DYNAMIQUE DES POPULATIONS DE CARIBOUS MIGRATEURS *(RANGIFER TARANDUS)* BASÉE SUR DES INDICES DE CONDITION CORPORELLE

par

Melanie Dawn Pachkowski

mémoire présenté au Département de biologie en vue

de l'obtention du grade de maître ès sciences (M.Sc.)

FACULTÉ DES SCIENCES

UNIVERSITÉ DE SHERBROOKE

Sherbrooke, Québec, Canada, Septembre 2012

Library and Archives
Canada

Published Heritage
Branch

395 Wellington Street
Ottawa ON K1A 0N4
Canada

Bibliothèque et
Archives Canada

Direction du
Patrimoine de l'édition

395, rue Wellington
Ottawa ON K1A 0N4
Canada

Your file Votre référence
ISBN: 978-0-494-91031-3

Our file Notre référence
ISBN: 978-0-494-91031-3

NOTICE:

The author has granted a non-exclusive license allowing Library and Archives Canada to reproduce, publish, archive, preserve, conserve, communicate to the public by telecommunication or on the Internet, loan, distrbute and sell theses worldwide, for commercial or non-commercial purposes, in microform, paper, electronic and/or any other formats.

The author retains copyright ownership and moral rights in this thesis. Neither the thesis nor substantial extracts from it may be printed or otherwise reproduced without the author's permission.

AVIS:

L'auteur a accordé une licence non exclusive permettant à la Bibliothèque et Archives Canada de reproduire, publier, archiver, sauvegarder, conserver, transmettre au public par télécommunication ou par l'Internet, prêter, distribuer et vendre des thèses partout dans le monde, à des fins commerciales ou autres, sur support microforme, papier, électronique et/ou autres formats.

L'auteur conserve la propriété du droit d'auteur et des droits moraux qui protege cette thèse. Ni la thèse ni des extraits substantiels de celle-ci ne doivent être imprimés ou autrement reproduits sans son autorisation.

In compliance with the Canadian Privacy Act some supporting forms may have been removed from this thesis.

While these forms may be included in the document page count, their removal does not represent any loss of content from the thesis.

Conformément à la loi canadienne sur la protection de la vie privée, quelques formulaires secondaires ont été enlevés de cette thèse.

Bien que ces formulaires aient inclus dans la pagination, il n'y aura aucun contenu manquant.

Canada

Le 14 septembre 2012

le jury a accepté le mémoire de Madame Mélanie Pachkowski

dans sa version finale.

Membres du jury

Professeur Marco Festa-Bianchet
Directeur de recherche
Département de biologie

Monsieur Steeve Côté
Codirecteur de recherche
Université Laval

Professeure Sophie Calmé
Membre
Département de biologie

Professeure Fanie Pelletier
Présidente rapporteur
Département de biologie

For my family and the boos

SOMMAIRE

Le suivi et la compréhension de la dynamique des populations sont essentiels pour la gestion et la conservation de la faune. Une taille de population ou une densité élevée peut affecter négativement les paramètres démographiques comme la reproduction, le recrutement et la survie. Chez les grands mammifères, ces paramètres sont intimement liés à la taille des individus et à leur condition corporelle. Le caribou migrateur (*Rangifer tarandus*) est une espèce clé dans la toundra. Les populations peuvent fluctuer considérablement et rapidement, rendant leur suivi et leur gestion difficiles. Les indicateurs écologiques indirects, qui sont des indices dépendants de la densité basés sur des caractéristiques physiques individuelles ou de performance, ont été proposés comme une alternative aux estimés de population pour gérer les populations d'ongulés. Des données morphologiques mesurées sur des nouveaux-nés, des individus âgés de 1 an et des femelles adultes pour quatre troupeaux de caribous migrateurs (Rivière-George, Rivière-aux-Feuilles, Beverly et Porcupine) ont été compilées. La relation entre la condition corporelle et la dynamique des populations au niveau individuel a été étudiée en regardant comment la taille individuelle, la condition corporelle et la taille de la population influencent la gestation des femelles adultes dans le troupeau de la Rivière-George. Au niveau de la population, l'efficacité des indices de condition corporelle pour estimer les tendances démographiques pour les quatre troupeaux a été évaluée.

La condition corporelle des femelles adultes était positivement liée à leur probabilité de gestation. La taille de la population influençait négativement le taux de gestation, mais les femelles n'ont pas adopté une stratégie conservatrice de reproduction. En effet, la masse minimale des femelles adultes requise pour la reproduction ne variait pas avec la taille de la population. Au niveau populationnel, il y avait des effets dépendants de la densité négatifs sur les traits morphologiques pour trois des quatre troupeaux. Cependant, les traits morphologiques n'étaient pas toujours corrélés avec la taille de la population et ils n'étaient pas de bons paramètres pour prédire les changements dans la taille des populations. Il a souvent été montré que les effets dépendants de la densité sur les traits physiques sont plus forts, voire même limités, aux périodes de croissance démographique. Les traits physiques des jeunes semblaient répondre aux changements de la taille de la population plus rapidement que ceux des femelles adultes. L'effet de la taille de la population à la naissance sur les traits physiques persistait pour les mesures squelettiques des femelles adultes. Les effets dépendants de la densité apparents chez certains troupeaux mettent en évidence l'importance de déterminer les facteurs influençant la dynamique des populations, en particulier pendant les périodes de déclin. Les relations entre la taille et la condition corporelle, les taux démographiques et la dynamique des populations sont complexes, de sorte que les changements dans la taille des populations ne peuvent pas être prédits de manière efficace par un suivi des traits physiques individuels.

SUMMARY

Monitoring and understanding wildlife population dynamics is key to their management and conservation. High population size or density can negatively affect demographic parameters including reproduction, recruitment and survival. These parameters are intricately linked to individual body size and condition. Migratory caribou (*Rangifer tarandus)* are a keystone species in the tundra. Populations can fluctuate drastically and rapidly and are challenging to monitor and manage. As an alternative to population estimates, indirect ecological indicators, which are density-dependent indices based on individual physical characteristics or performance, have been proposed to monitor ungulate populations. I amalgamated morphological data measured on newborns, yearlings and adult females for four migratory caribou herds; the Rivière-George, Rivière-aux-Feuilles, Beverly and Porcupine. I investigated how body condition relates to population dynamics at the individual level by determining how body size, condition and population size impact female reproductive success in the Rivière-George herd. At the population level, I determined the efficacy of body condition indices to estimate demographic trends for all four herds.

Body condition of adult females was positively related to the probability of gestation for the Rivière-George herd. Although population size negatively affected gestation rates, females did not adopt a conservative reproductive strategy as predicted, because the threshold adult female mass required for gestation did not vary with population size. At the population level, physical traits showed negative density dependence in three of the four herds. Physical traits, however, did not consistently correlate with population size nor did they predict numerical changes in population size. Physical traits often showed density dependence stronger, or even exclusively, during periods of demographic growth. Physical traits of juveniles seemed to respond to changes in population size more readily than those of adult females, and the effect of population size at birth persisted in skeletal measures of adults. Density dependence was apparent only in some herds, highlighting the importance of determining the drivers of population dynamics, particularly during periods of decline. Relationships between body

condition, demographic rates and population dynamics are complex, so that changes in population size cannot be predicted reliably by monitoring physical traits.

ACKNOWLEDGEMENTS

I have many thanks to give because "it's not just the journey but the people that carry you along the way". First and foremost I would like to thank my supervisors: Marco, for your incredible decisiveness and urgency, for setting the precedence and for putting me back on track when needed, and Steeve, pour m'avoir acceuillie, for countless insights, positive encouragement and the occasional but much needed compliments. I stood on the shoulders of giants and I sincerely thank you both for your patience considering I am the 'lagging strand', and for the unforgettable opportunities that accompanied working with you and researching caribou. I thank all my committee members: Sophie Calmé and the late Don Thomas for their direction and time, with special mention to Fanie Pelletier for going above and beyond. Statistical advices from Marc Bélisle were vital and constructive. This research was funded by several financial partners of Caribou Ungava including: ArcticNet, the Ministère des Resources naturelles et de la Faune du Québec (MRNF), Labrador and Newfoundland Wildlife Division, Natural Sciences and Engineering Research Council of Canada, Hydro-Québec, Fédération des Pourvoiries du Québec, Canadian Wildlife Federation, X-Strata Raglan Mine, Centre d'études nordiques, and in partnership with Université de Sherbrooke, Université Laval and the CircumArctic Rangifer Monitoring and Assessment network. This research was contingent on data from: Drolet, Dauphiné, Bergerud, Luttich, Parker, Huot, Manseau, Couturier, Taillon, the MRNF and the Government of Labrador, Russell, Allaye Chan-Mcleod, Thomas, Cooley and the Porcupine Caribou Technical Committee. Support and logistics from the Caribou Ungava group including Caroline, Jean-Pierre, Émilie, Glenn, Vincent and Maël, was indispensible. And in particular Joëlle, who was the blue to my pink and acted as much as my mentor and colleague as friend. I thank those that got their hands dirty collecting caribou samples up North; Aurélie, Elise, and Charles. Joëlle, Pascale and Jean-Yves, and my idol Stéphane, taught me the ropes and had my back on the calving grounds. Without encouragement from Richard, Norm and Rachelle I would not have embarked on this journey, and without Elise, Audrey and Sharon I would not have succeeded. I thank all who supported me throughout, including my family, friends and fellow grad students.

TABLE OF CONTENTS

SOMMAIRE ii
SUMMARY iv
ACKNOWLEDGEMENTS vi
TABLE OF CONTENTS vii
LIST OF TABLES ix
LIST OF FIGURES xii

GENERAL INTRODUCTION 1
  Population Dynamics and Monitoring 1
  General Objectives 1
  Demographic Parameters 2
  Linking Size and Condition to Demographic Rates 2
  Factors that Affect Body Size and Condition 3
  Effects of Density on Body Condition and Size 4
  Effects of Density on Survival and Reproduction 5
  Ecological Indicators 7
  Model Species and Specific Objectives 7

CHAPTER 1 12
SPRING-LOADED REPRODUCTION: EFFECTS OF BODY CONDITION AND POPULATION SIZE ON GESTATION RATES IN MIGRATORY CARIBOU 12
  ABSTRACT 12
  INTRODUCTION 12
  METHODS 15
    Study Area and Population Estimates 15
    Data Collection 15
    Caribou Body Condition 16
    Population Estimates 17
    Statistical Analyses 17
  RESULTS 19

Fertility 19
Adult female body condition 19
Gestation Predictors 19
Population Size as a Predictor of Pregnancy 20
DISCUSSION 24
Condition-Fecundity Relationships 26
Effect of Population Size 28
ACKNOWLEDGEMENTS 30

CHAPTER 2 31
MORPHOLOGICAL TRAITS OF MIGRATORY CARIBOU PREDICT POPULATION SIZE BETTER IN PERIODS OF DEMOGRAPHIC GROWTH THAN DECLINES 31
ABSTRACT 31
INTRODUCTION 32
STUDY AREA 34
METHODS 35
Population Counts, Interpolating Population Estimates 35
Morphological Data 36
Statistical Analyses 38
RESULTS 38
Correlation of population size and average physical traits 39
Correlation of population size and average leg lengths 47
DISCUSSION 48
Rivière-George 51
Rivière-aux-Feuilles 53
Beverly and Porcupine 54
Conclusion 55
ACKNOWLEDGEMENTS 57

GENERAL CONCLUSION 58
REFERENCES 60

LIST OF TABLES

1. Average mass (kg), body fat (%), hind foot length (hflT) (cm), number of warbles and age with standard error (se) and sample size (n) grouped by reproductive status (pregnant or barren) and demographic trend (low and increasing, high and increasing or low and decreasing) of known-age female caribou ($\geq$ 3 years) from the Rivière-George herd collected in 1980, 1984, 1986, 1987 and 2002. Presence or absence of a foetus was recorded during March and April, except for 5 individuals collected in late February in 1987. Values that differ significantly based on Tukey post-hoc tests for mass, body fat and hind foot length and based on Kruskal-Wallis tests for differences in age distribution and number of warbles, are denoted by different letters. Bonferonni correction was applied to determine significance between demographic trends for age (p=0.017).. 21

2. Model selection based on second order Akaike's information criterion corrected for small sample size (AICc) for the determinants of gestation in adult female migratory caribou of the Rivière-George herd in spring (March and April) 1980, 1984, 1986, 1987 and 2002. Models include 115 known-age individuals with all morphological measurements including mass (mass), percent body fat adjusted to March 23 (bodyfatC) and hind foot length (hflT). Population size (popest), and interactions denoted by asterisk (*) were also included in models along with a model containing no explanatory variables (null model). Models are listed in rank order with the 6 best models, with AICc values that do not differ by more than 2, in bold. Number of estimated parameters (k), change in AIC from lowest AICc value (ΔAICc), and cumulative weight of model (Cum. Wt) based on the likelihood that that model is the best model (LL) are presented.. 23

3. Model averaged parameter estimates, standard error (se) and 95% confidence intervals (CI) for variables from the 6 competing models from Table 2 for the determinants of gestation in adult female migratory caribou of the Rivière-George herd in spring (March and April) 1980, 1984, 1986, 1987 and 2002. Models included 115 known age individuals with all morphological measurements including mass (mass), percent body fat adjusted to March 23 (bodyfatC), hind foot length (hflT) and population size (popest).. 24

4. Model selection based on second order Akaike's information criterion corrected for small sample size (AICc) for the determinants of gestation in adult female migratory caribou of the Rivière-George herd in spring (March and April) 1980, 1984, 1986, 1987 and 2002. Models include 131 known age individuals with measured mass (mass) and hind foot length (hflT). Population size (popest) and interactions denoted by asterisk (*) were also included in models. Models are listed in ranked order with the best model in bold. Number of estimated parameters (k), change in AIC from lowest AICc value (ΔAICc), and cumulative weight of model (Cum. Wt) based on the likelihood that that model is the best model (LL) are presented...................... 25

5. Number of individuals and years where body condition variables were sampled in four migratory herds (Rivière-George, Rivière-aux-Feuilles, Beverly and Porcupine), according to age class (newborn, yearling, adult), season (summer, autumn, spring and autumn/winter), and physical traits measured (whole mass (mass), eviscerated mass (mass2), hind foot length (hfl), metatarsus length (meta), metatarsus bone length and percent body fat (fat)) with reference to publications. Traits with the same sample size are conjoined with a "+" and traits that differ appear in brackets, with associated sample sizes and changes in population size in brackets. Total number of individuals and years are shown for each trait, with the number of years during periods of population increase and decrease and the estimated change in population size for each growth and decline phases............... 40

6. Correlations between estimated population size and average morphological measures (whole body mass (mass) eviscerated mass (mass2), hind foot length (hfl), and percent body fat (fat)) with condition corrected for collection date denoted with a "C", according to age class (calves, yearling females (yearling) and adult (>2 years old) females and season (spring, summer, autumn and autumn/winter), of caribou from four migratory herds (Rivière-George, Rivière-aux-Feuilles, Beverly and Porcupine). Females were considered reproductive if they were pregnant in spring or lactating in summer and autumn. Parameter estimates are shown with their standard error (se), p-values (p), variation they explained in population size (r^2), degrees of freedom (df) and f-statistic (f). Significant models ($p<0.05$) are in bold.. 42

7. Correlations between estimated population size and average leg lengths (metatarsal length (meta) and hind foot length (hfl) for adult (≥2.5 years old) female caribou from four migratory herds (Rivière-George, Rivière-aux-Feuilles, Beverly and Porcupine). Data that included transformations of measurements are denoted with a "T" (see text). Parameter estimates are shown with associated standard error (se), p-values (p), variation explained in population size estimate (r^2) and degrees of freedom (df). Sample size of number of individuals and cohorts included in analyses are presented. Cohorts with fewer than 5 individuals were excluded from analyses. Significant parameters ($p<0.05$) are in bold... 50

LIST OF FIGURES

1. Distribution of major North American migratory tundra caribou herds with their associated calving grounds, including the four study populations: the Porcupine, Rivière-George, Rivière-aux-Feuilles and Beverly herds. Figure from (Hummel et al., 2008)........ 9

2. Population estimates (points) of the Rivière-George, Feuilles, Porcupine and Beverly migratory caribou herds over time. Bars represent 90% confidence intervals for the Rivière-aux-Feuilles and Rivière-George herds and standard error for the Beverly herd, when available. Lines depict population trajectories for all four herds based on loess smoothing........ 11

3. Logistic regressions of the probability of gestation according to body condition indices and population size for Rivière-George caribou females aged 3 to 16 years collected in spring of 1980, 1984, 1986, 1987 and 2002. Regressions predicting presence (1) or absence of foetus (0) for (A) mass, (B) percentage of body fat and (F) population size were significant. Regressions for (C) hind foot length and (D) age were not significant. Logistic regression of (E) the number of warbles was significant (solid line) but became marginally insignificant after removing the female with the highest warble count (dotted line). Raw data (points) are shown, except for (F), instead grey bars show the proportion of pregnant females at given population sizes........ 22

4. Model predictions, from best model with 131 individuals selected using AICc in Table 4, of gestation in relation to mass in April and May at average hind foot length (left panel), and in relation to hind foot length at average mass (right panel) for adult females of the Rivière-George herd in 1980, 1984, 1986, 1987 and 2002........ 26

5. Average calf birth mass and yearling mass in June (kg) (a,c) and average calf and yearling hind foot length (cm) (b,d) with standard errors, overlaid with estimated population size (red line) (based on average growth rate between population counts) over time for caribou of the Rivière-George herd... 45

6. Average calf birth mass and yearling mass in June (kg) (left panels) and average calf and yearling hind foot lengths (cm) (right panels) with standard errors overlaid on estimated population size (based on average growth rate between population counts) over time for caribou of the Rivière-aux-Feuilles herd.................................... 46

7. Average leg lengths (hind foot length (cm), metatarsus length (cm) and metatarsal bone length (mm) with standard error plotted according to year of birth, overlaid with estimated population size (based on average growth rate between population counts) over time, for caribou of the (a) Rivière-George, (b) Rivière-aux-Feuilles, (c) Beverly and (d) Porcupine herds.. 49

GENERAL INTRODUCTION

Population Dynamics and Monitoring

Wildlife management requires knowledge of population dynamics. Monitoring population size is not only fundamental (Morellet et al., 2007; Zannese et al., 2006), it is high priority for managers (Klein et al., 1999), yet it poses logistical difficulties. A plethora of ways to estimate population size or proxies of population size exist (Nugent and Frampton, 1994) but their accuracy and precision have been questioned (Jachmann, 2002; Pettorelli et al., 2007; Redfern et al., 2002). New statistical methods have been devised to analyze demographic data, but still offer an imperfect solution (Saether et al., 2007).

General Objectives

The overall objective of my research was to better understand population dynamics of migratory caribou *(Rangifer tarandus)* based on body condition indices, or individual physical traits. Individual body size and condition are associated to demographic parameters (ex.fecundity) that affect population dynamics, and are affected by a variety of factors including population density. The two main objectives of my research were to determine the effect of population size on the relationship between gestation and female size and condition and to determine the efficacy of physical traits to monitor population size. With the aim of improving our understanding of the factors that affect demographic parameters that in turn, influence population dynamics, to allow for more informed management decisions. Discovering new proxies of population size could improve methods of wildlife populations monitoring, especially populations of migratory caribou, where it is particularly difficult to obtain consistent population estimates.

Demographic Parameters

Changes in population size can be partitioned into their component demographic parameters such as age specific reproduction and survival (Fowler, 1987). For ungulates in general, juvenile survival is typically more sensitive to various ecological factors and variable over time compared to adult survival (Gaillard et al., 2000). Senescent individuals and males typically have relatively lower survival rates than prime-aged females (Dumont et al., 2000; Loison et al., 1999). Recruitment rates of juveniles affect population growth rates (Gaillard et al., 1998) but if adult female survival varies, it will typically have a dramatic impact on population growth (Crête et al., 1996; Eberhardt et al., 2007; Walsh et al., 1995).

Intrinsic factors such as the age-sex structure and density of a population (Coulson et al., 2001; Festa-Bianchet et al., 2003; Pelletier et al., 2011), along with extrinsic factors like predation (Sinclair et al., 2003), environmental stochasticity (Post and Forchhammer, 2002), disease (Joly and Messier, 2004), and catastrophes influence population dynamics through their impact on demographic rates. Similar factors influence several species but the relative importance of specific factors varies among species (Coulson et al., 2000) and populations. For example, the most important determinant of population growth was age structure in red deer *(Cervus elaphus)* (Pelletier et al., 2011), bighorn sheep *(Ovis canadensis)* and mountain goats *(Oreamnos americanus)* (Festa-Bianchet et al., 2003), but density superseded age structure for Soay sheep *(Ovis aries)* (Coulson et al., 2008). The effects of intrinsic and extrinsic factors can occur simultaneously (Coulson et al., 2000) or interact (Skogland, 1985). The effects of density can be exacerbated by harsh environmental conditions (Coulson et al., 2001; Pelletier et al., 2011).

Linking Size and Condition to Demographic Rates

Bone measurements proximate skeletal or "structural" size (Dobson, 1992), whereas measures of body condition assess the physical state of an individual and typically include a quantification of fat. Mass is therefore the combination of body size and condition, together, which represents phenotypic quality. Phenotypic quality affects life history traits (Bergeron et al., 2011) including survival and reproductive success, ultimately influencing individual fitness and affecting population growth rates.

Individual condition and size are positively associated to individual survival in juvenile roe deer (*Capreolus capreolus*) (Gaillard et al., 1997), mule deer *(Odocoileus hemionus)* (White and Bartmann, 1998), bighorn sheep (Festa-Bianchet et al., 1997), elk *(Cervus elaphus)* (Singer et al., 1997) and moose *(Alces alces)* (Keech et al., 2000). Adult body condition and size are positively linked to reproductive success for many species. Females that are heavier (Adams and Dale, 1998), fatter (Crête et al., 1993) or both heavier and fatter (Thomas, 1982), breed at a younger age (Messier et al., 1988), have a higher probability of pregnancy (Cameron et al., 1993; Gerhart et al., 1997; Reimers, 1983; Russell et al., 1998), produce more offspring, reproduce more frequently (Cameron, 1994) and produce better quality offspring (Tveraa et al., 2003).

Factors that Affect Body Size and Condition

Individual morphology is partly determined by resource availability (Simard et al., 2008; Zedrosser et al., 2006) and quality (Côté and Festa-Bianchet, 2001). Nutritional plane during development affects individual growth, which determines structural size that is fixed once growth is completed, and current condition. Morphology is therefore affected by a multitude of heritable, intrinsic and environmental factors. Time to complete somatic growth varies between species, sexes, and the different bones and the allocation of resources to bone, tissue and organ growth is species-specific (Hilton et al., 2000). For example, caribou leg bones may have growth priority (Klein et al., 1987) and take 2.5 years to complete growth compared to mandibles whose growth takes 4 years for females and 5 years for males (Parker, 1981). For neonates that rely on maternal nutrition, growth and condition are influenced by maternal traits from conception to weaning (Taillon et al., 2012a; Therrien et al., 2007).

Individual reproductive strategy can also influence body condition of females. Age of primiparity can affect adult body size of females as seen by hindered growth in bighorn ewes due to early reproduction (Festa-Bianchet et al., 1995). In caribou, mandible length was thought to be affected by age at first reproduction (Gerhart et al., 1997). Female condition typically differs between reproductive classes (Allaye Chan-McLeod et al., 1999) during pregnancy (Cameron et al., 1993; Russell et al., 1998) and lactation (Gerhart et al., 1997; Reimers et al., 2005). The cost of lactation is high (Barboza and Parker, 2008) and can cause reproductive pauses (Adams and Dale, 1998) due to decreased body condition.

Climate can directly impact body condition through energy expenditures (Couturier et al., 2010), or indirectly by affecting the availability and abundance of resources (Boelman et al. 2005, Barrette and Vandal 1986). Availability and abundance of resources can vary between seasons causing body condition to vary (Chan-McLeod et al., 1999; Crête and Huot, 1993). For most northern ungulates, mass and body fat content typically decrease over winter (Bergerud et al., 2008), with the exception of the Rivière George herd females that gain fat over winter (Couturier et al., 2009a).

Effects of Density on Body Condition and Size

Density dependence can be defined as a decrease in population growth rate as density increases. As population size increases, body condition typically decreases although not necessarily linearly (Moller et al., 2004). Although few studies have provided empirical evidence of this negative density dependent effect (Bonenfant et al., 2009), the mechanism is thought to be nutritional limitation due to increased competition. When nutrition is limited, it affects a variety of morphological measures. Due to differential nutritional requirements, the effects of density are often age and sex dependent (Coulson et al., 2001).

The negative effect of density on juvenile size and mass is well document in red deer (Mysterud et al., 2001), bighorn sheep (Leblanc et al., 2001), male moose (Ferguson et al., 2000), roe deer (Hewison et al., 2002; Zannese et al., 2006), caribou and reindeer (Couturier et al., 2009b; Post and Klein, 1999; Weladji et al., 2003). Female body mass in reindeer is negatively correlated to population density (Helle and Kojola, 1994). In roe deer, density had negative effects on body weight for juveniles and adult males, but not for adult females (Vincent et al., 1995). Yet an experimental increase of density in elk caused a reduction in the body condition of females (Stewart et al., 2005). Density dependent effects on adult body size have been documented in fallow deer (*Dama dama*) metacarpus length (Serrano et al., 2007), roe deer leg length (Zannese et al., 2006), diastema mandible height in fallow deer (Nugent and Frampton, 1994) and mandible length in roe deer (Hewison et al., 1996) and caribou (Couturier et al., 2010) but may differ between sexes as observed in muskox (Lyberth et al., 2007).

Different morphological measures may also respond differently to changes in resource availability. Juvenile mass may respond before skeletal measures to changes in density, as seen in roe deer (Toigo et al., 2006). White-tailed deer (*Odocoileus virginianus*) fawns under resource limitation allocated resources to lipogenesis before body growth, ultimately affecting body size (Lesage et al., 2001; Verme and Ozoga, 1980).

Effects of Density on Survival and Reproduction

Life history theory posits that under resource limitation, individuals must make trade-offs in the allocation of resources to growth, maintenance and reproduction (Stearns, 1992). In addition to the negative effects of density on growth and condition, negative effects on demographic rates including reproduction and survival have been well documented (Bonenfant et al., 2009). As a population increases and approaches carrying capacity, changes in its demographic parameters typically follow a predictable sequence beginning with an increase in juvenile mortality, followed by an increase in the age of primiparity, then a reduction in reproductive rates and lastly, in extreme cases, an increase in adult mortality (Eberhardt, 2002).

Density has been shown to reduce survival probability of juveniles in many species (Bonenfant et al., 2009 and Gaillard et al., 1998). Density affects juvenile survival more than adult survival, as adult female survival is buffered against density and environmental stochasticity (Gaillard et al., 1998). Density effects on adult survival have been reported for buffalo (*Syncerus cafer*) (Mduma et al., 1999), Soay sheep (Clutton-Brock et al., 1992) and reindeer (Helle and Kojola, 2008) where density interacted with climate. Females may buffer their own survival when resources are limited by reducing litter size (Sand et al., 1996), maternal care (Bårdsen et al., 2008; Martin and Festa-Bianchet, 2010), or fertility (Albon et al., 1983; Sand et al., 1996). During demographic growth, age of primiparity increases (Messier et al., 1988), gestation rates decrease (Mduma et al., 1999), fecundity decreases (Hewison, 1996; Stewart et al., 2005), and the threshold mass needed to conceive increases (Albon et al., 1983; Heard et al., 1997; Sand et al., 1996).

In theory, the effects of density should become apparent either as a population approaches its carrying capacity (Fowler, 1981) or after a threshold density has been reached (Getz, 1996). Most studies of density dependence document negative effects during demographic growth. Because density acts indirectly to limit body size and condition by limiting resources, effects on body condition should be reversible. Indeed, adult female caribou from the Rivière George herd fed *ad libitum* gained weight and became fatter (Crête et al., 1993). Similarly, experimental reduction of a feral donkey *(Equus asinus)* population increased juvenile growth rate and condition (Choquenot, 1991). Population reduction led to an increase in white-tailed deer male mass and hind foot length for fawns, yearling and adults (Ashley et al., 1998). Other examples of improved condition during periods of natural population declines include mandible size of female caribou (Couturier et al., 2010), birth weights of caribou (Skogland, 1990), and roe deer (Hewison et al., 2002). Demographic parameters have also been shown to improve as populations declined, including age of primiparity in caribou (Crête et al., 1993), mortality rates of donkeys (Choquenot, 1991), and survival of mule deer fawns (White and Bartmann, 1998).

Density dependence can have an immediate effect on body condition (Gaillard et al., 2000), or it can manifest after a time lag (Fryxell et al., 1991; Messier et al., 1988) due to delays in vegetation re-growth (Henry and Gunn, 1991) after overgrazing. Lags in density dependent responses can also be due to cohort effects as conditions at birth may affect reproductive rates only after sexual maturity has been reached years later (Forchhammer et al., 2001; Gaillard et al., 2003; Pettorelli et al., 2002; Simard et al., 2011).

Ecological Indicators

Ecological indicators are density-dependent physical characteristics or demographic parameters that reflect changes in a population relative to its environment (Morellet et al., 2007). Ecological indicators have been proposed to monitor ungulate populations including roe deer (Hewison et al., 1996; Morellet et al., 2007; Toigo et al., 2006; Zannese et al., 2006) and several African species (Du Toit, 2002). Examples of ecological indicators used in roe deer include fawn leg length (Toigo et al., 2006), fawn mass (Gaillard et al., 1996), cohort mandible length (Hewison et al., 1996), and female to young ratios (Vincent et al., 1995). However, density-dependent responses vary according to whether a population is increasing or decreasing (Fryxell et al., 1991) and ecological indicators have only been validated during periods of demographic growth or high density (Zannese et al. 2006, Morellet et al. 2007, Hewison et al. 1996 and Vincent et al. 1995).

Model Species and Specific Objectives

Migratory caribou and reindeer are found throughout the circum-arctic and have high cultural importance for many aboriginal communities (Kendrick and Manseau, 2008) as well as economical importance. Currently, most populations are declining (Festa-Bianchet et al., 2011; Vors and Boyce, 2009). Populations of migratory caribou appear to fluctuate more rapidly and drastically than those of other large mammals (Bergerud et al., 2008) presenting a challenge to consumptive management of this species. Due to large home ranges and northern distribution (Figure 1), aerial surveys are currently the only effective way to obtain population estimates. Because they are costly, population counts are infrequent (Figure 2). In addition, estimates often have large confidence intervals (Couturier et al., 2010) (Figure 2).

Factors that influence caribou population dynamics include large-scale climate patterns (Joly et al., 2011; Vors and Boyce, 2009), weather and predation (Adams and Dale, 1998; Boertje, 1990), parasites (Albon et al., 2002), density-dependent food limitation (Skogland, 1983) and reduced adult survival (Crête et al., 1996). Caribou managers have monitored growth, condition, survival and reproduction to better understand population fluctuations. However, the proximal causes of population fluctuations remain poorly understood. Density dependence in demographic parameters and morphology has been documented in many herds, along with the relationships linking body size and condition to demographic rates, but gaps in knowledge still exist. Body condition and size are positively correlated to fecundity and population size reduces productivity (Crête et al., 1996). Whether population size influences fecundity indirectly by affecting body condition or if females adopt a conservative reproductive strategy at high density as seen in other species, however, has yet to be investigated in migratory caribou. Similarly, many morphological measures of migratory caribou and vital rates have shown density dependence. However, unlike other species, morphological measures have not been validated as ecological indicators and the overall usefulness for ecological indicators to inform on changes at the population level during various phases of population abundance has not been assessed.

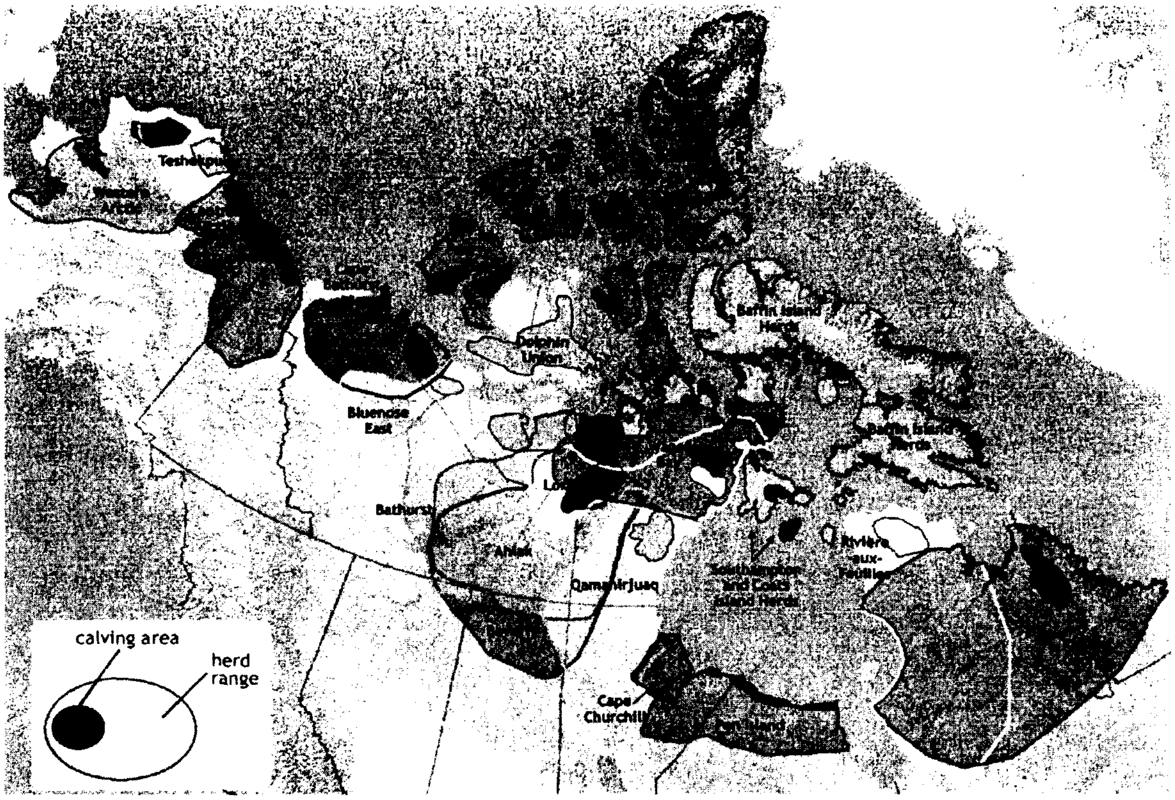

Figure 1. Distribution of major North American migratory tundra caribou herds with their associated calving grounds, including the four study populations: the Porcupine, Rivière-George, Rivière-aux-Feuilles and Beverly herds. Figure from (Hummel et al., 2008).

These gaps in knowledge led to the two main objectives of this study. Firstly, at the individual level, I sought to determine if females adopt a conservative reproductive strategy by investigating the mechanism by which population size affects fecundity rates through its interaction with body size and condition. More specifically, I wanted to determine which body size, condition or health indices, including mass, body fat, parasite infection and leg length, affect the probability of gestation. Also, I investigated the effect of population size on gestation rates and its effect on the relationship between physical condition and gestation rates. The Rivière George herd was examined to test this hypothesis since body condition data on pregnant and non-pregnant females were available over a large range of population sizes. I hypothesized that, similar to other herds, larger, heavier and fatter females with low parasite infections would have a higher probability of gestation. And similar to other long lived iteroparous mammals, females would adopt a conservative reproductive strategy at high population size.

The second objective, at the population level, was to determine which physical traits act as ecological indicators for migratory caribou and to assess their usefulness to predict population size. Specifically, my goal was to quantify correlations between juvenile morphology (mass and leg length), seasonal adult condition (mass and fat) and adult size (leg length) with population size for four migratory caribou herds. Because nutrition can determine adult size and current condition (Parker et al., 2009), I hypothesized that average physical traits would vary according to population size when nutrition was the limiting factor. An increase in density often limits resource availability, whereas reduced density is not always associated with an increase in resources (Bonenfant et al., 2009). Therefore, I hypothesized that density dependence would be more prominent during periods of demographic growth. And as seen in other ungulates, I hypothesized that juveniles would respond more readily than adults to changes in population size (Gaillard et al., 2000). Ecological indicators that inform on population size would act as an alternative to infrequent population counts and be invaluable for caribou managers and the conservation of migratory caribou.

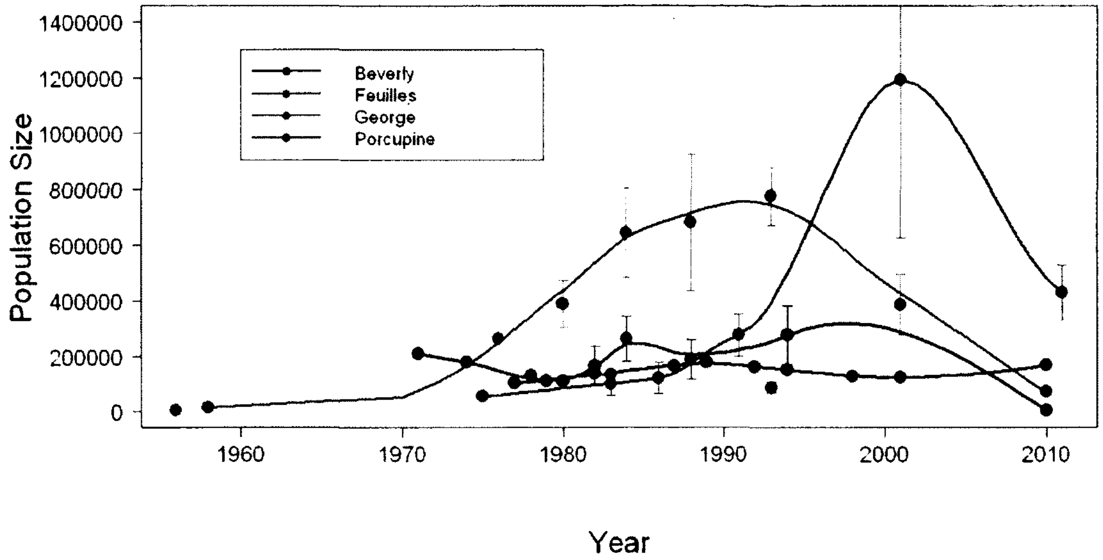

Figure 2. Population estimates (points) of the Rivière-George, Rivière-aux-Feuilles, Porcupine and Beverly migratory caribou herds over time. Bars represent 90% confidence intervals for the Rivière-aux-Feuilles and Rivière-George herds and standard error for the Beverly herd, when available. Lines depict population trajectories for all four herds based on loess smoothing.

CHAPTER 1

SPRING-LOADED REPRODUCTION: EFFECTS OF BODY CONDITION AND POPULATION SIZE ON GESTATION RATES IN MIGRATORY CARIBOU

ABSTRACT

In many ungulates, including caribou, female fecundity is affected by body condition and has important effects on population dynamics. In some species, females adopt a conservative strategy, reducing reproductive effort when population density is high. We investigated what factors affect the probability of gestation in adult female caribou from the Rivière-George herd in northern Québec and Labrador over five years that spanned various population sizes and trends. Similar to other populations of migratory caribou, the probability that a female was pregnant in spring increased with body mass and percentage of body fat. The probability of gestation appeared to be reduced by high warble infestation. The proportion of females pregnant varied between years and was reduced at high population size. Females of similar mass, however, were pregnant regardless of whether the population was increasing at low density, had reached a peak, or was declining. Compared to other ungulates that reduce maternal expenditure at high density, female caribou of the Rivière-George herd may have a risk-prone reproductive strategy.

INTRODUCTION

Life history theory assumes that limited resources force trade-offs among fitness components such as growth, reproduction and survival (Stearns, 1992). These trade-offs lead to variation in life history traits including fecundity, age at primiparity and reproductive lifespan or aging. Because fecundity affects population productivity (MacDonald et al., 2009; Promislow and Harvey, 1990), understanding female reproductive strategy is key to population dynamics and management (Festa-Bianchet and Côté, 2008). Indeed, measures of reproductive performance such as fecundity (Cameron and Hoef, 1994), female to young ratios and recruitment rates

(Couturier et al., 2009; Vincent et al., 1995) are regularly suggested as management tools to evaluate population performance.

Reproductive performance may vary with individual characteristics such as age (Festa-Bianchet, 1988; Ropstad, 2000; Sand et al., 1996), body condition (Sand et al., 1996; Testa and Adams, 1998) and previous reproductive experience. Extrinsic factors including density (Albon et al., 1983; Sand et al., 1996), predation, parasitism (Hughes et al., 2009) and weather (Adams and Dale, 1998; Post and Stenseth, 1999) may also affect reproductive performance. Most research has focused on how female body size and condition relates to reproductive success through age at primiparity (Jorgenson et al., 1993), lifetime reproductive success and fecundity (Crête et al., 1993; Dauphiné and McClure, 1974; Reimers, 1983). Good body condition allows females to reproduce earlier, more often, and produce more or larger offspring with high survival rates (Tveraa et al., 2003). Environmental factors such as climate may affect body condition indirectly by affecting food availability and energy expenditure (Solberg et al., 2001). High population density can limit resource availability through increased competition (Clutton-Brock et al., 1982).

When resources are limited, females may increase their survival by limiting investment in reproduction. Indeed, long lived iteroparous animals typically adopt a conservative reproductive strategy at high population densities by reducing litter size (Sand et al., 1996), maternal care (Bårdsen et al., 2008; Martin and Festa-Bianchet, 2010), or fertility (Albon et al., 1983; Sand et al., 1996). Few studies have revealed density-dependent effects on adult female survival (Gaillard et al., 2000) supporting the contention that females favor maintenance and survival over reproduction. That contention is also supported by the sequence with which vital rates usually change as population density increases: first survival of young decreases, then age of primiparity increases, after which reproductive rates decrease and lastly, but rarely, adult survival decreases (Eberhardt, 2002).

Potential mechanisms for how density impacts reproductive rates have been identified. Density affected age of primiparity through a reduction in body condition for bighorn sheep, but also selected for a more conservative reproductive strategy, independent of body condition (Jorgenson et al., 1993). Similarly, density reduced not only adult female mass but also age-specific fecundity in moose (*Alces alces*), beyond what could be explained by the decrease in body condition (Sand et al., 1996). In red deer hinds, the threshold mass required for females to conceive was higher at high than at low population density (Albon et al., 1983).

Understanding reproduction of migratory caribou is of particular interest because populations undergo rapid and extensive fluctuations (Morneau and Payette, 2000). Reproduction is one of the first vital rates affected by an increase in population size in migratory populations (Crête et al., 1996). In rapidly increasing populations, yearling females have high pregnancy rates (Ouellet et al., 1997; Parker, 1980) but yearlings may stop conceiving at high density (Crête and Huot, 1993). Reproduction in caribou is associated with body size (Gerhart et al., 1997) and condition in both autumn (Adams and Dale, 1998; Cameron and Hoef, 1994; Cameron et al., 1993) and spring (Russell et al., 1998). Female caribou that first reproduce at a young age are typically heavier (Adams and Dale, 1998), fatter (Crête et al., 1993) or both heavier and fatter (Thomas, 1982) than those that delay primiparity. Among adults, females that conceive are heavier and fatter than those that do not conceive (Allaye Chan-McLeod et al., 1999). Fecundity-body condition relationships for adults have been determined for several populations, including the Denali herd (Adams and Dale, 1998), the Porcupine herd (Gerhart et al., 1997), the Central Arctic Herd (Cameron et al., 1993) and Peary populations (Thomas, 1982).

The relationship between body condition and fecundity in caribou varies with age (Adams and Dale, 1998; Cuyler and Àstergaard, 2005), lactation status (Gerhart et al., 1997) and weather (Adams and Dale, 1998). Although the effect of density on reproductive rates has also been examined, its effect on the relationship between condition and fertility has yet to be assessed. Our objectives were to determine if (1) the relationship between body condition and fecundity seen in other herds was conserved in the Rivière-George herd and (2) if females adopted a conservative reproductive strategy at high population densities. We hypothesized that once age and body size were controlled for, females in better body condition (higher mass and percent body fat) and health (lower parasitic infection) would have a higher gestation rate in spring compared to females in poorer condition and/or health. As well, because caribou are long-lived and iteroparous, we expected females to adopt a conservative reproductive strategy, so that the threshold body condition required to reproduce would increase with population density.

METHODS

Study Area and Population Estimates

The Rivière-George herd is a migratory caribou herd in Northern Québec and Labrador. The annual range estimate was 213 390 km^2 in 2009 (Taillon, J. per. comm.), although range size varies with population size (Couturier et al., 2010). The Rivière-George increased from approximately 5000 in the 1950s to an apparent peak approximating 1 000 000 individuals in 1989 (Crête et al., 1996). It then declined to 776 000 in 2001 (Couturier et al., 2009b) and to less than 75 000 individuals in 2010 (Québec Government aerial count).

Data Collection

Scientific culls from the Rivière-George have been conducted for decades, but sampling methods and purposes differed between researchers and years. We restricted analyses to collections where the selection of females was not biased towards particular reproductive classes. Age of females was assessed by counting the cementum annuli of an incisor (Miller, 1974). Data we used were collected from late February to April and limited to known-age individuals, where the presence or absence of a foetus was recorded. Data meeting these requirements were collected in April 1980 by G. Parker; in April 1984 by J. Huot; and in March 1986-1987, February and April 1987, and March 2002 by S. Couturier.

Because not all age classes were sampled equally in all years and to avoid the possible complications associated with primiparity, we defined adult females as ≥ 3 years old. Limited number of old individuals sampled precluded the analysis of senescence effects. We therefore excluded the oldest female collected, a barren 17-year-old, from analyses. Our data set included 160 females, of which 23 were barren and 137 were pregnant.

Caribou Body Condition

Body condition indices typically measured included whole mass and/or eviscerated body mass, hind foot length and/or metatarsal length, kidney fat mass and kidney mass, percentage of femur marrow fat, and parasite load denoted by the absolute number of warbles (*Hypoderma tarandi*) counted. Protocols for animal culls and body condition measurements are described elsewhere (Couturier et al., 2009a; Huot, 1989; Parker, 1980). Percentage of body fat was calculated as 0.091*KFFI-1.382 based on (Crête et al., 1993), where KFFI is the kidney fat femur index (KFI + % Femur marrow fat) (Huot and Picard, 1988). KFI is the kidney fat index based on the Riney fat index (Riney, 1955). The average of the right and left kidney weights and kidney fat weights was used to calculate the KFI, except for 15 of 172 cases where only one kidney or kidney fat was weighed.

Because body condition varies seasonally, we used ANCOVAs to test for an effect of collection date on mass and percent body fat and for a possible interaction between these variables and pregnancy status. We used eviscerated masses collected from February to May in 1987 to test for an effect of collection date on body mass. Collection date did not affect eviscerated body mass ($F_{(1,38)}=0.94$, $p=0.34$) nor did it affect pregnant and barren females differently (interaction: $p=0.63$).

Pooling all years, percent body fat decreased from late February to April ($F_{(3,161)}=5.80$, $p<0.01$) and in interaction with pregnancy status ($p=0.02$) such that there was a decrease in body fat for gestating but not for barren females. We therefore adjusted body fat of pregnant females to March 23, the middle of the sampling period for all years. Pregnant females lost on average 0.05% body fat per day. The maximum number of days corrected for was 24 with a maximum correction of 1.08% body fat loss.

To compare metatarsal lengths measured in 1980 with hind foot lengths measured in 1984-2002, we transformed metatarsal lengths using a correlation based on 132 adult females from the Rivière-George from 8 years (1986-1988, 2001-2003 and 2007) including collections outside of this study ($F_{(1,129)}=275.80$, $r^2=0.68$, $p=2.20*10^{-16}$, hind foot length=1.31*metatarsal length+4.69).

Population Estimates

Population counts were available for two years when body condition data were collected (1980 and 1984). Population size for 1986, 1987 and 2002 was estimated by fitting a loess smoothing spline on available population counts. Aerial counts were made in 1988, 1993 and 2001, so all population estimates were within one or two years of actual counts. We accounted for population size and trend in three ways: (1) as a continuous vector using actual counts and inferred estimates, (2) grouped into two categories: above and below 500 000 individuals, following Couturier et al. (2009), and (3) grouped into three phases that accounted for both population density and trend: low and increasing (1980), high and approaching the peak (1984-1987), and declining (2002).

Statistical Analyses

We used R software version 2.12.1 (R Development Core Team 2010) for all statistical analyses. General Linear Models (GLM) with a binomial distribution were used to model the probability of gestation as a function of female age, mass, hind foot length, percent body fat, warble infection, population size and trend. Year of collection was tested as a random effect in mixed models but was not significant so analyses were performed using GLMs. Our data were non-orthogonal. Unequal sample sizes were due to missing data on several individuals. We first used maximum sample sizes (ranging from 86 to 160) to model the probability of gestation based on each variable separately. We then excluded warble counts from further multivariate analyses, as counts were only available for two of the five years, to test all other body condition variables with population size and trend. These analyses were performed using a data set with 115 individuals. Subsequent analyses excluded body fat and therefore only included variables that can be measured or estimated on live animals. Body fat was not available for 16 females. Therefore when body fat was excluded for analyses, the sample increased to 131 individuals.

We checked all explanatory variables for collinearity before combining them in the same model. We used the *vif* function in the "car" package to test the variance inflation factor of variables in all full models. Variables were not combined in models if the variance inflation factor exceeded 2. The highest correlation for both sample sets was between mass and body fat (0.47) in the set containing all variables ($n=115$). All other variables were only weakly correlated ($r<0.32$). Older females were larger, heavier and fatter than younger females. Warble count and population size were negatively correlated to all other variables such that older, larger, heavier and fatter females had fewer warbles and were mostly sampled at low population size.

We considered all results significant at $\alpha<0.05$ for univariate General Linear Models. Due to small sample size, model selection was performed using a second order Aikaike Information Criterion (AICc). The model with the lowest AICc was retained (Burnham and Anderson, 2002). Differences in AICc values of at least 2 were used to determine if one model was better than another. Because several models were indistinguishable based on AICc values, we used the *modavg* function from the "AICmodavg" package in R to calculate weighted (w_i) parameter estimates for explanatory variables along with their standard errors and 95% confidence intervals. Variables were considered significant if the confidence interval of their estimate did not overlap zero. Step-wise model selection following (McCullagh and Nelder, 1989) led to similar models being selected.

RESULTS

Fertility

When all years were pooled, 27% of 33 yearlings were pregnant. Gestation rates increased to 76% for 122 females aged two to four years and 90% for 103 females aged 5 years or older. Nine of 16 yearlings were gestating in 1980, when the population was low and increasing. These animals would have given birth as two-year-olds. In 1984, 1986 and 1987, none of 12 yearlings collected were pregnant. No yearlings were collected in 2002 when the population was decreasing.

Adult female body condition

Pregnant females were on average 13.5 kg heavier, 2.3% fatter, were older and had fewer warbles than barren females, but did not differ in hind foot length (Table 1). Females were in good condition when the population was low and increasing (1980), as they were heavier and larger (based on hind foot length) compared to when the population was high (1984-1987) or decreasing (2002) (Table 1). The different age distribution in 1980 compared to all other periods (Table 1) was likely due to differences in yearly sample sizes caused by variation in sampling methods. Based on percent body fat, females were in good condition with over 10% body fat for all periods of demographic trend (Table 1). However, females had 1.1 % less body fat when the population was nearing a peak compared to when the population was low (Table 1). Average number of warbles nearly doubled as the population increased (Table 1).

Gestation Predictors

For females aged 3 or older, hind foot length (estimate= 0.03 ± 0.17, n=140, p=0.90) and age (estimate= 0.26 ± 0.13, n=160, p=0.08) did not affect fecundity in simple logistic models (Figures 3C and 3D, respectively). Fecundity increased with both mass (estimate=0.17 ± 0.04, n=133, p<0.01) and percent body fat (estimate= 0.44 ± 0.04, n=132, p<0.01) (Figures 3A and

3B). Fewer females were pregnant at high population size than at lower population size (estimate= -0.0004 ± 0.0001, n=160, $p<0.01$) (Figure 3F). Warble infestation reduced the probability of gestation (estimate= -0.02 ± 0.01, n=84, p=0.01, Figure 3E). When the female with the highest infestation (336 warbles) was removed, however, the regression was not significant (estimate= -0.02 ± 0.01, p=0.06, n=83, Figure 3E). If we excluded this potential outlier but included 2-year-olds as in Gerhart et al. (1997) and Hughes et al. (2009), the negative effect remained significant.

In simple logistic models, body mass was the best predictor of pregnancy rate and explained 22.5% of the variation in fertility. Percent body fat was significant but explained only 12.1% of the variation. At average mass (91.2 kg), females had a 91% probability of being pregnant. All but 3 non-pregnant females were lighter than this threshold. At average percent body fat (10.9%), females had a 95% chance of being pregnant.

Population Size as a Predictor of Pregnancy

Population size as a continuous variable had the lowest AICc value (62.8) compared to population size grouped into 2 groups (AICc=64.3) or population trend (3 groups) (AICc=63.1). Therefore, we used population size as a continuous variable in AICc model selection. There were 115 females with all variables measured, including body fat. Both AICc and step-wise model selection with nested models suggested that mass was the most important factor affecting the probability of gestation (Tables 2 and 3). The inclusion of a quadratic effect of age did not affect model selection based on AICc and did not alter parameter estimates. Although hind foot length was included among the best models using AICc, its parameter estimate did not significantly differ from zero (Table 2) and it bordered on significance (p=0.07) in models obtained by a step-wise selection. Based on AICc model selection, the relationship between mass and fertility did not vary according to population size as no interaction between population size and body condition variables were retained (Table 2). Although population size did appear in one of the best models, its parameter estimate was not significantly different than zero (Table 3).

Table 1. Average mass (kg), body fat (%), hind foot length (hflT) (cm), number of warbles and age with standard error (se) and sample size (n) grouped by reproductive status (pregnant or barren) and demographic trend (low and increasing, high and increasing or low and decreasing) of known-age female caribou (≥3 years) from the Rivière-George herd collected in 1980, 1984, 1986, 1987 and 2002. Presence or absence of a foetus was recorded during March and April, except for 5 individuals collected in late February in 1987. Values that differ significantly based on Tukey post-hoc tests for mass, body fat and hind foot length and based on Kruskal-Wallis tests for differences in age distribution and number of warbles, are denoted by different letters. Bonferonni correction was applied to determine significance between demographic trends for age (p=0.02).

	Mass (kg)			Body fat (%)			HflT (cm)			Warbles			Age		
	mean	se	n	mean	se	n	mean	se	n	mean	se	n	mean	se	n
Reproductive status															
Pregnant	92.5a	0.8	117	11.1a	0.2	111	56.7a	0.1	122	35.3a	4.2	82	6.7a	0.2	137
Barren	79.0b	2.6	16	8.9b	0.6	14	56.6a	0.4	18	146.8b	67.3	4	5.6b	0.4	23
Demographic trend															
Low	94.0a	0.9	81	11.2a	0.2	76	57.0a	0.1	80	36.4a	4.5	76	7.2a	0.3	81
High	86.2b	1.9	39	10.2b	0.3	40	56.2b	0.2	47	71.9b	31.7	10	5.7b	0.2	66
Decreasing	85.5b	2.6	13	11.4ab	1.3	9	56.8ab	0.5	13				7.1b	0.6	13

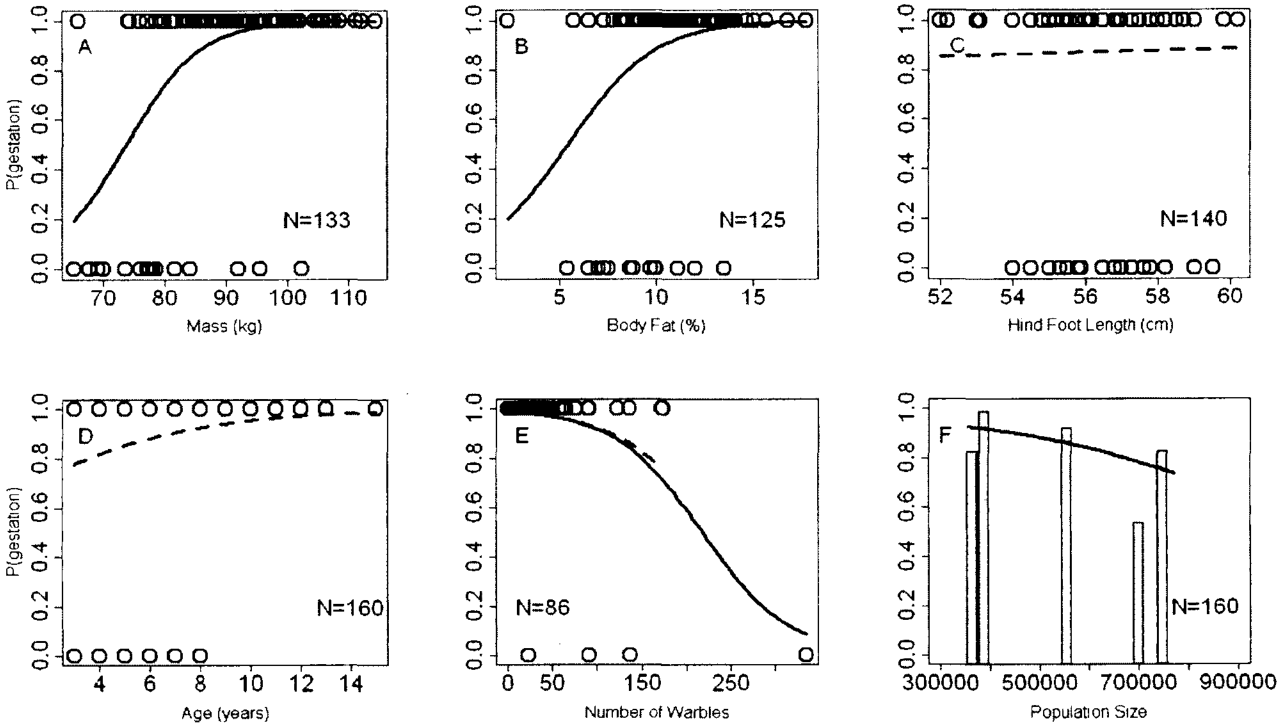

Figure 3. Logistic regressions of the probability of gestation according to body condition indices and population size for Rivière-George caribou females aged 3 to 16 years collected in spring of 1980, 1984, 1986, 1987 and 2002. Regressions predicting presence (1) or absence of foetus (0) for (A) mass, (B) percentage of body fat and (F) population size were significant. Regressions for (C) hind foot length and (D) age were not significant. Logistic regression of (E) the number of warbles was significant (solid line) but became marginally insignificant after removing the female with the highest warble count (dotted line). Raw data (points) are shown, except for (F), where grey bars show the proportion of pregnant females at given population sizes.

Table 2. Model selection based on second order Akaike's information criterion corrected for small sample size (AICc) for the determinants of gestation in adult female migratory caribou of the Rivière-George herd in spring (March and April) 1980, 1984, 1986, 1987 and 2002. Models include 115 known-age individuals with all morphological measurements including mass (mass), percent body fat adjusted to March 23 (bodyfatC) and hind foot length (hflT). Population size (popest), and interactions denoted by asterisk (*) were also included in models along with a model containing no explanatory variables (null model). Models are listed in rank order with the 6 best models, with AICc values that do not differ by more than 2, in bold. Number of estimated parameters (k), change in AIC from lowest AICc value (ΔAICc), and cumulative weight of model (Cum. Wt) based on the likelihood that that model is the best model (LL) are presented.

Model	K	AICc	ΔAICc	AICcWt	Cum.Wt	LL
mass+hflT	**3**	**60.64**	**0**	**0.19**	**0.19**	**-27.21**
mass	**2**	**61.14**	**0.5**	**0.15**	**0.34**	**-28.52**
age+mass+hflT+bodyfatC	**5**	**61.4**	**0.76**	**0.13**	**0.48**	**-25.42**
mass+bodyfatC	**3**	**61.59**	**0.95**	**0.12**	**0.6**	**-27.69**
mass+hflT+bodyfatC	**4**	**61.74**	**1.1**	**0.11**	**0.71**	**-26.69**
popest+mass	**3**	**62.49**	**1.85**	**0.08**	**0.79**	**-28.14**
mass+age	**3**	**62.51**	**1.87**	**0.08**	**0.86**	**-28.15**
age+mass+hflT+bodyfatC+popest	6	62.67	2.03	0.07	0.93	-24.95
popest*mass	4	63.64	3	0.04	0.97	-27.64
bodyfatC+age	3	65.43	4.8	0.02	0.99	-29.61
popest+bodyfatC	3	68.13	7.49	0	1	-30.96
popest*bodyfatC	4	70.17	9.54	0	1	-30.9
bodyfatC	2	70.92	10.28	0	1	-33.41
hflT+bodyfatC	3	72.97	12.34	0	1	-33.38
popest	2	74.86	14.22	0	1	-35.37
popest*age	4	75.91	15.27	0	1	-33.77
age	2	76.82	16.18	0	1	-36.36
popest+hflT	3	76.87	16.24	0	1	-35.33
popest*hflT	4	77.52	16.89	0	1	-34.58
null	1	78.98	18.34	0	1	-38.47
hflT	2	81.05	20.41	0	1	-38.47

Table 3. Model averaged parameter estimates, standard error (se) and 95% confidence intervals (CI) for variables from the 6 competing models from Table 2 for the determinants of gestation in adult female migratory caribou of the Rivière-George herd in spring (March and April) 1980, 1984, 1986, 1987 and 2002. Models included 115 known age individuals with all morphological measurements including mass (mass), percent body fat adjusted to March 23 (bodyfatC), hind foot length (hflT) and population size (popest).

variables	estimate	se	CI low	CI high	Significant
mass	0.15	0.07	0.01	0.3	YES
hflT	-0.42	0.28	-0.97	0.13	NO
bodyfatC	0.25	0.19	-0.3	0.62	NO
age	0.31	0.25	-0.18	0.81	NO
popest	0	0	0	0	NO

When body fat was not considered, the best model explaining gestation in adult females included hind foot length and mass (Table 4; AIC=67.3, and AIC≥69.7 for all other models). The relationship between mass and probability of gestation remained positive for mass (0.22 ± 0.07, CI: 0.09 to 0.34, Figure 4) but the effect of hind foot length became negative once mass was controlled (-0.58 ± 0.26, CI: -1.1 to -0.07, Figure 4). The model containing both hind foot length and mass explained 31% of the variation, 8.5% more than mass alone. To have a 50% chance of pregnancy, females had to be ~76kg in spring. However, females of a given mass were ~5% less likely to be pregnant if their hind foot length was ~4 cm larger.

DISCUSSION

Fecundity-condition relationships seen in other caribou herds were mainly confirmed in the Rivière-George. Mass and percent body fat positively affected gestation rates and there was no effect of age. High warble infection was associated with a reduced probability of pregnancy in spring. Hind foot length itself was not a good indicator of whether a female would reproduce, but reduced the probability of gestation after body mass was controlled.

Table 4. Model selection based on second order Akaike's information criterion corrected for small sample size (AICc) for the determinants of gestation in adult female migratory caribou of the Rivière-George herd in spring (March and April) 1980, 1984, 1986, 1987 and 2002. Models include 131 known age individuals with measured mass (mass) and hind foot length (hflT). Population size (popest) and interactions denoted by asterisk (*) were also included in models. Models are listed in ranked order with the best model in bold. Number of estimated parameters (k), change in AIC from lowest AICc value (ΔAICc), and cumulative weight of model (Cum. Wt) based on the likelihood that that model is the best model (LL) are presented.

Model	K	AICc	ΔAICc	AICcWt	Cum.Wt	LL
mass+hflT	**3**	**67.26**	**0**	**0.72**	**0.72**	**-30.53**
mass	2	70.96	3.7	0.11	0.83	-33.43
mass+age	3	71.68	4.43	0.08	0.91	-32.75
popest+mass	3	72.11	4.85	0.06	0.97	-32.96
popest*mass	4	73.84	6.58	0.03	1	-32.76
popest+age	3	93.38	26.12	0	1	-43.59
age	2	94.64	27.39	0	1	-45.27
popest	2	94.96	27.7	0	1	-45.43
popest*age	4	95.09	27.84	0	1	-43.39
hflT+age	3	96.55	29.29	0	1	-45.18
popest+hflT	3	96.71	29.45	0	1	-45.26
popest*hflT	4	98.65	31.39	0	1	-45.17
1	1	99.28	32.02	0	1	-48.62
hflT	2	101.26	34	0	1	-48.58

Population size negatively affected the proportion of females that were pregnant but contrary to our second hypothesis, threshold mass and body fat necessary for gestation did not vary with population size, suggesting that females did not adopt a conservative reproductive strategy when resources were scarce. Productivity of this herd remained high but was reduced by smaller mass at high population size.

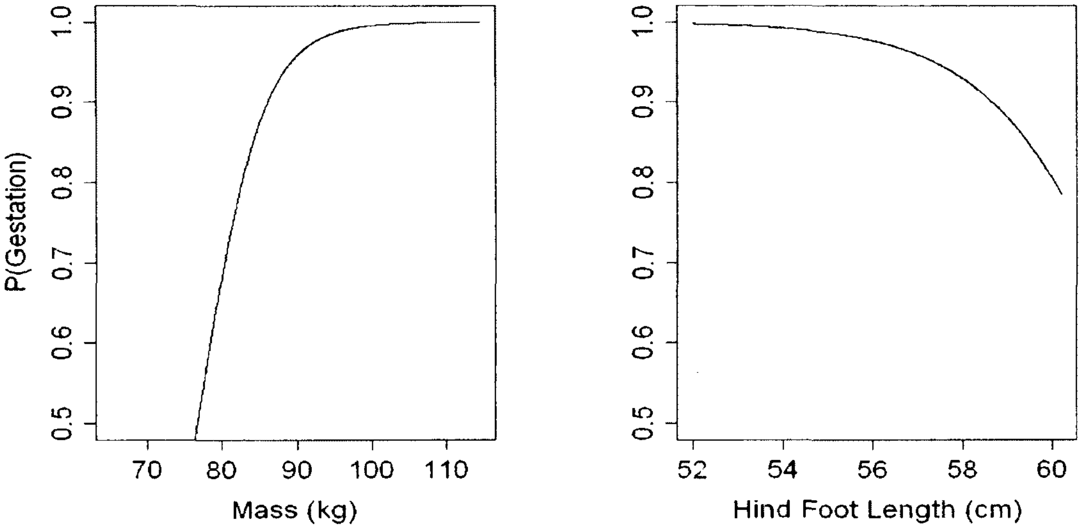

Figure 4. Model predictions, from best model with 131 individuals selected using AICc in Table 4, of gestation in relation to mass in April and May at average hind foot length (left panel), and in relation to hind foot length at average mass (right panel) for adult female caribou of the Rivière-George herd in 1980, 1984, 1986, 1987 and 2002.

Condition-Fecundity Relationships

As seen in other caribou herds, both mass and fat were important determinants of fecundity (Adams and Dale, 1998; Cameron et al., 1993; Dauphiné and McClure, 1974; Russell et al., 1998; Thomas, 1982). Although it has been proposed that a critical level of mass and fat are needed for caribou to conceive (Crête et al., 1993), we did not observe a sharp threshold. A threshold may have existed during autumn when ovulation occurred but did not persist until spring. We did not detect an effect of age on the probability of gestation. Congruent with results from the Porcupine caribou herd (Gerhart et al., 1997), hind foot length in simple logistic regressions did not affect the probability of gestation; its negative effect after accounting for body mass suggests that caribou with relatively fewer body reserves were less likely to be pregnant.

Warble infestation reduced the probability of gestation. When we included two-year-olds to compare with analyses of the Dolphin-Union herd (Hughes et al., 2009), our results corroborated the finding that the probability of gestation in spring decreases with warble abundance. Relationships between parasite load and fecundity, however, are often confounded by body condition. Because parasite load is correlated with body condition, it is difficult to ascertain whether individuals are in poor condition due to high parasite load or poor condition allows high intensity infections. Both parasite load and condition are correlated with fecundity. For caribou from the Dolphin Union herd, high warble infection was correlated to minimal back fat levels (Hughes et al., 2009) and for the Rivière-George in this study both mass (r=-0.22 (n=82)) and percent body fat (r=-0.26 (n=82)) were negatively correlated to infection intensity. Reduction of parasite infections improves body mass, back fat and fecundity in reindeer (Stien et al., 2002). Parasite infections may affect the assimilation of nutrients needed for maintenance (Hughes et al., 2009). Although condition may be more closely associated to fecundity, it is important to understand the role of parasites because parasite abundance may affect population growth in *Rangifer* (Albon et al., 2002). Since intensity of infection typically increases with host density (Arneberg et al., 1998), as observed in this population, it is important to monitor parasite loads, especially if parasite abundance is influenced by climate change (Brotton and Wall, 1997).

Mass was clearly the best predictor of gestation in the study herd. Our results contradicted those of the Porcupine herd in autumn, where body fat (Gerhart et al., 1997) was the best predictor of pregnancy. This could be due to several factors; firstly, in this study, body fat was calculated from direct measures of fat compared to body condition scores used for the Porcupine herd. Secondly, seasonal differences between the two herds could account for the different results obtained. For example, body condition for females of different reproductive classes in the Porcupine herd converged over winter (Allaye Chan-McLeod et al., 1999). Similarly, the percentage of body fat of pregnant females decreased over the collection period in the Rivière-George. Lastly, pregnancy-condition relationships may vary among herds.

Although percentage of body fat affected whether or not a female would be pregnant in spring, it did not improve on mass as a predictor of gestation. When body fat was excluded from models, our results corroborated those from the Porcupine herd; both mass and hind foot length were related to the probability of pregnancy (Gerhart et al., 1997). The effect size of hind foot length was small and in analyses with a smaller sample size that included percent body fat, only mass was a significant explanatory variable. Therefore, in the Rivière-George, the importance of hind foot length appears to be minor.

Effect of Population Size

Female fecundity was lower when population size was high. Contrary to our expectation, the threshold condition necessary for gestation did not vary with population size, despite an estimated difference of 400 000 individuals, suggesting a near-doubling of population size. Caribou, therefore, did not adopt the conservative reproductive strategy reported for other ungulates (Festa-Bianchet et al., 1998; Therrien et al., 2007), at least in terms of conception rates. This seemingly risky strategy could be due to a low potential cost of gestation compared with the potentially high fitness cost associated with foregoing reproduction. Outside Greenland (Cuyler and Àstergaard, 2005), caribou are not known to twin and consequently, their lifetime reproductive success is mostly affected by the number of years in which they reproduce. Therefore, unlike species that reduce litter size under resource restriction (Sand, 1998), caribou forego their yearly reproduction if they do not conceive. Perhaps caribou have a fixed pregnancy rate that depends on body condition but vary foetal growth or postpartum maternal investment based on their seasonal condition, as seen in reindeer (Bårdsen et al., 2008). For example, females may abort if their condition deteriorates (Russell et al., 1998). Calf mass is also affected by female condition (Adams, 2005), suggesting that females modulate allocation of resources to their foetus according to their own condition. Lactation is the most energetically costly component of reproduction (Gerhart et al., 1997) and when resources are scarce females may allocate more to maintenance than to offspring growth postpartum (Bårdsen et al., 2009). Females from the Rivière-George, however, appeared to prioritize gestation over their own condition, as suggested by the decrease in mass and not in gestation rate. We therefore hypothesize that for caribou, the fitness cost of foregoing reproduction is high relative to the investment of carrying a calf to term. Despite this apparently fixed reproductive strategy, we still observed a reduction in herd productivity during the population increase.

Similar to the Denali population (Adams and Dale, 1998), we suggest that the mechanism affecting gestation rates in Rivière-George females was a reduction in mass. However, our results contrast with those from the Porcupine herd where variation in body condition of females was not reflected in pregnancy rates (Gerhart et al., 1997). Despite a drastic increase in population size, pregnancy rates in the Rivière-George remained high compared to other populations. For example, in Peary caribou, pregnancy rates fell as low as 4% at high density (Thomas, 1982). One explanation for the high pregnancy rates could be that female condition, based on percent body fat, remained high throughout the period of increase and was maintained even during the beginning of the subsequent decline. During our study, percent body fat averaged 11.0 ± 0.2 % (n=115), consistent with high pregnancy rates if indeed the threshold of 7.3% body fat needed for females to conceive (Crête et al., 1993) holds true. Although we suggest that a decline in mass reduced reproductive rates, other demographic parameters including age at primiparity and survival may have also affected productivity.

Determining both the intrinsic and extrinsic factors that affect the probability of gestation in caribou is important to understand population dynamics. Although there is no known causal relationship between body condition and fertility, the relationship between body condition and gestation remains uncontested. For management purposes, adult female mass and hind foot length measurements in spring predict pregnancy rates in the Rivière-George. Both measures can be obtained through live captures. We showed that caribou prioritize reproduction even at high population densities as we were unable to detect a conservative reproductive strategy for gestation. High gestation rates, however, did not seem to affect changes in population size in this herd. That result highlights the importance of monitoring post-gestational demographic

ACKNOWLEDGEMENTS

This research was funded by Caribou Ungava and some of its many financial partners including: ArcticNet, Ministère des Resources naturelles et de la Faune du Québec (MRNF), Labrador and Newfoundland Wildlife Division, Natural Sciences and Engineering Research Council of Canada (NSERC), Hydro-Québec, Fédération des Pourvoiries du Québec, Canadian Wildlife Federation, Centre d'études nordiques, and in partnership with Université de Sherbrooke and Université Laval. We are especially thankful to G. Parker, J. Huot and S. Couturier for use of their data and to the many that contributed to the data collection making this research possible. We are thankful to F. Pelletier for advice on statistical approaches.

CHAPTER 2

MORPHOLOGICAL TRAITS OF MIGRATORY CARIBOU PREDICT POPULATION SIZE BETTER IN PERIODS OF DEMOGRAPHIC GROWTH THAN DECLINES

ABSTRACT

Population estimates are key to monitoring and managing wildlife. Migratory caribou populations are particularly difficult to monitor due to their northern location, immense range and drastic population fluctuations. Currently, aerial surveys are the main tool to obtain population estimates, but lack both accuracy and precision. Because they are costly, aerial surveys are infrequent. Ecological indicators that provide information about a population relative to its environment have been proposed to monitor ungulate density. These indicators include size, mass, and body fat. Density-dependent factors have been identified in caribou but the extent that individual traits inform on population size has not been assessed. We examined body condition and morphology of different age classes of caribou from four North American herds to determine which indices best predict population size. Most physical traits only predicted population size during periods of demographic growth. Traits that correlated with population size were age-dependent; juveniles responded more consistently than adults, but correlations also varied between herds. Adult mass was positively related to population size in the Beverly and Porcupine herds. Adult hind foot length decreased with increasing density in the Rivière-aux-Feuilles and Porcupine herds. Monitoring physical traits can be useful to determine whether resource limitation or other factors are mainly driving population dynamics, but the ability of morphological traits to quantify numerical change at the population level is restricted to particular ecological contexts. We recommend that mass in juveniles and bone measurements in adults be measured to inform on population size. However, monitoring physical traits can only complement and not replace costly aerial counts. To better manage populations of migratory caribou, continued research and monitoring is

needed to identify herd-specific factors driving population dynamics, and potential ecological indicators, particularly during periods of population decline.

INTRODUCTION

Successful monitoring and management of wildlife populations hinges on knowledge about population size and trend, which require reliable population estimates (Morellet et al., 2007; Williams et al., 2002). In ungulates, various techniques such as the number of animals seen per kilometer of transects, capture-mark-recapture and hunting success rates (Nugent and Frampton, 1994) are used as proxies for population density, and aerial surveys are typically conducted for species that have large home ranges (Redfern et al., 2002), such as migratory caribou. Indeed, aerial surveys are currently considered the only effective tool for monitoring migratory caribou. Although population estimates are a high priority for managers (Klein et al., 1999), aerial surveys are costly and therefore infrequent. The accuracy and precision of aerial counts have also been questioned (Jachmann, 2002; Pettorelli et al., 2007; Redfern et al., 2002). Estimates often have large confidence intervals, which tend to increase with herd size (Couturier et al., 2010).

Monitoring migratory caribou populations is of utmost importance since most populations are declining globally (Festa-Bianchet et al., 2011; Vors and Boyce, 2009). Migratory populations also fluctuate more rapidly and drastically than those of other large mammals (Bergerud et al., 2008). Such drastic fluctuations present a major challenge to consumptive management of this species. Migratory caribou have high cultural and economical importance for aboriginal communities (Kendrick and Manseau, 2008). Because population estimates are infrequent, annual management decisions, including harvest quotas, are based on imprecise information, often without recent information on demographic trends.

In lieu of population counts, ecological indicators have been proposed to monitor ungulate populations (Du Toit, 2002; Morellet et al., 2007; Zannese et al., 2006). Ecological indicators provide valuable information about a population relative to its environment. Indirect ecological indicators are density-dependent indices based on physical characteristics or performance of individuals, such as female reproductive success, juvenile body mass or other morphological measures (Morellet et al., 2007; Zannese et al., 2006) that reflect changes in population density. Ideally ecological indicators provide yearly information about a population for a fraction of the cost of population counts, but they require validation.

Indirect ecological indicators rely on the principle of density dependence; as density increases, the number of resources per individual decreases, affecting individual nutrition. The negative impact of density on ungulate size and condition is well documented. Hind foot length (Zannese et al., 2006) and fawn mass (Hewison et al., 2002) of roe deer (*Capreolus capreolus*), caribou calf mass (Couturier et al., 2009b; Post and Klein, 1999; Weladji et al., 2003), red deer birth mass (Nussey et al 2005), body size of adult red deer (Mysterud 2001), roe deer (Toigo et al. 2006) and brown bear (*Ursus arctos*) (Zedrosser et al. 2006) have all shown negative density dependence during periods of population growth.

Reversal of the negative effects of high density requires that the nutritional plane improve as a population is reduced. Fewer studies have examined this relationship than those documenting the negative effects of increasing density. Cohort mandible size of caribou (Couturier et al., 2010), reindeer birth mass (Skogland, 1990), roe deer birth mass (Hewison et al., 2002), white-tailed deer fawn mass, yearling male mass and hind foot lengths (Ashley et al., 1998), and juvenile body condition of feral donkeys (Choquenot, 1991) all tended to increase when populations were reduced or declined naturally. However, a response in demographic parameters or physical traits does not always occur after population reduction, as seen in white-tail deer (Shea et al., 1992).

The response of demographic parameters and physical traits to density may vary according to whether a population is increasing or decreasing (Fryxell et al., 1991), although this possibility has received little attention. Demographic parameters and physical traits may mirror changes in density during periods of population growth, as resources become scarce, but may lag during periods of decline (Fryxell et al., 1991) until forage quality recovers. Cohort effects can also cause delayed responses. For example, poor environmental conditions at birth can affect adult mass and reproductive success even if density declines by when those individuals reach maturity (Gaillard et al., 2003; Pettorelli et al., 2002).

In addition to conducting population estimates, caribou managers have monitored productivity (pregnancy rates, birth rates, calf recruitment in autumn), adult survival (Crête et al., 1996), calf mass (Couturier et al., 2009b) and survival (Whitten et al., 1992), annual ranges, movements (Couturier et al., 2010), and adult body condition (Huot, 1989; Parker, 1980; Taillon et al., 2012a) to improve understanding of populations and their limiting factors. Due to limited financial resources, such data are not collected consistently over time nor for all herds (Klein et al., 1999). Managers therefore must make decisions with limited knowledge about the current state of a population. Alternatives such as ecological indicators would therefore be invaluable to inform on a population's state.

Our objective was to quantify correlations between individual physical characteristics including juvenile morphology (mass and leg length), seasonal adult condition (mass and fat) and adult size (leg length) with population size in four migratory caribou herds. We hypothesized that (1) average physical traits would vary according to population size for food-limited herds, that (2) the correlation between physical traits and population size would be strongest in populations at or near peak density, assumed to reflect carrying capacity, and that (3) juveniles would respond more readily to changes in population size compared to adults (Gaillard et al., 2000).

STUDY AREA

We studied four demographically independent (Figure 2) migratory caribou herds in North America; the Rivière-George herd and the Rivière-aux-Feuilles herd in Quebec and Labrador, the Beverly herd in central Canada and the Porcupine herd in the Northwest Territories, Yukon and Alaska. The Rivière-George and Rivière-aux-Feuilles herds together range over 1.2 million km^2 north of 50°30'N (Couturier et al., 2010), are genetically undifferentiated

(Boulet et al., 2007) and despite winter range overlap in some years, have unique calving grounds (Taillon et al., 2012b) and summer ranges (Boulet et al., 2007), differ morphologically (Couturier et al., 2010) and are managed as distinct populations. The Porcupine herd ranges over 250 000km^2 from 64-70°N and 130-150°W in northeastern Alaska, northern Yukon Territory and northwestern Northwest Territories (Chan-McLeod et al., 1999). The Beverly herd ranges over 700 000km^2 (Klein et al., 1999) including part of Manitoba, Saskatchewan, the Northwest Territories and Nunavut.

METHODS

Population Counts, Interpolating Population Estimates

Population estimates were obtained from post calving photography surveys for the Porcupine (http://www.nwtwildlife.com/NWTwildlife/caribou/herds.htm) and Rivière-aux-Feuilles herds, as well as for the Rivière-George herd after 1993. Population estimates for the Beverly and Rivière-George herds from 1976 to 1993 were extrapolated from counts of reproductive females on the calving ground and autumn classification counts. Estimates of the Rivière-George herd before 1976 were extrapolated from visual aerial censuses of the winter population.

From 1976-2010, seven photographic aerial counts of the Rivière-George herd were conducted. Confidence intervals were calculated for population counts beginning in 1980. The herd increased from about 5000 individuals in the 1950s to an estimated 776 000 in 1993, then declined to approximately 400 000 by 2001 (Couturier et al., 2009b) and 74 000 in 2010 (Quebec Government aerial survey). The population trajectory for the Rivière-George herd was validated up to the year 2000 using tree ring analyses (Boudreau et al., 2003). Based on population counts, we assumed that the Rivière-George peaked in 1993. Because dendroecological analyses (Boudreau et al., 2003) and population simulations (Crête et al., 1996) suggested that the herd actually peaked in 1989, we also verified a population trajectory with a peak in 1989.

Discovered by Le Hénaff (1976) in 1975, the Rivière-aux-Feuilles herd has had six population estimates conducted. The population was estimated at 56 000 in the 1975, increased to over 1.1 million in 2001 (Couturier et al., 2009b), and declined to 430 000 individuals in 2011 (Quebec Government aerial count).

Nine counts have been conducted for the Beverly herd. The herd decreased from more than 200 000 in 1971 to half as many in 1980. It increased again to 250 000 caribou in 1994 (http://www.enr.gov.nt.ca/_live/pages/wpPages/Beverly_herd.aspx) then decreased to 5 160 in 2009 (CARMA Network). Poor census conditions in 1993 led to a recount in 1994. Therefore, the 1994 estimate was exclusively used in analyses. Dendroecological analyses have also confirmed historical abundance in the Beverly herd (Zalatan et al., 2006).

Since 1977, ten population counts of the Porcupine herd have been conducted. Originally estimated at over 110 000 in 1977, it peaked in 1989 at over 170 000. The herd had declined to 123 000 by 2001 (CARMA network) and the 2010 estimate showed an increase to 169 000 individuals (Alaska Department of Fish and Game and Canadian wildlife agencies - aerial count: http://www.adfg.alaska.gov/index.cfm?adfg=pressreleases.pr03022011).

We assumed constant population growth rate between counts and estimates of population size each year, for all herds.

Morphological Data

Data were collected over various years and seasons for different purposes, including studies of body condition, organochlorine and heavy metal contamination, range quality, calf survival and maternal investment (Table 5). Measurements were obtained on hunted animals, live-captured animals and scientific culls and in one instance from a mass drowning. Measures obtained included whole mass, eviscerated mass, leg length measured as hind foot length (tip of the calcaneus to the hoof), metatarsus length, and/or metatarsal bone length and body fat percent.

For analyses of adult body condition, we followed Couturier et al. (2010), and included only adult females ≥2 years old. For leg length analyses we included only females ≥2.5 years old since leg length growth is completed at that age (Parker, 1981; Thomas and Barry, 2005). Leg length analyses required cohort assignation, therefore only caribou with precise age estimates were included. Methods of age determination have been presented elsewhere (see Table 5 for references), with the exception of live-captured yearlings. Yearlings were identified from helicopters and sex and age were confirmed at capture. Yearling age was determined by tooth eruption pattern, i.e. the presence of tricuspid molars.

Reproductive females were lactating in summer or autumn and pregnant in spring. Only lactating females from the Rivière-aux-Feuilles and Rivière-George herds were collected in summer and autumn in 2007-2009. Because reproductive status affects female condition (Chan-McLeod et al., 1999) we restricted autumn and summer analyses for the Rivière-aux-Feuilles and Rivière-George herd to reproductive females. For the Rivière-George, Beverly and Porcupine herds in spring, as well as the Porcupine herd in autumn, both reproductive classes were collected. Therefore we performed analyses on average condition of pooled reproductive classes, as well as using reproductive females only. Results using pooled classes were not significant so we presented results from reproductive females only. Lactation status was not assigned to Beverly females collected in December so all females were included in analyses.

Because body condition varies seasonally (Couturier et al., 2009a; Crête and Huot, 1993) we analyzed seasons separately and assessed within season effects for collection date. Both lactating and non-lactating females of the Porcupine herd lost mass and gained fat at the same rate from September to November. We corrected for a decrease in mass, of 0.11kg per day, and an increase of percent body fat, of 0.012% per day, for adult females from the Porcupine by adjusting condition to the mean collection date (September 25) using linear regressions.

Metatarsal lengths (n=101) for adult (≥2.5 years) Rivière-George females measured in 1980 were transformed into hind foot lengths using the regression (transformed hind foot length=0.99*metatarsal length +16.64, $F_{(1,143)}=84.6$, $p<0.0001$, $r^2=0.37$) to compare to hind foot lengths measured in other years. Results that excluded transformed metatarsal lengths did not differ significantly from when transformed measures were included; therefore we present results including transformed data from 1980.

Statistical Analyses

We modeled population size based on average morphological measures for each herd and age class using linear models. We only included years or cohorts where at least 5 individuals were measured.

For both calves and yearlings, we included mass and leg length in the same model as both measures are associated with year of birth. For these multivariate regressions we used the *vif* function in the "car" package to test for multi-collinearity between explanatory variables. None of the variance inflation factors exceeded 10 (Kleinbaum, 1988). Adult condition (mass and body fat) were modeled according to population size at year of collection and adult leg lengths were modeled according to population size in the year of birth.

Rivière-George calf birth masses and cohort leg lengths were analyzed separately for periods of population growth and decline. Small sample size for adult female body condition precluded similar analyses. We used stepwise model selection following (McCullagh and Nelder, 1989) and variables were considered significant at $\alpha<0.05$. Due to small sample sizes we reported adjusted r^2 values. All analyses were performed using R software version 2.12.1 (R Development Core Team 2010).

RESULTS

We assessed the usefulness of juvenile mass and leg length, adult seasonal condition (mass and fat) and adult leg length to predict population size in four migratory caribou herds. All herds underwent an increase and a decrease phase during the period of sampling, with only the

Beverly herd having two periods of increase. The Rivière-aux-Feuilles and the Rivière-George herds underwent larger fluctuations in size than the Beverly and Porcupine, with the Rivière-aux-Feuilles herd fluctuating with the largest amplitude (Figure 2). Data were non-orthogonal due to the different purposes and methods of collection, therefore not all physical traits were measured during both phases for each age class and herd (Table 5 and 6).

Correlation of population size and average physical traits

For the Rivière-George herd, the longest time series was for calf mass, which spanned an increase of ~460 000 and a decrease of ~710 000 individuals (Table 5). Calf mass was not correlated with population size over the whole time series (Table 6). Calf hind foot length was not correlated to population size either (Table 6, Figure 5B) but there were fewer years with data on calf hind foot lengths than on calf mass. Calf mass was strongly and negatively correlated to population size (parameter estimate=-168309±56474) during a population increase from 1978 to 1992 ($F_{(1,6)}$=8.9, p=0.02, Figure 5A) and explained 53% of the variation in population size, but there was no correlation during the decline from 1993 onward ($F_{(1,16)}$=0.13, p=0.88, r^2=0, Figure 5A). For an average calf mass of 5, 6 and 7 kg, during a period of population growth, the predicted population size and 95% confidence interval would be ~812 000 ± 243 000, 645 000 ± 129 000 and 476 000 ± 113 000, respectively. The relationship between population size and hind foot length during a period of population growth could not be determined since hind foot length was only measured in 3 years of demographic growth (Figure 5B). During the decline however, the negative correlation of population size and calf hind foot approached significance ($F_{(1,14)}$=3.8, p=0.07, r^2=0.16) reflecting the positive trend of hind foot length during the decline (Figure 5B).

Table 5. Number of individuals and years where body condition variables were sampled in four migratory herds (Rivière-George, Rivière-aux-Feuilles, Beverly and Porcupine), according to age class (newborn, yearling, adult), season (summer, autumn, spring and autumn/winter), and physical traits measured (whole mass (mass), eviscerated mass (mass2), hind foot length (hfl), metatarsus length (meta), metatarsus bone length and percent body fat (fat)) with reference to publications. Traits with the same sample size are conjoined with a "+" and traits that differ appear in brackets, with associated sample sizes and changes in population size in brackets. Total number of individuals and years are shown for each trait, with the number of years during periods of population increase and decrease and the estimated change in population size for each growth and decline phases.

				sample size		period (n) years		change in pop			
Herd	Age Class	Season	trait	individuals	years	increase	decrease	growth	decline	years (range)	References
Rivière-George	newborn	summer	mass (hfl)	27 (10)	2					1978 -1979	Bergerud (unpub) in Couturier et al. 2009b
				118 (0)	2					1981, 1985	Luttich (unpub) in Couturier et al. 2009b
				438 (384)	15 (13)					1986-2003	(Couturier et al., 2009b)
				20 (20)	1					2010	MRNF
				240 (134)	7					1999, 2000, 2002, 2004, 2005, 2007, 2008	Government of Labrador
				46 (46)	3					2007-2009	(Taillon et al., 2012a)
				888 (592)	25 (20)	8 (3)	17 (17)	459734	690978	All years	
	yearling	summer	mass + hfl	132	12	0	12	NA	639979	1994-2010	MRNF
	adult reproductive	fall	mass (fat)	15 (15)	1					1983	(Huot, 1989)
				44 (73)	3					1985-1987, 2001, 2002	(Couturier et al., 2009a)
				45 (36)	3					2007-2009	(Taillon et al., 2012a)
				104 (124)	7 (9)	2 (4)	5 (5)	165145	535427	All years	
		summer	mass2 (fat)	18	1					1988	(Crête and Huot, 1993)
				20	1					1993	(Manseau et al., 1996)
				27	2					2001-2002	(Couturier et al., 2009a)
				45	3					2007-2009	(Taillon et al., 2012a)
				110 (106)	7 (7)	1	6	114579	690978	All years	
		spring	mass (fat)	21						1976	Drolet and Dauphine 1976 in (Couturier et al. 2009b)
				100						1980	(Parker, 1980)
				12						1984	(Huot, 1989)
				50						1986,1987, 2002	(Couturier et al., 2009a)
				183 (134)	6 (5)	5 (4)	1 (1)	381609	324008	All years	

Table 5. (Continued)

				sample size		period (n) years		change in pop			
Herd	Age Class	Season	trait	individuals	years	increase	decrease	growth	decline	years (range)	References
Rivière-aux-Feuilles	newborn	summer	mass (hfl)	208 (204)	12					1991-2003	(Couturier et al., 2009a)
				59 (58)	3					2007-2009	(Taillon et al., 2012a)
				53	2					2010-2011	MRNF
				315	15	9	8	917000	763000	All years	
	yearling	summer	mass + hfl	99	9	1	8	162454	716804	2001-2010	MRNF
	adult reproductive	autumn	mass (fat)	24	2					2001-2002	(Couturier et al., 2010b)
				48 (46)	3					2007-2009	(Taillon et al., 2012a)
			total	72 (70)	5	0	5	NA	665645	All years	
		summer	mass (fat)	15						1988	(Crête and Huot, 1993)
				24						2001-2002	(Couturier et al., 2010)
				48						2007-2009	(Taillon et al., 2012a)
				88 (87)	6	1	5	1024719	665645	All years	
Porcupine	adult reproductive	spring	mass (fat)	16 (16)	2					1987-1998	(Chan-McLeod et al., 1999)
				66 (48)	6					1990-1992, 1994, 1996, 1997	(PCTC) 1990-1998
				36	2					1994-1995	(Russell et al., 1998)
				118 (67)	9 (7)	2	7 (5)	6785	42785	All years	
		autumn	mass (fat)	16	2					1987-1988	(Chan-McLeod et al., 1999)
				131	6					1990-1995	(Russell et al., 1998)
				87	10					1989-1998	PCTC
				231 (76)	11 (8)	2	9 (6)	13000	49000	All years	
Beverly	adult	spring	mass+ fat	425	8	4	4	153691	57825	1980-1987	(Couturier et al., 2009a)
		autumn	mass+ fat	153	5	2	3	99353	40117	1982-1986	(Couturier et al., 2009a)
Rivière-George	adult	all	hflT (meta)	101 (101)						1980	(Parker, 1980)
				187 (17)						1983-1993	(Couturier et al., 2010a)
				136 (25)						2000-2002	(Couturier et al., 2010a)
				84 (66)						2007-2009	(Taillon et al., 2012a)
				470 (190)	28 (18)	16 (7)	12 (11)	675000 (609110)	557682 (491792)	Cohort :1973-2006	
Rivière-aux-Feuilles	adult	all	Hfl (meta)	93 (43)						2000-2002	(Couturier et al., 2010a)
				87 (82)						2003	Couturier (unpub.)
				102 (83)						2007-2009	(Taillon et al., 2012a)
				274 (208)	16	11	5	958963 (823125)	399820 (399820)	Cohort: 1991-2005	
Beverly	adult female	all	metatarsus	653	15	4	9 and 2	153691	100000 and 20885	1980-1987 Cohort :1971-1985	Thomas,D.(unpub)
Porcupine	adult female	all	metatarsal bone	137	11	8	3	59650	12212	1989-1997 Cohort :1980-1992	PCTC

PCTC: Porcupine Caribou Technical Committee

Table 6. Correlations between estimated population size and average morphological measures (whole body mass (mass) eviscerated mass (mass2), hind foot length (hfl), and percent body fat (fat)) with condition corrected for collection date denoted with a "C", according to age class (calves, yearling females (yearling) and adult (>2 years old) females and season (spring, summer, autumn and autumn/winter), of caribou from four migratory herds (Rivière-George, Rivière-aux-Feuilles, Beverly and Porcupine). Females were considered reproductive if they were pregnant in spring or lactating in summer and autumn. Parameter estimates are shown with their standard error (se), p-values (p), variation they explained in population size (r^2), degrees of freedom (df) and f-statistic (f). Significant models ($p<0.05$) are in bold.

				Sample Size (N)								
Herd	class	season	model	individuals	years	parameter	estimate	se	p	r^2	df	f
Rivière-George	newborn	summer	mass	888	25	intercept	335195	415186	0.43	0	1,23	0.05
						mass	15952	68068	0.82			
			mass+ hfl	592	20	intercept	2512183	2027838	0.23	0	1,18	1.08
						hfl	-64387	62053	0.31			
						mass	193031	142539	0.19			
	yearling	summer	**mass+hfl**	**137**	**14**	**intercept**	**1760752**	**629413**	**0.02**	**0.25**	1,12	5.27
						mass	**-34096**	**14860**	**0.04**			
						hfl	66584	50144	0.21			
	reproductive females	spring	mass	140	5	intercept	2381559	1833875	0.29	0.01	1,3	1.04
						mass	-20930	20529	0.38			
			fat	134	5	intercept	1237947	805901	0.22	0	1,3	0.81
						fat	-61697	68357	0.43			
		autumn	**mass**	**104**	**7**	**intercept**	**4996531**	**1627970**	**0.03**	**0.55**	1,5	8.32
						mass	**-48169**	**16695**	**0.03**			
			fat	**124**	**9**	**intercept**	**-500985**	**359133**	**0.21**	**0.39**	1,7	6.10
						fat	**124103**	**50260**	**0.04**			
		summer	mass2	127	8	intercept	834137	1820431	0.66	0	1,6	0.06
						mass2	-8385	34311	0.82			
			fat	127	8	intercept	620368	251519	0.06	0.05	1,5	1.35
						fat	-83313	71798	0.30			

Table 6. (Continued)

				Sample Size (N)								
Herd	class	season	model	individuals	years	parameter	estimate	se	p	r^2	df	f
Rivière-aux-Feuilles	newborn	summer	mass	320	17	intercept	1788983	729829	0.03	0.08	1,15	2.37
						mass	-191148	124298	0.15			
			hfl	315	17	intercept	5046291	2133461	0.03	0.17	1,15	4.21
						hfl	-133919	65273	0.06			
	yearling	summer	mass +hfl	90	10	intercept	331263	1096915	0.77	0	1,8	0.19
						mass	11786	27400	0.68			
						hfl	132984	115050	0.29			
	:productive	summer	mass2	88	6	intercept	4234336	1347343	0.03	0.54	1,4	6.93
						mass2	-71160	27042	0.06			
			fat	87	6	**intercept**	**1380333**	**85700**	**0.00**	**0.94**	1,4	78.54
						fat	**-195348**	**22042**	**0.00**			
		autumn	mass	72	5	intercept	6213579	4953510	0.30	0.05	1,3	1.19
						mass	-59514	54494	0.36			
			fat	70	5	intercept	-1345151	875164	0.22	0.56	1,3	6.11
						fat	362604	146745	0.09			
Beverly	reproductive	spring	mass	428	8	intercept	-862594	620029	0.21	0.21	1,6	2.91
						mass	12596	7388	0.14			
			fat	**372**	**7**	**intercept**	**-420057**	**173309**	**0.06**	**0.67**	1,5	12.96
						fat	**47204**	**13110**	**0.02**			
	adult	autumn/winter	mass	196	5	intercept	-976372	481443	0.14	0.56	1,3	6.18
						mass	14641	5888	0.09			
			fat	161	5	intercept	-631808	541374	0.33	0.27	1,3	2.48
						fat	75869	48173	0.21			
Porcupine	reproductive	spring	mass	118	9	intercept	121703	146471	0.43	0	1,7	0.05
						mass	370	1625	0.83			
			fat	67	7	intercept	252356	40148	0.00	0.44	1,5	5.76
						fat	-7709	3213	0.06			
		autumn	**massC**	**234**	**12**	**intercept**	**-33430.9**	**80035.5**	**0.69**	**0.29**	1,10	5.60
						massC	**2097.2**	**886.2**	**0.04**			
			fatC	78	9	intercept	190281	64813	0.02	0	1,7	0.29
						fatC	-3499	6525	0.61			

Data on yearling females from the Rivière-George herd were mainly collected during a period of decline. Female yearling mass but not hind foot length was negatively correlated to population size and explained 25% of the variation (Table 6, Figures 5C, D). Of three seasons with available data (spring, summer and autumn), body condition of reproductive females was correlated to population size in autumn only. Autumn mass of reproductive females decreased. whereas percent body fat increased with population size (Table 6). Both autumn mass and body fat explained more variation in population size (55% and 39% respectively) compared to yearling mass, however, fewer years of data were available (7 and 9 years respectively).

In general, morphological measures of calves and yearlings were not correlated to population size for the Rivière-aux-Feuilles herd (Table 6, Figure 6). Although calves in the Rivière-aux-Feuilles herd were measured for fewer years compared to the Rivière-George, calf measurements spanned a larger range in population size; an increase of ~920 000 and a decrease of ~760 000 caribou. Calf mass was not correlated with population size but the negative relationship with calf hind foot length approached significance (Table 6). In contrast to the Rivière-George herd, yearling morphology was not correlated to population size despite a similar decrease of ~700 000 caribou. Body fat of lactating females in summer but not autumn was negatively correlated with population size (Table 6) and explained 94% of the variation over the 6 years where caribou were collected. The negative relationship with eviscerated mass of lactating females in summer approached significance (Table 6). Although not significant, the relationship between autumn body fat of lactating females and population size was positive (Table 6), confirming the pattern observed in the Rivière-George.

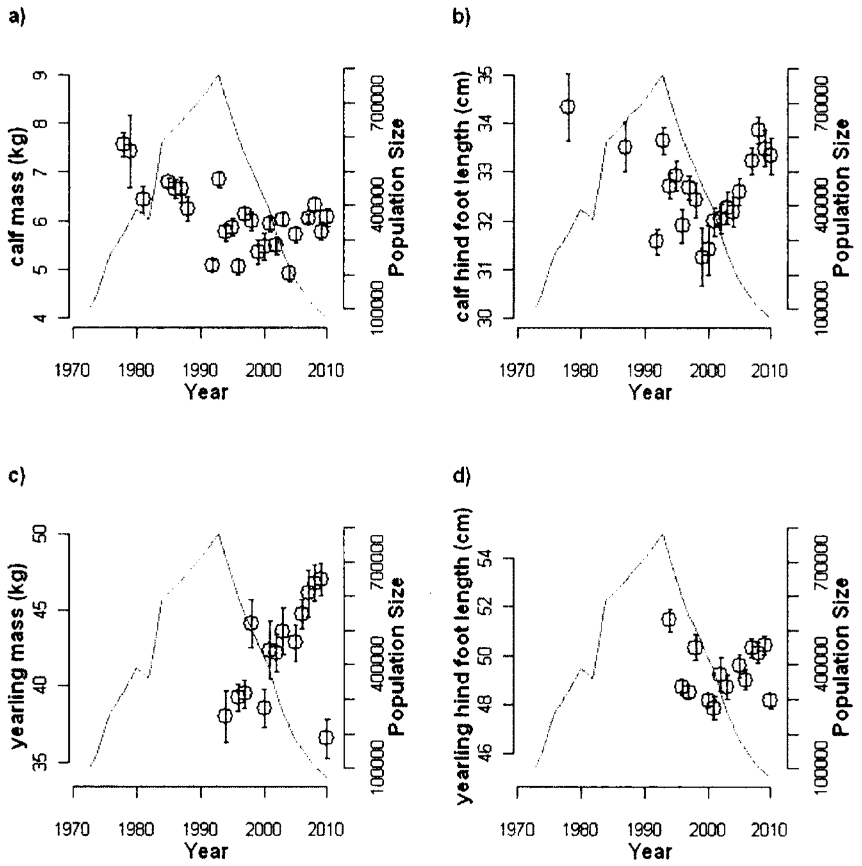

Figure 5. Average calf birth mass and yearling mass in June (kg) (a,c) and average calf and yearling hind foot length (cm) (b,d) with standard errors, overlaid with estimated population size (red line) (based on average growth rate between population counts) over time for caribou of the Rivière-George herd.

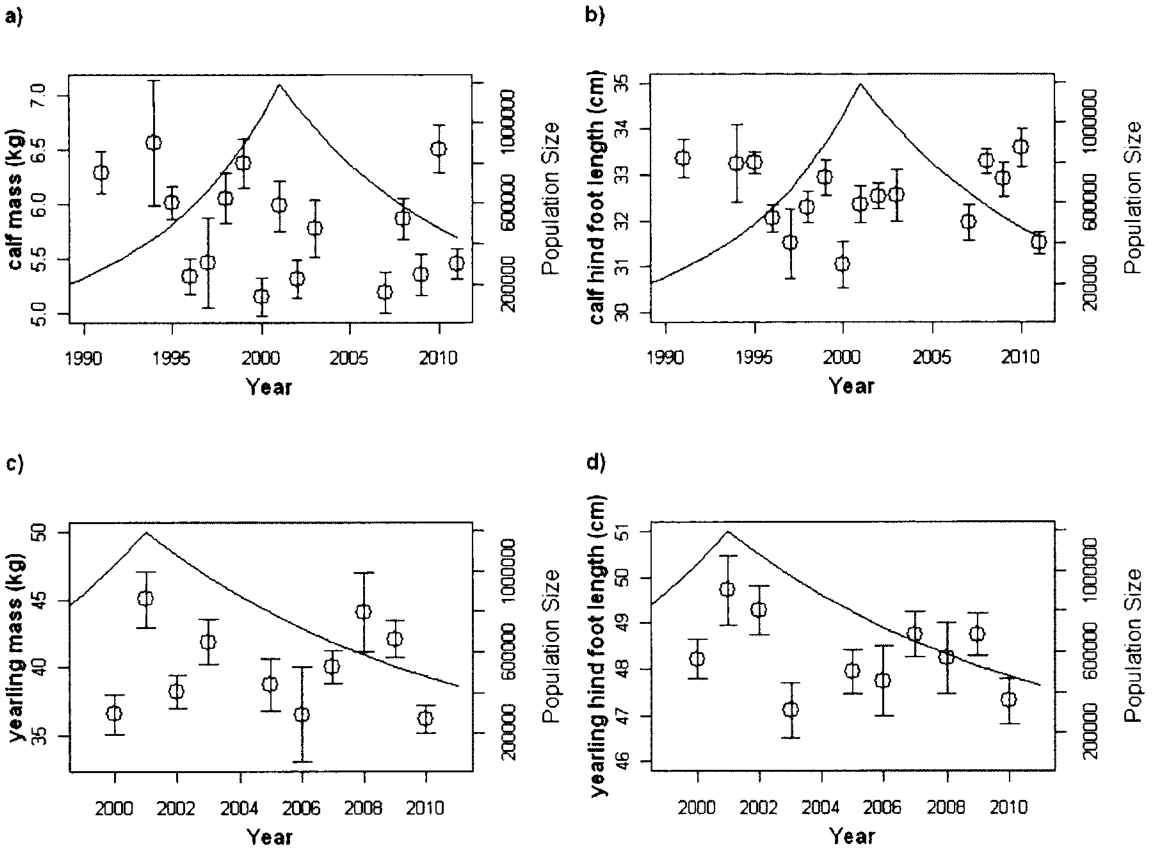

Figure 6. Average calf birth mass and yearling mass in June (kg) (left panels) and average calf and yearling hind foot lengths (cm) (right panels) with standard errors overlaid on estimated population size (based on average growth rate between population counts) over time for caribou of the Rivière-aux-Feuilles herd.

Body condition and size of adult females was not useful to predict population size in the Beverly herd as no traits were negatively correlated with population estimates. Although the range in population size was much smaller for the Beverly herd compared to the Rivière-George and Rivière-aux-Feuilles herds, the ~154 000 increase represented a doubling of the population. The positive relationship between population size and body fat of adult females in spring was significant (Table 6) and explained 67% of the variation. Both early winter mass and body fat of adult females were positively associated to population size, but only mass approached significance (Table 6).

Body condition, mass and body fat of females of the Porcupine herd in spring were not correlated to population size. In contrast to the positive relationship between mass and population size seen in the Beverly herd in spring, the nearly-significant relationship between body fat and population size was negative (Table 6). Autumn mass and population size of Porcupine females was positively correlated to population size and explained 29% of the variation.

Correlation of population size and average leg lengths

Average cohort leg length varied over time for all four herds (Figures 7A-D), but was negatively correlated to population size only in the Rivière-aux-Feuilles and Porcupine herds (Table 7). Neither metatarsus length nor hind foot length correlated with population size in the Rivière-George herd. Although metatarsal length was not correlated with population size in the Rivière-aux-Feuilles herd, average hind foot length explained 70% of the variation in population size at birth. This negative relationship reflected a decrease in hind foot length during a period of population growth (up to 2001) (Figure 7B). An additional 9% of variation in population size was explained by hind foot length when we analyzed cohorts born during a period of population growth, but there was no correlation during the period of decline (Table 3). Average metatarsal bone lengths of Porcupine females declined over time and were negatively correlated to population size (Table 7, Figure 7D). Variation explained in population size at year of birth increased by 26% when analyses were restricted to cohorts born during a period of population growth (Table 7), but lack of leg length measurements for cohorts born after 1989 precluded assessing the relationship during a decline. Metatarsal lengths of Beverly caribou were not significantly correlated to population size (Table 7).

DISCUSSION

Physical traits of migratory caribou correlated with population size in some instances, but these correlations were context dependent and varied between morphological measures, age groups and herds. Our findings from the Rivière-George herd supported our first hypothesis that physical traits are correlated to population size. However, this was not true for other herds despite large changes in population size. In support of our hypothesis that density dependence will be more prominent during demographic growth; calf mass and population size in the Rivière-George were only correlated when the population was growing and not during a period of decline. Lastly, our finding that female yearling mass in the Rivière-George herd increased during a period of population decline supports our hypothesis that juveniles respond to changes in population size more consistently than adults. Between-herd comparisons were particularly difficult since populations differed in demographic trajectories, time periods when data was collected, sampling effort and ecology. Therefore we discuss the results of each herd within its ecological context and limits before presenting overall conclusions.

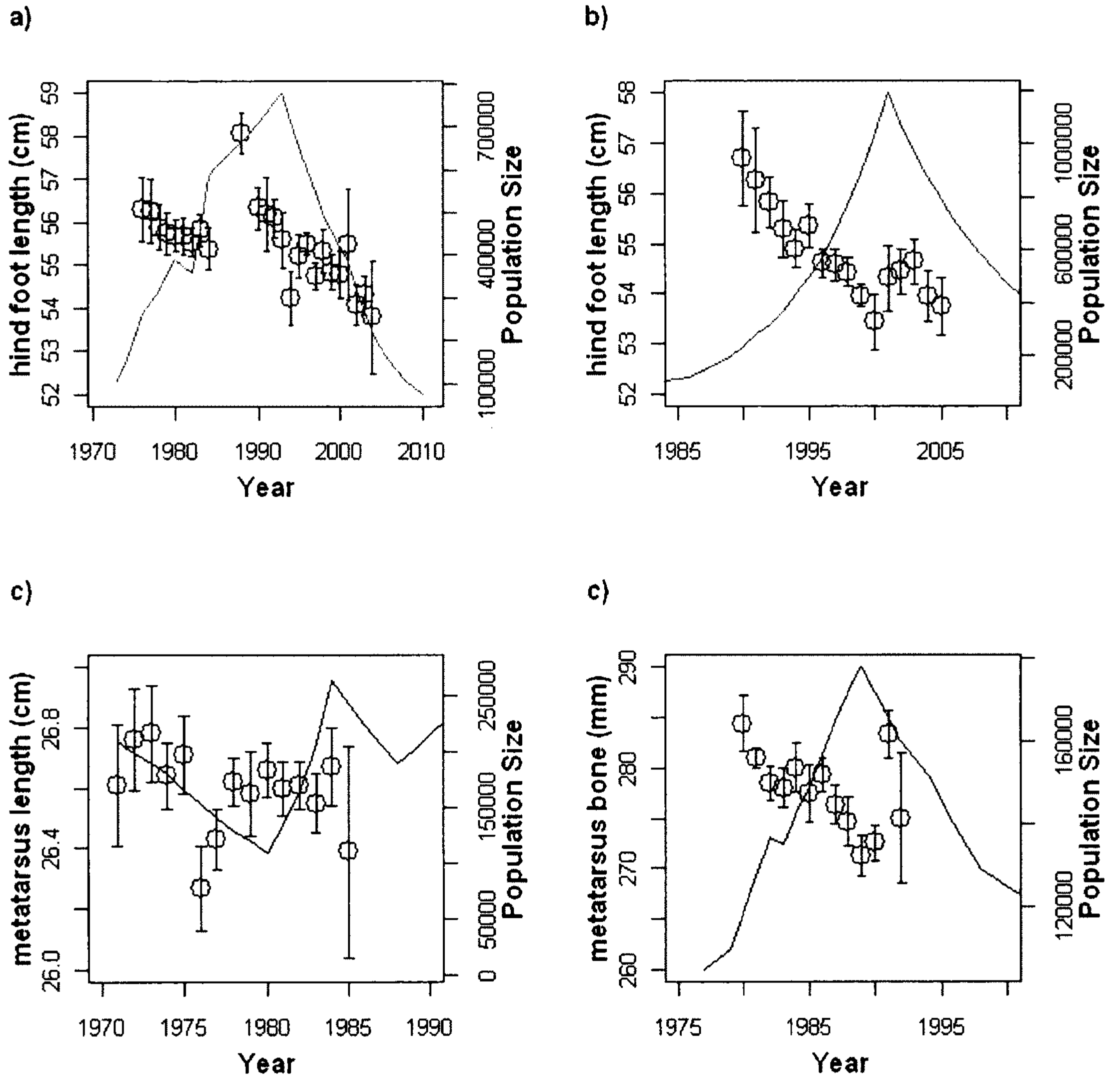

Figure 7. Average leg lengths (hind foot length (cm), metatarsus length (cm) and metatarsal bone length (mm) with standard error plotted according to year of birth, overlaid with estimated population size (based on average growth rate between population counts) over time, for caribou of the (a) Rivière-George, (b) Rivière-aux-Feuilles, (c) Beverly and (d) Porcupine herds.

Table 7. Correlations between estimated population size and average leg lengths (metatarsal length (meta) and hind foot length (hfl) for adult (≥2.5 years old) female caribou from four migratory herds (Rivière-George, Rivière-aux-Feuilles, Beverly and Porcupine). Data that included transformations of measurements are denoted with a "T" (see text). Parameter estimates are shown with associated standard error (se), p-values (p), variation explained in population size estimate (r^2) and degrees of freedom (df). Sample size of number of individuals and cohorts included in analyses are presented. Cohorts with fewer than 5 individuals were excluded from analyses. Significant parameters ($p<0.05$) are in bold.

		all available years					period of population growth					period of decline				
Herd	parameter	estimate	se	p	r^2	df	estimate	se	p	r^2	df	estimate	se	p	r^2	df
Rivière-George	intercept	5502777	3966849	0.18	*0.04*	*1,17*	5823843	2736505	0.09	0.34	1,5	4048321	4974913	0.44	-0.05	1,10
	meta	-129760	100884	0.22			-141642	69526	0.10			-90571	126595	0.49		
	intercept	-2098394	2483956	0.41	*0.00*	*1,26*	-7481110	4772658	0.14	0.10	1,14	-8381545	4108888	0.07	0.25	1,10
	hflT	45913	44756	0.31			141083	85220	0.12			161819	74949	0.06		
Rivière-aux-Feuilles	**intercept**	**14314660**	**2368668**	**>0.001**	**0.70**	**1,13**	**13715503**	**2251231**	**>0.001**	**0.79**	**1,8**	-14529420	10230089	0.25	0.25	1,3
	hfl	**-246977**	**43011**	**>0.001**			**-236700**	**40567**	**>0.001**			286132	188695	0.23		
	intercept	9402851	10686290	0.40	-0.03	1,11	16916758	10825753	0.17	0.15	1,6	-7598104	11277842	0.55	-0.12	1,3
	meta	-220259	272951	0.44			-415297	276425	0.18			219295	288208	0.50		
Beverly	intercept	-397624	2409734	0.87	-0.07	1,13	23051375	6984779	0.08	0.76	1,2	-1077012	2488992	0.68	-0.08	1,9
	meta	21501	90619	0.82			-860633	262536	0.08			47330	93614	0.63		
Porcupine	**intercept**	**1042519**	**312357**	**0.01**	**0.42**	**1,9**	**1572107**	**367472**	**0.01**	**0.67**	**1,6**					
	meta	**-3200**	**1124**	**0.02**			**-5116**	**1319**	**0.01**							

Rivière-George

In the Rivière-George herd, the density dependence of calf birth mass (Couturier et al., 2009b) existed exclusively during a period of population growth. Calf mass decreased by an average of 1.1 kg or 20% during 15 years of population growth. Because birth mass in ungulates is often associated with survival (Clutton-Brock et al., 1987; Festa-Bianchet et al., 1997), the decrease in average calf mass would likely reduce recruitment. Indeed, calf mass has previously been correlated to autumn recruitment rates in this herd during demographic growth (Couturier et al., 2009b). A decline in birth mass over time can therefore indicate that the population is approaching carrying capacity. Despite the strong correlation between birth mass and population size during demographic growth, large confidence intervals for predicted population size highlight that the predictive power is low. The lack of relationship between population size and calf mass during a population decline could partly be due to constraints on calf mass variability. Females are physiologically limited by the upper size-limit of calves they can produce, so regardless of how small the population size becomes, calves cannot be born any larger. Low calf mass during periods of decline could also reflect maternal effects (Taillon et al., 2012b). On average, Rivière-George adult females were heavy in autumn during the population decline but had little fat reserves (discussed below). Nutrition based on forage availability may have been sufficient for females to conceive in autumn, but not adequate enough to gain fat reserves and produce heavy calves (Cook et al. 2002). Alternatively, harsh environmental conditions with high calf mortality during the decline could have relieved females from the burden of energetic lactation such that they could subsequently breed the following year (Adams and Dale, 1998; Gerhart et al., 1997). Unlike reindeer calf mass that improved 5 years after the onset of a decline (Skogland, 1990), calf mass in the Rivière-George remained low for 18 years. Continued light calf mass for extended periods is concerning since birth weight is often correlated with survival (Festa-Bianchet et al., 1997).

Yearling female mass in the Rivière-George herd increased during a population decline. That relationship can be explained by either cohort effects of calf mass or by a direct sensitivity to changes in density. If there was a strong selective pressure on calf mass, only large calves would survive and presumably become large yearlings. In other ungulate species individuals that are heavy as adults were heavy at birth (Festa-Bianchet et al., 1996). Lack of a correlation between average calf birth mass and autumn calf mass (Couturier et al., 2009b) in this herd, could reflect variability in mortality rates and therefore changes in selection pressure favoring larger calves. Evidence is accumulating that selection pressure is strongest in harsh environments with low survival (Pelletier et al., 2007). Alternatively, regardless of birth mass, yearlings could benefit from reduced food competition during a population decrease and therefore could grow quickly. Juvenile ungulates are known to be more sensitive than adults to changes in population density (Bonenfant et al., 2009; Festa-Bianchet et al., 2003; Gaillard et al., 2000). Our results identify yearlings as ecological indicators in the Rivière-George herd, although whether they respond negatively to increases in population size remains to be established.

Adult female condition in autumn, but not in summer or spring, was correlated with population size. Female mass and body fat, however, had opposing relationships with population size. These results differ from Couturier et al. (2009) where autumn condition (mass and body fat) was independent of herd size. Once data from 2007-2009 were included, however, the trend in body condition was apparent; average female mass increased from 1983 to 2009 by an average of ~10kg, and percent body fat decreased by ~2% from 1985-1987 to 2007-2009. Summer forage was thought to be the limiting factor for this herd up to 1993 (Crête et al., 1996) which could account for the increase in adult autumn mass during a period of population decline. In this herd, the accumulation of fat but not protein reserves seems to be limited over summer (Huot, 1989). If summer nutrition is the limiting factor, specifically limiting accumulation of fat reserves, then our results suggest that the summer range continued to deteriorate while the population declined, since females were leaner. Low population size is not necessarily indicative of good environmental conditions as forage recovery time may lag by over 20 years for slow growing lichen (Henry and Gunn, 1991).

Many traits responded to changes in population size in the Rivière-George with the exception of adult female leg length. Although leg length was not correlated to population size, there appears to be a decreasing trend in leg length that continued throughout the population decline. Perhaps leg length was slow to respond as it may have high growth priority (Klein et al., 1987). Selection pressure on leg length may be strong for migratory caribou due to the large distances they travel each year. Density-dependent effects may be more evident in skeletal measures that have lower growth priority, as seen in cohort mandible size for this herd (Couturier et al., 2010).

In support of our first hypothesis, we observed several correlations of physical traits and population size in a herd thought to be limited by nutrition. Summer nutritional limitation was further supported by the response in average yearling and adult autumn mass during a population decline. We also confirmed our second hypothesis, that the relationship between physical traits, (e.g. calf mass) and population size was stronger during periods of population growth. Although there is support for food-limited regulation in this herd (Arseneault et al., 1997; Messier et al., 1988), low adult survival has previously been determined as the proximate cause of the population decline (Crête et al., 1996; Hearn et al., 1990).

Rivière-aux-Feuilles

The Rivière-aux-Feuilles herd underwent similar fluctuations in size as the Rivière-George so we expected to see density dependent effects. However, neither of mass and hind foot length for calves and yearlings in the Rivière-aux-Feuilles was correlated to population size. The decrease in calf mass from 1991-2003 was nearly significant (Couturier et al., 2009b), but calf mass was not correlated with population size during a period of population growth nor during a decline. Density effects on calf mass may not have been detected because the range of calf mass was relatively small compared to the Rivière-George. Range of yearling mass was similar to that in the Rivière-George, but there was no trend as average mass varied extensively from year to year. Variation in calf and yearling morphological measures could have been caused by density-independent factors therefore masking any density dependent effects. Adult female body fat in summer was negatively correlated to population size, confirming previous findings (Couturier et al., 2009a). Although adult body fat appeared to explain most of the observed variation in population size, the r^2 value is not very reliable since the regression was based on 6 data points.

The relationship between adult female leg length and population size in the Rivière-aux-Feuilles herd was not clear because hind foot length was negatively associated with population size whereas metatarsal length was not. The larger range of hind foot lengths compared to metatarsal lengths meant that statistically, the probability of detecting a difference in hind foot length was greater. Both measures of leg length have substantial measurement error leading to low repeatability and large observer differences (Martin, J. unpub.). Despite the lack of precision, the ~4 cm decrease in leg length in the 16 cohorts over an increase of 959 000 individuals likely reflected a real temporal trend. Inferences regarding the Rivière-aux-Feuilles herd are difficult since analyses were especially limited by imprecise and infrequent population estimates in this herd. We assumed that the Rivière-aux-Feuilles herd peaked in 2001 when the population count was obtained. Although it is very likely that the herd peaked near or after 2001, since the population more than doubled from 1991 to 2001 (from 276 000 to at least 628 000 caribou), the peak might have happened between the 1991 and 2011 counts. Imprecise estimate of the population peak could have affected our results.

Beverly and Porcupine

The Beverly and Porcupine herds underwent smaller changes in population size compared to the Québec-Labrador herds. Therefore, we did not anticipate large density-dependent effects. Contrary to our predictions, population size was positively associated with spring fat in the Beverly and with autumn mass in the Porcupine. The only measurement that showed a negative effect of population size was leg length in the Porcupine herd. The unexpected positive relationship between body fat of reproductive Beverly females in spring and population size may be an artifact of low sample size. Relatively low body fat (11.4%) in 1980 occurred at the lowest population size and was highly influential in the statistical analysis. Casting further doubts on this result, the lowest and highest body fat averages (11.4% and 14.2%) were observed in consecutive years; 1980 and 1981. The relationship between population size and autumn mass of Porcupine females was also not robust. Using weighted regression to account for differences in sample size (results not shown) or by removing one of the two years when mass was low, the effect disappears. Average autumn mass of adult females in the Porcupine herd fluctuated by as much as 6.3 kg from one year to the next. We may have observed positive relationships in adult females if a lag was present since few years of data were available for these herds.

Population size was negatively correlated with cohort leg length of adult females in the Porcupine but not the Beverly herd. This relationship may have manifested in the Porcupine herd, despite having the smallest change in population size, because most cohorts were born during a period of growth and the metatarsal bone was measured. Measurement error associated with bone length is minimal compared to live measures, making small differences in bone length easier to detect. Indeed, the decrease of 11mm while the population increased by ca. 60 000 individuals was significant. Similar decreases in leg length with increasing population size were observed in roe deer (Toigo et al., 2006; Zannese et al., 2006). Leg length of adult females was correlated with population size for two of the four herds we studied. The variation in population size explained by leg length in both herds increased when only cohorts born during demographic growth were included in analyses. Measuring leg length of harvested animals that can be aged from tooth section has a relatively low cost and appears to be informative of population size increases in migratory caribou. Managers should be aware of the large error associated with leg length measures and ensure that measurement error and observer differences are minimized over time by using specifically designed tools (Garel et al., 2010) or take more accurate measures like bone lengths instead.

Conclusion

We showed that analyzing periods of population growth and decline simultaneously can mask density dependent effects on ecological indicators. This finding highlights the importance of taking the phase of the population cycle into consideration. Although juveniles responded to changes in density more consistently than adults, there were inconsistencies between herds.

Direction of correlations between adult female condition and population size varied between herds perhaps because size and condition of adult females is less likely to respond to changes in density compared to juveniles or males (Ashley et al., 1998; Clutton-Brock et al., 1982; Vincent et al., 1995). Or because adult mass can be confounded by environmental conditions present at birth (Solberg et al., 2004) and females can buffer their own condition by allocating more resources to maintenance compared to reproduction (Festa-Bianchet and Jorgenson, 1998; Therrien et al., 2007).

The effects of phenotype on population growth are just beginning to be studied (Schoener, 2011) and although they may contribute to population growth rate, their relative contribution appears to be small (Pelletier et al., 2011). Therefore, the main drivers of population dynamics should be investigated. Density independent factors were thought to be the primary drivers of population dynamics in Peary caribou (Tews et al., 2007) and several large scale climate patterns have been correlated to population dynamics of *Rangifer* regionally (Joly et al., 2011) and globally (Vors and Boyce, 2009). Despite being buffered against environmental stochasticity, adult female survival can have the greatest impact on population growth. Few studies have identified the role of starvation in adult survival (Owen-Smith and Mason, 2005) whereas the role of predation for population regulation is well documented (Owen-Smith et al., 2005). When predation is the limiting factor in a population, body condition is not associated with population size or changes in population size as seen in a mountain caribou population (McLellan et al., 2011). Although predation did not seem to be regulating the Rivière-George herd (Messier et al., 1988), whether predation rates and hunting pressure are implicated in population declines as seen in other species (Patterson and Power, 2002) requires investigation.

From a management perspective, the ability of physical traits to predict population size of caribou is limited. Ecological indicators can complement, but not replace population counts. As previously proposed, rather than rely on a single indicator, a suite of ecological indicators is recommended (Dale and Beyeler, 2001; Morellet et al., 2007). If caribou managers intend to measure physical traits as ecological indicators, we recommend they focus on juvenile mass, which seems to respond quickly to changes in population size, and restrict measurement of adults to more accurate bone measurements. To predict and monitor changes at the population level, factors limiting and influencing population dynamics should be identified.

ACKNOWLEDGEMENTS

This research was funded by Caribou Ungava and some of its many financial partners including: ArcticNet, Ministère des Resources naturelles et de la Faune du Québec (MRNF), Labrador and Newfoundland Wildlife Division, Natural Sciences and Engineering Research Council of Canada (NSERC), Hydro-Québec, Fédération des Pourvoiries du Québec, Centre d'études nordiques, and in partnership with Université de Sherbrooke and Université Laval. This research was possible because of the many researchers and agencies that collected data on caribou including Drolet, Dauphiné, Bergerud, Luttich, Parker, Huot, Manseau, Couturier, Taillon, MRNF, Government of Labrador and through the CARMA network from: Russell, Allaye-Chan Mcleod, Cooley, Thomas, the Porcupine Caribou Technical Committee, Alaska Department of Fish and Game, and Canadian wildlife agencies.

GENERAL CONCLUSION

The positive relationship between condition and probability of gestation for female caribou in the Rivière-George herd did not vary with population size. Therefore, these caribou did not adopt a conservative reproductive strategy, at least in terms of conception rates. However, density-dependent changes in female condition affected gestation rates. My analysis of the interactions between individual mass and population size was limited by the small sample of non-pregnant females and by the availability of data over a limited number of years. Although a larger sample size of non-pregnant caribou may have enabled the detection of subtle differences in the relationship between morphological measures and the probability of gestation, there were no light females when the population was at low density and increasing. That made it difficult to evaluate independently the effects of population density and female condition. At the individual level, reproductive success increases with adult body condition and size. Population size influences productivity, thereby influencing recruitment rates and affecting population dynamics. Therefore, monitoring adult condition and gestation rates for the Rivière-George herd will provide insight regarding changes in population size.

To determine which physical traits of migratory caribou predict numerical changes in population size, I had planned to examine which trait, sex, and age class best predicted changes at the population level for periods of population increase and decline. My analysis, however, was constrained by the available data from previous monitoring and research initiatives. Despite a total of over 6000 measurements, the number of years with data available for a given herd-age-season-trait and reproductive class ranged from 5 to 25 (with a maximum of 28 for cohort year) and from 0 to 17 when divided according to population phase. Unfortunately, adequate comparisons between sexes and between most population phases were not possible. In addition, sample size was equivalent to the number of years where data were collected, because population size was modeled on the average of traits per year. Small sample size precluded most multivariate analyses, did not allow for the inclusion of non-linearity in models and led to poor model fit.

Despite these limitations, this research produced several important conclusions. Firstly, physical traits did not predict population size consistently or accurately in migratory caribou. Similar results were obtained from long term studies of other ungulates with complete data on recruitment and survival rates which showed that the influence of individual traits on population growth was minimal (Coulson et al., 2011; Pelletier et al., 2011). Secondly, traits that are useful ecological indicators for three of the four populations of migratory caribou during periods of population growth, and one herd-specific trait useful during a decline, were identified.

Most importantly, I provided a rare empirical example supporting the view that density-dependence is stronger during demographic growth than during declines (Bonenfant et al., 2009). This finding stresses the importance of taking population phase into consideration when analyzing trends in morphological measures. It has important management implications: managers should not use ecological indicators out of context, because traits respond differently to changes in density in different contexts or population phases. Managers also need to be aware that ecological indicators provide information about a population relative to its environment and the changes therein, but population estimates are required to put changes in traits into context. Ecological indicators may be useful for the management of overabundant ungulates to show when populations are becoming a nuisance, but are less useful for migratory caribou populations where managers are more concerned about drastic population declines. Future research should continue to monitor female yearling mass in the Rivière George herd and attempt to determine factors that regulate other herds including the Rivière-aux-Feuilles herd. My research also highlighted that physical traits that respond to population increases do not necessarily drive population declines. For migratory caribou, more research is needed to determine the factors that contribute to population declines and crashes. I suggest that monitoring how predation and hunting may affect adult survival may be particularly important. We cannot predict the future, but we should work to ensure that caribou are a part of ours.

REFERENCES

Adams, L.G. (2005). Effects of maternal characteristics and climatic variation on birth masses of Alaskan caribou. Journal of Mammalogy *86*, 506-513.

Adams, L.G., and Dale, B.W. (1998). Reproductive performance of female Alaskan caribou. Journal of Wildlife Management *62*, 1184-1195.

Albon, S.D., Mitchell, B., and Staines, B.W. (1983). Fertility and body weight in female red deer: a density-dependent relationship. Journal of Animal Ecology *52*, 969-980.

Albon, S.D., Stien, A., Irvine, R.J., Langvatn, R., Ropstad, E., and Halvorsen, O. (2002). The role of parasites in the dynamics of a reindeer population. Proceedings of the Royal Society B: Biological Sciences *1500*, 1625-1632.

Allaye Chan-McLeod, A.C., White, R.G., and Russell, D.E. (1999). Comparative body composition strategies of breeding and nonbreeding female caribou. Canadian Journal of Zoology *77*, 1901-1907.

Arneberg, P., Skorping, A., Grenfell, B., and Read, A.F. (1998). Host densities as determinants of abundance in parasite communities. Proceedings of the Royal Society B: Biological Sciences *265*, 1283-1289.

Arseneault, D., Villeneuve, N., Boismenu, C., Leblanc, Y., and Deshaye, J. (1997). Estimating lichen biomass and caribou grazing on the wintering grounds of northern Quebec: an application of fire history and Landsat data. Journal of Applied Ecology *37*, 65-78.

Ashley, E.P., McCullough, G.B., and Robinson, J.T. (1998). Morphological responses of white-tailed deer to a severe population reduction. Canadian Journal of Zoology *76*, 1-5.

Barboza, P.S., and Parker, K.L. (2008). Allocating protein to reproduction in arctic reindeer and caribou. Physiological and Biochemical Zoology *81*, 835-855.

Bårdsen, B.J., Fauchald, P., Tveraa, T., Langeland, K., and Nieminen, M. (2009). Experimental evidence of cost of lactation in a low risk environment for a long-lived mammal. Oikos *118*, 837-852.

Bårdsen, B.J., Fauchald, P., Tveraa, T., Langeland, K., Yoccoz, N.G., and Ims, R.A. (2008). Experimental evidence of a risk-sensitive reproductive allocation in a long-lived mammal. Ecology *89*, 829-837.

Bergeron, P., Baeta, R., Pelletier, F., Réale, D., and Garant, D. (2011). Individual quality: tautology or biological reality? Journal of Animal Ecology *80*, 361-364.

Bergerud, A.T., Luttich, S.N., and Lodewijk, C. (2008). The return of caribou to Ungava (Montréal, McGill-Queen's University Press).

Boertje, R.D. (1990). Diet quality and intake requirements of adult female caribou of the Denali herd, Alaska. Journal of Applied Ecology *27*, 420-424.

Bonenfant, C., Gaillard, J., Coulson, T., Festa-Bianchet, M., Loison, A., Garel, M., Loe, L.E., Blanchard, P., Pettorelli, N., Owen-Smith, N., *et al.* (2009). Chapter 5 Empirical Evidence of Density-Dependence in Populations of Large Herbivores. In Advances in Ecological Research, pp. 313-357.

Boudreau, S., Payette, S., Morneau, C., and Couturier, S. (2003). Recent decline of the George River caribou herd as revealed by tree-ring analysis. Arctic, Antarctic and Alpine Research *35*, 187-195.

Boulet, M., Couturier, S., Côté, S.D., Otto, R.D., and Bernatchez, L. (2007). Integrative use of spatial, genetic, and demographic analyses for investigating genetic connectivity between migratory, montane, and sedentary caribou herds. Molecular Ecology *16*, 4223-4240.

Brotton, J., and Wall, G. (1997). Climate change and the Bathurst caribou herd in the Northwest Territories, Canada. Climate Change *35*, 35-52.

Burnham, K.P., and Anderson, D.R. (2002). Model Selection and Multimodel Inference: A practical Information-Theoretic Approach, 2nd edn (Springer).

Cameron, R.D. (1994). Reproductive pauses by female caribou. Journal of Mammalogy *75*, 10-13.

Cameron, R.D., and Hoef, J.M.V. (1994). Predicting parturition rate of caribou from autumn body mass. Journal of Wildlife Management *58*, 674-679.

Cameron, R.D., Smith, W.T., Fancy, S.G., Gerhart, K.L., and White, R.G. (1993). Calving success of female caribou in relation to body weight. Canadian Journal of Zoology *71*, 480-486.

Chan-McLeod, A.C., White, R.G., and Russell, D.E. (1999). Comparative body composition strategies of breeding and nonbreeding female caribou. Canadian Journal of Zoology *77*, 1901-1907.

Choquenot, D. (1991). Density-dependent growth, body condition, and demography in feral donkeys: testing the food hypothesis. Ecology *72*, 805-813.

Clutton-Brock, T.H., Albon, S.D., and Guinness, F.E. (1987). Interactions between population density and maternal characteristics affecting fecundity and juvenile survival in red deer. Journal of Animal Ecology *56*, 857-871.

Clutton-Brock, T.H., Guinness, F.E., and Albon, S.D. (1982). Red deer: behavior and ecology of two sexes (Chicago, University of Chicago).

Clutton-Brock, T.H., Price, O.F., Albon, S.D., and Jewell, P.A. (1992). Early development and population fluctuations in Soay sheep. Journal of Animal Ecology *61*, 381-396.

Côté, S.D., and Festa-Bianchet, M. (2001). Birthdate, mass and survival in mountain goat kids: effects of maternal characteristics and forage quality. Oecologia *127*, 230-238.

Coulson, T., Catchpole, E.A., Albon, S.D., Morgan, B.J.T., Pemberton, J.M., Clutton-Brock, T.H., Crawley, M.J., and Grenfell, B.T. (2001). Age, sex, density, winter weather, and population crashes in Soay sheep. Science *292*, 1528-1531.

Coulson, T., Ezard, T.H.G., Pelletier, F., Tavecchia, G., Stenseth, N.C., Childs, D.Z., Pilkington, J.G., Pemberton, J.M., Kruuk, L.E.B., Clutton-Brock, T.H., *et al.* (2008). Estimating the functional form for the density dependence from life history data. Ecology *89*, 1661-1674.

Coulson, T., MacNulty, Stahler, D.R., vonHoldt, B., Wayne, R.K., and Smith, D.W. (2011). Modeling Effects of Environmental Change on Wolf Population Dynamics, Trait Evolution, and Life History Science *334*, 1275-1278.

Coulson, T., Milner-Gulland, E.J., and Clutton-Brock, T.H. (2000). The relative roles of density and climatic variation on population dynamics and fecundity rates in three contrasting ungulate species. Proceedings of the Royal Society B: Biological Sciences *1454*, 1771-1779.

Couturier, S., Côté , S.D., Huot, J., and Otto, R.D. (2009a). Body-condition dynamics in a northern ungulate gaining fat in winter. Canadian Journal of Zoology *87*, 367-378.

Couturier, S., Côté, S.D., Otto, R.D., Weladji, R.B., and Huot, J. (2009b). Variation in calf body mass in migratory caribou: the role of habitat, climate, and movements. Journal of Mammalogy *90*, 442-452.

Couturier, S., Otto, R.D., Côté, S.D., Luther, G., and Mahoney, S.P. (2010). Body size variations in caribou ecotypes and relationships with demography. Journal of Wildlife Management *74*, 395-404.

Crête, M., Couturier, S., Hearn, B.J., and Chubbs, T.E. (1996). Relative contribution of decreased productivity and survival to recent changes in the demographic trend of the Rivière George caribou herd. Rangifer *9*, 27-36.

Crête, M., and Huot, J. (1993). Regulation of a large herd of migratory caribou: summer nutrition affects calf growth and body reserves of dams. Canadian Journal of Zoology *71*, 2291-2296.

Crête, M., Huot, J., Nault, R., and Patenaude, R. (1993). Reproduction, growth and body composition of Rivière George caribou in captivity. Arctic *46*, 189-196.

Cuyler, C., and Àstergaard, J.B. (2005). Fertility in two West Greenland caribou Rangifer tarandus groenlandicus populations during 1996/97: Potential for rapid growth. Wildlife Biology *11*, 221-227.

Dale, V.H., and Beyeler, S.C. (2001). Challenges in the development and use of ecological indicators. Ecological Indicators *1*, 3-10.

Dauphiné, T.C., and McClure, R.L. (1974). Synchronous mating in barren-ground caribou. Journal of Wildlife Management *38*, 54-66.

Dobson, F.S. (1992). Body mass, structural size, and life-history patterns of the Columbian ground squirrel. American Naturalist *140*, 109-125.

Du Toit, J.T. (2002). Wildlife harvesting guidelines for community-based wildlife management: A southern African perspective. Biodiversity and Conservation *11*, 1403-1416.

Dumont, A., Crête, M., Ouellet, J.P., Huot, J., and Lamoureux, J. (2000). Population dynamics of northern white-tailed deer during mild winters: evidence of regulation by food competition. Canadian Journal of Zoology *78*, 764-776.

Eberhardt, L.L. (2002). A paradigm for population analysis of long-lived vertebrates. Ecology *83*, 2841-2854.

Eberhardt, L.L., White, P.J., Garrott, R.A., and Houston, D.B. (2007). A seventy-year history of trends in Yellowstone's Northern elk herd. Journal of Wildlife Management *71*, 594–602.

Ferguson, S.H., Bisset, A.R., and Messier, F. (2000). The influences of density on growth and reproduction in moose *Alces alces*. Wildlife Biology *6*, 31-39.

Festa-Bianchet, M. (1988). Age-specific reproduction of bighorn ewes in Alberta, Canada. Journal of Mammology *69*, 157-160.

Festa-Bianchet, M., and Côté, S.D. (2008). Mountain goats: ecology, behavior and conservation of a mountain ungulate (Washington, Island Press).

Festa-Bianchet, M., Gaillard, J.-M., and Côté, S.D. (2003). Variable age structure and apparent density-dependence in survival of adult ungulates. Journal of Animal Ecology *72*, 640-649.

Festa-Bianchet, M., Gaillard, J.-M., and Jorgenson, J.T. (1998). Mass- and density-dependent reproductive success and reproductive costs in a capital breeder. American Naturalist *152*, 367-379.

Festa-Bianchet, M., and Jorgenson, J.T. (1998). Selfish mothers: reproductive expenditure and resource availability in bighorn ewes. Behavioral Ecology *9*, 144-150.

Festa-Bianchet, M., Jorgenson, J.T., Bérubé, C.H., Portier, C., and Wishart, W.D. (1997). Body mass and survival of bighorn sheep. Canadian Journal of Zoology *75*, 1372-1379.

Festa-Bianchet, M., Jorgenson, J.T., King, W.J., Smith, K.G., and Wishart, W.D. (1996). The development of sexual dimorphism: seasonal and lifetime mass changes of bighorn sheep. Canadian Journal of Zoology *74*, 330-342.

Festa-Bianchet, M., Jorgenson, J.T., Lucherini, M., and Wishart, W.D. (1995). Life-history consequences of variation in age of primiparity in bighorn ewes. Ecology *76*, 871-881.

Festa-Bianchet, M., Ray, J.C., Boutin, S., Côté, S.D., and Gunn, A. (2011). Conservation of caribou (Rangifer tarandus) in Canada: an uncertain future. Canadian Journal of Zoology *89*, 419-434.

Forchhammer, M.C., Clutton-Brock, T.H., Lindstrom, J., and Albon, S.D. (2001). Climate and population density induce long-term cohort variation in a northern ungulate. Journal of Animal Ecology *70*, 721-729.

Fowler, C.W. (1981). Density Dependence as Related to Life History Strategy. Ecology *62*, 602-610.

Fowler, C.W. (1987). A review of density dependence in populations of large mammals. In Current Mammalogy, H.H. Genoways, ed. (New York, Plenum Press), pp. 401-441.

Fryxell, J.M., Hussell, D.J.T., Lambert, A.B., and Smith, P.C. (1991). Time lags and population fluctuations in white-tailed deer. Journal of Wildlife Management *55*, 377-385.

Gaillard, J.-M., Boutin, J.-M., Delorme, D., Laere, G.V., Duncan, P., and Lebreton, J.-D. (1997). Early survival in roe deer: causes and consequences of cohort variation in two contrasted populations. Oecologia *112*, 502-513.

Gaillard, J.-M., Delorme, D., Boutin, J.-M., Laere, G.V., and Boisaubert, B. (1996). Body mass of roe deer fawns during winter in 2 contrasting populations. Journal of Wildlife Management *60*, 29-36.

Gaillard, J.-M., Festa-Bianchet, M., and Yoccoz, N.G. (1998). Population dynamics of large herbivores: variable recruitment with constant adult survival. Trends in Ecology and Evolution *13*, 58-63.

Gaillard, J.-M., Festa-Bianchet, M., Yoccoz, N.G., Loison, A., and Toïgo, C. (2000). Temporal variation in fitness components and population dynamics of large herbivores. Annual Review of Ecology and Systematics *31*, 367-393.

Gaillard, J.M., Loison, A., Toigo, C., Delorme, D., and Van Laere, G. (2003). Cohort effects and deer population dynamics. Ecoscience *10*, 412-420.

Garel, M., Gaillard, J.M., Chevrier, T., Michallet, J., Delorme, D., and Van Laere, G. (2010). Testing reliability of body size measurements using hind foot length in roe deer. Journal of Wildlife Management *74*, 1382-1386.

Gerhart, K.L., Russell, D.E., DeWetering, D.V., White, R.G., and Cameron, R.D. (1997). Pregnancy of adult caribou (*Rangifer tarandus*): evidence for lactational infertility. Journal of Zoology *242*, 17-30.

Getz, W.M. (1996). A hypothesis regarding the abruptness of density dependence and the growth rate of populations. Ecology *77*, 2014-2026.

Heard, D., Barry, S., Watts, G., and Child, K. (1997). Fertility of female moose (*Alces alces*) in relation to age and body composition. Alces *33*, 165-176.

Hearn, B.J., Luttich, S.N., Crete, M., and Berger, M.B. (1990). Survival of radio-collared caribou (Rangifer tarandus caribou) from the George River herd, Nouveau-Quebec - Labrador. Canadian Journal of Zoology *68*, 276-283.

Helle, T., and Kojola, I. (1994). Body mass variation in semidomesticated reindeer. Canadian Journal of Zoology *72*, 681-688.

Helle, T., and Kojola, I. (2008). Demographics in an alpine reindeer herd: effects of density and winter weather. Ecography *31*, 221-230.

Henry, G.H.R., and Gunn, A. (1991). Recovery of tundra vegetation after overgrazing by caribou in Arctic Canada. Arctic *44*, 38-42.

Hewison, A.J.M. (1996). Variation in the fecundity of roe deer in Britain: effects of age and body weight. Acta Theriologica *41*, 187-198.

Hewison, A.J.M., Gaillard, J.M., Angibault, J.M., Van Laere, G., and Vincent, J.P. (2002). The influence of density on post-weaning growth in roe deer *Capreolus capreolus* fawns. Journal of Zoology *257*, 303-309.

Hewison, A.J.M., Vincent, J.P., Bideau, E., Angibault, J.M., and Putman, R.J. (1996). Variation in cohort mandible size as an index of roe deer (*Capreolus capreolus*) densities and population trends. Journal of Zoology *239*, 573-581.

Hilton, G.M., Lilliendahl, K., Solmundsson, J., Houston, D.C., and Furness, R.W. (2000). Geographical variation in the size of body organs in seabirds. Functional Ecology *14*, 369-379.

Hughes, J., Albon, S.D., Irvine, R.J., and Woodin, S. (2009). Is there a cost of parasites to caribou? Parasitology *136*, 253-265.

Hummel, M., Ray, J.C., and Bateman, R. (2008). Caribou and the north : a shared future. (Toronto, Canada.).

Huot, J. (1989). Body composition of the George River caribou (*Rangifer tarandus caribou*) in fall and late winter. Canadian Journal of Zoology *67*, 103-107.

Huot, J., and Picard, G. (1988). A Simplified Method for Assessment of Caribou Body Composition. Journal of Wildlife Management *52*, 606-609.

Jachmann, H. (2002). Comparison of aerial counts with ground counts for large African herbivores. Journal of Applied Ecology *39*, 841-852.

Joly, D.O., and Messier, F. (2004). Testing hypotheses of bison population decline (1970–1999) in Wood Buffalo National Park: synergism between exotic disease and predation. Canadian Journal of Zoology *82*, 1165–1176.

Joly, K., Klein, D.R., Verbyla, D.L., Rupp, T.S., and Chapin, F.S. (2011). Linkages between large-scale climate patterns and the dynamics of Arctic caribou populations. Ecography *34*, 345-352.

Jorgenson, J.T., Festa-Bianchet, M., Lucherini, M., and Wishart, W.D. (1993). Effects of body size, population density and maternal characteristics on age of first reproduction in bighorn ewes. Canadian Journal of Zoology *71*, 2509-2517.

Keech, M.A., Bowyer, R.T., Ver Hoef, J.M., Boertje, R.D., Dale, B.W., and Stephenson, T.R. (2000). Life-history consequences of maternal condition in Alaskan moose. Journal of Wildlife Management *64*, 450-462.

Kendrick, A., and Manseau, M. (2008). Representing traditional knowledge: Resource management and inuit knowledge of barren-ground Caribou. Society and Natural Resources *21*, 404-418.

Klein, D.R., Meldgaard, M., and Fancy, S.G. (1987). Factors Determining Leg Length in Rangifer tarandus. Journal of Mammalogy *68*, 642-655.

Klein, D.R., Moorehead, L., Kruse, J., and Braund, S.R. (1999). Contrasts in use and perceptions of biological data for caribou management. Wildlife Society Bulletin *27*, 488-498.

Kleinbaum, D.G., Kupper, Lawrence L., Muller, Keith E. (1988). Applied Regression Analysis and Other Multivariable Methods, 2nd edition edn (Belmont, California, PWS-KENT Publishing Company, a division of Wadsworth Publishing Company).

Leblanc, M., Festa-Bianchet, M., and Jorgenson, J.T. (2001). Sexual size dimorphism in bighorn sheep (*Ovis canadensis*): effects of population density. Canadian Journal of Zoology *79*, 1661-1670.

Lesage, L., Crête, M., Hout, J., and Ouellet, J.P. (2001). Evidence for a trade-off between growth and body reserves in northern white-tailed deer. Oecologia *126*, 30-41.

Loison, A., Festa-Bianchet, M., Gaillard, J.-M., Jorgenson, J.T., and Jullien, J.-M. (1999). Age-specific survival in five populations of ungulates: evidence of senescence. Ecology *80*, 2539-2554.

Lyberth, B., Landa, A., Nagy, J., Loison, A., Olesen, C.R., Gunn, A., and Forchhammer, M.C. (2007). Muskoxen in the high Arctic-temporal and spatial differences in body size. Journal of Zoology *272*, 227-234.

MacDonald, D.W., Newman, C., Nouvellet, P.M., and Buesching, C.D. (2009). An analysis of Eurasian badger (Meles meles) population dynamics: Implications for regulatory mechanisms. Journal of Mammalogy *90*, 1392-1403.

Manseau, M., Huot, J., and Crête, M. (1996). Effects of summer grazing by caribou on composition and productivity of vegetation: community and landscape level. Journal of Ecology *84*, 503-513.

Martin, J.G.A., and Festa-Bianchet, M. (2010). Bighorn ewes transfer the costs of reproduction to their lambs. American Naturalist *176*, 414-423.

McCullagh, P., and Nelder, J.A. (1989). Generalized linear models (Chapman and Hall, London).

McLellan, M., Serrouya, R., McLellan, B., Furk, K., Heard, D., and Wittmer, H. (2011). Implications of body condition on the unsustainable predation rates of endangered mountain caribou. Oecologia, 1-8.

Mduma, S.A.R., Sinclair, A.R.E., and Hilborn, R. (1999). Food regulates the Serengeti wildebeest: a 40-year record. Journal of Animal Ecology *68*, 1101-1122.

Messier, F., Huot, J., Le Henaff, D., and Luttich, S. (1988). Demography of the George River caribou herd: evidence of population regulation by forage exploitation and range expansion. Arctic *41*, 279-287.

Miller, F.L. (1974). Age Determination of Caribou by Annulations in Dental Cementum. Journal of Wildlife Management *38*, 47-53.

Moller, H., Berkes, F., Lyver, P.O.B., and Kislalioglu, M. (2004). Combining science and traditional ecological knowledge: monitoring populations for co-management, pp. 2.

Morellet, N., Gaillard, J.-M., Hewison, A.J.M., Ballon, P., Boscardin, Y., Duncan, P., Klein, F., and Maillard, D. (2007). Indicators of ecological change: new tools for managing populations of large herbivores. Journal of Applied Ecology *44*, 634-643.

Morneau, C., and Payette, S. (2000). Long-term fluctuations of a caribou population revealed by tree-ring data. Canadian Journal of Zoology *78*, 1784-1790.

Mysterud, A., Yoccoz, N.G., Stenseth, N.C., and Langvatn, R. (2001). Effects of age, sex and density on body weight of Norwegian red deer: evidence of density-dependent senescence. Proceedings of the Royal Society B: Biological Sciences *268*, 911-919.

Nugent, G., and Frampton, C. (1994). Microgeographic and temporal variation in mandible size within a New Zealand fallow deer (Dama dama) population. Journal of Applied Ecology *31*, 253-262.

Ouellet, J.-P., Heard, D.C., Boutin, S., and Moulders, R. (1997). A comparison of body condition and reproduction of caribou on two predator-free arctic islands. Canadian Journal of Zoology *75*, 11-17.

Owen-Smith, N., and Mason, D.R. (2005). Comparative changes in adult vs. juvenile survival affecting population trends of African ungulates. Journal of Animal Ecology *74*, 762-773.

Owen-Smith, N., Mason, D.R., and Ogutu, J.O. (2005). Correlates of survival rates for 10 African ungulate populations: density, rainfall and predation. Journal of Animal Ecology *74*, 774-788.

Parker, G.R. (1980). Physical and reproductive parameters of pre-calving caribou (Rangifer tarandus caribou) in northern Labrador, N.B. Sackville, Canada, ed. (Sackville, New Brunswick, Canada, Canadian Wildlife Service, Sackville, New Brunswick, Canada), pp. 86.

Parker, G.R. (1981). Physical and Reproductive Characteristics of an Expanding Woodland Caribou Population (Rangifer-Tarandus-Caribou) in Northern Labrador. Canadian Journal of Zoology *59*, 1929-1940.

Parker, K.L., Barboza, P.S., and Gillingham, M.P. (2009). Nutrition integrates environmental responses of ungulates. Functional Ecology *23*, 57-69.

Patterson, B.R., and Power, V.A. (2002). Contributions of forage competition, harvest, and climate fluctuation to changes in population growth of northern white-tailed deer. Oecologia *130*, 62-71.

Pelletier, F., Clutton-Brock, T.H., Pemberton, J.M., Tuljapurkar, S., and Coulson, T. (2007). The evolutionary demography of ecological change: linking trait variation and population growth. Science *315*, 1571-1574.

Pelletier, F., Moyes, K., Clutton-Brock, T.H., and Coulson, T. (2011). Decomposing variation in population growth into contributions from environment and phenotypes in an age-structured population. Proceedings of the Royal Society B: Biological Sciences *279*, 394-401.

Pettorelli, N., Côté, S.D., Gingras, A., Potvin, F., and Huot, J. (2007). Aerial surveys vs hunting statistics to monitor deer density: the example of Anticosti Island (Québec, Canada). Wildlife Biology *13*, in press.

Pettorelli, N., Gaillard, J.M., Van Laere, G., Duncan, P., Kjellander, P., Liberg, O., Delorme, D., and Maillard, D. (2002). Variations in adult body mass in roe deer: the effects of population density at birth and of habitat quality. Proceedings of the Royal Society B: Biological Sciences *269*, 747-753.

Post, E., and Forchhammer, M.C. (2002). Synchronization of animal population dynamics by large-scale climate. Nature *420*, 168-171.

Post, E., and Klein, D.R. (1999). Caribou calf production and seasonal range quality during a population decline. Journal of Wildlife Management *63*, 335-345.

Post, E., and Stenseth, N.C. (1999). Climatic variability, plant phenology, and northern ungulates. Ecology *80*, 1322-1339.

Promislow, D.E.L., and Harvey, P.H. (1990). Living fast and dying young: a comparative analysis of life-history variation among mammals. Journal of Zoology *220*, 417-437.

Redfern, J.V., Viljoen, P.C., Kruger, J.M., and Getz, W.M. (2002). Biases in estimating population size from an aerial census: A case study in the Kruger National Park, South Africa. South African Journal of Science *98*, 455-461.

Reimers, E. (1983). Reproduction in wild reindeer in Norway. Canadian Journal of Zoology *61*, 211-217.

Reimers, E., Holmengen, N., and Mysterud, A. (2005). Life-history variation of wild reindeer (*Rangifer tarandus*) in the highly productive North Ottadalen region, Norway. Journal of Zoology *265*, 53-62.

Riney, T. (1955). Evaluating condition of free-ranging red deer with special reference to New Zealand. New Zealand Journal Science Technology *36 (B)*, 429-463.

Ropstad, E. (2000). Reproduction in female reindeer. Animal Reproduction Science *60-61*, 561-570.

Russell, D.E., Gerhart, K.L., White, R.G., and Vandewetering, D. (1998). Detection of early pregnancy in caribou - evidence for embryonic mortality. Journal of Wildlife Management *62*, 1066-1075.

Saether, B.E., Lillegard, M., Grøtan, V., Filli, F., and Engen, S. (2007). Predicting fluctuations of reintroduced ibex populations: the importance of density dependence, environmental stochasticity and uncertain population estimates. Journal of Animal Ecology *76*, in press.

Sand, H. (1998). Costs of reproduction in female moose (*Alces alces*) as measured by means of phenotypic correlations. Canadian Journal of Zoology *76*, 187-193.

Sand, H., Bergströlm, R., Cederlund, G., Ölstergren, M., and Stålfelt, F. (1996). Density-dependent variation in reproduction and body mass in female moose Alces alces. Wildlife Biology *2*, 233-245.

Schoener, T.W. (2011). The newest synthesis: Understanding the interplay of evolutionary and ecological dynamics. Science *331*, 426-429.

Serrano, E., Angibault, J.-M., Cargnelutti, B., and Hewison, A.J.M. (2007). The effect of animal density on metacarpus development in captive fallow deer. Small Ruminant Research *72*, 61-65.

Shea, S.M., Breault, T.A., and Richardson, M.L. (1992). Herd density and physical condition of white-tailed deer in Florida flatwoods. Journal of Wildlife Management *56*, 262-267.

Simard, M.A., Côté, S.D., Weladji, R.B., and Huot, J. (2008). Feedback effects of chronic browsing on life-history traits of a large herbivore. Journal of Animal Ecology *77*, 678-686.

Simard, M.A., Coulson, T., Gingras, A., and Côté, S.D. (2011). Influence of density and climate on population dynamics of a large herbivore under harsh environmental conditions. Journal of Wildlife Management *74*, 1671-1685.

Sinclair, A.R.E., Mduma, S., and Brashares, J.S. (2003). Patterns of predation in a diverse predator-prey system. Nature *425*, 288-290.

Singer, F.J., Harting, A., Symonds, K.K., and Coughenour, M.B. (1997). Density dependence, compensation, and environmental effects on elk calf mortality in Yellowstone National Park. Journal of Wildlife Management *61*, 12-25.

Skogland, T. (1983). The effects of density dependent resource limitation on size of wild reindeer. Oecologia *60*, 156-168.

Skogland, T. (1985). The effects of density-dependent resource limitations on the demography of wild reindeer. Journal of Animal Ecology *54*, 359-374.

Skogland, T. (1990). Density dependence in a fluctuating wild reindeer herd: maternal vs. offspring effects. Oecologia *84*, 442-450.

Solberg, E.J., Jordhøy, P., Strand, O., Aanes, R., Loison, A., Sæther, B.E., and Linnell, J.D.C. (2001). Effects of Density-Dependence and Climate on the Dynamics of a Svalbard Reindeer Population. Ecography *24*, 441-451.

Solberg, E.J., Loison, A., Gaillard, J.-M., and Heim, M. (2004). Lasting effects of conditions at birth on moose body mass. Ecography *27*, 677-687.

Stearns, S.C. (1992). The Evolution of Life Histories (Oxford, Oxford University Press).

Stewart, K.M., Bowyer, R.T., Dick, B.L., Johnson, B.K., and Kie, J.G. (2005). Density-dependent effects on physical condition and reproduction in North American elk: an experimental test. Oecologia *143*, 85-93.

Stien, A., Irvine, R.J., Ropstad, E., Halvorsen, O., Langvatn, R., and Albon, S.D. (2002). The impact of gastrointestinal nematodes on wild reindeer: Experimental and cross-sectional studies. Journal of Animal Ecology *71*, 937-945.

Taillon, J., Brodeur, V., Festa-Bianchet, M., and Côté, S.D. (2012a). Is mother condition related to offspring condition in migratory caribou (rangifer tarandus) at calving and weaning? Canadian Journal of Zoology *90*, 393-402.

Taillon, J., Festa-Bianchet, M., and Côté, S.D. (2012b). Shifting targets in the tundra: Protection of migratory caribou calving grounds must account for spatial changes over time. Biological Conservation *147*, 163-173.

Testa, J.W., and Adams, G.P. (1998). Body condition and adjustments to reproductive effort in female moose (*Alces alces*). Journal of Mammalogy *79*, 1345-1354.

Tews, J., Ferguson, M.A.D., and Fahrig, L. (2007). Modeling density dependence and climatic disturbances in caribou: a case study from the Bathurst Island complex, Canadian High Arctic. Journal of Zoology *272*, 209-217.

Therrien, J.-F., Côté, S.D., Festa-Bianchet, M., and Ouellet, J.-P. (2007). Conservative maternal care in an iteroparous mammal: a resource allocation experiment. Behavioral Ecology and Sociobiology *62*, 193-199.

Thomas, D., and Barry, S. (2005). Antler mass of barren-ground caribou relative to body condition and pregnancy rate. Arctic *58*, 241-246.

Thomas, D.C. (1982). The relationship between fertility and fat reserves of Peary Caribou. Canadian Journal of Zoology *60*, 597-602.

Toigo, C., Gaillard, J.M., Van Laere, G., Hewison, M., and Morellet, N. (2006). How does environmental variation influence body mass, body size, and body condition? Roe deer as a case study. Ecography *29*, 301-308.

Tveraa, T., Fauchald, P., Henaug, C., and Yoccoz, N.G. (2003). An examination of a compensatory relationship between food limitation and predation in semi-domestic reindeer. Oecologia *137*, 370-376.

Verme, L.J., and Ozoga, J.J. (1980). Effects of Diet on Growth and Lipogenesis in Deer Fawns. Journal of Wildlife Management *44*, 315-324.

Vincent, J.P., Bideau, E., Hewison, A.J.M., and Angibault, J.M. (1995). The influence of increasing density on body weight, kid production, home range and winter grouping in roe deer (*Capreolus capreolus*). Journal of Zoology *236*, 371-382.

Vors, L.S., and Boyce, M.S. (2009). Global declines of caribou and reindeer. Global Change Biology *15*, 2626-2633.

Walsh, N.E., Griffith, B., and McCabe, T.R. (1995). Evaluating Growth of the Porcupine Caribou Herd Using a Stochastic Model. The Journal of Wildlife Management *59*, 262-272.

Weladji, R.B., Holand, O., Steinheim, G., and Lenvik, D. (2003). Sex-specific preweaning maternal care in reindeer (*Rangifer tarandus t.*). Behavioral Ecology and Sociobiology *53*, 308-314.

White, G.C., and Bartmann, R.M. (1998). Effect of density reduction on overwinter survival of free-ranging mule deer fawns. Journal of Wildlife Management *62*, 214-225.

Whitten, K.R., Garner, G.W., Mauer, F.J., and Harris, R.B. (1992). Productivity and Early Calf Survival in the Porcupine Caribou Herd. Journal of Wildlife Management *56*, 201-212.

Williams, B.K., Nichols, J.D., and Conroy, M.J. (2002). Analysis and Management of Animal Populations (San Diego, CA).

Zalatan, R., Gunn, A., and Henry, G.H.R. (2006). Long-term abundance patterns of barren-ground caribou using trampling scars on roots of Picea mariana in the Northwest Territories, Canada. Arctic, Antarctic, and Alpine Research *38*, 624-630.

Zannese, A., Baisse, A., Gaillard, J.M., Hewison, A.J.M., Saint-Hilaire, K., Toigo, C., Van Laere, G., and Morellet, N. (2006). Hind foot length: An indicator for monitoring roe deer populations at a landscape scale. Wildlife Society Bulletin *34*, 351-358.

Zėdrosser, A., Dahle, B., and Swenson, J.E. (2006). Population density and food conditions determine adult female body size in brown bears. Journal of Mammalogy *87*, 510-518.