MODELLING THE POPULATION DYNAMICS OF THE ITCHA-ILGACHUZ CARIBOU HERD TO DETERMINE THE EFFECTS OF REMOVALS FOR TRANSLOCATION

by

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ABSTRACT

The Purcells-South mountain caribou herd in British Columbia has declined to very low numbers and is now in imminent danger of extirpation. To aid recovery, wildlife managers plan to augment the Purcells-South herd with caribou from another area. A potential donor herd is the Itcha-Ilgachuz caribou herd in west central BC. This herd is important to First Nations, resident hunters, and guide outfitters, all of whom hunt caribou from this herd. This project modelled the population dynamics of the Itcha-Ilgachuz herd in order to determine what effect the removal of 40 caribou over two years would have on the herd. I used three model variations to reflect different hypothesis about the current dynamics of the Itcha-Ilgachuz herd. I concluded that removals would have very little effect on the abundance and age and sex ratios of the Itcha-Ilgachuz herd and therefore, hunting opportunities should not be affected by removals for translocation.

Keywords: Bayesian; modelling; caribou; translocation; population dynamics

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INTRODUCTION

The conservation of native species and ecosystems is a growing challenge. Around the world, habitat destruction and fragmentation, over-exploitation, competition with invasive species, and climate change are causing the extirpation and extinction of species at a rate 100 to 1000 times higher than historical averages (Millennium Ecosystem Assessment 2005; Pimm et al. 1995). In British Columbia, these threats have contributed to the listing of 43% of the province's assessed species as "at risk". Forty-nine species have already gone extinct or been extirpated from the province (Austin et al. 2008). In the face of this species loss and the potential for many more extinctions, the importance of conserving and restoring biodiversity has been recognized at regional, national and international levels.

Global concerns about biodiversity loss led to the International Convention on Biological Diversity, to which Canada is a signatory, which aims to halt biodiversity declines and conserve species. The Canadian Biodiversity Strategy outlines Canada's approach to meeting its commitments under the Convention; it includes the goal "to conserve biodiversity and use biological resources in a sustainable manner" (Government of Canada 1995). This strategy resulted in the creation of the *Species at Risk Act* (SARA), federal legislation aimed at preventing species from becoming extinct and providing for their recovery. The management of wildlife and natural resources, however, falls largely under the jurisdiction of the provincial and territorial governments. Therefore, cooperation between federal, provincial, and territorial governments is necessary to manage species at risk and ensure Canada meets its obligations under the Convention. The National Accord on the Protection of Species at Risk (Government of Canada 1996) outlines this cooperative arrangement. The BC government, in keeping with its jurisdiction over wildlife management and its responsibilities under the Accord, leads the preparation and implementation of recovery plans for species at risk in the province (Province of British Columbia 2009).

Caribou (*Rangifer tarandus*) is a species of concern worldwide. Anthropogenic changes to the landscape and climate warming are blamed for declines of caribou populations throughout their global range (Vors & Boyce 2009). The woodland caribou subspecies (*Rangifer tarandus caribou)* occupies mountainous and forested regions across Canada and is at risk across most of the country due to habitat loss (caused by human activities) and predation (possibly facilitated by human activities) (COSEWIC 2002). In BC, the distribution of caribou has remained consistent with historic levels in the northern half of the province, but caribou have experienced both a marked range retraction (Spalding 2000) and a decline in numbers (Thomas & Gray 2002) in the southern half of the province. All caribou in BC belong to the same subspecies—woodland caribou—but the province classifies the subspecies into three different “ecotypes” that are based on habitat use and feeding behaviours (Mountain Caribou Technical Advisory Committee 2002; Stevenson & Hatler 1985). The mountain caribou ecotype occurs in the mountainous south- and central-eastern regions of the province, from the US border north to the Hart Ranges. The BC Conservation Data Centre (2011) lists mountain caribou as critically imperilled because of their declining numbers and small, fragmented herds. The northern caribou ecotype occupies the mountainous western and northern parts of BC. Northern caribou are listed as special concern because they are considered vulnerable to becoming imperilled if factors like forest harvesting and other human activities are not managed to prevent caribou declines (BC Conservation Data Centre 2011). The boreal caribou ecotype is found in the north-eastern corner of BC (Stevenson & Hatler 1985; Edmonds 1991); boreal caribou are listed as imperilled because of their low density and the fragmentation of their habitat (BC Conservation Data Centre 2011).

Over the past two decades, mountain caribou numbers have declined and mountain caribou herds have become increasingly fragmented and isolated. Several herds are now in imminent danger of extinction (Wittmer et al. 2005a). The decline has been attributed to high predation rates resulting from anthropogenic landscape change (Spalding 2000; Wittmer et al. 2005a; Wittmer et al. 2005b). Logging, which creates young forest stands in the place of older stands, can increase the number of other, more abundant ungulates, and lead to increases in populations of wolves and cougars that may then opportunistically prey on caribou (Rettie & Messier 2000; Mountain Caribou Technical Advisory Committee 2002; Wittmer et al. 2005b). From 1996 to 2010, the estimated number of mountain caribou declined from 2300 animals in 17 herds to 1710 animals in 15 herds (McNay & Hamilton 2010). Although the overall drop in numbers is concerning, it is the decline of the smallest herds that is of most concern. Ten mountain caribou herds now have fewer than 50 animals, including eight with fewer than 20 animals (McNay & Hamilton 2010). Two herds have been extirpated since 1996. These declines lead the provincial government, following its responsibilities under the National Accord for Species at Risk, to develop the Mountain Caribou Recovery Strategy (Mountain Caribou Technical Advisory Committee 2002), which identified strategies deemed necessary to protect and recover mountain caribou. The Recovery Strategy identified a short term goal to reverse the decline, with a long term goal to increase the number of mountain caribou to 2500-3000 animals (pre-1995 levels). The 2007 Mountain Caribou Recovery Implementation Plan (Ministry of Environment 2007) reiterated these goals, with a timeline to halt the decline within seven years and recover the population to 2500 animals within twenty years. Through the Implementation Plan, the provincial government committed to several management actions to reach these goals, including habitat protection, managing human recreational activities, managing predator populations and the primary prey of those predators, and augmenting herds with caribou from elsewhere to ensure that mountain caribou herds achieve critical mass for self-sufficiency.

The Purcells-South herd is one of the smallest and most isolated of the mountain caribou herds and has been identified as the first candidate to receive translocated animals. With a current population estimate of 14 animals, it is very unlikely to recover without augmentation (Kinley 2010). This herd experienced a precipitous decline from 63 animals in 1995 to 13 animals in 2000 and has been roughly stable at about 14 animals since then. Its small size and the lack of immigration from other areas makes it vulnerable to extinction from stochastic events, and it likely already has significantly reduced genetic heterozygosity (Kinley 2010).

The translocation of animals from one area to another can rebuild populations where a species has been extirpated or is nearing extirpation (Griffith et al. 1989; Wolf et al. 1996; IUCN 1998; Fischer & Lindenmayer 2000). In a review of 37 caribou introductions, reintroductions, and augmentations, Kinley (2009 as cited in Kinley 2010) found that at least 67% were successful in establishing new or larger herds. Careful consideration of the choice of donor animals, the size of the release group, and the habitat and environmental conditions at the release site will ensure a translocation has the best chance of successfully achieving a self-sustaining population (IUCN 1998; Armstrong & Seddon 2008). However, it is also important to assess the impacts on the donor population to ensure that population will not suffer negative effects from the removal of animals for translocation (IUCN 1998; Armstrong & Seddon 2008).

While the importance of considering the impact to donor populations in a translocation project is recognized (IUCN 1998; Armstrong & Seddon 2008; BC Gov. Translocation Policy 4-7-13.02, 29 May 2001), few studies report the potential or actual impacts to donor populations. There are two exceptions:

1) A study of a bighorn sheep population in Alberta, Canada (Stevens & Goodson 1993) that assessed the effects of an actual removal event on a

donor population and made recommendations for any future removals that might take place; and

2) A study on a robin population in New Zealand (Dimond & Armstrong 2007) that used population modelling to determine the appropriate number of removals from the donor population. Removals were then conducted and the effects monitored. The information gained through monitoring was used to update the model and make recommendations for future removals.

Both of these studies were considering large removals relative to the size of the donor population (36-44%).

Augmentation of the Purcells-South herd will immediately boost numbers, but in order for augmentation to be successful in recovering the herd, habitat and environmental conditions must allow the herd to grow and achieve self-sufficiency. Predation is expected to be the main limiting factor for the Purcells-South herd. Any plan to translocate animals will include predator management to limit mortality in the herd and provide the best chance of survival for the translocated animals (Mountain Caribou Technical Advisory Committee 2002; Mountain Caribou Science Team 2005). Efforts have already been made to reduce wolf numbers in the area (G. Mowat, Ministry of Forests Lands and Natural Resource Operations, personal communication). The provincial government has recently protected over 1400km^2 of habitat from forest harvesting in the South Purcell planning unit and several parks in the area are already protected. This habitat protection within caribou range will lead to a greater component of older seral stands over time and therefore provide good habitat for caribou while becoming less desirable for other ungulate species (e.g. moose, deer) and their associated predators (Kinley 2010). In addition, access restrictions for snowmobiles aim to minimize disturbance and prevent predators gaining easy access via snowmobile tracks to otherwise unreachable higher elevation areas (Kinley 2010). With these factors addressed, augmentations will have the best chance of success in recovering the Purcells-South herd.

The best donor population for the Purcells-South herd would be one of same ecotype (i.e. another mountain caribou herd) (The Mountain Caribou Technical Advisory Committee 2002). Differing behavioural characteristics between ecotypes may mean that mountain caribou are more suitable for translocation to another mountain caribou herd (Warren et al. 1996). However, all of the mountain caribou herds are at risk of extinction, and the removal of females from any mountain caribou herd could have negative impacts on the donor population (Wittmer et al. 2010). From a genetic perspective, there is no reason why caribou from the northern ecotype cannot be translocated to a mountain caribou herd (Mountain Caribou Technical Advisory Committee 2002). The northern ecotype has, in fact, been used in the past to augment the South Selkirk mountain caribou herd (Compton et al. 1995). Although the northern ecotype experienced higher mortality than the mountain caribou that were translocated at the same time, the northern caribou had less emigration of animals away from the release site (Compton et al. 1995, Warren et al. 1996). The Mountain Caribou Recovery Implementation Plan identified the Itcha-

Ilgachuz herd, located in west-central BC, as a potential source of animals to augment the Purcells-South mountain caribou herd. The Itcha-Ilgachuz herd belongs to the northern ecotype; it is the closest northern caribou herd to the Purcells-South herd and is one of the largest caribou herds in the province (CCLUP Caribou Strategy Committee 2002).

The Itcha-Ilgachuz herd has been used as a donor population for translocations twice in the past. In 1987 and 1988, a total of 26 caribou were taken from the Itcha-Ilgachuz herd, along with 34 caribou from other herds, to augment a herd of 20 animals in the south Selkirk Mountains in northern Idaho (Compton et al. 1995). In later years, another 43 animals from other herds were also translocated to the same area. The recipient population initially declined due to mortality and dispersal and then grew to an estimated 46 individuals in 2009. Although the recipient population has not grown greatly over the past two decades, it is likely that the translocations have enabled the herd to persist over that time (G. Woods, Ministry of Environment, personal communication, via Ian Hatter, Ministry of Forest, Lands and Natural Resource Operations). Between 1984 and 1991, a reintroduction program translocated 52 caribou from the Itcha-Ilgachuz herd to the nearby Charlotte Alplands area, which had previously supported a northern ecotype herd (Young et al. 2001). The first group of translocated animals travelled back to the Itcha-Ilgachuz herd, but a second group was successful in increasing numbers at the re-introduction site over the short term. The longer-term status is unknown, although animals were still present in 2009 (Kinley 2010). The impact of these removals on the Itcha-

Ilgachuz herd was not quantitatively assessed prior to, or following, the translocations.

An earlier population viability analysis on the Itcha-Ilgachuz herd, undertaken when translocations were first contemplated as part of the Mountain Caribou Recovery Plan, concluded that translocations of 20 caribou annually for six years could occur with minimal risk to the herd (Hatter & Young 2004). The Itcha-Ilgachuz herd was considered a possible donor at that time because of its large size and long-term increasing trend. From the early 1970s to 2003 the herd was estimated to have grown from approximately 400 to 2800 animals (Young & Freeman 2003). Since 2003, however, population surveys have documented fewer and fewer animals. There is uncertainty as to whether this indicates that the herd is declining or that animals are not being observed with the same accuracy due to changes in seasonal migrations and distribution. Concerns about a possible decline of the Itcha-Ilgachuz herd called for another assessment to take into account this new survey information and determine whether the Itcha-Ilgachuz caribou may still be a suitable donor herd.

In keeping with the provincial government's translocation policy (4-7-13.02, 29 May 2001) to "minimize the risk of adverse side effects that may occur as a result of translocations," this project provides information to help evaluate potential impacts on the donor (Itcha-Ilgachuz) herd as a result of removals for translocation. Specifically, the objectives of this project were to evaluate how different removal options would affect short-term and long-term population abundance and examine how these removals may change the age and sex composition of the herd. Because the Itcha-Ilgachuz herd is hunted by First Nations, resident hunters, and non-resident hunters, it was also important to evaluate what effect a translocation program could have on hunting opportunities. Predicted changes in abundance and sex composition were examined to evaluate if tradeoffs would exist between removals for hunting and removals for translocation: for example, if it would be necessary to reduce hunter harvest to mitigate the impacts of removals for a translocation.

STUDY AREA

The Itcha-Ilgachuz herd inhabits an area approximately 10,042 km^2 in the Itcha and Ilgachuz mountain ranges and surrounding areas in the rain shadow of the Coast Mountains in west-central British Columbia (Figure 1) (CCLUP Caribou Strategy Committee 2002). This area once consisted of active isolated shield volcanoes that are now gently rolling alpine areas rising up to 2400 meters above sea level. The Itcha and Ilgachuz mountains occur primarily in the Fraser Plateau Ecoregion (CCLUP Caribou Strategy Committee 2002) and the western Chilcotin Uplands ecosection, and are located in a plateau of mature lodgepole pine forest, interspersed with wetlands and meadows. The biogeoclimatic zones at higher elevations are the Alpine Tundra zone and Engelmann Spruce – Subalpine Fir zone and at lower elevations, the Montane Spruce zone and Sub-Boreal Pine – Spruce zone. The alpine areas of the Itcha and Ilgachuz mountain ranges are within Itcha-Ilgachuz Provincial Park, created in 1995 to protect the summer habitat of the caribou. Further description of the study area may be found in the Northern Caribou Strategy (CCLUP Caribou Strategy Committee 2002).

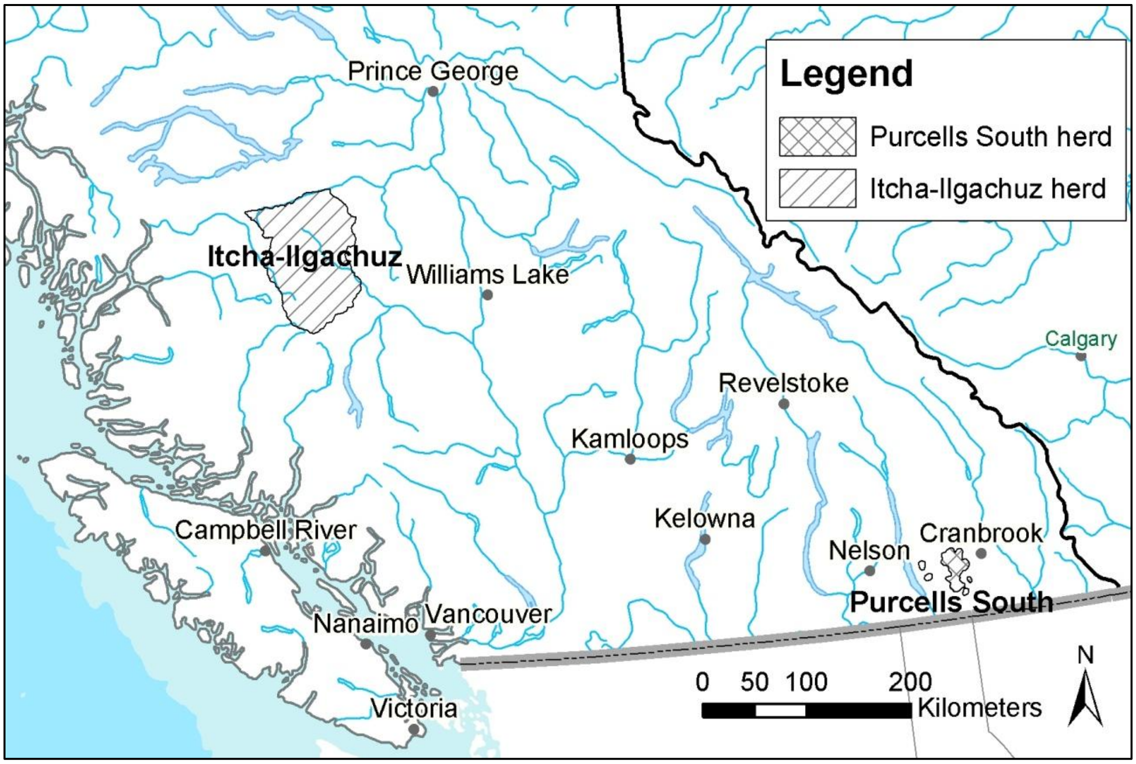

Figure 1. Location of the Itcha-Ilgachuz and Purcells South caribou herds in British Columbia. (Herd location data provided by the Ministry of Environment (2008), accessed August 2011.)

METHODS

I constructed a Bayesian stock assessment model to estimate the current population size and structure of the Itcha-Ilgachuz caribou herd and project potential population size and structure into the future based on different translocation removal options. Bayesian stock assessment models are commonly used in fisheries management and are gaining popularity in wildlife management because of their value in incorporating uncertainty in population parameters into the model and evaluating the outcomes of different management actions (Pascual & Hilborn 1995; Hatter 1998; Cooper et al. 2003; Conn et al. 2008). Bayesian methods are also useful in that they allow prior knowledge about the parameters being estimated to be incorporated into the analysis (Hobbs & Hilborn 2006).

Data

To fit the stock assessment model, I used data collected by the BC Ministry of Environment from 1995 to 2010. The available data included annual hunter harvest reports, periodic population surveys, and sightability correction factors from a radio telemetry project. I only used data from the period 1995 to 2010 because the methodology for the population surveys was standardized from 1995 onwards and is therefore considered to be more reliable (Hatter & Young 2004).

Annual hunter harvest reports provided the number of caribou killed each year by hunters. Harvested caribou are required to be inspected by provincial government staff or their contractors within 30 days of the kill. During this inspection, data on the sex, age, and location of the kill are collected. First Nations' harvest for food, social, and ceremonial purposes is not required to be reported. These unreported harvests, along with unreported illegal harvest and wounding losses, were not explicitly modelled, but are assumed to be accounted for in the natural mortality rate. That is, unreported harvest and wounding loss was assumed to be proportional to abundance, and as such the natural mortality rate included mortalities due to natural causes (e.g. predation) plus unreported human caused mortality.

Provincial government biologists have conducted aerial population surveys of the Itcha-Ilgachuz herd up to three times annually. In late June, post-calving surveys documented the number of adult females (cows), adult males (bulls), yearling females, yearling males and juveniles (calves) (Young & Freeman 2003). A total count method was used which attempts to enumerate all animals using 100% flight coverage of the area inhabited by the population (Resources Information Standards Committee 2002). Even with the total count method, however, it is almost impossible to observe every individual in a free-ranging ungulate population. Therefore, it was necessary to correct the population counts to account for the animals missed using a sightability correction factor. The sightability correction factor is a measure of the number of animals in the population relative to the number of animals observed. One way to estimate a sightability correction factor is by using mark-resight methods. In the Itcha-Ilgachuz herd, radio-collared cows provided marked individuals, allowing the calculation of the total abundance of cows using the Joint Hypergeometric Maximum Likelihood Estimator (JHE) in the NOREMARK computer statistical package for mark-resight data (White 1996; Young & Freeman 2003). The radio-collared animals were part of a radio-telemetry project conducted from 1995 to 2003 that collared 40 adult female caribou to study habitat use (Young & Roorda 1999). The sightability correction factor derived for the June cow abundance was also applied to the calf count in June. Because calves are with their mothers in June, it was reasonable to expect they would have been seen with the same accuracy as cows. Sightability correction factors were only available for 1996-2003, so the mean sightability correction factor from these years was used for all other years. At the time of the June survey, adult and yearling males and some yearling females were often using lower elevation habitats than the adult females, and therefore would not be seen with the same accuracy (Resources Information Standards Committee 2002; N. Freeman, Ministry of Environment, personal communication). Because bulls and yearlings had an unknown sightability, abundance estimates for these animals could not be derived from the survey counts. In addition, the June bull:cow ratios were not included in the model fitting because they were assumed to be biased due to their different sightabilities.

The rut survey was conducted in October after the fall hunt and documented the number of cows, calves and bulls to determine bull:cow and calf:cow ratios (Young & Freeman 2001). Due to difficulties in distinguishing yearlings of both sexes from cows, yearlings were included in the cow classification. It was not possible to attempt total population counts at this time because many groups of caribou were believed to be missed under tree cover (N. Freeman, personal communication). However, during the survey, the animals were in mixed groups, and the sightability of the different classes was thought to be similar. Therefore, bull:cow and calf:cow ratios were considered representative of the population.

The late-winter survey in March documented adults (bulls, cows, and yearlings combined) and calves to determine calf:adult ratios (Young & Freeman 2001). Similar to the October survey, total counts were not possible in March because many animals were concealed in habitats where they were difficult to observe. However, the relative sightability of adults and calves was not believed to be affected by vegetative cover at that time of year, and therefore calf:adult ratios based on the observed animals were considered representative of the population.

The October and March surveys were used only to determine sex and age ratios, not total abundance because the sightability of the animals during these surveys was unknown and likely changed from year to year. The only abundance data used in fitting the model were the calf and cow data in June because only this segment of the population had a sightability correction factor.

Model Structure

I built a sex and stage-based population dynamics model with the software package AD Model Builder (ADMB Project 2009). Because the population surveys occurred at three different times during the year, the population (calves, yearlings and adults) was modelled accounting for these time periods so that the survey data could be fit to the model (Figure 2).

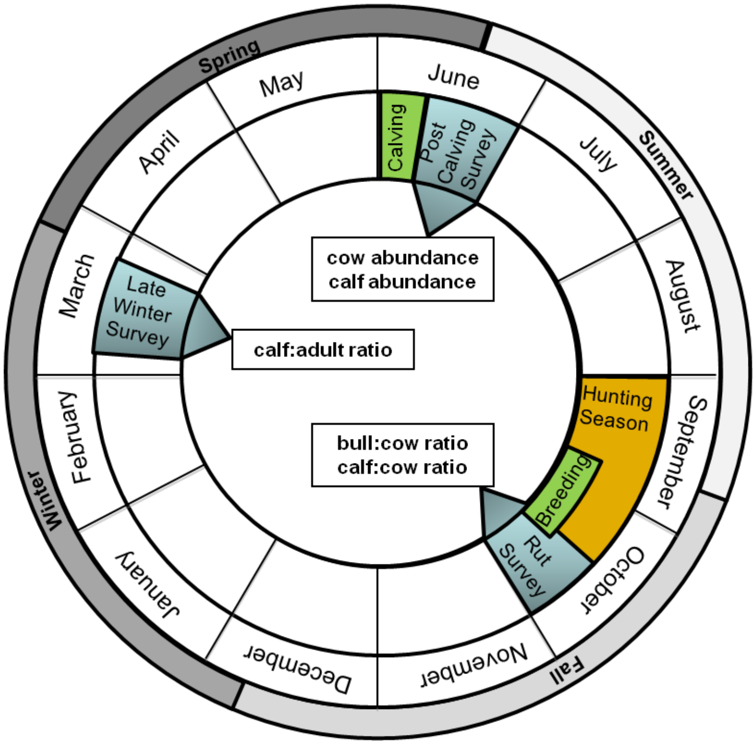

Figure 2. A "caribou year." The year starts at the beginning of June just prior to calving. A survey occurs after calving that provides data on cow and calf abundance. The hunting season runs from early September to mid-October. The rut, or breeding period, occurs in September and October. The rut survey is conducted after the hunt, in the latter part of October and provides bull:cow and calf:cow ratios. The late winter survey occurs in March and provides a calf:adult ratio.

The year starts in the beginning of June just prior to calving. The initial population size of calves, cows and bulls in June were estimated parameters in the model. The model was not able to estimate an initial population size for yearlings because there was no data to which yearling abundance may be fit. Therefore, the initial population size of yearling classes were derived from the initial population of calves assuming a stable age distribution, such that, at time=1:

$$N_{yf,j,1} = p * N_{c,j,1} * S_c \tag{1}$$

$$N_{ym,j,1} = (1 - p) * N_{c,j,1} * S_c \tag{2}$$

where $N_{yf,j,1}$ is the number of yearling females (yf) in June (j) in year 1, $N_{ym,j,1}$ is the number of yearling males (ym) in June (j) in year 1, p is the proportion of female calves at the end of their first year, $N_{c,j,1}$ is the number of calves (c) in June (j) in year 1 and S_c is the annual calf survival. There would be little impact on the results if the assumption of the stable age distribution were not correct. An under or over estimation in the abundance of a one year age class, such as yearlings, does not have much impact on the model because this is a relatively small component of the entire population. After June of year 1, the population abundances for each stage in June were modelled as follows:

$$N_{c,j,t} = N_{af,m,t-1} * R \tag{3}$$

$$N_{yf,j,t} = p * N_{c,m,t-1} \tag{4}$$

$$N_{ym,j,t} = (1 - p) * N_{c,m,t-1} \tag{5}$$

$$N_{af,j,t} = N_{yf,m,t-1} + N_{af,m,t-1} \tag{6}$$

$$N_{am,j,t} = N_{ym,m,t-1} + N_{am,m,t-1} \tag{7}$$

where R is recruitment rate (calves per adult female), $N_{x,z,t}$ is the number of individuals at stage x (c, calf; yf, yearling female; ym, yearling male; af, adult female; am, adult male), in month z (j, June; o, October; m, March) for a caribou year, t. The notation $t-1$ refers to the parameter value for the previous year. p is the proportion of calves entering the yearling age class that are female. The value of p was set equal to 0.5, because the sex ratio at birth and through the first year of life is likely close to 1:1 (Fancy et al. 1994, Bergerud 2000). Note that recruitment in this model refers to the number of calves per female that survive until the time of the June survey (the end of the calving period) and includes early neonatal mortality. In October and March the population abundances for each stage were modelled as follows:

$$N_{x,o,t} = N_{x,j,t} * S_{x,s} - H_{x,t} \tag{8}$$

$$N_{x,m,t} = N_{x,o,t} * S_{x,w} \tag{9}$$

where $S_{x,s}$ is the survival for stage x in the summer (s), $S_{x,w}$ is the survival for stage x in the winter (w) and $H_{x,t}$ is the known harvest on stage x in year t. Unreported mortality, including First Nations' harvest, wounding loss, and illegal harvest was assumed to be proportional to caribou abundance and included as part of the natural mortality rate.

Yearling females and yearling males were included in the cow classification during the October and March surveys because they were indistinguishable from adult females at that time. Therefore, the estimates of yearling males and yearling females were included in the estimated cow portions of the calf:cow and bull:cow ratios. The modelled calf:cow ratio in October was:

$$N_{c,o,t}/(N_{yf,o,t} + N_{ym,o,t} + N_{af,o,t}). \tag{10}$$

The modelled bull:cow ratio in October was:

$$N_{am,o,t}/(N_{yf,o,t} + N_{ym,o,t} + N_{af,o,t}). \tag{11}$$

The modelled calf:adult ratio in March was:

$$N_{c,m,t}/(N_{yf,m,t} + N_{ym,m,t} + N_{af,m,t} + N_{am,m,t}). \tag{12}$$

In the population projections, removals for translocation were assumed to occur between March and June (i.e. after winter mortaily had taken place), so that the modelled June abundance changed from equations (6) and (7) to

$$N_{af,j,t} = N_{yf,m,t-1} + N_{af,m,t-1} - R_{af,t} \tag{13}$$

$$N_{am,j,t} = N_{ym,m,t-1} + N_{am,m,t-1} - R_{am,t} \tag{14}$$

where $R_{am,t}$ and $R_{af,t}$ represent the number of removals each year (t) of adult males (am) and adult females (af), respectively.

Because sightability corrected data on yearling abundance was unavailable, there was not enough information for the model to estimate survival rates for male and female yearlings. Yearling survival rates were assumed to equal the adult natural survival rates for each sex (Bergurud 1980). This avoided having to estimate two additional parameters (male and female yearling survival) or give the model a fixed yearling survival rate. Yearlings were still included as a separate age group from adults for three reasons: (1) in the June survey, the female yearlings did not have the same sightability as the cows so the data could not be summed to fit a combined yearling and adult age class in the model; (2) in the October survey both male and female yearlings were counted in the cow classification, so the model had to be able to put the yearlings and cows together to fit the data, which would not have been possible if the yearling males were grouped with the bulls; and (3) yearling females only minimally contribute to the production of calves (Bergerud 1980; Fancy et al. 1994), and as such, their abundance should not be combined with adult females.

Survival for each age class was calculated using an instantaneous mortality rate and proportion of mortality in each season. Using an instantaneous mortality rate provides a way to calculate mortality rates for different time periods (Hilborn & Walters 1992), and is used here to partition mortality between summer and winter. The model was set up to have hunter harvest mortality occur after the summer survival rate was applied and before the winter survival rate was applied Therefore, natural mortality during the hunting season (September–October) was assumed to be zero. Hunting mortality and natural mortality likely do occur simultaneously, however, the resulting bias of having all the natural mortality occur first would be very minimal. In order for the model to provide the best fit for the bull:cow ratio in October the summer survival rate may be estimated very slightly higher as a result of the natural mortality occurring before any hunting mortality. I did not estimate a third survival rate (in addition to the summer and winter survival) for the mortality in April-May: mortality in these months was assumed to be zero. The majority of caribou mortality occurs in the other ten months of the year (Wittmer 2004; McLoughlin et al. 2003), and because the March data that the model is fitting to is a ratio (calves:adults), mortality in April and May would only affect the model if the mortality was very different between adults and calves, which is not expected (Wittmer 2004; Bergerud 2000). Summer (June–August) and winter (November–March) survival were modelled as

$$S_{x,summer} = e^{-(m_x * b_x)} \tag{15}$$

$$S_{x,winter} = e^{-\left(m_x * (1-b_x)\right)} \tag{16}$$

where m is the instantaneous mortality rate for the stage of animal (x) and b is the proportion of mortality that occurs in the summer. The proportion of mortality that occurs over the winter is $1 - b$. Annual survival was the product of summer survival and winter survival.

June population surveys showed a decline in numbers after 2003. The cause is unknown, but multiple hypotheses were developed and explored with the population model. Three model variations were used to test the sensitivity of the results to different hypotheses about what might be causing the decline in observed June numbers. The first model attributed the decline in observed numbers to be the result of random observation error and assumed the underlying process (i.e. population dynamics) of this herd to be constant over the time period for which data was fit. All data from 1995 through 2010 was used to fit this model. The second model assumed the three June population surveys after 2003 reflect the actual abundance of caribou and that there has been a change in the natural processes acting on the herd. This model allowed a change in the survival and recruitment parameters after the June 2003 survey. Calves, cows and bulls had two survival rates: one for the period 1995–2002 and one for the period 2003–2010 (the second time period for the survival rates starts in 2003 because survival rates are applied after the June abundance estimate). Similarly, recruitment rates were also allowed to vary between the two time periods such that there was one recruitment rate for the period 1995-2003 and another for 2004-2010 (the second time period for the recruitment rate starts in 2004 because recruitment is applied before the June abundance estimate). The population projections used the mortality and recruitment rates that were estimated for the latter time period. The third model attributed the decline in the number of caribou observed in recent years to a change in the accuracy of the population survey; specifically, animals dispersed to new areas and were not counted in the survey. An additional parameter was estimated to give a sightability correction factor for the post-2003 June calf and cow numbers instead of using an average of the sightability from the earlier surveys. It was assumed that the survival and recruitment parameters did not change, they remained constant throughout the time period 1995–2010. These three models represent different "states of nature," which explicitly recognize the uncertainty in the population dynamics model (Peterman & Anderson 1999).

I considered and rejected a model that included density-dependent regulation. There was no indication in the data that density dependence was acting on the Itcha-Ilgachuz herd over the time period studied. Density dependent regulation normally first affects fecundity and juvenile survival (Eberhardt 2002). Using linear regression, I explored the relationship between the summer calf survival (calculated by dividing the October calf:cow ratio by the

June calf:cow ratio) and the abundance of adult females June (an index of population size). The linear regression showed no significant relationship between the two variables (R^2 =0.0302 slope= 0.00006 p=0.16). Regressing the June calf:cow ratio (an index of fecundity) against the number of adult cows also showed no significant relationship (R^2 =0.0524, slope=-0.000065, p=0.47). Because neither calf survival nor fecundity showed a decline with increasing cow population size (from 800 to 1700 animals), I assumed density dependence had not affected the population in a manner that I could readily model.

Model Fitting

Bayesian estimation is used in model fitting to calculate a probability distribution for estimated parameters and outcomes of interest. This is called the posterior probability distribution and can be used to calculate the probability of each hypothesized parameter truly taking on a value within any specified range. Calculation of the posterior probability distribution requires two things: a prior probability distribution for the estimated parameters and a likelihood function for the data. The prior probability distribution is based on prior knowledge about the parameter and states a probability for the parameter taking on hypothesized values within a range before the data are considered. If there is no previous information available about a parameter, a uniform prior can be used which gives equal weight to all hypothesized parameter values (Walters & Ludwig 1994). The likelihood function is used to calculate the fit of the model to the data over a range of parameter values.

I constructed prior probability distributions for annual calf, cow, and bull survival as well as recruitment. Each of these priors took the form of a beta distribution which has a range from zero to one (Law & Kelton 1982). The probability distribution function is described by the equation

$$P(S) = \frac{S^{\alpha-1}(1-S)^{\beta-1}}{B(\alpha,\beta)} \tag{17}$$

where S is the survival parameter (taking values from 0 to 1), and α and β are shape parameters that define the shape of the distribution. B is a normalization constant that ensures the total probability integrates to unity. I used estimates of female survival from the radio telemetry study as the prior for adult female survival (N. Freeman, unpublished data). Survival rates of the collared females from 1996 to 2002 were calculated using the Kaplan-Meier estimator (N. Freeman unpublished data) (Kaplan & Meier 1958; White 1996). I constructed prior probability distributions for calf survival based on Seip & Cichowski (1996); adult male survival based on Fancy et al. (1994) and Bergerud (2000); and recruitment based on Seip (1992) and Seip & Cichowski (1996) (Figure 3). The mean of the prior for adult female survival was 0.90 (SD 0.069), calf survival was 0.60 (SD 0.200), adult male survival was 0.83 (SD 0.103) and recruitment was 0.56 (SD 0.178). Priors were applied to annual survival rates (summer survival * winter survival). For the remaining parameters—including the initial population size of each stage and the proportion of survival in the summer— uninformative or uniform priors were used because there were no reliable data to develop prior distributions. See Appendix 1 for detailed information on the choice of priors.

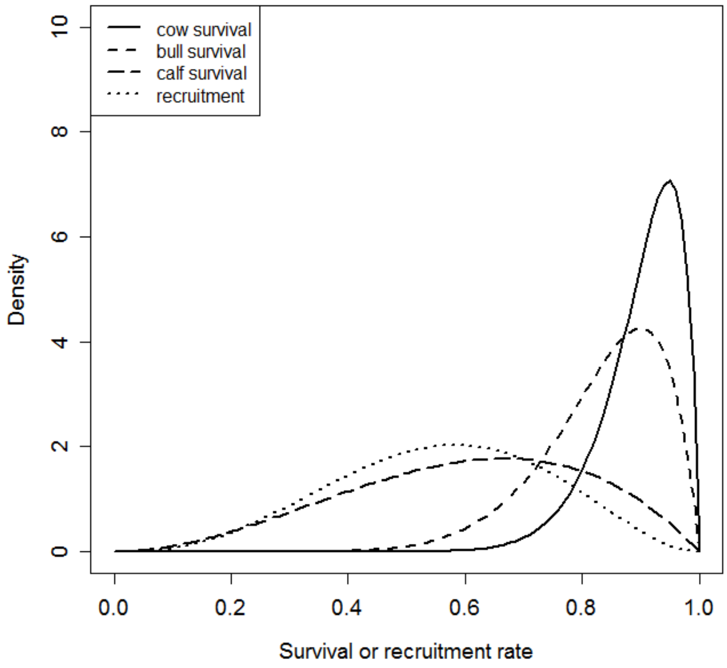

Figure 3. Prior probability distributions for cow survival (shape parameters α = 16.62, β = 1.85), bull survival (shape parameters α = 10, β = 2), calf survival (shape parameters α = 3, β = 2), and recruitment (shape parameters α = 3.8, β = 3).

Likelihood functions were used to determine the relative degree of fit of the model to the data. I used lognormal likelihood functions for the abundance of calves and cows in June, for the bull:cow ratio and calf:cow ratio in October, and for the calf:adult ratio in March. The lognormal likelihood was used because the lognormal distribution is similar in appearance to the gamma distribution (Castella & Berger 1990) which was recommended by Dennis and Constantino (1988) for indices of abundance, and the ratio of two log-normally distributed variables is lognormal (Evans et al. 1993). Cooper et al. (2003) also modelled age and sex ratios and abundance estimates with the lognormal distribution. The lognormal likelihood function for the set of parameters (θ) given the data on the abundance of cows in June (x_1) is described by the equation:

$$L(\theta|x_1) = \prod_{t=1995}^{2010} \left[\frac{1}{\sqrt{2\pi}\sigma_1 x_{1,t}} \exp\left(\frac{-\left[\log(x_{1,t}) - \log(u_{1,t})\right]^2}{2\sigma_1^2} \right) \right]^{I_{1,t}} \qquad (18)$$

where t refers to the year in the time series of data that goes from 1995 to 2010, σ_1 is the residual standard deviation of the observed data, $x_{1,t}$ is the data for abundance of cows in year t and $u_{1,t}$ is the model-derived estimate for cows in June in year t provided by the population dynamics model. $I_{1,t}$ equals 1 if data is available for year t and equals zero otherwise. This allowed the likelihood function to be fit with an incomplete time series of data. The parameter set was estimated by minimizing the negative log-likelihood, such that equation 18 was transformed to

$$-\log L(\theta|x_1) = \sum_{t=1995}^{2010} \left[\left(\frac{\log(2\pi)}{2} + \log\left(\sigma_1 x_{1,t}\right) + \frac{\left[\log(x_{1,t}) - \log(u_{1,t})\right]^2}{2\sigma_1^2} \right) I_{1,t} \right]. \qquad (19)$$

The same equation was applied to the abundance of calves (x_2), the bull:cow ratio (x_3), the calf:cow ratio (x_4), and the calf:adult ratio (x_5). The total likelihood of the parameter set was then

$$-\log L(\theta|x_1, x_2, x_3, x_4, x_5) =$$

$$-\log L(\theta|x_1) - \log L(\theta|x_2) - \log L(\theta|x_3) - \log L(\theta|x_4) - \log L(\theta|x_5). \qquad (20)$$

Posterior probability distributions for parameter estimates and projections were calculated using Markov chain Monte Carlo methods. ADMB uses a version of the Metropolis-Hastings algorithm to search the parameter space and determine the relative probability of parameter values (Gelman et al. 1995). For model 1, the MCMC chain was run for 1,000,000 iterations with a burn-in of 400, and then thinned to every 200. For model 2, the MCMC chain was run for 2,000,000 iterations with a burn-in of 800 and thinned to every 400. For model 3, the MCMC chain was run for 1,000,000 iterations with a burn in of 400 and thinned to every 200. Autocorrelation dropped to near zero with this thinning. The chains were visually inspected for convergence. In addition, the R package CODA (Plummer et al. 2006) was used to implement the Heidelberger and Welch stationary and halfwidth tests; all parameters passed.

Population Projections

The population projections were done simultaneously with model fitting to allow uncertainty in model parameters and the correlation between parameter estimates to be propagated into the projections. For model 2, which had two periods for the recruitment and survivals parameters, the parameter values for the latter period were used to model the future projections. Population projections were made ten years into the future. Translocation removals occurred during the first two years of projections. The population was projected another eight years after the translocation removals were completed to see how removals would affect the subsequent population trajectory. Hunter harvest for 2010 onwards was set at 35 bulls per year, which was the average of the hunter harvest for the ten-year period 2000-2009. Hunter harvest has been relatively stable over the past 20 years, so it was reasonable to assume this trend would continue into the future.

Three different removal scenarios were tested with each of the three models. The first scenario modelled the option of not using the Itcha-Ilgachuz herd for translocations and thus provided a baseline for assessing the impacts of the translocation removals. The second scenario removed 17 adult females and 3 adult males for translocation in each of two years, which was the recommended number of animals for translocation to the Purcells-South herd (Kinley 2010). The third scenario was to increase the removals to 170 adult females and 30 adult males. This third scenario was provided as a sensitivity analysis to illustrate how the population would react to a ten-fold increase in the recommended number of removals. For each management action, the model calculated the posterior probability distribution of the estimated population size for each stage in each future year. The effects of the removals for translocation on the Itcha-Ilgachuz herd were evaluated by calculating the ratio of the population size under the removal scenario to the population size with no removals for translocation.

Sensitivity Analysis

It was important to test the sensitivity of the model results to the priors used in the model. The amount of information contained in the data relative to the prior can be determined by comparing the posterior distribution of each parameter to its prior distribution. If the two are very similar, it indicates the data is uninformative and the results are being largely determined by the prior. I also calculated the posterior distributions using uniform priors for all the parameters to see how that changed the posterior distributions. If the posterior does not change as the prior distribution is changed, it indicates the data are informative and have a large influence on the posterior distribution (Cooper et al. 2003).

RESULTS

Model 1, or the constant growth model, had constant parameters and was not able to capture the post-2003 decline in the observed cow abundance; instead, it fit a gradual increase in abundance over the time period (Figure 4). Model 2, or the predation hypothesis model, allowed parameters to change after June 2003, and was able to capture the steep 1995-2003 increase in observed cow abundance followed by a post-2003 decrease. Model 3, or the dispersal hypothesis model, with a post-2003 change in the June calf and cow sightability correction factor, was also able to fit the steep decrease in observed cow abundance. The trend in the fit of the models to the June calf abundance was similar to the June cow abundance and is shown in Appendix 2. The observed October bull:cow ratio was fairly constant over the time period studied and all models were able to fit the trend in the bull:cow ratio (Figure 5). The observed October calf:cow ratio dropped after 2003; only model 2 was able to fit this decline (Figure 6). The trend of the fit of the March calf:adult ratio was similar to the October calf:cow ratio and is also shown in Appendix 2.

The ratio of the total population size (all age classes) in 2020 with removals to the population size in 2020 with no removals was calculated to determine the effect of the removals on the population size (Figure 7, Table 1). In the recommended removal scenario, this ratio is over 0.95 with all three models. The ratios with the extreme removals are lower and the probability distributions of the ratios are much wider (Figure 8, Table 1). The extreme removals affect the population in the same way, but at a much larger scale.

The model was fit to sightability corrected abundance data for cows and calves, and in some instances, the lower 95% credibility interval bound for the estimated cow or calf abundance was below the number of cows or calves actually observed during the survey. Model 1 (constant growth) had three years when the observed number of cows was higher than the estimated lower credibility interval bound and five years when the observed number of calves was higher than the estimated lower credibility interval bound. Model 3 (dispersal hypothesis) had one year when the number of cows was higher than the estimated lower credibility interval bound and three years when the observed number of calves was higher than the estimated lower credibility interval bound. This is a result of the model attempting to fit constant survival and recruitment rates to data that has an initial increase in observed numbers followed by a decrease. For these models, the abundance is underestimated in some years. This did not occur in model 2 (predation hypothesis), because it allowed parameter estimates to vary between the two time periods.

The average sightability correction factor for cows was 1.33, calculated using mark-resight methods from the radio-telemetry study. This means that on average, 76% of the cows and calves were counted in the surveys. In model 3, the estimated sightability correction factor from the model for the post-2003 surveys was 2.56 with a 95% credibility interval of 1.70–3.58. As such, the model estimated that only about 40% of the cows and calves were counted in the surveys. This means that to account for the observed survey numbers after 2003 if survival and recruitment parameters had remained constant, sightability would have dropped by about half. This is a substantial drop and is larger than the annual variation in sightability from the 1996-2003 surveys, which ranged from 1.1 to 1.6 (or 62-90% of animals observed).

The posterior distributions for the annual calf, cow and bull survival rates do not appear to be heavily informed by the priors, as they are significantly narrower than the prior distributions (Figure 9, Figure 10, Figure 11 and Figure 12). In fact, the survival and recruitment rate estimates changed very little when uniform priors were used, indicating that the posterior distributions were informed by the data, with the priors having little to no influence (for posterior probability distributions with uniform priors see Appendix 2). In model 2 (predation hypothesis), the posterior distributions for the survival and recruitment rates in the second time period were wider and therefore less precise than the distributions for the first period. There were fewer data points to inform the estimates for the second time period because the second time period is shorter and surveys were not conducted as frequently, with only three post calving surveys, one rut survey, and no late winter surveys occurring after 2003. The posterior distributions for cow survival were the narrowest, followed by bull survival, with calf survival being the widest. The wide posterior for the calf survival rate is likely due to the fact that calf survival is highly variable (Gaillard et al. 1998) which causes uncertainty (lack of precision) in the estimate of the average survival rate, whereas female survival is the least variable (Gaillard et al.

1998) and therefore is estimated more precisely. In model 2, the survival and recruitment parameters declined from the first to the second time period. All of the models estimated that the majority of the mortality occurs in the summer (model 1—86%, model 2—83%, model 3—87%), consistent with findings in other studies. Seip & Cichowski (1996) reported mortality causes in eight caribou herds, six of which had the major cause of mortality occurring in summer (this included an earlier study of the Itcha-Ilgachuz herd). McLoughlin et al. (2003) found that 78.8% of caribou mortality occurred from April through October.

In all three models, there very little difference between the removal and no removal scenarios for the projected June cow abundance (Figure 13, Figure 14, and Figure 15), the October bull:cow ratio (Figure 16, Figure 17 and Figure 18), and the October calf:cow ratio (Figure 19, Figure 20 and Figure 21). Under the extreme removal scenario, the projected cow abundance initially declines during the removals in all three models and then shows a similar trend to the no removal and recommended removal scenarios. The projected bull:cow ratio initially increases under the extreme removal scenario in all three models due to the reduction in cows and then follows the same trend as the no removal and recommended removal scenarios. The projected calf:cow ratio dips very slightly with the extreme removal scenario in all three models but then rises again to the same level as the no removal and recommended removal scenario. Projections of future June calf abundance had a similar trend to cow abundance and are presented in Appendix 2. Projections of future March calf:adult ratios had a similar trend to the projections of future October calf:cow ratios and are also presented in Appendix 2. The uncertainty in the estimates of future herd abundance and age and sex ratios propagates over time leading to greater uncertainty with more distant projections.

In model 2 there is a large amount of uncertainty in the projected bull abundance (Figure 22) relative to the projected cow abundance (Figure 14). This is due to the uncertainty in the bull survival rate after June 2003, which has only one data point to inform the estimate. With the large uncertainty in the bull abundance, there is some probability that the bull abundance will drop to zero before 2020 (i.e. the lower 95% credibility interval goes to zero). Generally, the abundance of males is not a limiting factor for reproduction because of the harem breeding system; though a ratio of less than 1:10 bulls to cows would likely cause recruitment to drop (Holand et al. 2002). This is not accounted for in the model, however the model also does not account for management feedback, which would reduce harvest before bull abundance dropped to a critical level. Therefore, it is unlikely that the situation would occur where bull abundance was limiting productivity.

The uncertainty in the projected bull abundance in model 2 results in a very wide range in the projected October bull:cow ratio (Figure 17). Nonetheless, the median bull:cow ratio is declining because the bull abundance is declining faster than cow abundance. This is attributed to the 35 bull per year hunter harvest. If the harvest were stopped the bull:cow ratio would increase slightly and level off as the population reached a stable age distribution (Figure 23).

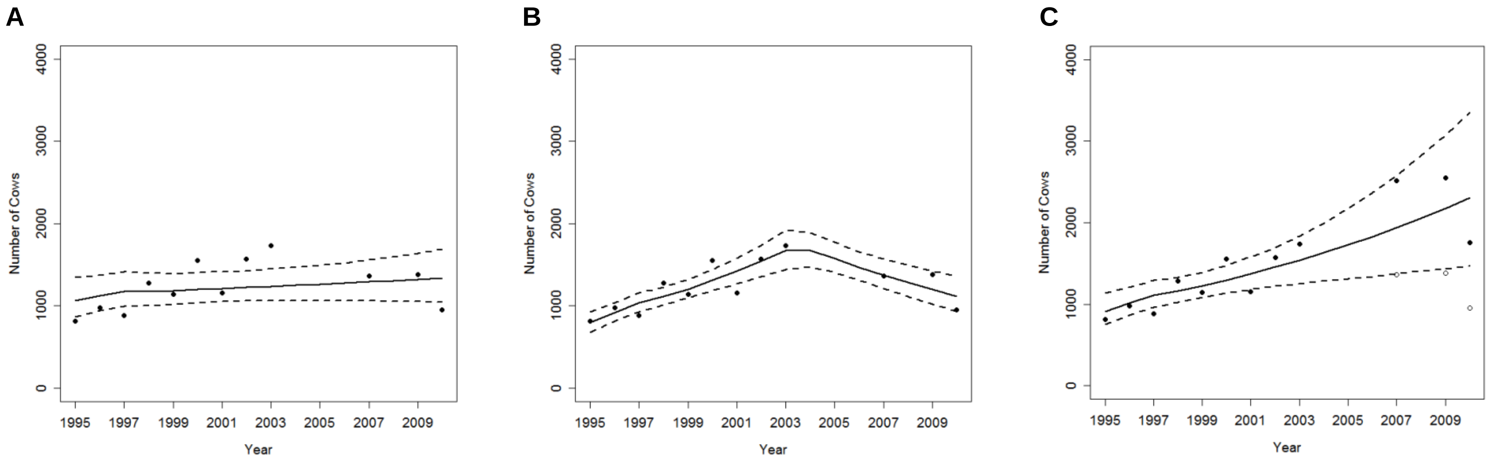

Figure 4. Fit of the model to the number of cows in June. Models 1, 2 and 3 (A, B and C, respectively), shown with median (solid line) and 95% credibility interval (dotted lines). The dots represent the data points being fit. In model 3, the open circles show the non-corrected data, for reference.

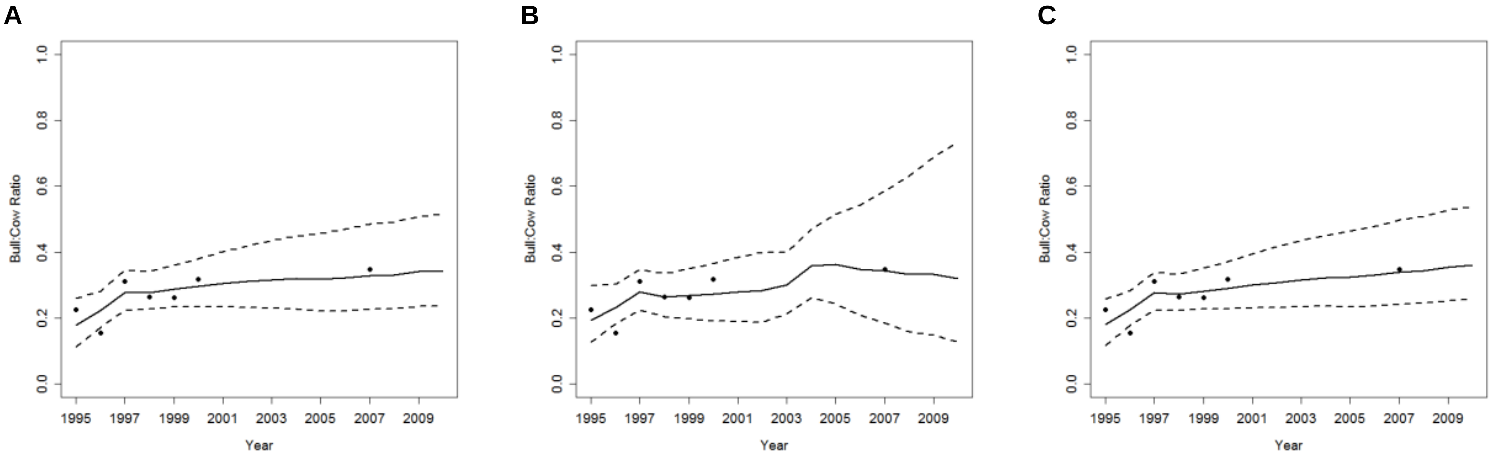

Figure 5. Fit of the model to the bull:cow ratio in October. Models 1, 2 and 3 (A, B and C, respectively), shown with median (solid line) and 95% credibility interval (dotted lines). The dots represent the data points being fit.

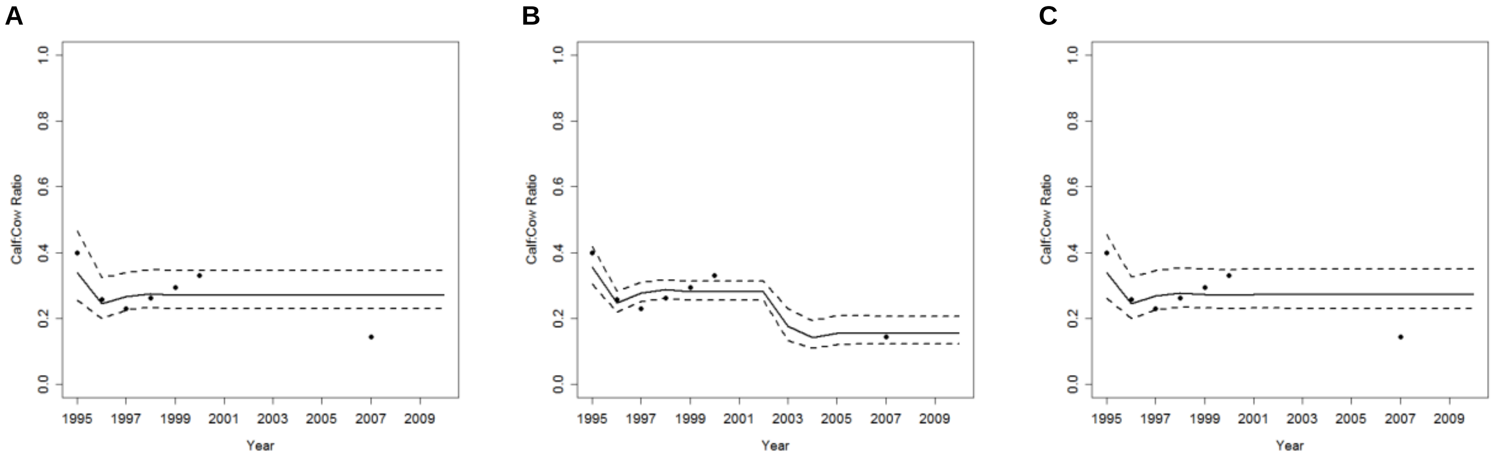

Figure 6. Fit of the model to the calf:cow ratio in October. Models 1, 2 and 3 (A, B and C, respectively), shown with median (solid line) and 95% credibility interval (dotted lines). The dots represent the data points being fit.

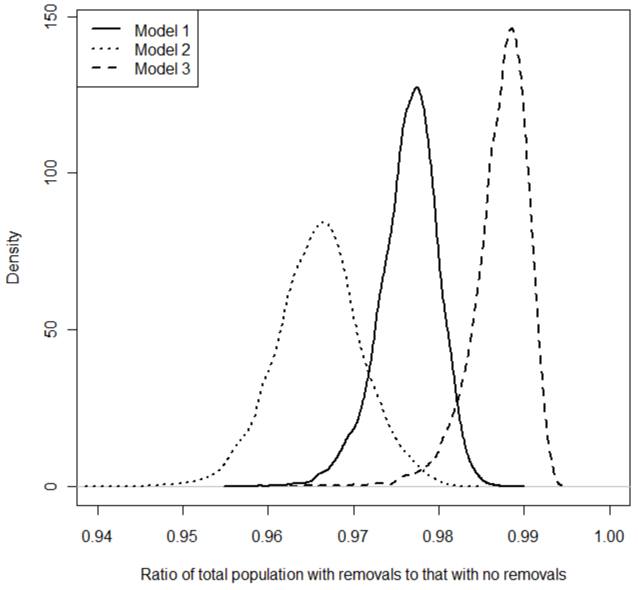

Figure 7. **The posterior probability distribution of the ratio of the total number of caribou in 2020 under the recommended removal scenario to the total number of caribou in 2020 with no removals. The results from all models are shown.**

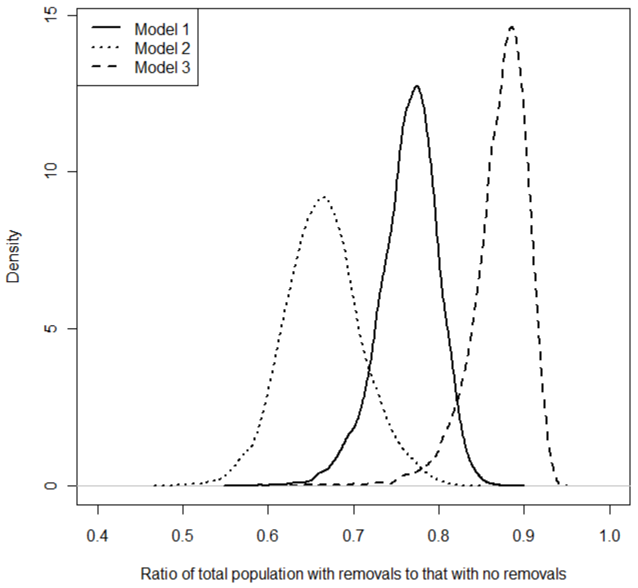

Figure 8. **The posterior probability distribution of the ratio of the total number of caribou in 2020 under the extreme removal scenario to the total number of caribou in 2020 with no removals. The results from all models are shown. Note the difference in the scale of the x- and y-axis compared to Figure 7.**

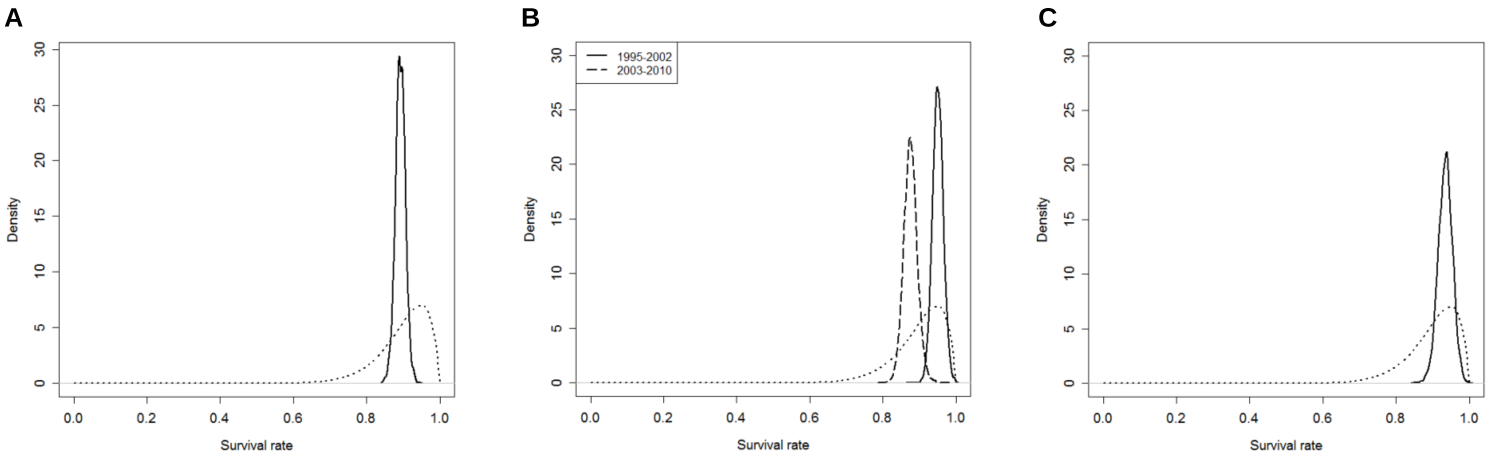

Figure 9. Prior (dotted line) and posterior (solid or dashed line) probability distributions for annual cow survival. Models 1, 2 and 3 (A, B and C, respectively).

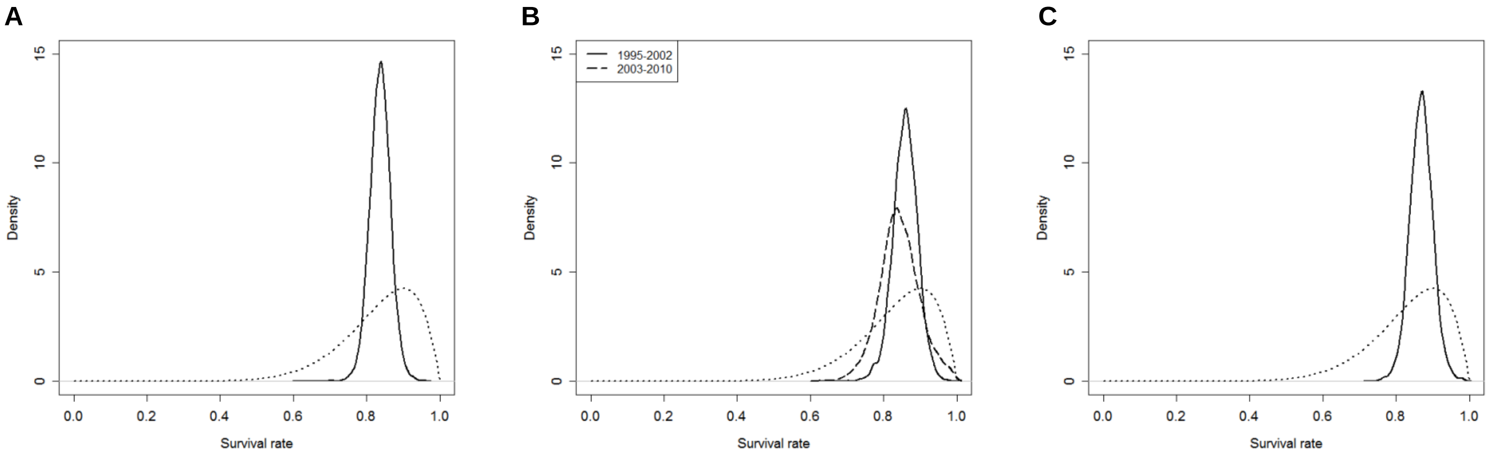

Figure 10. Prior (dotted line) and posterior (solid or dashed line) probability distributions for annual bull survival. Models 1, 2 and 3 (A, B and C, respectively).

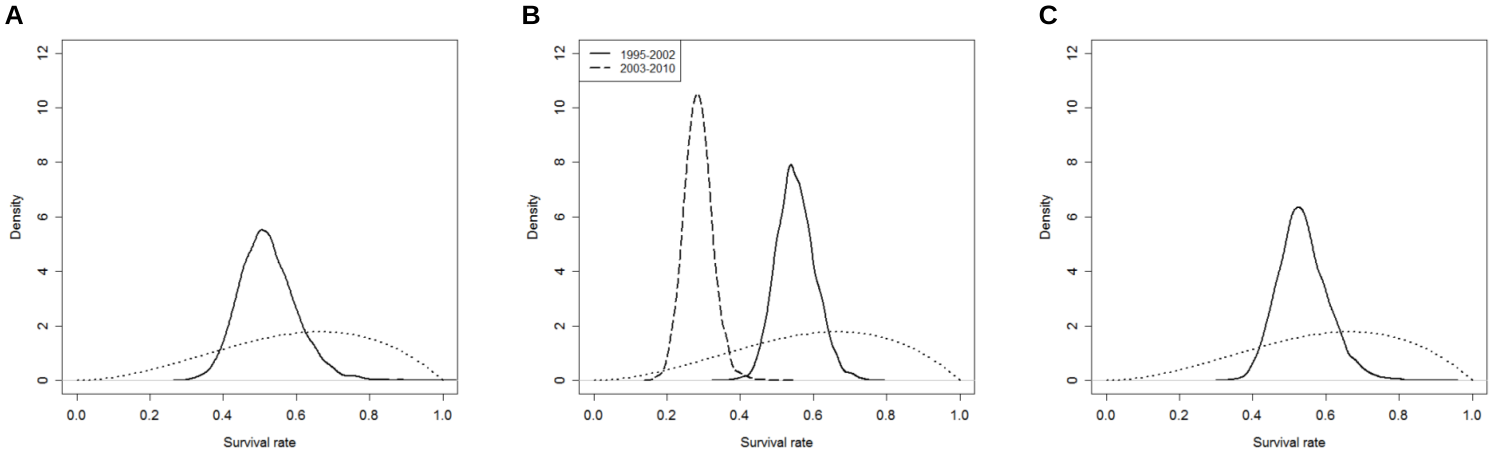

Figure 11. Prior (dotted line) and posterior (solid or dashed line) probability distributions for annual calf survival. Models 1, 2 and 3 (A, B and C, respectively).

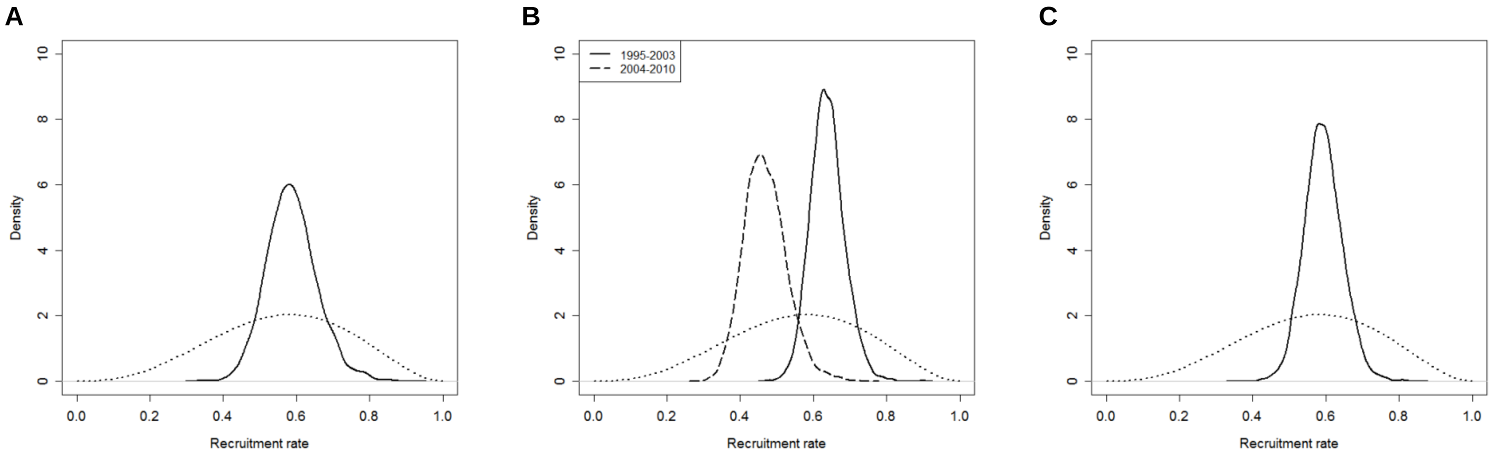

Figure 12. Prior (dotted line) and posterior (solid or dashed line) probability distributions for recruitment. Models 1, 2 and 3 (A, B and C, respectively).

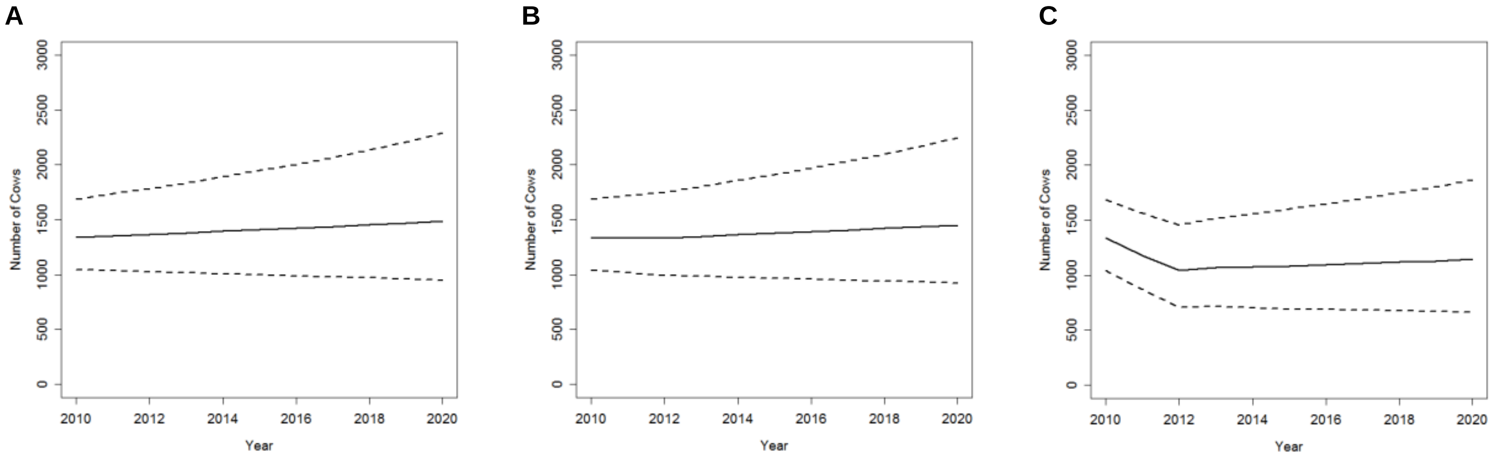

Figure 13. Model 1 projections of the number of cows in June. No removal, recommended removal and extreme removal scenarios (A, B and C, respectively), shown with median (solid line) and 95% credibility interval (dotted lines).

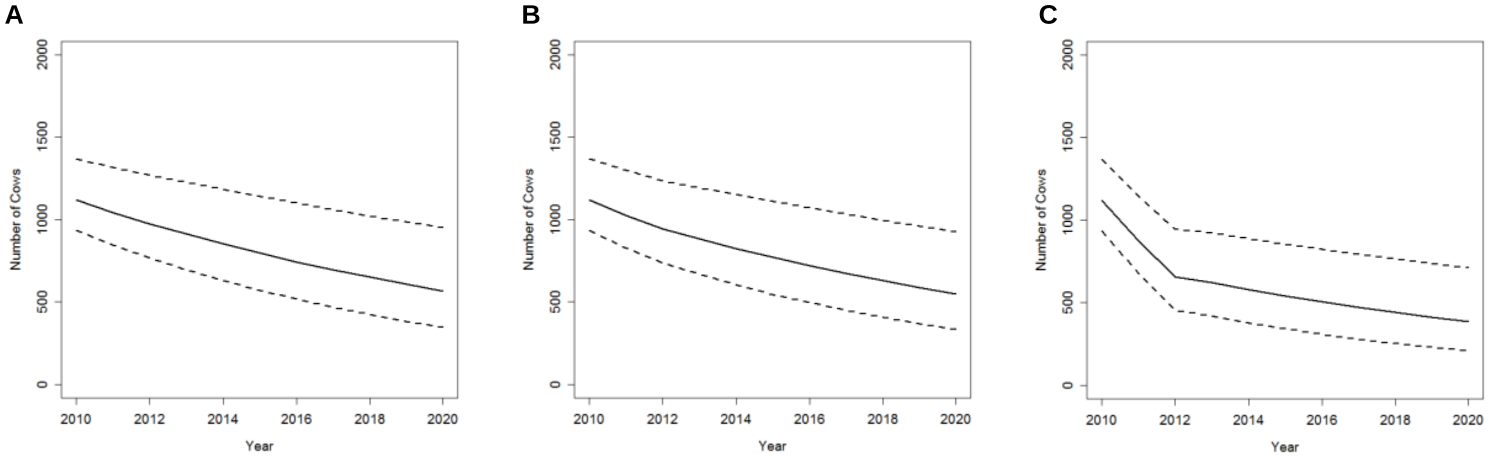

Figure 14. Model 2 projections of the number of cows in June. No removal, recommended removal and extreme removal scenarios (A, B and C, respectively), shown with median (solid line) and 95% credibility interval (dotted lines).

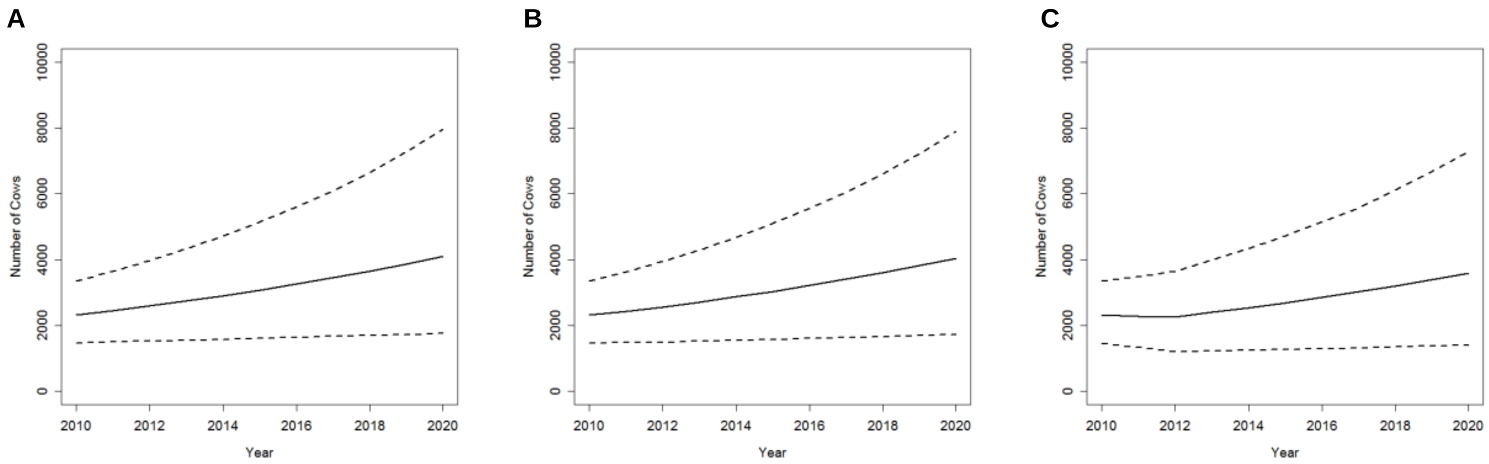

Figure 15. Model 3 projections of the number of cows in June. No removal, recommended removal and extreme removal scenarios (A, B and C, respectively), shown with median (solid line) and 95% credibility interval (dotted lines).

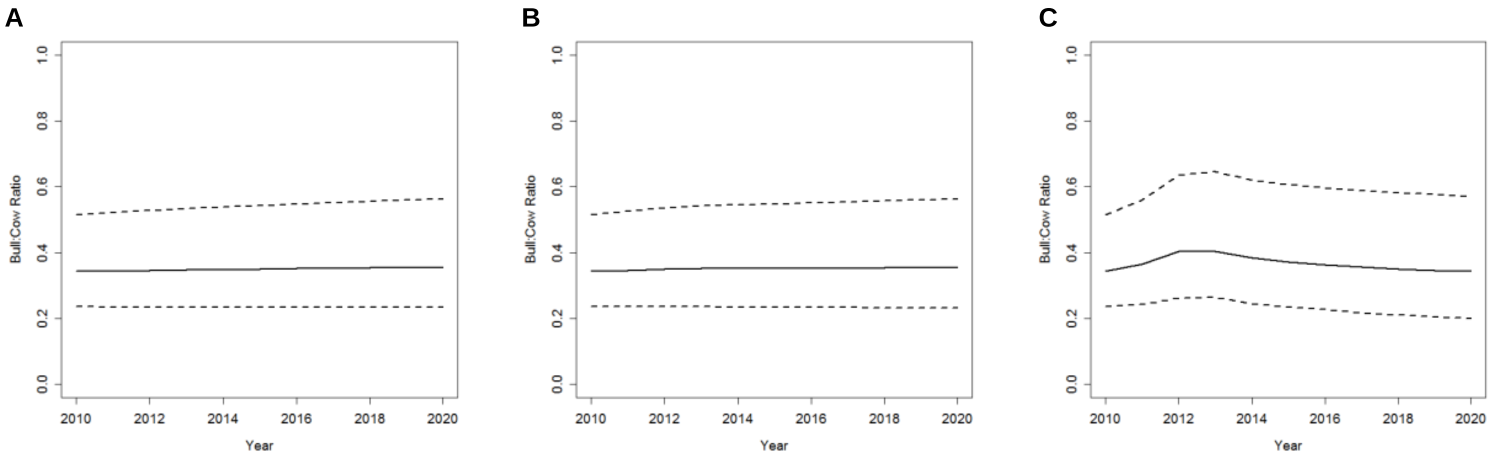

Figure 16. Model 1 projections of the bull:cow ratio in October. No removal, recommended removal and extreme removal scenarios (A, B and C, respectively), shown with median (solid line) and 95% credibility interval (dotted lines).

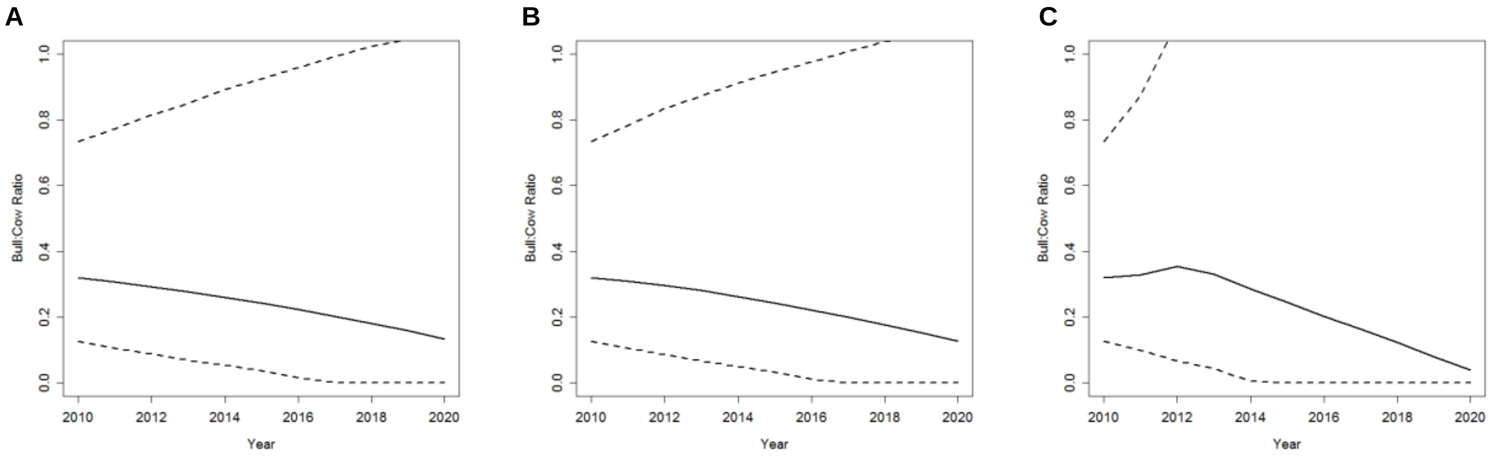

Figure 17. Model 2 projections of the bull:cow ratio in October. No removal, recommended removal and extreme removal scenarios (A, B and C, respectively), shown with median (solid line) and 95% credibility interval (dotted lines).

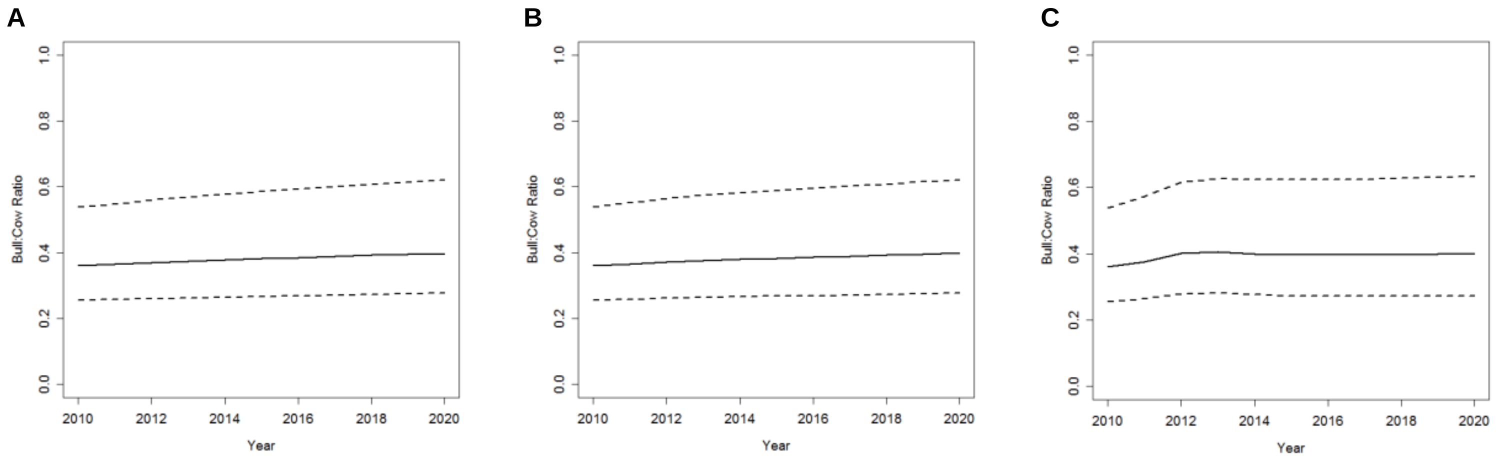

Figure 18. Model 3 projections of the bull:cow ratio in October. No removal, recommended removal and extreme removal scenarios (A, B and C, respectively), shown with median (solid line) and 95% credibility interval (dotted lines).

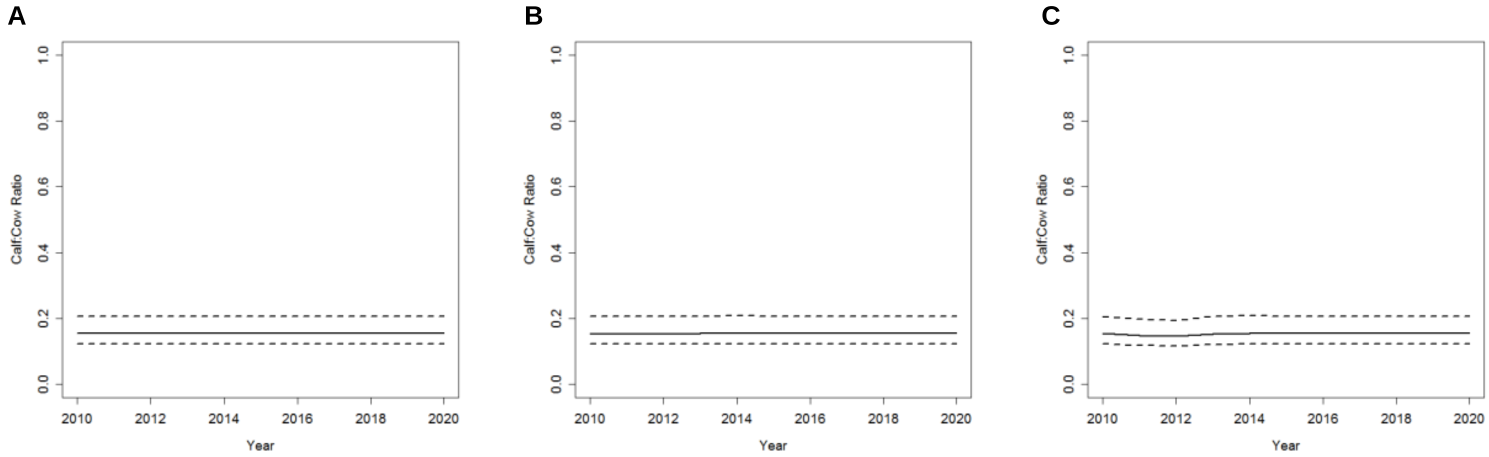

Figure 19. Model 1 projections of the calf:cow ratio in October. No removal, recommended removal and extreme removal scenarios (A, B and C, respectively), shown with median (solid line) and 95% credibility interval (dotted lines).

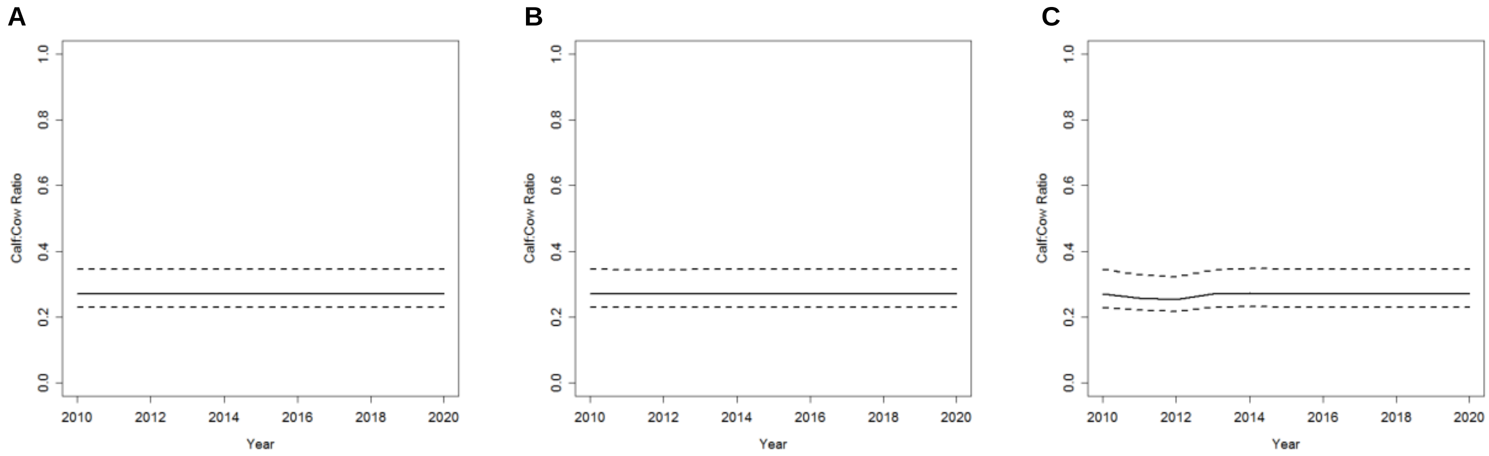

Figure 20. Model 2 projections of the calf:cow ratio in October. No removal, recommended removal and extreme removal scenarios (A, B and C, respectively), shown with median (solid line) and 95% credibility interval (dotted lines).

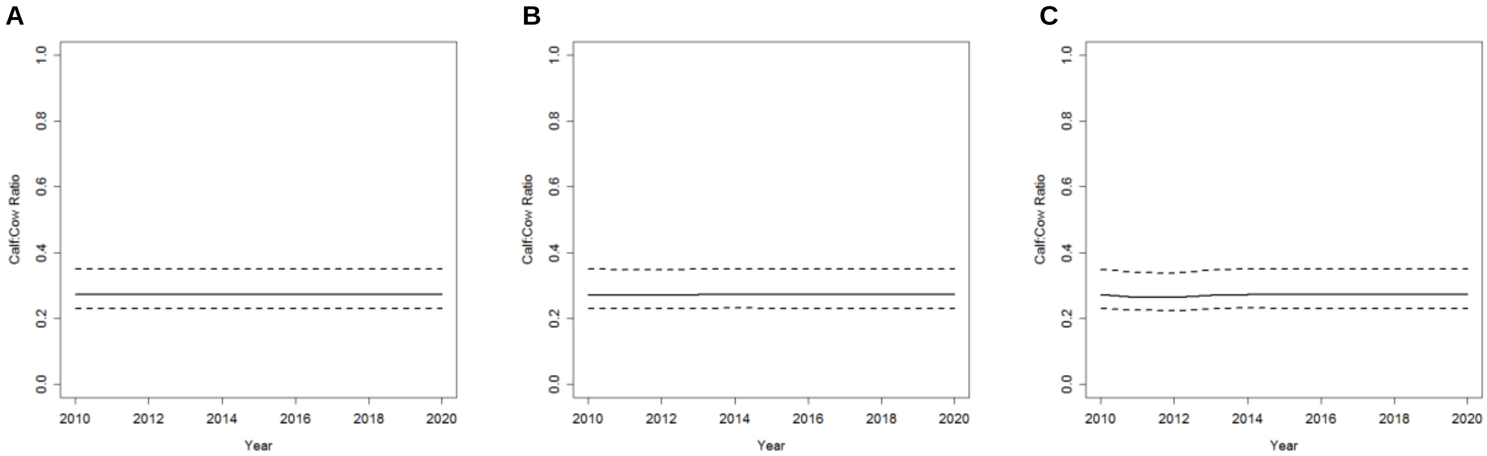

Figure 21. Model 3 projections of the calf:cow ratio in October. No removal, recommended removal and extreme removal scenarios (A, B and C, respectively), shown with median (solid line) and 95% credibility interval (dotted lines).

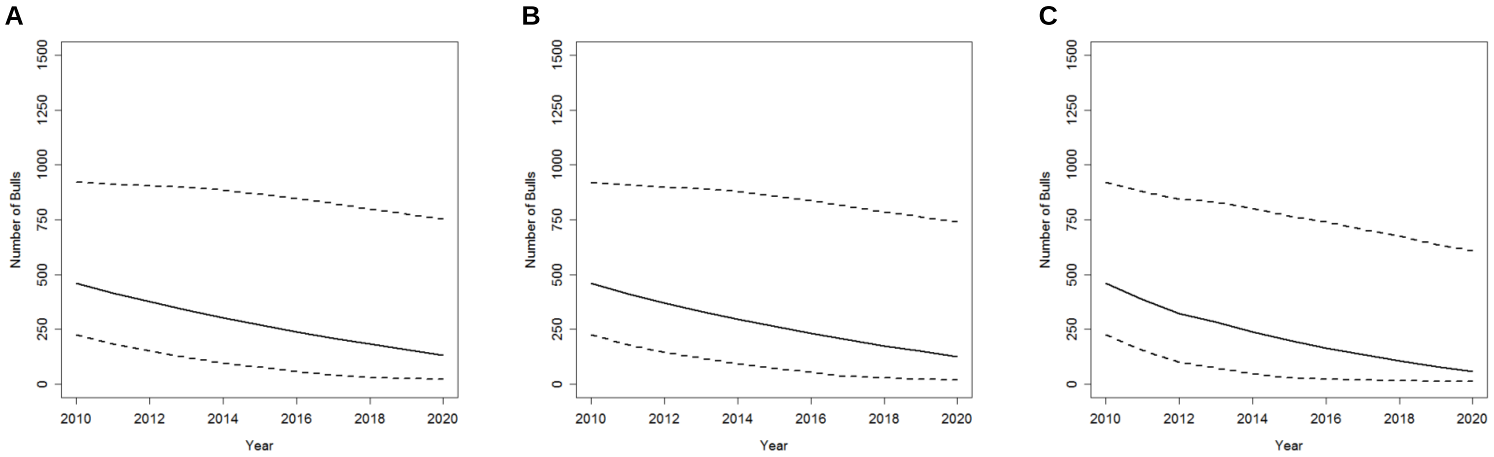

Figure 22. Model 2 projections of bull abundance in June. No removal, recommended removal and extreme removal scenarios (A, B and C, respectively), shown with median (solid line) and 95% credibility interval (dotted lines).

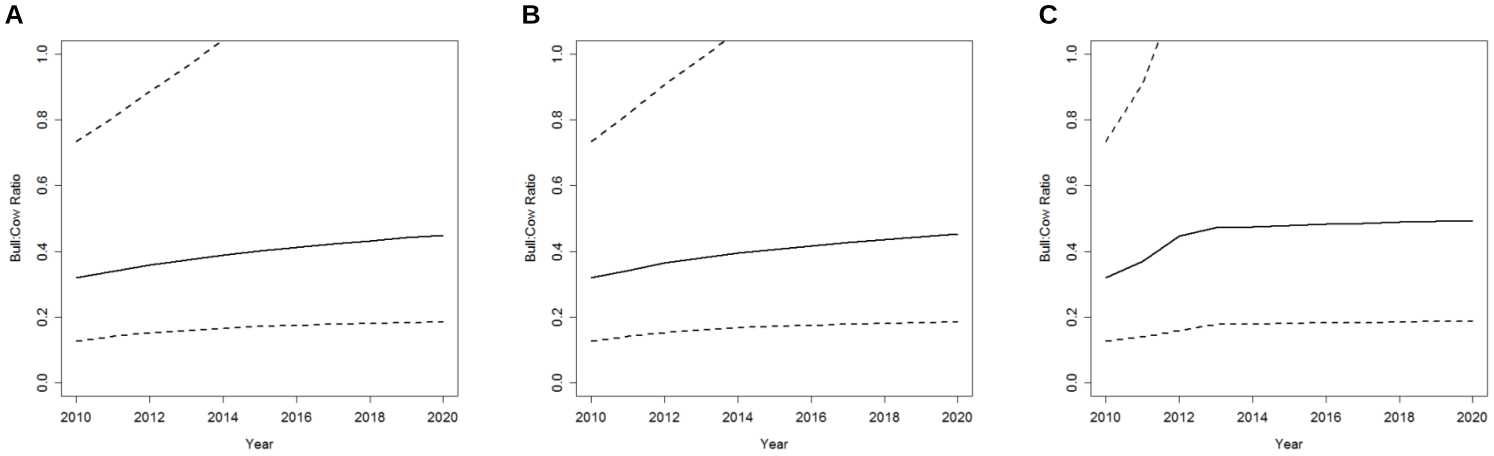

Figure 23. Model 2 projections of the bull:cow ratio in June with no hunter harvest occurring after 2010. No removal, recommended removal and extreme removal scenarios (A, B and C, respectively), shown with median (solid line) and 95% credibility interval (dotted lines).

Table 1. Total population size in year 2020 and the ratio of the total population size with removals to the total population size with no removals for each of the three models. The median and 95% credibility interval from the posterior probability distribution are shown.

		No Removals		**Recommended Removals**		**Extreme Removals**	
		Median	95% Credibility Interval	Median	95% Credibility Interval	Median	95% Credibility Interval
Model 1	Population size	3401	2132-5331	3321	2066-5237	2611	1468-4381
	Ratio			0.977	0.969-0.982	0.767	0.686-0.824
Model 2	Population size	1048	606-1970	1013	581-1920	693	364-1503
	Ratio			0.966	0.956-0.976	0.664	0.575-0.760
Model 3	Population size	9574	4026-18916	9456	3942-18771	8407	3194-17390
	Ratio			0.988	0.979-0.992	0.878	0.791-0.920

DISCUSSION

I constructed three models to examine the population dynamics of the Itcha-Ilgachuz caribou herd. These models represent three possible states of nature, or different hypotheses about the processes that could have been acting upon this herd over the period from 1995 to 2010. The constant growth model (model 1) assumed there was no change in the population dynamics over the 16 years and that the variation in survey numbers is due to random observation error. The predation hypothesis model (model 2) and dispersal hypotheses model (model 3) assume that some change after the June 2003 survey led to a decline in survey numbers: either caribou experienced lower survival and recruitment causing the herd to decline (model 2), or the caribou are using different areas, causing the sightability to drop significantly in later years (model 3). There are anecdotal reports of increased wolf numbers within the range of the Itcha-Ilgachuz herd, suggesting that higher predation rates may have caused a decline in caribou numbers. There are also anecdotal reports of caribou sightings in areas where caribou have not been seen before, suggesting that caribou may have expanded or shifted their range. However, whether changes in observed numbers are due to changes in actual numbers of caribou or changes in sightability is not known with certainty and I have not attempted to answer that question here. Further research and data collection are needed to determine the true trend in the population and the causes of that trend. The question of primary interest in this study is how the Itcha-Ilgachuz herd would react to removals for translocation. Given the uncertainty in the current trend of the population, the models illustrate the effects of removals under different possible states of nature.

These three states of nature are based on different assumptions about the data and how it represents the true abundance of caribou. In a decision analysis, this uncertainty in the population dynamics can be explicitly accounted for in determining the effect of different management options (i.e. removal scenarios). In a decision analysis, a relative probability value would be assigned to each model, based on how probable it is that each of the models represents what the true state of nature is (Peterman & Anderson 1999). These probability values are often elicited from expert opinion–the opinions of those that are experienced in the subject areas and are familiar with the system. Then, each of the management options (e.g. no removals, recommended removals) for each of the models would be given a utility value, which is a way to quantify in one value the benefit to the receiving herd and the potential cost to the source herd. The results from this modelling analysis would be used in quantifying the cost to the source herd (e.g. the probability of decline below some threshold). An expected utility value would then be calculated for the different management options, which takes into account the utility value of each management option across the different models weighted by the probability of each of those models being the true state of nature. The outcome is a rank of the management options based on their expected utility values. It was not necessary to conduct a formal decision analysis here because the results from each of the models were very similar, and therefore the decision to use the Itcha-Ilgachuz herd as a donor population does not depend on which state of nature is actually true.

The predicted effects of removing the recommended number of caribou (40 over two years) are very similar among the models. Although the predicted 2020 population size varied widely among the models, the predicted population size with the removals does not differ by more than 5% from the predicted population size with no removals in any of the three models. The number of animals proposed for removal is so low relative to the total population size that according to these models it does not affect the trajectory of the population, regardless of whether the population is increasing or decreasing. The effect of the recommended removals on the modelled calf:cow and bull:cow ratios was minimal even though the removals focus on adult females. The removals occur in early spring, before females give birth. The random removal of cows means that the proportion of pregnant cows in the removal group is similar to the proportion of pregnant cows in the population, thereby leaving the calf:cow ratio in October unaffected. In models 1 and 3 the calf numbers increase, and in model 2 the calf numbers decrease, but in all cases the calf numbers are changing in the same manner as the cow numbers, leaving the calf:cow ratio constant. The removal of 17 females and 3 males annually over two years was not large enough to affect the bull:cow ratios, even though the ratio of bulls to cows in the removal group (0.18) is lower than the bull:cow ratio of the population in 2010 (~0.35).

The median bull:cow ratio in model 2 (predation hypothesis) declines over the projected time period 2010 to 2020, but remains fairly constant in models 1 and 3 (constant growth and dispersal hypothesis). In model 2, the hunter harvest of 35 bulls per year was a large enough to cause the bull component of the herd to decline faster than the cow component, thus causing the bull:cow ratio to drop over time. In models 1 and 3 the population is growing and the hunter harvest of 35 bulls per year is not large enough to cause the bull:cow ratio to decline. In order to ensure there are a sufficient number of mature males for breeding and hunting, caribou populations in BC are managed to maintain a post hunt (October) bull:cow ratio of 0.35 (Province of BC 1996). Bull:cow ratios below 0.35 may indicate that the hunting pressure is too great and harvest levels need to be reduced. Although the recommended level of removals for translocation does not affect the bull:cow ratio in any of the models, the modelling results suggest that if the herd is shrinking (as in model 2), the bull:cow ratio will decline with a continued bull harvest. Bull:cow ratios should be monitored over time and action taken to reduce harvest levels if a declining trend is observed. However, this is irrelevant to the matter of removals for translocation. The ongoing hunter harvest has a much greater effect on the bull component than the proposed two years of removals for translocation, particularly if the population is declining. This is because the harvest continues on an annual basis removing the same number of animals as the bull population gets smaller, therefore having a greater and greater effect each year.

The results from the extreme removal scenario (400 animals over two years) show how a large number of removals could affect the herd. Under this scenario, there would be a noticeable difference in the number of animals compared to when there were no removals, regardless of the model considered. However, the calf:cow ratios are again unaffected by removals because the females are removed prior to calving. Bull:cow ratios are initially affected by this level of removals. Under the extreme removal scenario, there is an initial increase in the bull:cow ratio due to the removal of females, and then the bull:cow ratio levels off and follows the same trend as in the no removal scenario.

Since the recommended removals are not expected to influence overall abundance or age and sex ratios, there would be no need to alter hunter harvest from the current levels to offset the impact of removals for translocation. In addition, the minimal impact on caribou abundance means that recommended number of removals for translocations would not affect the ability of First Nations, local hunters and guide outfitters to hunt caribou, nor should it affect opportunities for wildlife viewing. If the population were in decline as represented by model 2, there likely would be an impact on the availability of caribou for hunting and viewing in the future, but this would be independent of whether or not translocation removals occurred.

I did not examine how a change in the level of hunter harvest would affect the population trajectory. The models assume that the reported hunter harvest will remain consistent with the average reported hunter harvest over the last ten years. If the reported hunter harvest increased or decreased from this level, the population trajectory of bulls may change. As harvest is only on bulls, this would not affect the population of cows or calves. The model accounted for First Nations' harvest in the natural mortality rates (because it is not required to be reported if for food, social or ceremonial use). This assumes that First Nations' harvest is a proportion of the total population and that it will increase when there are more caribou and decrease when there are fewer caribou. If First Nations' harvest does not increase or decrease proportionally with population size, as I have assumed, the mortality rates in the projections would be over- or under-estimated, respectively.

A density dependent response was not included in the model because there was no evidence that density dependence was acting on the population during the time period studied. If, in fact, density dependence were present, the removals would be compensatory, not additive, to natural mortality. As such, the removals would have less of an effect on the population, because the removal of animals would be compensated for by increased survival rates.

In a situation where the population is declining, it is possible that predation could have a depensatory effect (Wittmer 2010). This occurs when predators take an increasing proportion of the prey as the population declines such that the mortality rate increases as the population gets smaller. This could occur under a scenario like model 2, where the population is declining; however, I did not model this type of response. If a depensatory response did occur, the rate of population decline would be greater than that estimated by model 2. In addition, translocation removals could have a greater effect on the population size because they would reduce the population causing an increase mortality rates. However, the recommended level of removals is small and is not expected to cause a major change in the population size, so the depensation effect, if present would not increase as a result of this level of removals. However, if the number of removals was large relative to the total population size, as in the extreme removal scenario, the effect of depensatory predation could have a significant impact. With a depensatory response, the projections with the extreme removals under the modelled decline scenario (model 2) would underestimate the impact of the removals.

As with most management decisions, there are a variety of social and economic factors that managers must consider, in addition to the biological factors, before implementing a translocation project. This is especially true for the Itcha-Ilgachuz herd where First Nations, stakeholders, and local residents have a great interest in caribou. The present concern among these groups, as well as wildlife managers, is the suspected decline of the herd as suggested by the drop in survey numbers. In the context of a possible decline in the herd, removing animals for translocation becomes much more complex when social-economic factors are considered. Even though this study has shown that the removals will have little additional impact on the population dynamics of the herd, managers must address the larger debate as to whether or not removing animals from a potentially declining population is an appropriate management policy. Unfortunately, the question of whether the population is in decline, how serious that decline may be, and what the causes are cannot be answered in the time frame under which decisions need to be made about this translocation project. A radio-telemetry study to track caribou mortality and movement would provide key information to determine if mortality rates have increased or if caribou are using different habitats. Collecting this type of data could take a number of years and translocations were planned for the spring of 2011. While further data collection could determine if there is a real decline in the herd, it would not change the conclusion of this study that removals will have little additional effect on the herd's future population trajectory.

This study has evaluated the impacts of removals from a donor population—the Itcha-Ilgachuz herd—to determine if there could be detrimental effects associated with removing 40 animals over two years. This study indicates that the recommended number of translocation removals would not adversely influence the population trajectory of the Itcha-Ilgachuz herd. Even if the Itcha-Ilgachuz herd was declining after 2003, it appears that the herd is sufficiently large to sustain the removal of 40 animals over two years. While the findings of this study show there are no significant population concerns associated with this level of translocation removal, I acknowledge that there are social-economic concerns that could trump a purely biological decision to proceed with the translocation. I recommend that managers develop a communication strategy, in part using the results of this study to gain First Nation and stakeholder support for the translocation project.

As resource managers continue to face challenges with the loss of biodiversity, translocations of wildlife are an important tool that can be used to conserve and restore native species and ecosystems (Seddon 2010; Griffith et al. 1989). However, translocations are often a complex undertaking that must consider biological, social and economic factors (IUCN 1998) that together reflect the public interest. Biological analysis of potential outcomes provides information to managers and can be used to inform discussions with stakeholders and the public to determine the level of support for such projects.

APPENDICES

Appendix 1

Table A1.1. Information on the choice of priors used in the model.

Parameter	Reference		
Calf Survival	Siep & Cichowski 1996	Reported 20-40% calf mortality between June and March after the initial period of neonatal mortality, with some herds as high as 60%; equates to survival rate of 40-80%	Shape parameters: a=3, b=3 Mean=0.6 SD=0.200
Cow Survival	N. Freeman, unpublished data.	Mean and standard deviation from annual survival rates in the 1995-2003 radio telemetry study. Annual survival rates were calculated for 1995 through 2000.	Shape parameters: a=16.62 b=1.85 Mean=0.90 SD=0.069
Bull Survival	Bergerud 2000 Fancy et al. 1994	Bergerud estimated male mortality at 16%. Fancy reported male survival of 82%.	Shape parameters: a=10 b=2 Mean=0.83 SD=0.103
Recruit-ment	Siep & Cichowski 1996 Siep 1992	Mean of % cows with calves in late June in four radio telemetry studies on BC herds. Standard deviation between these observations increased 3 fold for a more diffuse prior.	Shape parameters: a=3.8 b=3 Mean=0.56 SD=0.178

Appendix 2

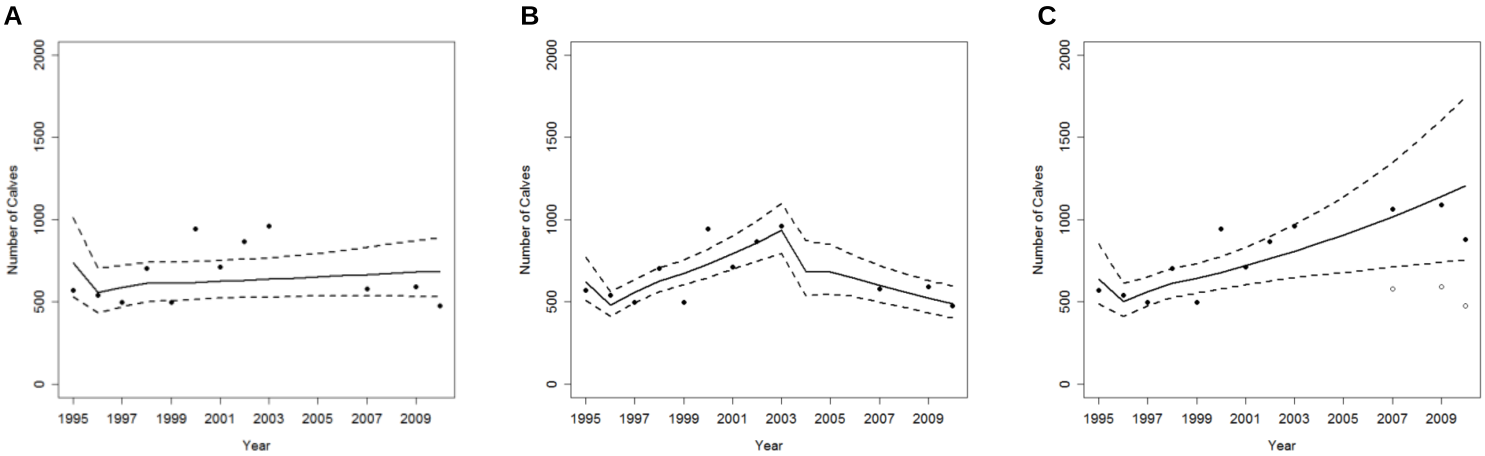

Figure A2.1. Fit of the model to the number of calves in June. Models 1, 2 and 3 (A, B and C, respectively), shown with median (solid line) and 95% credibility interval (dotted lines). The dots represent the data points being fit. In model 3, the open circles show the non-corrected data, for reference.

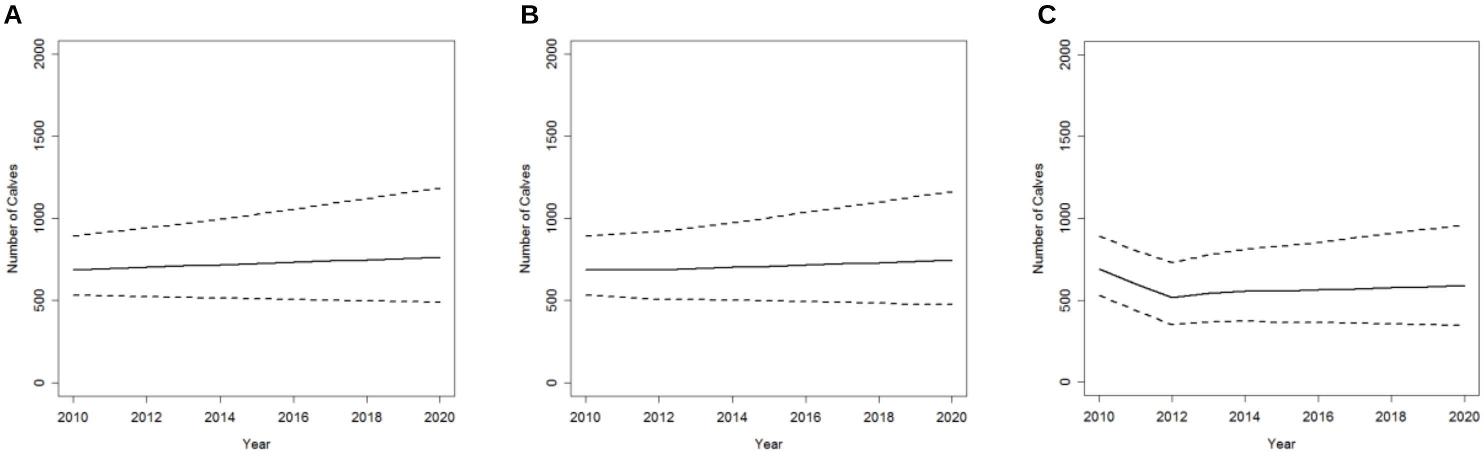

Figure A2.2. Model 1 projections of the number of calves in June. No removal, recommended removal and extreme removal scenarios (A, B and C, respectively), shown with median (solid line) and 95% credibility interval (dotted lines).

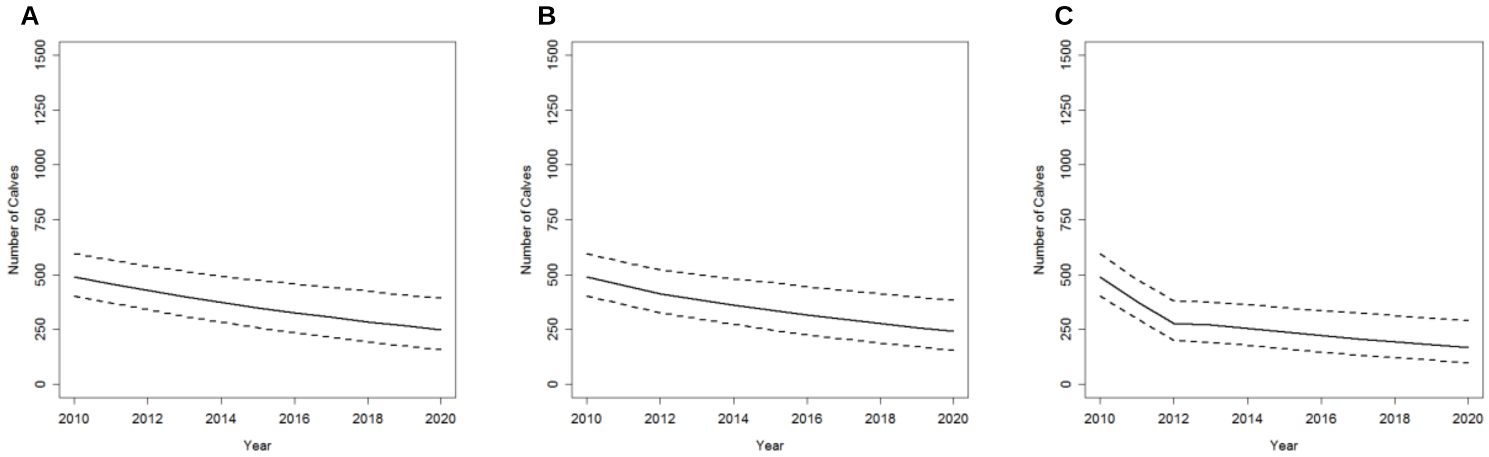

Figure A2.3. Model 2 projections of the number of calves in June. No removal, recommended removal and extreme removal scenarios (A, B and C, respectively), shown with median (solid line) and 95% credibility interval (dotted lines).

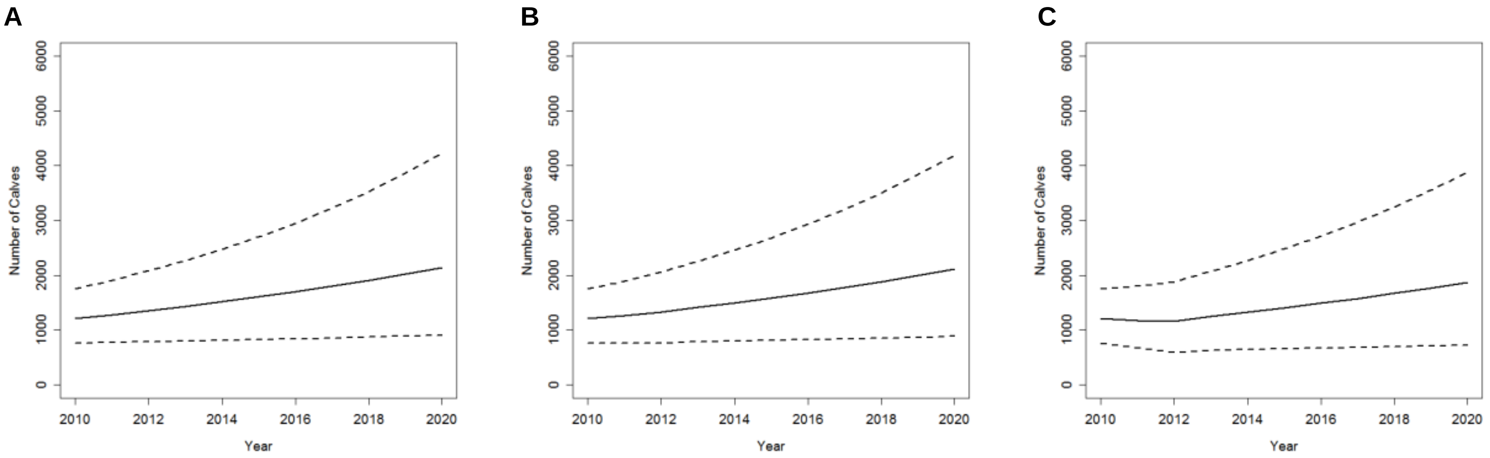

Figure A2.4. Model 3 projections of the number of calves in June. No removal, recommended removal and extreme removal scenarios (A, B and C, respectively), shown with median (solid line) and 95% credibility interval (dotted lines).

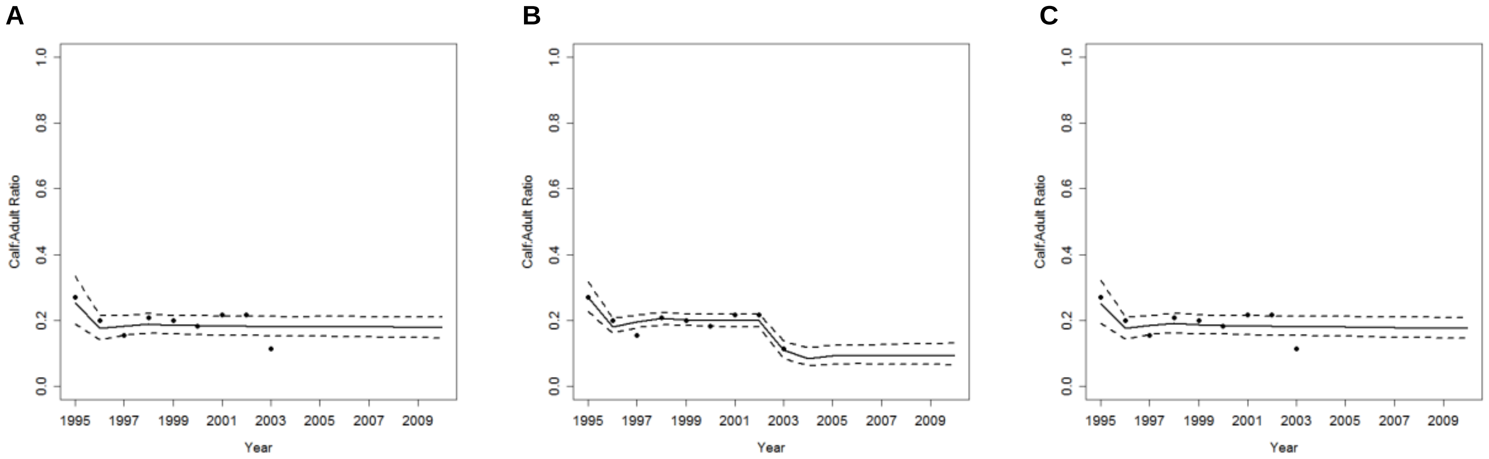

Figure A2.5. Fit of the model to the calf:adult ratio in March. Models 1, 2 and 3 (A, B and C, respectively), shown with median (solid line) and 95% credibility interval (dotted lines). The dots represent the data points being fit. Note that the “Year” is a caribou year. For March, the caribou year is one year behind the calendar year.

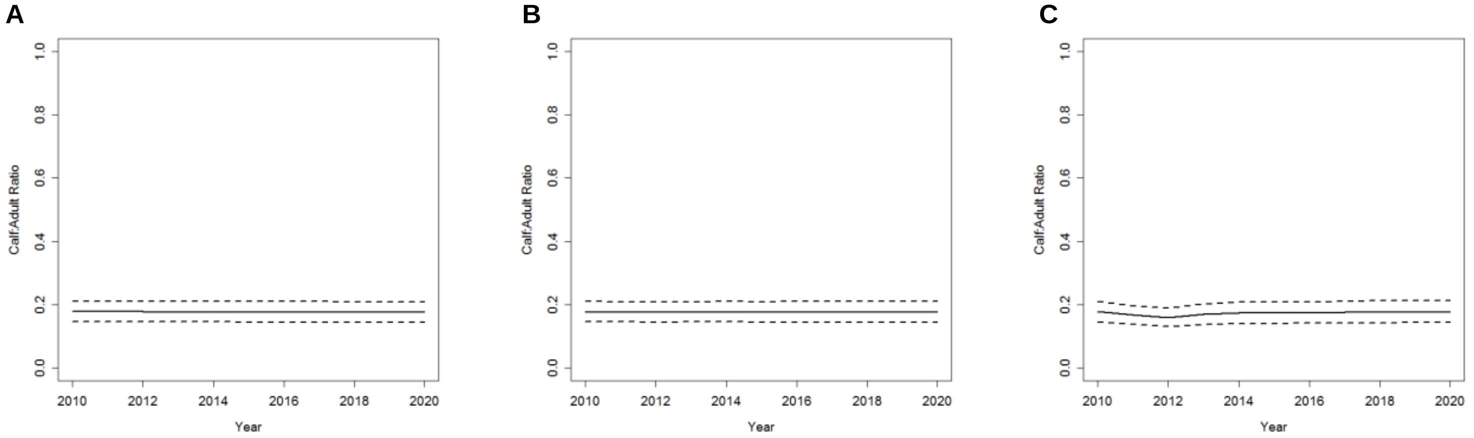

Figure A2.6. Model 1 projections of the calf:adult ratio in March. No removal, recommended removal and extreme removal scenarios (A, B and C, respectively), shown with median (solid line) and 95% credibility interval (dotted lines). Note that the “Year” is a caribou year. For March, the caribou year is one year behind the calendar year.

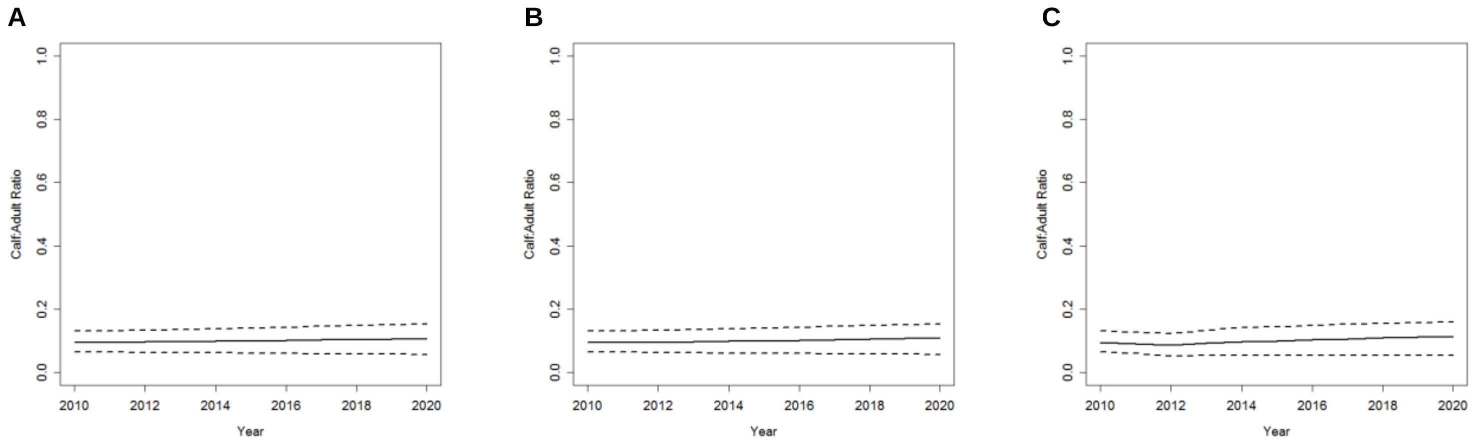

Figure A2.7. Model 2 projections of the calf:adult ratio in March. No removal, recommended removal and extreme removal scenarios (A, B and C, respectively), shown with median (solid line) and 95% credibility interval (dotted lines). Note that the "Year" is a caribou year. For March, the caribou year is one year behind the calendar year.

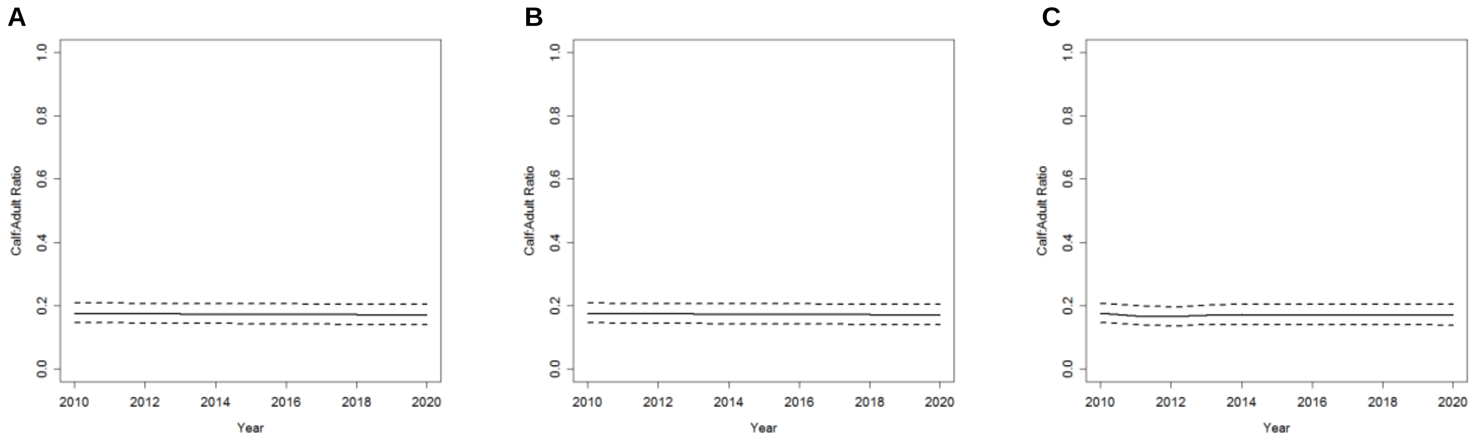

Figure A2.8. Model 3 projections of the calf:adult ratio in March. No removal, recommended removal and extreme removal scenarios (A, B and C, respectively), shown with median (solid line) and 95% credibility interval (dotted lines). Note that the "Year" is a caribou year. For March, the caribou year is one year behind the calendar year.

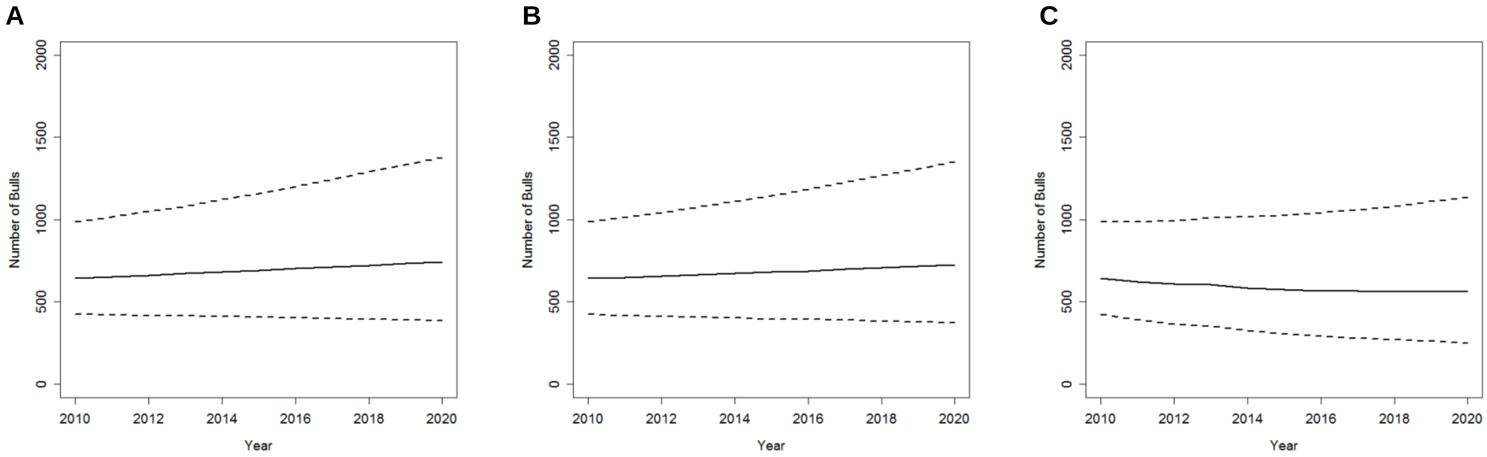

Figure A2.9. Model 1 projections of bull abundance in June. No removal, recommended removal and extreme removal scenarios (A, B and C, respectively), shown with median (solid line) and 95% credibility interval (dotted lines).

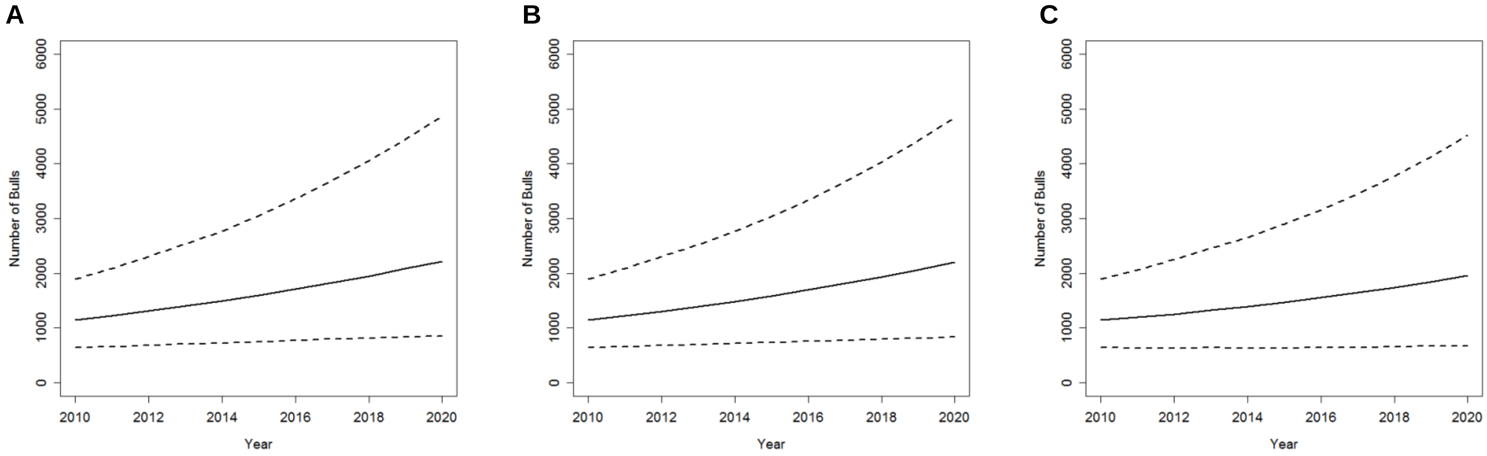

Figure A2.10. Model 3 projections of bull abundance in June. No removal, recommended removal and extreme removal scenarios (A, B and C, respectively), shown with median (solid line) and 95% credibility interval (dotted lines).

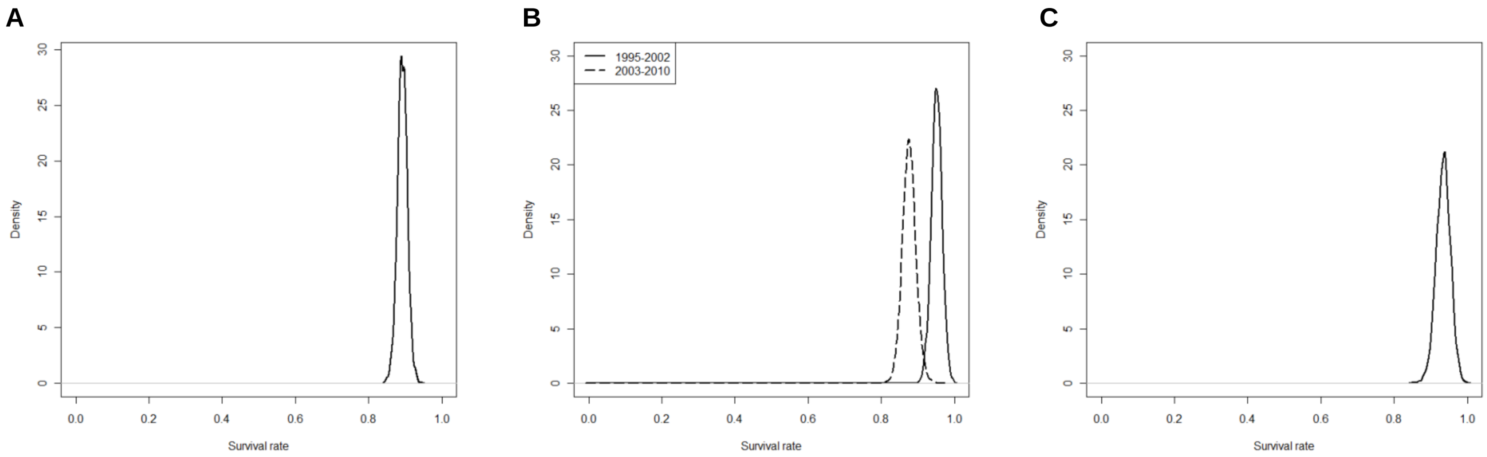

Figure A2.11. Posterior probability distributions for annual cow survival when a uniform prior is used. Models 1, 2 and 3 (A, B and C, respectively).

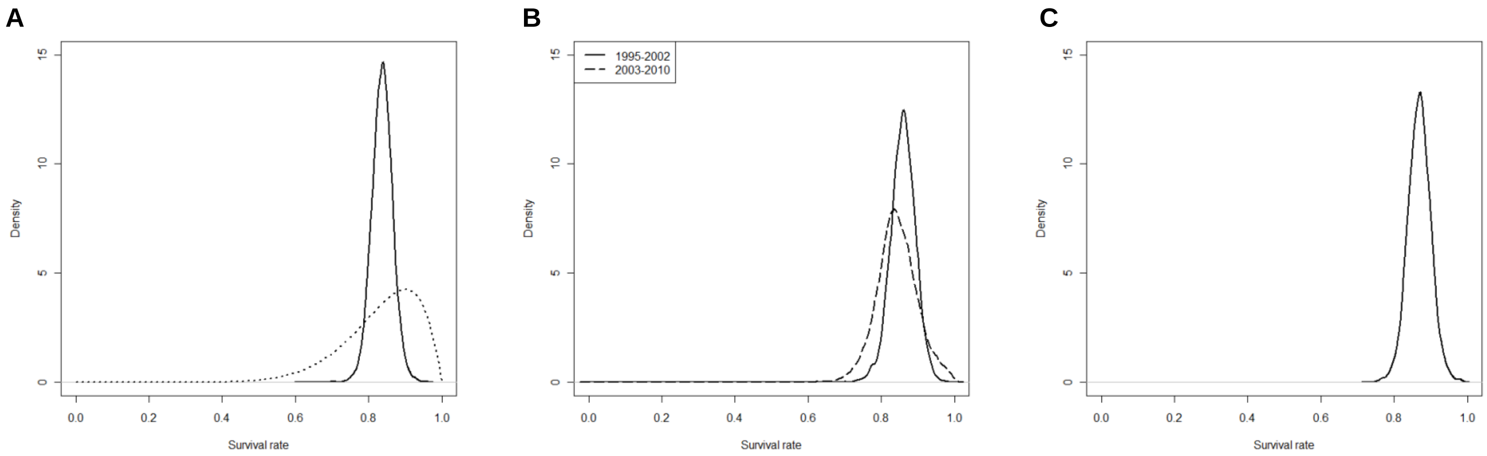

Figure A2.12. Posterior probability distributions for annual bull survival when a uniform prior is used. Models 1, 2 and 3 (A, B and C, respectively).

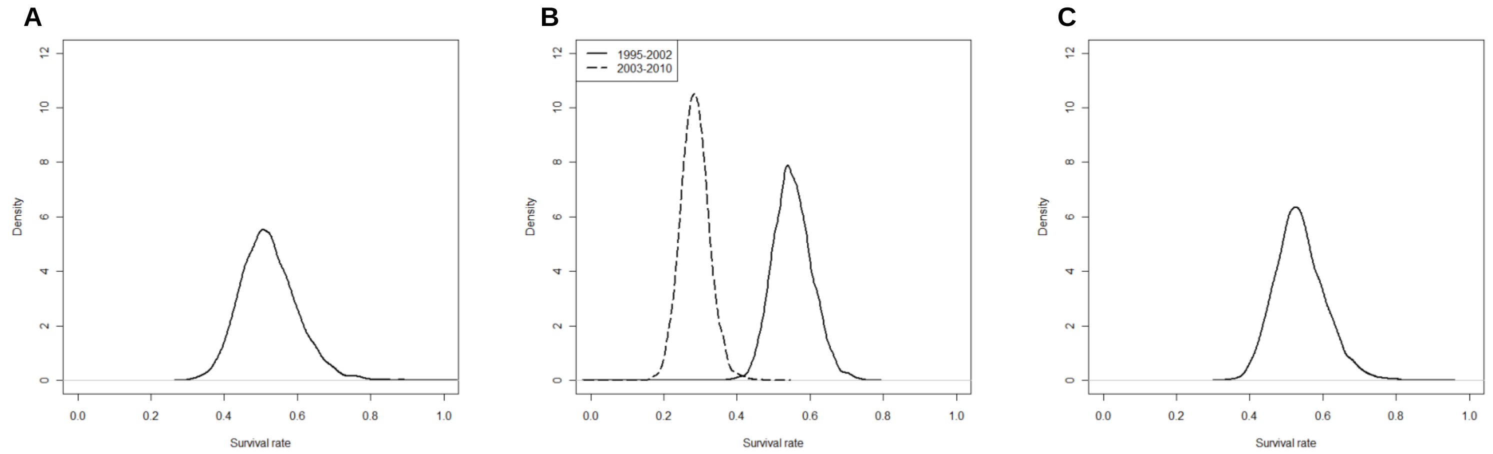

Figure A2.13. Posterior probability distributions for annual calf survival when a uniform prior is used. Models 1, 2 and 3 (A, B and C, respectively).

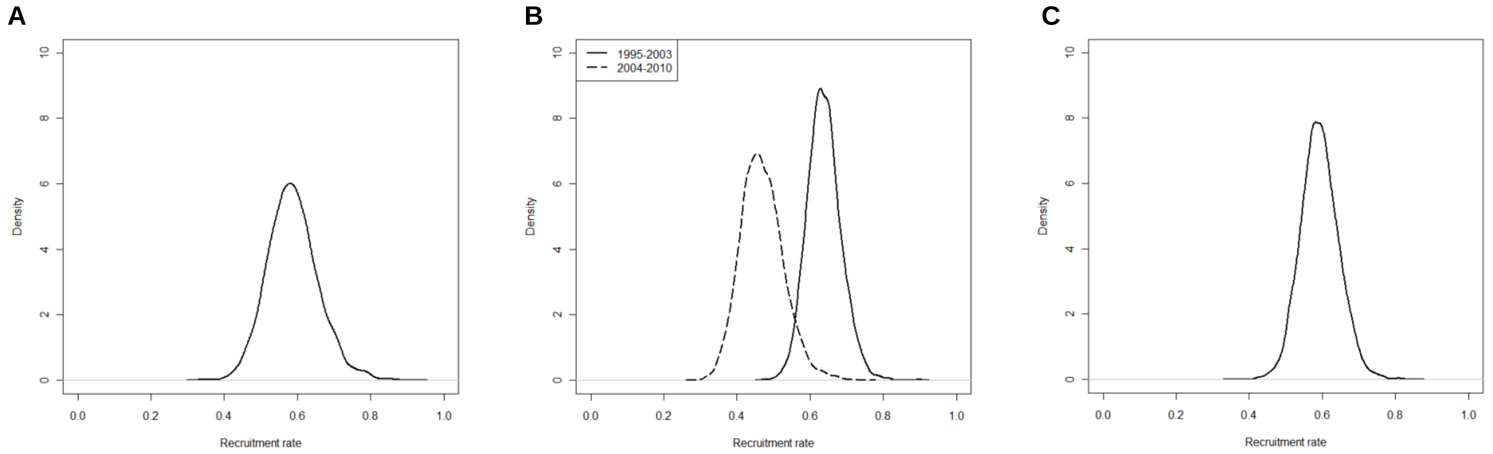

Figure A2.14. Posterior probability distributions for recruitment when a uniform priors is used. Models 1, 2 and 3 (A, B and C, respectively).

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