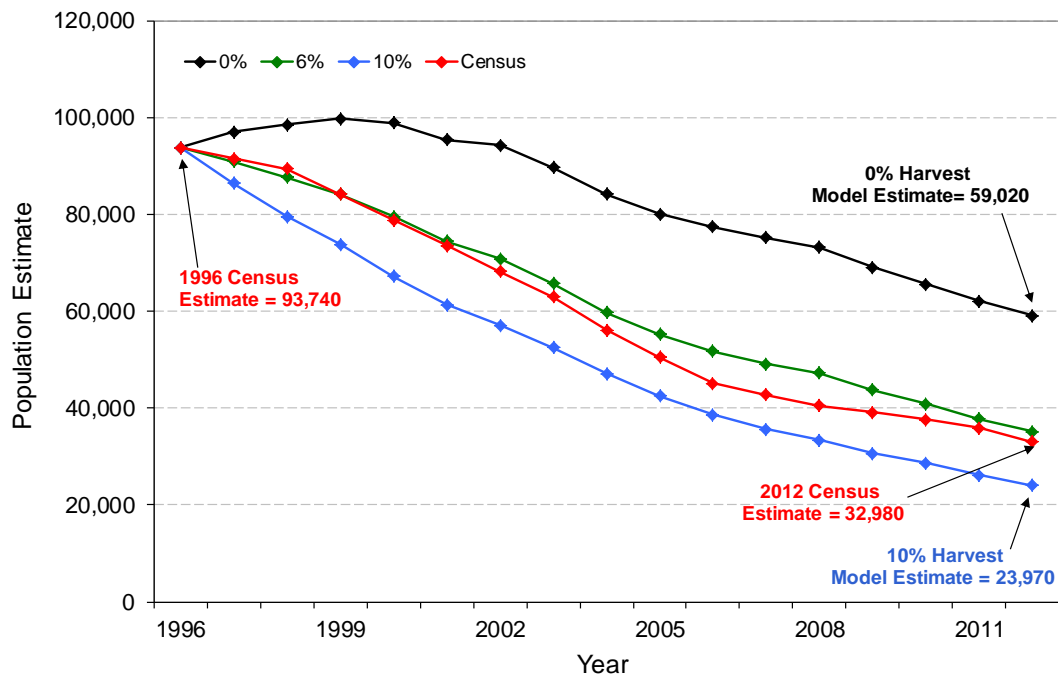


Figure 23: Projected population size (Vortex v 9.99b; Lacy *et al.* 2003) for Newfoundland caribou, 1996–2012, based upon scenarios of various levels of hunting intensity (0%, 6%, and 10% per annum), and projected population size estimated from census data.

Climate

Climatic conditions, such as the North Atlantic Oscillation (NAO; Hurrell 1995), are known to affect ungulate population demographics and morphology often through factors related to winter severity (Post *et al.* 1997; Post and Stenseth 1998; Forchhammer *et al.* 2002; Mysterud *et al.* 2003; Helle and Kojola 2008). Population abundance and climate/weather patterns may also interact with each other such that the influence of weather varies depending on population size, with negative impacts of weather observed at higher population densities (Ferguson and Mahoney 1991; Heard and Ouellet 1994; Aanes *et al.* 2000).

Our research revealed an association between the NAO and the decline in adult jawbone size, and this relationship did in fact vary with population abundance, age class, and individual herd (Mahoney *et al.* 2011; SDSS, unpublished data). However, variation in the NAO could not explain patterns of caribou calf survival (Lewis and Mahoney 2014) or antler size (Mahoney *et al.* 2011). Furthermore, an exhaustive analysis of the influence of local climate variables (i.e., temperature, precipitation, frost-free days, etc.) on demographic trends (Mahoney 2000) did not indicate climate as a significant driver of these trends. Significant relationships were sporadic and varied among herds and over time. Similarly, we did not detect any relationship between adult survival and severe winter weather (depth of snow) or freeze–thaw cycles (SDSS, unpublished data).



As discussed in Lewis and Mahoney (2014), winter severity may not be important for Newfoundland caribou for several reasons. First, *Rangifer* are superbly adapted to winter climates and are at the southern limits of their range on the island of Newfoundland, where winter weather is mild relative to most of *Rangifer*'s species range. Second, *Rangifer* are highly vagile, allowing them to escape locally extreme conditions through movement to more sheltered or ice-free areas. Third, many studies have shown that climate is

more likely to influence ungulate populations in systems where adults are subject to year-round predation by wolves (Post and Stenseth 1998, 1999; Post *et al.* 1999; Hegel *et al.* 2010). On the island of Newfoundland, there is an absence of large, overwinter predators of caribou. Predation pressure is minimal in the winter because bears are hibernating, calves are too large for lynx, and eagles are not present. Coyote predation on Newfoundland caribou beyond six months of age is minimal (Trindade *et al.* 2011; Lewis and Mahoney 2014).

Disease and Parasites

Newfoundland caribou are known to be affected by a debilitating neurologic disease known as cerebrospinal elaphostrongylosis (CSE), caused by the nematode *Elaphostrongylus rangiferi* (Ball *et al.* 2001). *Elaphostrongylus rangiferi* was introduced to Newfoundland in 1908 during the importation of 300 Norwegian reindeer (*R. t. tarandus*) (Lankester and Fong 1989). The intensity of infection is positively correlated with moderate summer temperatures and mild winters, but not correlated with caribou herd density (Ball *et al.* 2001). Almost all of Newfoundland caribou have been infected by *E. rangiferi*, but only a small percentage will manifest symptoms or succumb to the disease (Ball *et al.* 2001; Drover 2009). Increased mortality of caribou following CSE epizootics was implicated in the decline of the Avalon herd that decreased from 7000 to 2500 caribou in 3 years following *E. rangiferi* infection (Lankester and Fong 1989; Mahoney 2000) and dropped below 400 animals by 2005. The great majority of caribou develop resistance to *E. rangiferi* such that reinfections are less common in later years as calves and yearlings are more susceptible than older age classes (Ball *et al.* 2001). Caribou appear to be developing immunity to *E. rangiferi*; there are no data to indicate this infection played any role in the most recent population decline.

Newfoundland caribou are also known to be exposed to oestrid fly infestations (nasal bots and warbles) and undoubtedly harbour undocumented numbers of intestinal parasites. Parasites and biting flies are thought to be able to impose large energetic costs on their hosts, and poor nutrition can increase susceptibility. Although we do not have a clear understanding of the role of parasites and biting flies in the current decline, consistently high adult survival implies their impact, if any, was minimal.

Habitat Alteration and Disturbance

Woodland caribou are affected, to varying degrees, by habitat alteration and human activity throughout their North American range (e.g., Bradshaw *et al.* 1997; Dyer *et al.* 2001, 2002; Dalerum *et al.* 2007; Vors *et al.* 2007). Woodland caribou are sensitive to changes in their habitat and may avoid human activity and human-created features on the landscape (e.g., roads). Newfoundland caribou have access to relatively large sections of undisturbed landscape, their habitat is vulnerable to disturbance in the long term as less than 3% of the landscape is currently within protected areas (Wells *et al.* 2011).

Several research endeavours have attempted to identify the effects of human activity on Newfoundland caribou. An analysis of the summer habitat use of 35 collared caribou in east-central Newfoundland indicated that clearcutting affected their distribution and movements (Chubbs *et al.* 1993). The effects varied by individual caribou, but most female–calf pairs avoided clearcut areas (Chubbs *et al.* 1993), although more recent data suggests caribou may use clearcuts following timber harvest (Hebert and Weladji 2013). In a more recent study of 70 collared individuals, caribou avoided recently harvested areas, areas with higher moose densities, and areas with low forage availability and greater likelihood of encountering predators, black bears specifically (Mahoney and Virgl 2003). Adult female caribou appear more sensitive to forestry activities than adult males (Schaefer and Mahoney 2007), demonstrating larger avoidance distances (9.2 km) from active timber harvest operations.



Other types of human activity have also been shown to affect Newfoundland caribou. Hydroelectric development disrupted the timing of caribou migration during its construction, and facilities were avoided by up to 3 km for at least 2 years following the completion of construction activities (Mahoney and Schaefer 2002a). Similarly, mining activities resulted in caribou avoiding areas within 4–6 km of the area, and the effect was most pronounced during late winter and the period before and during calving (Mahoney *et al.* 1991; Weir *et al.* 2007). Seemingly lesser disturbances such as snowmobiling (Mahoney *et al.* 2001) and hiking (Soulliere 2008) are also known to displace Newfoundland caribou.



While these various studies demonstrate that caribou will often avoid ongoing human disturbance and may, over time, adjust to in-situ constructions or habitat change, no studies have explored the link between habitat alteration/human activity in Newfoundland and individual- or population-level fitness. In other words, our research to date has not evaluated demographic or numeric responses at the population level. Certainly, some relationship may be implied from caribou behavioural responses to these various changes.

SUMMARY

While many of the overall patterns and trends reported by Mahoney and Weir (2009) are still evident in the Newfoundland caribou population, some demographic and morphological patterns have reversed and there are indications of improvements in population performance in recent years.

- The Newfoundland population continued to decline, but the rate of decline has slowed, possibly because of improvements in calf survival since 2007 and the reduction in hunting quotas since 2006. The slower decline is predicted to continue however unless rates of calf survival rise consistently above 40%–45% annually. The Newfoundland population is not at risk of extinction in the next 20 years, based on current demographics (Morrison *et al.* 2012; Randell *et al.* 2012).
- The proportion of the Newfoundland population harvested increased for several years after the decline in population size began. There was an 8-year lag between population peak and the reduction in quotas — this mismatch resulted in high rates of harvest (particularly for males) in the early years of the population decline and likely exacerbated the rate of decline.
- The mean age of male and female caribou increased from the 1980s to the early 2000s but this trend has reversed.
- The survival of adult females, 2-year-olds, and yearlings remained high and constant; calf survival (based on radio-collars) has increased since 2007, but remains insufficient for population stability or growth.
- Predation remained the primary cause of death for calves. While most calves died during the first 8–12 weeks of life, overwinter survival remained high. Coyotes and bears were major predators in recent years. Rates of predation and the number of predator species increased in the 2000s as compared with the 1980s and 1990s.
- The decline in recruitment (observed from the 1980s to the early 2000s) has halted averaging ~11% in recent years, though this is still insufficient for population increase.
- There has been an increase in the percentage of males in the adult population since 2006 possibly because of changes in quota allocation, but the sex ratio is still well below historically recorded levels. The dramatic change in the adult sex ratio observed from the late 1980s to the mid-2000s was likely due to a male-biased harvest strategy, particularly

in the years immediately following the start of the population decline when harvest rates for males were at their highest.

- While the average rate of productivity has declined since the 1970s and 1980s, this reduction in productivity was not synchronous or consistent across the island, nor was the decline significant enough to explain the synchronous and drastic decline in caribou numbers.
- The birth weight (i.e., capture weight) of male and female calves increased since the early 2000s following a reduction from the 1980s to the 1990s; heavier calves have a higher probability of survival (Lewis and Mahoney 2014).
- Body size (jawbone length and antler size) increased since the mid-2000s following a decrease that began in the late 1980s. Both morphological indicators have returned to pre-decline levels.
- Harvested caribou born in the early 2000s experienced accelerated tooth wear when compared with caribou born in previous decades, possibly indicating that these caribou likely fed on rougher, low quality forage in poor quality habitats.
- Changes in habitat use, site fidelity, and timing of migration occurred as the population rose and fell. These changes suggest summer forage reduction, as a consequence of high numbers of caribou in the late 1990s, may have contributed to the population decline.

Based on these research findings we eliminated the following mechanisms as cause of the current decline:

- **Increase in natural adult mortality:** current rates of adult mortality are low and are comparable with those observed in the 1980s and 1990s.
- **Winter predation of calves and adults by coyotes:** overwinter survival of calves is high and rates are comparable with those of adults. Adult mortality has not increased over time. We found no evidence that winter predation by coyotes (or any other predator) has influenced the abundance of Newfoundland caribou.
- **Low birth rates:** overall rates of productivity are high and cannot explain the reduction in recruitment observed in the 2000s. While slight reductions in productivity were detected for a few herds, this cannot explain the drastic population decline observed in all major herds. That said, productivity rates are currently low for the Cape Shore, Northern Peninsula, Avalon, and Mount Peyton herds and monitoring should continue.
- **Brain worm:** *E. rangiferi* is now confirmed in all herds on the island of Newfoundland. Given the timing of brain-worm arrival and infestation of the major island herds, the recent population decline is not explained by brain-worm infestation. Further, throughout the intensive field research conducted during the last 5 years very few caribou suspected to manifest brain-worm disease symptoms were observed. No other diseases or parasites are known to directly affect the survival of caribou in Newfoundland, and there is no evidence, scientific or anecdotal, to suggest the decline was precipitated by an epidemic.
- **Climate:** There is no evidence to suggest local and large-scale weather patterns caused the observed significant decline in calf survival or the current population decline (see Lewis and Mahoney 2014 for further discussion on climate).

- **Harvest:** Legal hunting did not cause the population to decline but likely exacerbated the rate of decline in the early 2000s. Population modelling showed that even in the absence of hunting from 1996 to 2012 the Newfoundland population would still have declined (although at a slower rate).

The best-supported hypothesis to explain the observed patterns in the Newfoundland caribou population revolves around the influence of density dependence. Generally, caribou populations at high densities exhibit classic signs of density dependence through reduced juvenile survival (Bergerud 1971; Skogland 1985; Mahoney and Schaefer 2002b), lower fecundity and delayed reproductive maturity (Reimers *et al.* 1983; Skogland 1983), diminished recruitment (Messier *et al.* 1988; Couturier *et al.* 1990; Mahoney and Schaefer 2002b), and smaller stature (Skogland 1983; Couturier *et al.* 1990; Mahoney and Schaefer 2002b). Behavioural changes may also occur, including dramatic changes in the timing of migration (Mahoney and Schaefer 2002a; Schaefer and Mahoney 2013).

Almost all of these density-dependent responses are now well documented in the Newfoundland caribou population. As detailed in this report and in Mahoney and Weir (2009), we recorded changes in numerous demographic (age, sex ratio, calf survival, and reproduction), behavioural (site fidelity, migration timing, and habitat use), and morphological indices (calf birth weight, body stature, and tooth wear) consistent with changes in population abundance. While predation was the proximate (or immediate) cause of low calf survival, the ultimate (or underlying) cause of the decline was density-dependent forage limitation that led to smaller calves and increased vulnerability to predation.

Newfoundland caribou have experienced a 66% drop in numbers and recently several population indices reflect a positive response to this reduction in abundance. Behavioural changes such as reduced movement rates, increased site fidelity, and increased time spent on summer range indicate that competition for forage has been reduced coincident with a reduction in numbers of caribou. In addition, many decreasing morphological trends have reversed — adults are larger, antlers are bigger, and calves weigh more at birth. As a likely consequence of these improvements in physical stature and forage availability, calf survival increased in recent years. While optimistic that these trends will continue, rates of calf mortality remain high, predation remains the predominate cause of death, and the island-wide population continues to decline, though at a much reduced rate. Predator manipulation experiments do suggest that improvements to calf survival, in rather restricted areas, can be achieved through intensive lethal removal of primary predators.

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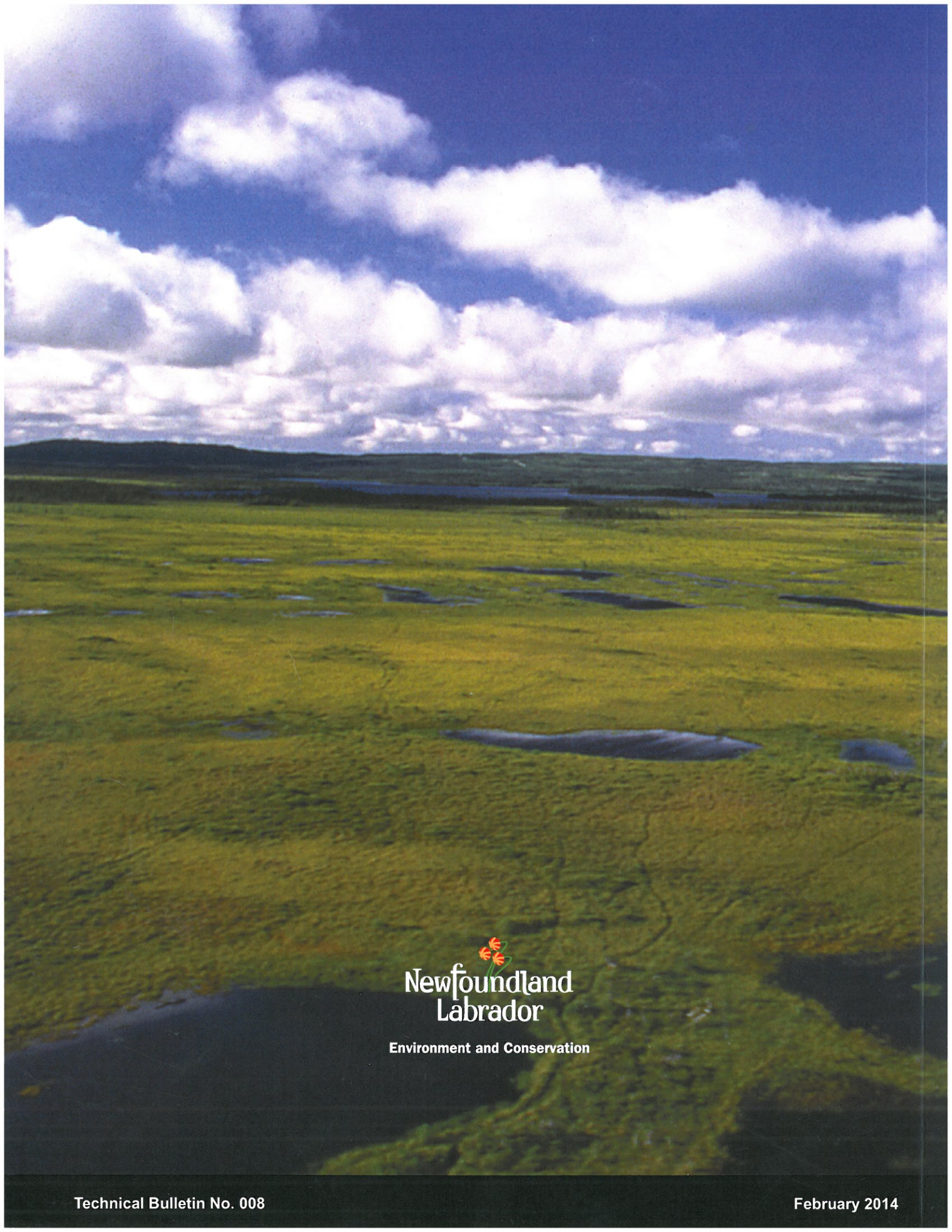
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