

**DENNING ECOLOGY OF BARREN-GROUND WOLVES IN THE CENTRAL
CANADIAN ARCTIC**

by

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ABSTRACT

My study focused on investigating wolf-caribou dynamics on the summer range of the Bathurst caribou herd. I used a multi-scale study design to investigate the behavioural and population responses of wolves during a severe decline in caribou numbers. The summer ranges of the Bathurst herd contracted north towards their calving grounds as the herd declined and caribou remained farther from the summer territories of wolves for relatively longer portions of the denning period. Density-dependent range contraction of caribou correlated with increases in den abandonment and lower pup recruitment, eventually leading to a decrease in wolf density. At low caribou abundance, variation in wolf movements indicated that prey were more readily available for some packs than others; extended movements away from the den in search of prey correlated with higher rates of pup mortality. My results documented a strong numerical response of wolves to a single declining prey base.

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CHAPTER 1: THESIS INTRODUCTION

CONTEXT

The distribution and survival of gray wolves (*Canis lupus*) is based predominantly on the accessibility of ungulate prey (Fuller et al. 2003). Prey availability varies considerably for wolves by season, where changing environmental conditions influence the distribution, behaviour, and body condition of ungulates. These aspects either promote or hinder the ability of wolves to find and kill prey (Mech and Peterson 2003). On the barrenlands of Canada's central Arctic, the tundra wolf has specialized to prey on migratory barren-ground caribou (*Rangifer tarandus groenlandicus*; Kelsall 1968, Parker 1973). Their behaviour is unique among wolf populations in that they do not maintain and defend annual territories. Instead, tundra wolves undergo long-distance migrations following barren-ground caribou throughout most of the year (Walton et al. 2001, Hansen et al. 2013). They are considered a unique ecotype of gray wolf; genetically, phenotypically, and behaviourally distinct from boreal forest wolves that hunt a more diverse prey base of relatively sedentary ungulates in more southern forested landscapes (Musiani et al. 2007).

In early spring, wolves migrate from their wintering range in the boreal forest to denning areas on the Arctic tundra. Tundra wolves show strong fidelity to den sites or traditional denning ranges and most wolves restrict their movements around a den by late-April (Walton et al. 2001). Wolves den on eskers because they provide some of the only suitable conditions for excavation within the tundra landscape (Mueller 1995), however, these sand and gravel substrates are often frozen until late-spring, so wolves reuse dens excavated from previous years. Pups are born between mid-May and early-June and remain within close proximity of the den until mid-September when they are old enough to travel with the pack (Frame et al. 2008). Adult wolves generally remain in close proximity to their pups from late-May to early-September (wolf

denning period) leaving occasionally to hunt for prey (Williams 1990, Walton et al. 2001, Frame et al. 2004). As such, the behavior of tundra wolves is likely more territorial during the denning period (Walton et al. 2001).

While tundra wolves are the main predator of barren-ground caribou, the extent that they influence caribou population dynamics is unknown (Thomas 1995, Valkenburg 2001, Boulanger et al. 2011). Some studies suggest that wolf predation has a limited influence on the dynamics of large migratory populations of caribou (Messier et al. 1988, Couturier et al. 1990). However, wolves may have more influence when caribou densities are low (Bergerud 1996, Thomas 1995, Valkenburg 2001). For example, Bergerud (1996) generalized that wolf densities > 6.5 wolves/1000 km² may limit population growth for migratory caribou, although results varied among herds and were dependent on the availability of alternate prey such as moose (*Alces alces*), which could maintain wolf populations when caribou numbers decline. Low densities of alternate prey in the central Arctic combined with the unpredictable movements of migratory barren-ground caribou suggest that tundra wolves have a limited capacity to reduce caribou populations to low densities (Thomas 1995). Nevertheless, small changes in adult female mortality strongly influence population trends (Gaillard et al. 2000; Boulanger et al. 2011) and strong correlations have been found between wolf density and both caribou recruitment and adult mortality (Bergerud 1980). Consistent with theory and empirical evidence, wolf predation interacts with other regulatory factors (Klein 1991), which may limit and/or lengthen herd recovery after a population decline (Seip 1995, Thomas 1995, Paquet and Carbyn 2003).

Barren-ground caribou herds have declined throughout much of Canada over the past two decades (Gunn et al. 2009, Festa-Bianchet et al. 2011, Gunn et al. 2011). Aboriginal traditional knowledge and scientific studies suggest that caribou populations fluctuate naturally between

periods of high and low abundance, over a timespan of decades (Zalatan et al. 2006; Tesar 2007; Gunn et al. 2009, 2011; Beaulieu 2012). The Bathurst caribou herd is one of eight migratory barren-ground caribou herds in the Northwest Territories (Environment and Natural Resources 2011). Once estimated at over 450,000 animals in the mid-1980s, the Bathurst herd declined drastically to 30,000 animals by 2009 (Figure 1; Adamczewski et al. 2009). Results from the latest reconnaissance survey in 2014 indicate that the Bathurst herd may have declined to 15,000 animals (Adamczewski et al. 2014).

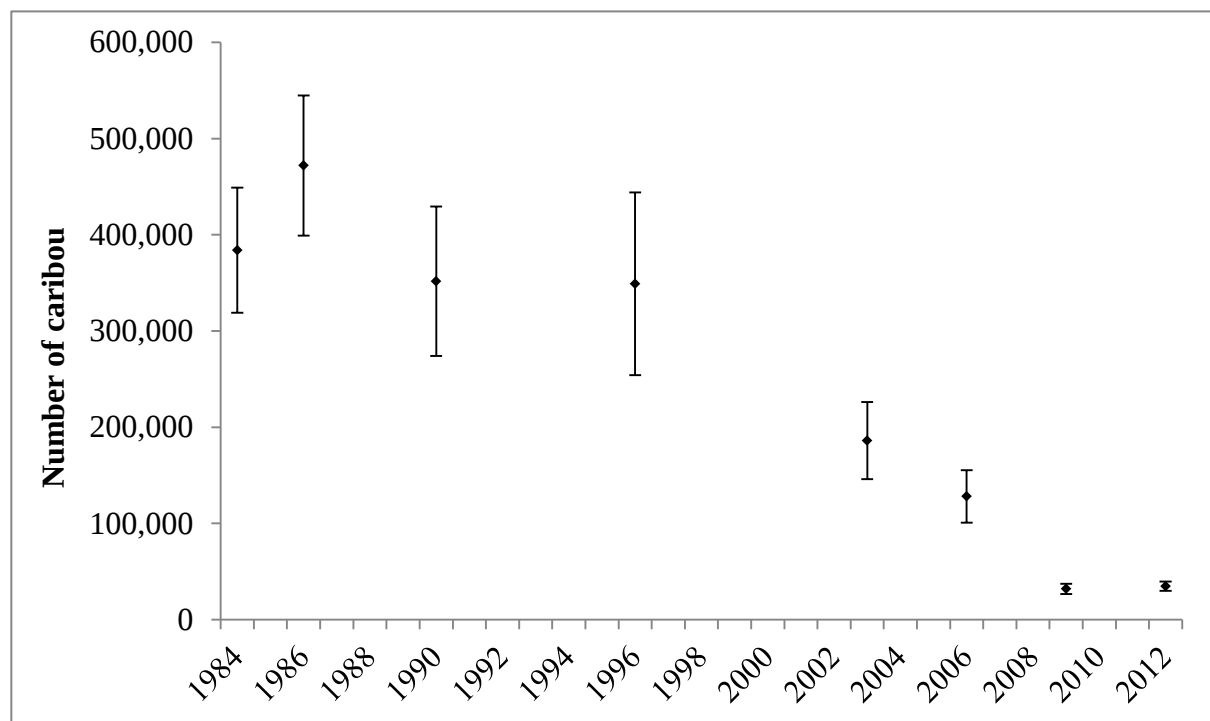


Figure 1. Population estimates ($\pm$ SE) for the Bathurst caribou herd based on calving ground aerial photo surveys.

The factors that influence the population dynamics of barren-ground caribou herds are complex (Bergerud 1980, Bergerud 1996, Valkenburg 2001, Gunn et al. 2009, Festa-Bianchet et al. 2011, Joly and Klein 2011). Each caribou range is inherently unique as weather patterns, physical topography, ungulate and predator densities, and forage availability all vary across time and space. In the past, forage limitation and predation were the key mechanisms hypothesized to

influence the population dynamics of caribou (Valkenburg 2001, Gunn et al. 2011).

Contemporary theories suggest that other factors, such as hunting pressure, anthropogenic development, insect harassment, disease, and the influence of changing climate patterns on range condition, also influence caribou populations numerically (Klein 1991, Thomas 1995, Gunn et al. 2009, Festa-Bianchet et al. 2011, Gunn et al. 2011). Several studies have focused on the ecological and environmental processes that regulate migratory barren-ground caribou populations, although results are not consistent across herds leading to debate about the key drivers and appropriate management responses (Van Ballenberghe 1985, Bergerud and Ballard 1989, Valkenburg 2001, Tyler 2010, Joly et al. 2011). Attention is now focused on the cumulative interaction of these factors in the context of population declines.

The severity of recent declines across several herds in northern Canada has led to concerns that caribou may be more vulnerable to the cumulative threats that now occur across much of their range (Vors and Boyce 2009, Gunn et al. 2011). Even though fluctuations and cycles are characteristic of caribou population dynamics, it is unclear whether the pattern of recovery has changed (Vors and Boyce 2009, Festa-Bianchet et al. 2011, Gunn et al. 2011). Such uncertainty confounds management responses such as reducing harvest or predator control. Theoretically, an estimate of overall predation rate from wolves can be calculated as the product of the functional and numerical response of the predator (Seip 1991, 1995; Messier 1995). Here, the number of predators (numerical response) and the number of prey killed by each predator (functional response) vary according to prey density and have a multiplicative effect on predation rate (Seip 1991, 1995; Messier 1995). Based on their dependence on barren-ground caribou for prey, it is not clear how the tundra wolf population on the Bathurst caribou summer range responds, either numerically or functionally, when caribou populations decline.

Identifying this relationship between predator and prey is challenging because the interactions are complex, dynamic, and occur over areas that are vast and remote. The implication of these responses for caribou herd recovery is unclear.

STUDY OBJECTIVES

The purpose of my research was to provide further insight into the denning ecology of tundra wolves on the summer range of the Bathurst caribou herd and to evaluate the behavioural and population responses of wolves relative to changes in the distribution and abundance of caribou. Results of my research provide insight into the population and distribution dynamics between tundra wolves and barren-ground caribou which can support future management decisions. I used long-term data sets in combination with field-based methods to quantify the relationship between wolves and caribou. My specific research objectives were:

1. Describe mechanisms that influence den selection and den distribution for tundra wolves and determine if selection and distribution changed in response to a decrease in caribou density.
2. Document production and recruitment of wolf pups on the Bathurst caribou summer range, investigate mechanisms that may influence pup survival, and evaluate the resulting dynamics of the tundra wolf population.
3. Investigate the fine-scale movements of wolves during the denning period throughout a period of low caribou abundance to assess the hunting strategies of wolves to reduced prey availability.

To meet these objectives, I divided the thesis into three research chapters. In Chapter 2, I used locations of active den sites of wolves denning on the Bathurst summer range between

1996 and 2012 to investigate the temporal variation in the selection of dens as a function of caribou abundance. In Chapter 3, I used repeated surveys of pup survival to assess the potential influence of the density and migration patterns of caribou on pup recruitment. I developed a population model based on those vital rates to provide insight into the dynamics of the tundra wolf population on the Bathurst caribou summer range. In Chapter 4, I used location data collected from GPS-collared adult tundra wolves to document hunting patterns throughout the denning period and investigated the relationship between hunting strategy and wolf reproductive success. I concluded the thesis with a summary of my main research findings, discussion of the management implications, and future research needs.

CHAPTER 2: BEHAVIORAL RESPONSE OF WOLVES TO DECLINING CARIBOU DENSITY IN THE CENTRAL CANADIAN ARCTIC

ABSTRACT

Wolves (*Canis lupus*) that den on the tundra of the central Arctic prey primarily on migratory barren-ground caribou (*Rangifer tarandus groenlandicus*). Prey densities in the vicinity of den sites are low, however, for a period each summer when caribou migrate to their calving and post-calving ranges. Eskers provide substrate where wolves can excavate den sites, but these landforms make up only a small proportion of the tundra landscape. I investigated the factors that influenced den site selection for wolves on the summer range of the Bathurst caribou herd, Northwest Territories, Canada. I used a long-term dataset (1996-2012) of wolf den locations to develop a series of resource selection function (RSF) models representative of broad land-cover types, esker density, and annual variation in seasonal prey availability. I compared a temporal sequence of RSF models to investigate whether wolves altered selection patterns in response to a 90% decline in caribou abundance (1996-2012). Eskers were selected denning habitat; the distribution of eskers may be limiting when wolf density is high. Covariates representing the seasonal distribution of caribou from early (5-18 July) and late (19 July-22 August) summer were the best predictors of den occurrence; these areas represented reliable concentrations of caribou over the greatest portion of the denning period. As the caribou herd declined, the seasonal summer ranges contracted northward toward the calving ground. Wolves did not exhibit a similar response. As such, the period of spatial separation between breeding wolves at den sites and the main distribution of caribou increased when herd abundance was low. The lack of a behavioural response is consistent with wolf-prey dynamics observed in other studies that suggest wolves strive to maintain consistent territories even following large decreases in resource availability. Such behaviour may reduce fitness and have implications for pup survival and population growth.

INTRODUCTION

In most areas of North America, the gray wolf (*Canis lupus*) is considered to be a habitat generalist (Mech and Boitani 2003). Wolves are highly territorial and their distribution is based predominately on the accessibility of ungulate prey (Fuller et al. 2003). Pup survival is tied to prey biomass (Fuller et al. 2003), and as such, prey availability is likely an important factor in determining the location of den sites within a territory (Paquet and Carbyn 2003). Other important factors include the spatial proximity to neighboring wolf packs, suitable vegetation and soil conditions to provide structural support for den excavation (Ciucci and Mech 1992, Paquet and Carbyn 2003), and hiding cover (Norris et al. 2002, Kaartinen et al. 2010).

Several studies have focused on the spatial distribution and selection of den sites by wolves (Ballard and Dau 1983, Fuller 1989, Ciucci and Mech 1992, Theuerkauf et al. 2003, Ahmadi et al. 2013). Most, however, have occurred within forested landscapes or mountainous regions where wolves are likely to exploit a more consistently available and sedentary prey base than in arctic ecosystems. In the Arctic, barren-ground caribou (*Rangifer tarandus groenlandicus*) are the primary prey of tundra wolves (Kuyt 1972, Parker 1973, Williams 1990). These wolves follow the seasonal movements of caribou throughout most of the year (Walton et al. 2001, Hansen et al. 2013). During the denning period (May through August), however, reproducing wolves are constrained to more southerly den sites, closer to treeline, while caribou continue their spring migration north to calving grounds near the arctic coast (Heard and Williams 1992, Walton et al. 2001). Alternative prey, such as moose (*Alces alces*) or muskoxen (*Ovibos moschatus*), are scarce in this region, resulting in a landscape with a low density of prey during a significant portion of the denning period. Past studies suggest that wolves select den sites where they can optimize the availability of caribou during the denning period; these areas

include major migration routes (Clark 1971, Kuylt 1972, Frame et al. 2008) or near treeline, where caribou are more abundant in September (Banfield 1954, Kelsall 1968, Heard and Williams 1992).

The Bathurst herd of barren-ground caribou, estimated at 349,000 animals ($\pm 94,900$ SE) in 1996, slowly declined through the late 1990s and then more rapidly during the 2000s (Environment and Natural Resources [ENR] 2011). The herd was estimated at 32,000 animals ($\pm 5,300$ SE) in 2009 representing a 70% decline over three years (Adamczewski et al. 2009). The distribution of barren-ground caribou is density-dependent such that range expansion and contraction are a function of the size of the herd (Simmons et al. 1979, Bergerud et al. 1984, Heard and Calef 1986, Messier et al. 1988, Couturier et al. 1990, Gunn et al. 2012). Gunn et al. (2013) reported that the winter range of the Bathurst herd has contracted since 2002, corresponding to the decline of the herd. In recent years, biologists also have noted fewer caribou in the southern portions of the Bathurst summer range (D. Cluff, pers comm) compared to periods of higher abundance when scattered groups of caribou remained along the treeline throughout the summer (Banfield 1954, Parker 1973, Miller and Broughton 1974, Darby 1978, 1979, Heard et al. 1996).

Heard and Calef (1986) and Heard and Williams (1992) hypothesized that wolf populations demonstrate a numerical response to caribou abundance, where density-dependent range expansion or contraction by caribou influences prey availability. For wolves limited to the area of caribou range adjacent to the den site, fewer prey result in higher pup mortality and pup recruitment strongly influences wolf population dynamics (Fuller et al. 2003). Rettie and Messier (2000) noted that animals should avoid areas that limit their fitness, with the strongest patterns apparent at larger scales (population range, home range). Theoretically, with over a

90% decline in their main prey source since the mid-1990s, a behavioural response of tundra wolves on the Bathurst range should act at broad spatial and temporal scales.

In a landscape dominated by bedrock, permafrost, and water, tundra-denning wolves select eskers or similar habitats because they consist of sandy soils that provide suitable conditions for den excavation (Mueller 1995, McLoughlin et al. 2004). However, eskers make up only 1-2% of the tundra landscape and their distribution is not uniform across the central Arctic (Mueller 1995). Thus, McLoughlin et al. (2004) suggested that the availability of eskers may be a limiting factor for wolves.

I investigated the mechanisms that influence the distribution of den sites for tundra wolves across the central Canadian Arctic relative to variation in prey availability over time. Specifically, I constructed and compared a temporal sequence of resource selection function (RSF) models using covariates representative of broad habitats, esker density, and annual variation in seasonal prey availability. I hypothesized that selection of den sites by wolves would vary in response to changing abundance of barren-ground caribou, the primary prey species during summer (Williams 1990). Changes observed in the distribution of dens provide insight into how wolves respond behaviorally to declines in the availability of caribou over time.

METHODS

Study Area

The study area in the Northwest Territories, Canada, extends from the boreal forest in the south, across a transition zone of forest tundra and onto low arctic tundra in the north (Figure 2). Climate is characterized by short summers and very cold and long winters. The southwestern portion of the study area encompasses Northern Canadian Shield Taiga (ECG 2012) where common forest types include open spruce-lichen woodlands and black spruce (*Picea mariana*)

peatlands. This area includes portions of the late winter/early spring distribution of the Bathurst caribou herd. The treeline is characterized as a transition zone between taiga and tundra, where stunted white spruce (*Picea glauca*) and black spruce occur in small patches before giving way to open tundra to the northeast.

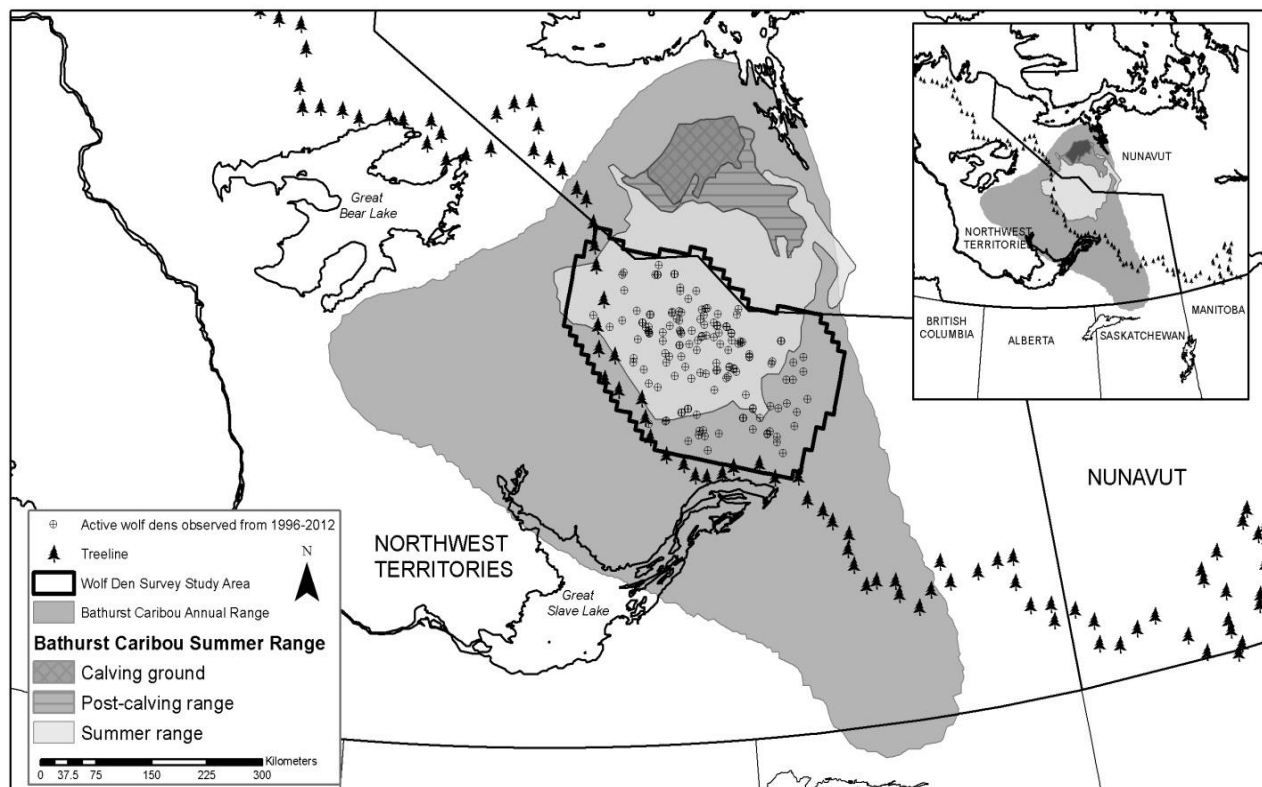


Figure 2. Study area for wolf den surveys on the summer range of the Bathurst caribou herd in the Northwest Territories, Canada. Active wolf dens ($n = 303$) were recorded during aerial surveys conducted in late May and early June, 1996-2012. The annual home range (calving, summer, and winter range) of the Bathurst herd is approximately 350,000 km². Range boundaries were delineated from locations of satellite- and GPS- collared caribou.

The wolf study area is comprised of rolling uplands of Canadian Shield rock and upland tundra while lowlands contain fens, bogs, and numerous lakes (ECG 2012). This area is used by Bathurst caribou during spring migration and again during the mid and late-summer, after the majority of the herd returns from their calving ground. The herd typically remains along the treeline during the late-fall rutting period before returning to the taiga during winter.

The entire region was covered by the last continental ice sheet where eskers formed from riverbed deposits during the melt from once fast-flowing glacial rivers. Eskers occur across both tundra and boreal ecozones (ECG 2012) and provide an ice-free surface of sand and gravel substrate where wolves can excavate den sites in a landscape otherwise dominated by rock, permafrost, and water (Mueller 1995, McLoughlin et al. 2004).

Animal Data

From 1996-2012, the Government of the Northwest Territories, Department of Environment and Natural Resources conducted annual wolf den surveys on the Bathurst caribou summer range, an area encompassing approximately 54,000 km² in the Northwest Territories (Figure 2). Surveys were stratified according to esker habitat. Over 95 individual den sites were recorded during the 17-year period; these data represent a time series of active den locations across periods of relatively high and low abundance of caribou. Likewise, as part of ongoing monitoring of the Bathurst herd, adult female caribou were fitted with satellite and GPS collars (Gunn et al. 2013). From 1996-2008, Argos satellite collars were used exclusively and recorded locations from weekly to daily intervals. From 2008-2013, both GPS and Argos satellite collars were deployed, resulting in the collection of animal locations at daily and hourly intervals. Location fix-rate varied by collar type and sample sizes varied both by year and season (Gunn et al. 2013).

Study Design

Resource Selection Functions

I developed a series of resource selection function (RSF) models to determine factors that influence den site selection and to investigate the behavioural response of wolves to changes in relative abundance of the Bathurst caribou herd. An RSF is a statistical model that quantifies the spatial relationship between location data collected for an individual or population and specific

factors or mechanisms that might influence the distribution of those location data (Boyce et al. 2002, Manly et al. 2002). Coefficients from RSF models represent selection or avoidance of a particular resource.

Resource Availability

The links between the behaviour and ecology of tundra wolves and the distribution of barren-ground caribou have been well established (Parker 1973, Williams 1990, Heard and Williams 1992, Walton et al. 2001, Frame et al. 2008, Hansen et al. 2013). Thus, I defined resource availability for den selection as the area occupied by caribou from 01 April to 30 September (1996-2012). During this interval, pregnant female wolves undergo long-distance migrations from the boreal forest to the tundra, select a den site, and restrict their movements within a summer territory (Walton et al. 2001, Frame et al. 2008). The area of availability for wolf dens was identified as the 95% minimum convex polygon (MCP) calculated from the locations of satellite- and GPS-collared caribou for each year of the study (Appendix A). I removed the locations of collared caribou that did not calve on the Bathurst calving ground (Gunn et al. 2002, 2013; Adamczewski et al. 2009). For six of the study years (1996 to 2012, inclusive) the 95% caribou MCP did not completely cover the extent of all wolf dens (1-2 dens). To ensure complete representation of available habitat, I merged caribou polygons with a 100% MCP around the locations of all active wolf dens recorded for each year.

I limited the northern extent of the analysis area to the political boundary of the Northwest Territories and Nunavut (Figure 2) as annual wolf den surveys occurred mainly in the Northwest Territories. Bathurst wolves are known to den near caribou calving and post-calving ranges in Nunavut (Heard and Williams 1992; D. Heard, unpublished data; D. Cluff, unpublished data), but previous studies and incidental sightings of wolves report that the majority of wolves

den on the caribou summer range, closer to treeline, in the Northwest Territories (Figure 2; Heard and Williams 1992, Walton et al. 2001, Frame et al. 2008). I quantified resource availability using 5 random sites per den selected within the merged 95% MCP for caribou range during the year of the den survey. For each year of the study, random locations were matched to each active den site and were replaced if they fell directly on a water feature.

Resource Variables

Land cover

I identified land-cover types that were expected to explain the distribution of wolf dens at the landscape scale. I modified Northern Landcover/EOSD 30-m vegetation cover (Wulder et al. 2003, Olthof et al. 2009) into 6 classes representative of the broad cover types that occur in the study area (Table 1). I used CanVec Relief and Forms vector data (Natural Resources Canada 2007) to overlay the distribution of eskers across both boreal and tundra ecozones, resulting in a total of seven land-cover types. To model den site selection, I calculated the percent cover of each land-cover type within a 500-m radius of each den and random site. I used the methods of Johnson et al. (2004) to calculate the density of esker pixels representing regional variation in the availability of esker habitat. This involved applying a 73-km² rectangular moving window to a binary image of esker habitat and calculating the density of pixels (ha/km²) across the study area (see Johnson et al. 2004, 2005).

Distance to Caribou Migration Routes

The distribution and movement of barren-ground caribou vary considerably by season (Fancy et al. 1989, Gunn et al. 2002, 2013). These dynamics influence the availability of prey (Heard and Williams 1992) and thus the reproductive success for denning wolves (Frame et al. 2008). I hypothesized that wolves would select den sites in areas where caribou were available through a longer portion of the summer when adults were restricted to the den area

Table 1. Variables used to model resource selection by tundra denning wolves on the summer range of the Bathurst caribou herd from 1996-2012.

Variable	Description
Land cover types	
Lowland tundra	Moist tussock tundra with < 25% dwarf shrubs < 40-cm tall, wet sedge, includes bryoids and lichen.
Upland tundra	Well drained non-tussock tundra, with low to prostrate dwarf shrub heath > 70% cover.
Shrub	Shrub height > 40 cm and < 2m, consisting mainly of dwarf birch (<i>Betula</i> spp.) and / or willow (<i>Salix</i> spp.); remaining cover consists of graminoids, lichen and may contain prostrate dwarf shrubs and bare soil.
Wetlands	Vegetated areas where the water table intersects the land surface all or part of the year; includes tree and shrub areas near and below treeline and is represented by sedge, moss, and low-shrub wetlands within the tundra.
Esker	Linear structures of sand or gravel which vary in length from a few to several hundred kms; provide topographic relief and are sparsely vegetated aside from base of slopes, where taller bands of shrub can be found up to 1.5-m high.
Forest	Boreal spruce-lichen forests extending to the northern limit of trees where the transition zone between taiga and tundra (treeline) is characterized by small patches of dwarf white spruce (<i>Picea glauca</i>) and black spruce (<i>P. mariana</i>).
Water	Small shallow tundra ponds < 2 m, deep lakes > 2 m, and river systems.
Esker density	Density of esker pixels within a 73-km ² (8.54 km x 8.54 km) moving window across the study area.
Caribou migration routes ¹	Median straight-line distance from each den/random site to each seasonal caribou movement path.

¹ Seasonal designations (Gunn et al. 2013): spring migration (01 April*-02 June), calving (03 June-13 June), post-calving (14 June-05 July), early summer (06 July-18 July), late summer (19 July-22 August), fall migration (23 August-04 October)

*01 April used to match wolf availability polygons (Gunn et al. 2013 used 15 April as the start of the spring migration)

caring for newborn pups. I used the locations of satellite-collared (Argos and GPS) adult females from 1996-2012 to quantify the seasonal variation in the spatio-temporal distribution of caribou (Gunn et al. 2013; Table 1). I created movement paths from the successive locations of each collared caribou for six seasonal distributions: spring migration (01 April-02 June), calving (03 June-13 June), post-calving (14 June-05 July), early summer (06 July-18 July), late summer (19 July-22 August), and fall migration (23 August-04 October). I measured the straight-line

distance from each den and random site to the closest edge of each caribou seasonal movement path. From each den, I then calculated the median distance from all seasonal paths and used this measure to represent the distance from each den to seasonal areas, assumed from migration routes, typically used by caribou (Appendix B).

Model Development and Assessment

I developed a set of four candidate RSF models to serve as hypotheses for testing factors to explain the distribution of wolf den sites relative to temporal and spatial variation in the availability of caribou (Table 2). First, I ran the set of candidate models using pooled den site data across all years (1996-2012) to assess general factors that influence den selection by wolves. To assess the behavioural response of wolves to changing caribou densities, I used den site data to fit RSF models over three time periods (interval models) that represented significant changes in the abundance of the Bathurst herd: 1) High 1996-2000 (~349,000-300,000 animals), 2) Medium 2003-2006 (186,000-128,000 animals), and 3) Low 2009-2012 (32,000-35,000

Table 2. Candidate RSF models for quantifying selection of den sites by tundra wolves on the summer range of the Bathurst caribou herd, 1996-2012.

Model Theme	Model Parameters
Land cover	Percent cover of seven land-cover variables (Table 1) within 500-m radius of a den or random site
Land cover + esker density	Percent cover of seven land-cover variables within 500-m radius; number of esker pixels per 73-km ² moving window
Land cover + caribou + caribou ²	Percent cover of seven land-cover variables within 500-m radius; median Euclidean distance to seasonal caribou migration routes (pre-calving, early summer, late summer, fall migration) including Gaussian terms if applicable [*]
Full model	Percent cover of seven land-cover variables within 500-m radius; median Euclidean distance to seasonal caribou migration routes (pre-calving, early summer, late summer, fall migration) including Gaussian terms if applicable ¹ ; esker density

^{*} Models were run with and without the squared (Gaussian) term to compare linear and nonlinear responses of wolves to caribou migration paths.

animals). A behavioural response would be inferred by a significant change in the value of coefficients between periods. I excluded 1998 from my analysis as only three caribou collars were functional over the majority of the denning period. To identify variation in selection patterns as caribou declined I excluded 2001-2002 and 2007-2008 from the response analysis (interval models).

I used a conditional (matched) logistic regression to model resource selection. Because merged caribou MCPs varied annually, I grouped the used and available data by year to represent annual changes in resource availability for wolves. I used a robust variance estimator to control for autocorrelation within the dataset, as dens were used more than once during the study period (Rogers 1993). I tested model parameters for multicollinearity using variance inflation factors (VIFs). Individual model parameters with a $VIF > 10$ were removed from candidate models (Hosmer and Lemeshow 2004). I used Akaike's Information Criterion (AIC) to select the most parsimonious model explaining selection of den sites. The most parsimonious model had the lowest AIC score, explaining the greatest amount of variation in the observed data with the fewest parameters. I calculated ΔAIC as the difference in AIC values between each model and the highest ranked model (Table 3). For further comparison, I calculated Akaike weights ($AICw_i$) for each model; this score represented the approximate probability that the selected model was the best among the proposed models (Anderson et al. 2000). I used a Gaussian function to model the nonlinear response of wolves to seasonal caribou migration paths. Because of variation in caribou migration paths over time, I used ΔAIC to determine if a linear or a Gaussian term was appropriate. The nonlinear term was retained in RSF models if the additional quadratic parameter improved $\Delta AIC \geq 2$ points.

Information theoretic approaches, such as AIC, provide relative measures of model fit. Thus, I used the receiver operating characteristic (ROC) to assess the predictive accuracy of each model. I conducted a one-fold cross-validation technique where each record was withheld sequentially from the model-building process, and that record was then used to calculate a predicted probability of it being a wolf den. Those independent probabilities were used to calculate the Area Under the Curve (AUC) for the ROC test. An AUC of 1.0 indicated that the model was a perfect predictor; values between 0.7 and 0.9 were considered to have good predictive capacity, with values of 0.5 having no predictive capacity (Fielding and Bell 1997, Boyce et al. 2002). I used 95% confidence intervals to assess the strength of each predictor covariate. I conducted all analyses in Stata v. 12.1 (Statacorp, College Station, Texas, USA).

Descriptive Analyses

Previous studies of wolves note that the spatial proximity of neighboring packs should influence den site selection at the landscape scale (Paquet and Carbyn 2003). To help interpret RSF results, I measured the Euclidean distance between active wolf dens (interden distance; Ballard and Dau 1983) recorded on the Bathurst caribou range for each year. I averaged this metric across the same periods used in the interval RSF models (High 1996-2000; Medium 2003-2006; Low 2009-2012).

Barren-ground caribou show a density-dependent mechanism where range expansion and contraction is a function of the size of the herd (Simmons et al. 1979, Bergerud et al. 1984, Heard and Calef 1986, Messier et al. 1988, Couturier et al. 1990). Such dynamics may influence the distribution of wolves (Heard and Williams 1992). I measured the Euclidean distance from the centroid of the Bathurst calving ground (Adamczewski et al. 2009) to each seasonal movement path delineated from locations of individual Argos- and GPS- collared caribou over

the 17-year period. I then averaged the distance measurements by model period (High, Medium, Low) to index broad changes in the seasonal distributions of the herd over the course of the study.

RESULTS

Surveys of wolf dens conducted by the Government of the Northwest Territories from 1996-2012 resulted in a total of 347 active den sites, of which 303 occurred within the study area. On average, active den sites were reused 2.2 times (SD = 1.9) over the 17-year study period. I used locations from 135 Argos- and GPS- collared adult female caribou ($\bar{X}$ = 14 collars/year; SD = 4.53) to stratify seasonal migration routes from 1996-2012. I developed four sets of RSF models, one set to describe general den site selection patterns (all years n = 303) and three model sets representing the periods of caribou abundance: High (n = 80), Medium (n = 72), and Low (n = 83).

Den site selection

Across all years, the most parsimonious model for den site selection included covariates for land cover, distance to caribou migration routes, and esker density (AIC w_i = 0.99; Table 3). The best model had good discriminatory ability (AUC = 0.82 ± 0.01 SE). Within a 500-m radius of the den, wolves selected for esker and upland tundra features. The coefficient for esker was the strongest; no other land-cover covariates besides these two influenced den site selection (Figure 3A). Wolves selected areas with a relatively high density of eskers (Figure 3A). The pooled RSF model indicated selection by wolves for den sites that were relatively close to caribou during the late-summer season, while spring migration routes were avoided (Figure 3B). On average, wolf dens were located closer to calving, post-calving, early-summer, late-summer and fall caribou migration routes than were the random sites (Figure 4).

Table 3. Results from resource selection function models used to identify denning habitat for tundra wolves on the summer range of the Bathurst caribou herd. The number of model parameters (k), differences in Akaike's Information Criterion scores (ΔAIC) and weights (w_i) were compared over three time periods (High, Medium, Low) when the population size of the Bathurst herd varied significantly as well as the full set of observations (1996-2012) excluding 1998.

Model	k				$\Delta_i AIC$				$AICw_i$			
	High	Medium	Low	All	High	Medium	Low	All	High	Medium	Low	All
Land cover	7	7	7	7	4.94	8.07	5.99	31.63	0.05	< 0.01	0.03	< 0.01
Land cover + esker density	8	8	8	8	6.30	8.94	3.53	22.97	0.03	< 0.01	0.12	< 0.01
Land cover + dist caribou + dist caribou ^{2*}	14	13	14	15	0.00	0.00	2.04	10.06	0.62	0.56	0.22	< 0.01
Full model**	15	14	15	16	1.41	0.52	0.00	0.00	0.30	0.43	0.63	0.99

*Gaussian term only included where appropriate

** Full model = landcover + esker density + dist caribou + dist caribou²

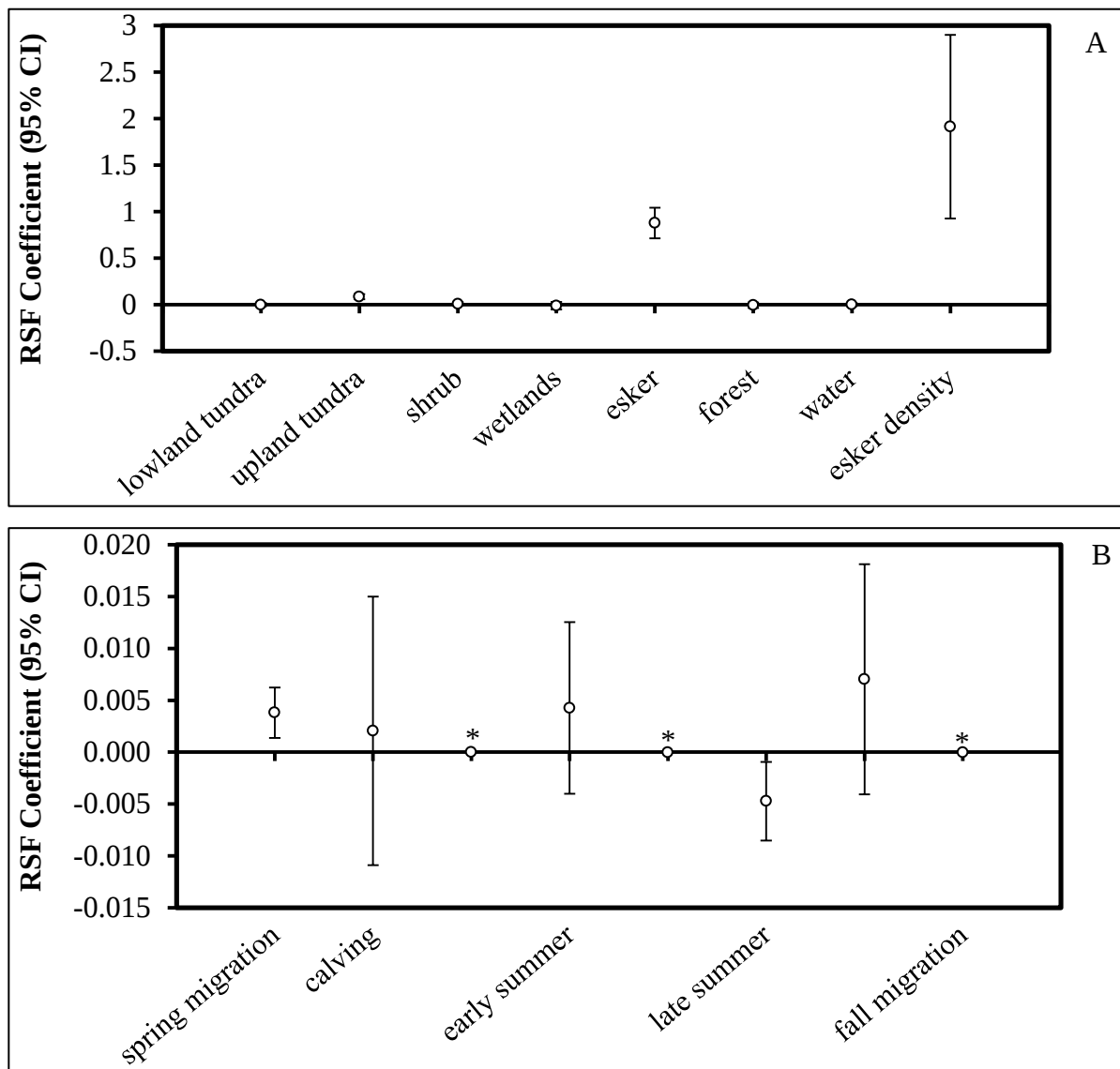


Figure 3. Coefficients and 95% confidence intervals from the most parsimonious resource selection function model developed to investigate selection of wolf dens relative to A) land-cover types and B) distribution of seasonal caribou migration routes on the Bathurst caribou summer range from 1996-2012 (excluding 1998). Positive distance coefficients (graph B) indicate a relative increase in the likelihood of a wolf den occurring as the distance to caribou routes increase (avoidance); negative coefficients indicate a decrease in the likelihood as distance increases (selection). * Indicates the Gaussian (squared) term was included for distance to seasonal migration path.

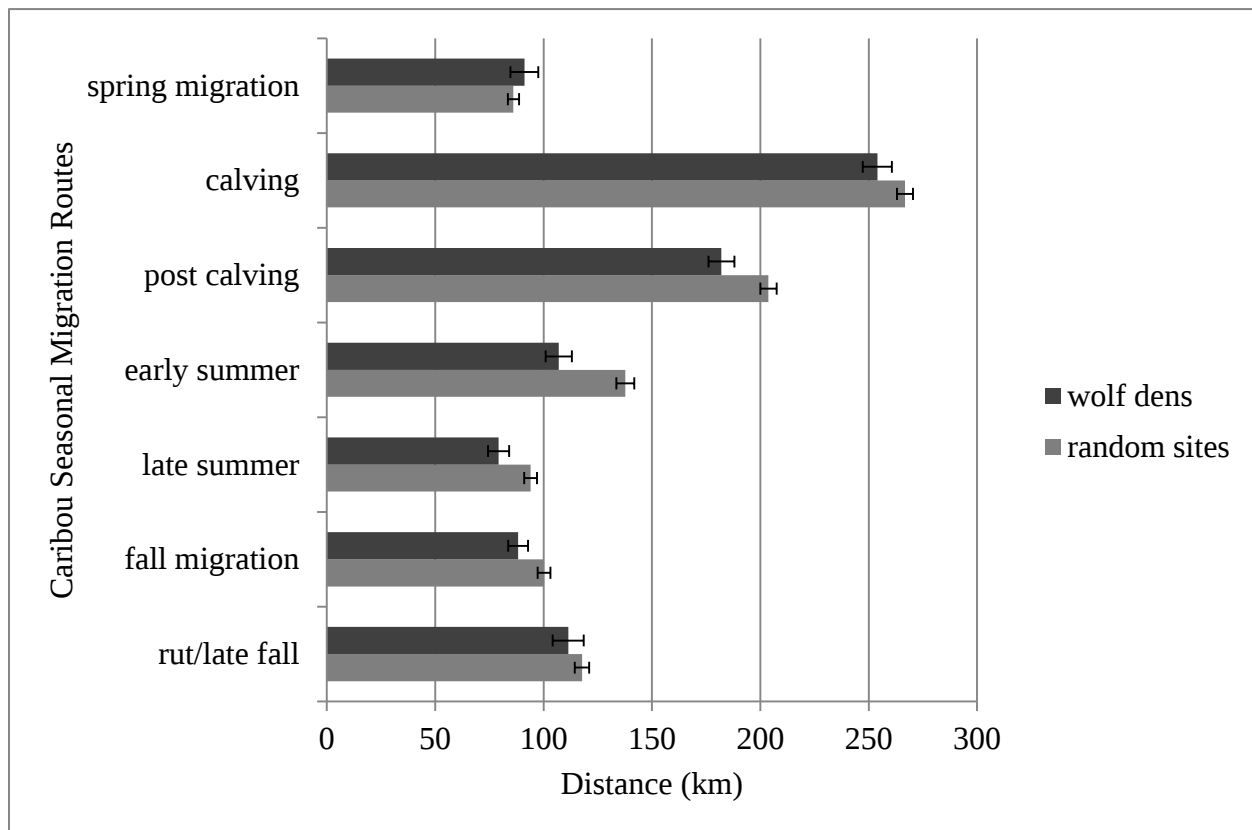


Figure 4. Average ($\pm$ 95% confidence intervals) distances (km) of wolf dens ($n = 303$) and random sites ($n = 1515$) from seasonal caribou migration routes on the Bathurst range from 1996-2012 (excluding 1998).

Response of wolves to changes in caribou density

The summer range for caribou contracted significantly from the late 1990s when the herd was estimated at $> 300,000$ animals to current estimates of 35,000 animals (ENR 2011). The 95% caribou MCPs (based on locations 01 April to 30 September) to stratify annual availability decreased over time, from an average of $94,670 \text{ km}^2$ ($\pm 20,466 \text{ km}^2 \text{ SE}$) during the High period, $79,465 \text{ km}^2$ ($\pm 11,481 \text{ km}^2$) during the Medium period, to $59,185 \text{ km}^2$ ($\pm 8512 \text{ km}^2$) during the period of Low abundance of caribou. As the herd declined in abundance, the area of occupancy from early summer through to late-fall rut contracted northward toward the centroid of the calving ground (Figure 5). The spatial distribution of wolf dens changed between model periods, but the pattern was inconsistent relative to the contraction in caribou range. The interden distance between wolf packs increased from an average of 21.7 (± 1.16) km to 28.9 (± 1.88) km

from High to Medium periods, respectively. Interden distance remained at 28.32 km (± 1.94) during Low caribou years.

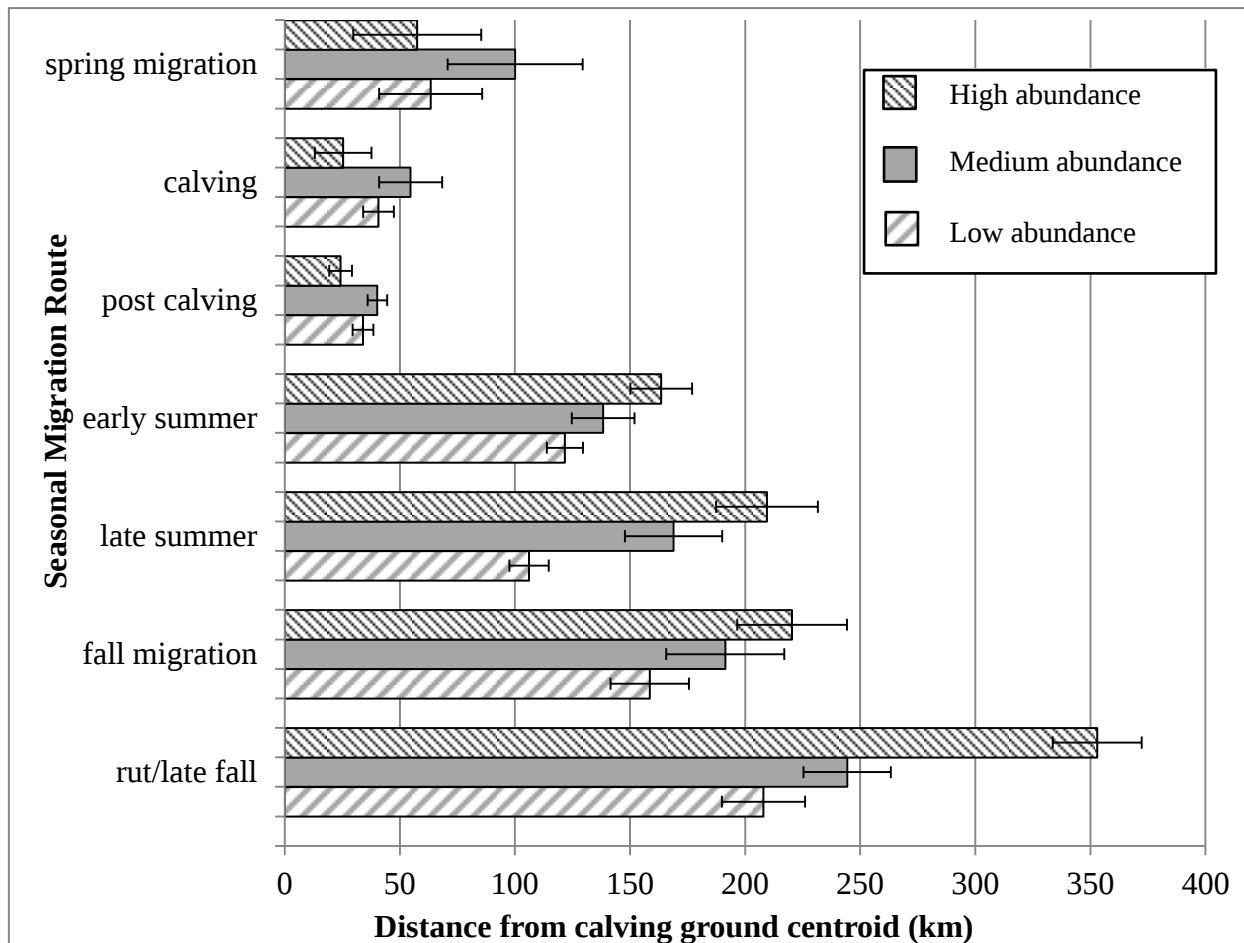


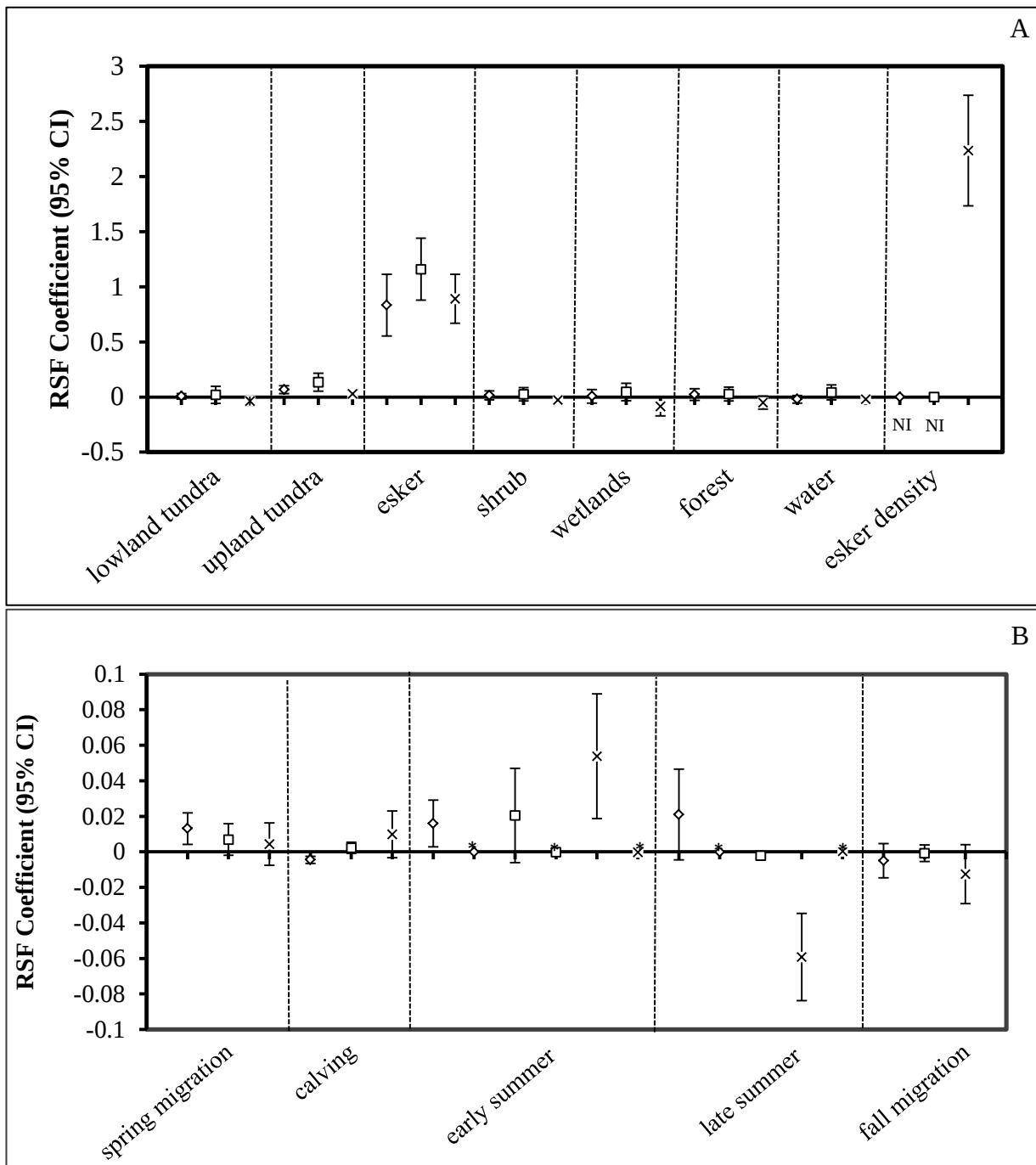
Figure 5. Relative change in the seasonal distribution of the Bathurst caribou herd ($\pm 95\%$ confidence intervals) as represented by distance from calving ground. For each year, the Euclidean distance from the centroid of the Bathurst calving ground (constant) was measured to seasonal movement paths of Argos- and GPS- collared adult female caribou. The mean distance was summarized by periods when the population size of the Bathurst herd declined significantly: High (1996-1997; 1999-2000), Medium (2003-2006), and Low (2009-2012).

During years of high abundance in caribou, the most parsimonious resource selection model for wolves included covariates for land-cover type and distance to caribou migration routes (AIC $w_i = 0.62$, Table 3). The second ranked model included an additional covariate for esker density and differed by < 2 AIC points (AIC $w_i = 0.30$, Table 3). Likewise, during the Medium period of caribou abundance, the model with the lowest AIC score included covariates

for land cover and caribou migration route (AIC $w_i = 0.56$) and the next most parsimonious model included the additional covariate for esker density (AIC $w_i = 0.43$, Table 3). During the Low period, the order of the top two models was reversed. The model with the lowest AIC score contained covariates for percent cover of land cover, caribou migration routes, and esker density (AIC $w_i = 0.63$, Table 3) and the next most parsimonious model included only covariates for land cover and caribou migration route (AIC $w_i = 0.22$, Table 3). All models had relatively large ROC scores, ($AUC = 0.75 \pm 0.02$ SE, 0.79 ± 0.01 , 0.75 ± 0.02 ; High, Medium, Low periods, respectively) indicating good predictive performance.

Although there was some variation in the selection and avoidance of land-cover types between periods of caribou abundance, in general, the top-ranked RSF models from each period were consistent in that wolves strongly selected for eskers (Figure 6A). The remaining covariates suggested weak selection or were not significant predictors of den site selection. Upland tundra was selected during High and Medium intervals, but the coefficient was relatively small and not statistically significant during years of low caribou density. The influence of esker density on den site selection varied with time (Figure 6A). Wolves selected for dens in areas of high esker density only when caribou abundance was low (Table 3, Figure 6A).

The covariates representing the distance to seasonal distribution of caribou were included in the top-ranked RSF models for all time periods (Table 3). The relationship between den selection and early summer migration routes was nonlinear, with coefficients for the linear term being positive across all model periods (Figure 6B). Selection did not statistically differ between model periods; however, quadratic plots indicated that the peak probability of occurrence for a



◇ High abundance □ Medium abundance X Low abundance

Figure 6. RSF coefficients and 95% confidence intervals from the best conditional fixed-effect logistic regression models used to investigate selection of wolf dens relative to A) land-cover types and B) the distribution of seasonal caribou migration routes over three periods of abundance in the Bathurst caribou herd. Positive coefficients indicate a relative increase in the likelihood of a wolf den occurring as the distance to caribou routes increase (avoidance); negative coefficients indicate a decrease in the likelihood as distance increases (selection). NI refers to covariates that were not included during the model selection process. * Indicates the Gaussian (squared) term was included for distance to seasonal migration path.

den increased with distance from the early summer migration route as the abundance of caribou declined (55 km, 80 km and 105 km during High, Medium, and Low periods, respectively; Figure 7A). The late-summer distribution of caribou was also an important predictor of wolf den occurrence during the period of Low caribou abundance, although the coefficient was significantly different from Medium and High periods (Figure 6B, 7B). The quadratic term for late summer was not included during the Medium period and the remaining covariates representing the distances to spring migration, calving ground and fall migration routes were relatively weak or not statistically significant (Figure 6B).

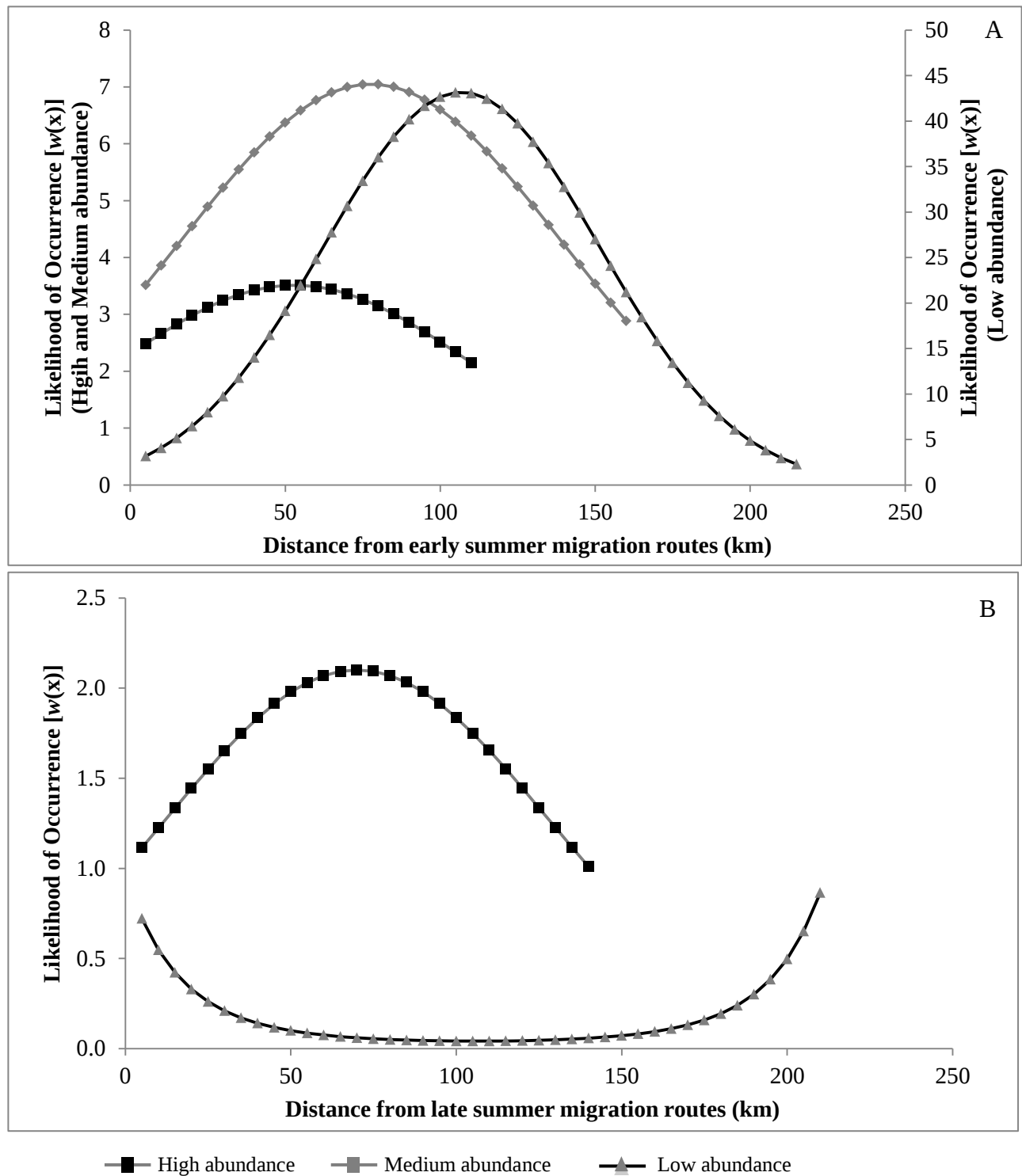


Figure 7. Plots representing the strength of selection [$w(x)$] for den sites of tundra wolves relative to caribou migration routes in A) early summer and B) late summer on the summer range of the Bathurst caribou herd. Occurrence of wolf dens was allowed to vary with distance from caribou migration routes while all other model covariates were held at their mean values.

DISCUSSION

The application of resource selection functions to long-term and spatially extensive data of wolf den occupancy in the Arctic allowed me to investigate the behavioural dynamics of wolves responding to a large change in the abundance of their primary prey. These findings corroborate earlier studies that report eskers as important habitat for tundra-denning wolves (Heard and Williams 1992, Mueller 1995, McLoughlin et al. 2004, Johnson et al. 2005). Across all model periods, wolves consistently showed strong selection for eskers within a 500-m radius of their den. Den surveys, however, were stratified by esker habitat which likely resulted in some observer and ultimately model bias which account for the consistent selection of esker across model periods. Nevertheless, in the central Arctic, eskers provide optimal environmental conditions as denning habitat in a landscape dominated by Precambrian shield rock, water, and permafrost (Mueller 1995). In my study, active den sites were located in areas of higher esker density than random sites, suggesting that the distribution of eskers across the Bathurst summer range influenced den site selection. Wolves also selected for upland tundra habitat although selection for this land-cover type was relatively weak compared to eskers and upland tundra was only selected when caribou abundance was relatively high. Upland tundra may be used by wolves as ancillary denning habitat.

In other studies, wolves selected den sites within 500 m of water (Ballard and Dau 1983, Norris et al. 2002, Trapp 2004, Ahmadi et al. 2013), likely due to greater requirements for hydration of the breeding female during lactation (Peterson and Ciucci 2003). Water availability, however, is not likely to be a limiting factor in the central Arctic as the tundra landscape is covered with a mosaic of small ponds, creeks, and lakes (ECG 2012). In my study

area, dens were on average 190 m (SD = 201) from the nearest water source and random sites were only 30 m farther ($\bar{X} = 220 \text{ m} \pm 168 \text{ m}$).

The Importance of Seasonal Caribou Distribution for Den Selection

I assumed that the distribution patterns of collared caribou would represent the seasonal variation in prey availability during a period when breeding wolves were non-migratory and remained in areas adjacent to the den sites caring for dependent pups. The use of these data was not without some key assumptions. Satellite and GPS-collared caribou provided detailed information at the scale of the individual, but they were only used to track adult female caribou and the number of collared individuals represented a small proportion of the overall herd. Gunn et al. (2013), however, reported that collared individuals represented higher densities of the herd during calving and Bathurst females showed high fidelity to post-calving and summer ranges. Aerial surveys have confirmed that collared females are predictive of caribou densities in the study area (Boulanger et al. 2004, Rescan Environmental Services 2006). Most adult male caribou follow the northern migration of females in spring and the distributions of both sexes occupy the same general areas from late June through to September (Heard et al. 1996). Gunn et al. (2013) suggested that it is reasonable to assume that male caribou show fidelity to females and maintain a closer geographic proximity during summer and fall, prior to the rutting season; this behaviour is also recognized for other species of deer (Jarman 1974, 1983, Apollonio et al. 1989).

Space-use patterns of barren-ground caribou are influenced by a variety of environmental and biological factors including whether, insect harassment, forage availability, and predation risk (Kelsall 1968, Bergerud 1996, Fancy et al. 1989, Gunn et al. 2002, 2013). These factors vary among caribou, making it challenging to infer the aggregate behaviour of the herd from

observations of individual animals. Nonetheless, location data collected on collared animals over multiple years should identify general patterns of space-use which would represent areas of varying prey concentrations for wolves at relatively large spatial and temporal scales.

Denning along major caribou migration routes (Clark 1971, Kuyt 1972, Frame et al. 2008) optimizes the availability of prey when the nutritional demands of wolf pups are the greatest. My results support these observations, with the exception of the spring migration by caribou. The southbound (post-calving) migration had more influence on selection of den sites than the northbound (pre-calving) migration. Wolves, on average, denned closer to the distribution of caribou from early-June (calving) until early October (end of fall migration) relative to random sites. In contrast, wolves did not select for spring migration routes, even though the distance was considerably closer when compared to the calving and post-calving ranges. The distribution of caribou during the spring migration may not be as important for denning wolves. Caribou move through the wolf study area in mid-May (median date = 12 May; interquartile range = 6 May to 21 May), 2-3 weeks prior to when pups are born (Frame et al. 2008, M. Klacek, unpublished data). Further, spring migration routes are strongly influenced by the winter distribution of the herd, the most variable of the seasonal distributions of barren-ground caribou (Gunn et al. 2002, 2013).

My results provide new insights into the spatio-temporal relationship between migratory caribou and denning wolves. Results from both pooled and interval RSF models revealed the importance of the early and late-summer caribou ranges in predicting wolf den occurrence. Caribou are more available to breeding wolves during these seasons than any other during the denning period. During this period, the distribution of male caribou typically overlaps with the early summer ranges of adult female caribou returning with calves on their southbound migration

(Heard et al. 1996). Gunn et al. (2013) reported that range overlap between consecutive years (range fidelity) for female Bathurst caribou increases after calving and is highest during late summer. Thus, spatially, the early and late-summer distributions represent the most reliable concentrations of caribou on the Bathurst summer range, while the occurrence of caribou calves in the denning areas increases biomass of more vulnerable prey base. Bathurst caribou were at their farthest distance from monitored wolf dens during the calving and post-calving seasons, when the average distance between wolf dens and the distribution of the herd was 250 and 180 km, respectively. In early July the caribou begin to disperse south (Gunn et al. 2013) and during early summer the peak probability of wolf den occurrence ranged from 55–105 km from caribou movement paths. This proximity provides breeding wolves with consistent access to caribou following the period when spatial separation between den sites and the main distribution of the herd was the greatest. Previous research on the movement dynamics (timing, direction, and distance) of Bathurst wolves reported extraterritorial movements away from dens sites only during a 3-week period in late June and early July (Walton et al. 2001, Frame et al. 2004). Hunting excursions lasted 2–4 days and occurred in a northerly direction, generally 40–50 km outside of the summer territory of a denning wolf. In late summer, breeding wolves are still tied to their dens or nearby rendezvous sites, as pups are too young to travel long distances with the pack (M. Klaczek, unpublished data). Caribou movement rates decrease considerably in August as insect harassment ceases and caribou focus on feeding to regain body mass prior to the rut and winter (Gunn et al. 2013).

Response of Wolves to Changing Caribou Densities

I hypothesized that denning wolves would demonstrate a behavioural response to changing caribou densities on the Bathurst range. I quantified changes in the selection of den sites over a 17-year period that coincided with a rapid and substantial decline in the abundance of

the Bathurst herd. During that time, the area of the summer range (95% MCP to define availability) of caribou decreased consistently and seasonal ranges from post-calving through fall migration contracted northward towards the calving ground; these results indicated that the Bathurst herd experienced density-dependent range contraction (Simmons et al. 1979, Messier et al. 1988, Fancy et al. 1989, Gunn et al. 2013). Wolves, however, did not select den sites closer to the seasonal caribou ranges as they contracted northwards. Covariates that represented both early and late-summer distributions of caribou changed considerably as the herd declined. As the distribution of caribou contracted, the probability of den site occurrence increased with distance from the early summer range. Furthermore, range contraction resulted in a more clustered distribution of collared caribou relative to when caribou abundance was high (Appendix D). Thus the probability of occurrence increased considerably during the period of low caribou abundance, but at a greater distance from the early summer range. Similarly, the late-summer distribution of caribou, as reflected by the distance of the migration route from the calving ground, was reduced by half between periods of High and Low abundance. Relative to when caribou abundance was High, quadratic plots (Figure 7) during Low caribou abundance indicated that late-summer probabilities of den occurrence decreased as distance increased from late-summer caribou migration routes. As caribou range contracted, the extent of spatial separation increased between denning wolves and the main distribution of the herd.

Upland tundra was selected by wolves during periods of High and Medium caribou abundance. This response could be explained by a density-dependent selection that was correlated with decreasing caribou abundance. During periods of abundant caribou, higher wolf densities would result in stronger competition, thus forcing breeding wolves to den in suboptimal habitats. These would be patches of upland tundra or areas with a relatively low density of esker

habitat. In contrast, esker density was included as a covariate in RSF models during periods when there were few caribou, but selection for upland tundra was not significant. These results, in addition to a significant increase in the interden distance from High to Medium periods of caribou abundance, suggest that currently, in a period of low caribou abundance, there may be relatively fewer wolf packs occupying core habitats on the Bathurst summer range. Furthermore, the availability of eskers, the most suitable areas for excavating dens, may influence the distribution of wolves during periods when Bathurst caribou are abundant and the wolf population is at peak density relative to available prey biomass.

CONCLUSION

Habitat selection by wolves is a hierarchical process that varies across spatial and temporal scales (McLoughlin et al. 2004). Arctic wolves across this study area show strong fidelity to den sites or denning areas, and yet because they are migratory, they do not establish or maintain annual territories (Walton et al. 2001). I investigated mechanisms that influenced den site selection relative to changes in the abundance of their primary prey, barren-ground caribou. Eskers were important denning habitat for wolves, although den site selection also was driven by the distribution of caribou during early and late summer. Spatially, these seasonal distributions represented areas where caribou were more reliably concentrated on the summer range over the greatest temporal period when wolves were restricted to areas adjacent to den sites.

Corresponding with a decline in caribou abundance, the distribution of the Bathurst herd contracted north towards the calving grounds. I hypothesized that wolves would respond behaviourally, selecting den sites that maintained a relative proximity to the retreating caribou. However, the RSF models did not indicate such a response, suggesting that the length of the

period of spatial separation between caribou and wolves, supporting pups at dens, increased as the herd declined. Changes in selection of dens did occur among model periods, but these patterns were more indicative of a competition effect, where fewer wolf packs occupied better denning habitat within the core area of their distribution.

Across much of its North American range, the gray wolf is highly territorial and once established, a breeding pair strongly resists losing its occupied range (Mech 1994, Mech and Boitani 2003). Wolf populations typically adjust to fluctuating prey densities through changes in dispersal and productivity (Peterson and Page 1988, Boertje and Stephenson 1992, Hayes and Harestad 2000, Fuller et al. 2003, Mech and Boitani 2003). Although a breeding pair can maintain a territory for long periods, it may be less productive or even refrain from breeding during times of low resource availability (Boertje and Stephenson 1992, Mech and Boitani 2003). Thus, varying prey densities and subsequent changes in wolf numbers may not influence the actual spatial mosaic of wolf territories at the population scale (Fuller 1989, Mech and Boitani 2003). Mech (1986), for example, reported a > 50% decrease in wolf abundance after a drastic decline in the deer (*Odocoileus virginianus*) population in the Superior National Forest, Minnesota, while the number of packs only dropped from 13 to 11.

Territoriality during the denning period has not been well documented for migratory tundra wolves. Movement patterns from satellite collar data reveal that breeding female wolves return to previously used denning areas and defend their summer ranges while they support pups (Walton et al. 2001). In my study, the lack of a behavioural response by wolves to significant changes in both the abundance and distribution of caribou may result in lower fitness with implications for pup survival and population growth (Heard and Williams 1992, Frame et al. 2008). Higher rates of den site abandonment and lower pup recruitment have been documented

for wolves denning on the Bathurst range in recent years (D. Cluff, unpublished data). In Chapter 3 of my thesis, I investigate the population dynamics of wolves relative to changes in the abundance and distribution of the Bathurst caribou herd. Such results provide further insight into the numerical response of wolves to changing caribou densities.

CHAPTER 3: WOLF-CARIBOU DYNAMICS WITHIN THE BARRENLANDS OF THE CENTRAL CANADIAN ARCTIC: ASSESSING A NUMERICAL RESPONSE

ABSTRACT

Wolves are the main predator of barren-ground caribou. The extent that wolves influence the decline and recovery of migratory caribou herds in the central Canadian Arctic, however, is unknown. I investigated wolf-caribou dynamics on the summer range of the Bathurst caribou herd in Northwest Territories and Nunavut, Canada. Caribou experienced a > 90% decline in abundance over the study period (1996-2014). Wolf productivity may be limited by changes in the abundance or spatial distribution of caribou, where low caribou densities result in food shortages leading to high pup mortality. I monitored the movements of GPS-collared adult female tundra wolves, representing individual packs, throughout the 2013 and 2014 denning periods to investigate pup recruitment at a time of low caribou abundance. Using long-term data sets (1996-2012), I developed regression models to investigate relationships between abundance indices of wolves and range-use patterns of caribou. I developed a series of stochastic population models to understand how pup recruitment influenced wolf densities on the Bathurst range over the period of caribou decline. High rates of den abandonment and low pup recruitment were observed during 2013 and 2014. As caribou abundance decreased, the late-summer distribution of the Bathurst herd contracted towards the calving ground. These movements correlated with low rates of wolf pup recruitment rates and high den abandonment, suggesting a regulatory mechanism whereby wolf reproductive success was limited by the low availability of caribou within the denning areas. Furthermore, these data suggested a numerical response, where wolf densities decreased as caribou numbers declined. Currently, wolf density is estimated at < 4 wolves/1000km² on the Bathurst caribou summer range. My results are

consistent with other studies that document a strong relationship between the population dynamics of wolves and the biomass of their ungulate prey.

INTRODUCTION

The tundra wolf (*Canis lupus*), a distinct ecotype of gray wolf (Musiani et al. 2007), has evolved to exist on the barrenlands of northern Canada by preying almost exclusively on migratory barren-ground caribou (*Rangifer tarandus groenlandicus*; Kuyt 1969, Parker 1973, Heard and Williams 1992, Walton et al. 2001, Frame et al. 2008). For most of the year, wolves maintain a close association with caribou (Walton et al. 2001, Hansen et al. 2013). The exception occurs from May to August when the migrating caribou herds move farther north to their calving and post-calving ranges near the Arctic coast, while breeding wolves are restricted to their denning areas generally farther south (Heard and Williams 1992, Walton et al. 2001). Prey availability may be low during that period of spatial separation (Heard and Williams 1992, Walton et al. 2001, Frame et al. 2004) as alternate prey, such as moose (*Alces alces*) or muskoxen (*Ovibos moschatus*) occur at low densities in the central Arctic (Ecosystem Management Group [ECG] 2012). For wolves, pup survival is dependent on prey biomass (Fuller et al. 2003); in the central Arctic, the distances from dens to caribou can influence their reproductive success (Frame et al. 2008).

Heard and Calef (1986) and Heard and Williams (1992) suggested that tundra wolf populations respond numerically to changing caribou densities. Space-use patterns of barren-ground caribou are density-dependent where the expansion and contraction of their range is a function of the population size of the herd (Simmons et al. 1979, Bergerud et al. 1984, Heard and Calef 1986, Messier et al. 1988, Couterier et al. 1990, Gunn et al. 2012). When caribou are abundant, the herd returns earlier to the southern portions of the summer range and within closer proximity to the denning areas of wolves, thus providing wolves with greater access to prey when the nutritional demands of pups are high. However, as caribou populations decline,

subsequent range contraction could result in the main distribution of the herd being farther from wolf dens for relatively longer periods of the summer (Heard and Williams 1992). Ensuing prey shortages would likely lead to higher pup mortality. Thus, the density of barren-ground caribou may regulate wolf populations denning in the central Arctic (Heard et al. 1996). Although several studies have empirically tested the effects of ungulate availability on wolf population dynamics (Keith 1983, Fuller 1989, Fuller et al. 2003), a numerical response has not been demonstrated for wolves and barren-ground caribou.

The Bathurst herd of barren-ground caribou, estimated at 350,000 ($\pm$ 94,900 SE) animals in 1996, slowly declined through the 1990s and then more rapidly during the 2000s. The herd was estimated at 32,000 ($\pm$ 5,300 SE) animals in 2009, representing a 70% decline over three years (Adamczewski et al. 2009). Survey data now indicate that there are fewer breeding wolves and dens are abandoned earlier in the summer (D. Cluff, unpublished data). The implications of these trends for both the abundance and dynamics of wolf populations in the central Arctic, however, are unclear.

I investigated wolf-caribou dynamics on the summer range of the Bathurst caribou herd. My primary objective was to test for a numerical response of wolves to changes in both the abundance and spatial distribution of caribou. I used a long-term data set of den occupancy and pup recruitment collected on the range of the Bathurst herd during a period of significant decline in caribou abundance. I used indices of wolf abundance to test for a relationship between caribou migration patterns and the population dynamics of dependent wolf populations. I hypothesised that wolves show a numerical response to changing caribou densities where pup survival and ultimately wolf abundance are dependent on the availability of caribou in the

denning areas. I developed stochastic population models to understand how pup recruitment, relative to caribou density, might influence wolf density on the Bathurst summer range.

METHODS

Study Area

I conducted my research within the summer range of the Bathurst caribou herd, an area encompassing approximately 71,000 km² in the Northwest Territories and Nunavut, Canada (Figure 8). As part of ongoing monitoring of the Bathurst herd, satellite collars (Argos and GPS) were used to track the movements of adult female caribou since 1996 (Gunn et al. 2002). The study area was delineated based on the movement patterns of Bathurst collared caribou between 1996-2008 (Adamczewski et al. 2009), and is situated in the Slave Geological Province and Southern Arctic Ecozone (ECG 2012). The region is influenced by a continental Arctic climate and experiences short cold summers and very cold and long winters (ECG 2012). The landscape is comprised of rolling uplands of Canadian Shield rock and lowlands that contain fens, bogs, and tundra lakes (ECG 2012). During the summer months, this area is only accessible by aircraft.

Wolf Population Monitoring

Aerial den surveys

From 1996-2012, the Government of the Northwest Territories conducted annual aerial surveys of wolf dens during early spring (late May/early June) and late summer (mid-late August) to monitor den occupancy, pack size, and pup recruitment on the summer range of the Bathurst caribou herd (Figure 8). Active dens during the spring (i.e., wolves were observed) were checked again in mid or late summer to count pups; these data provided an estimate of recruitment. Over 95 individual wolf dens were recorded.

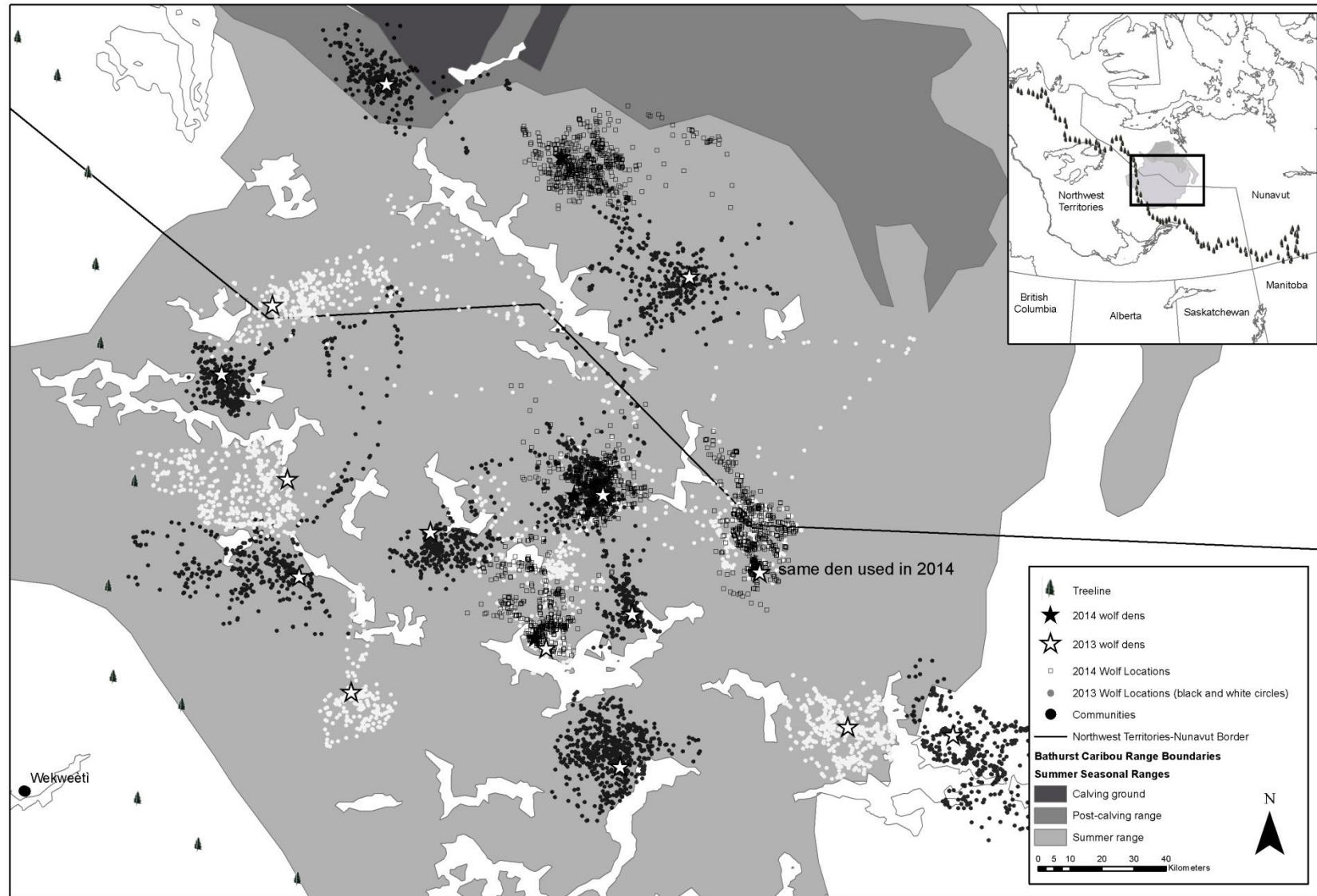


Figure 8. Location of wolf study area on the summer range of the Bathurst barren-ground caribou herd. Boundaries were delineated based on movements of caribou monitored with satellite collars from 1996-2008. Map shows the locations and movements of GPS-collared adult female tundra wolves (circles, $n = 15$, 2013; squares, $n = 4$, 2014) representing individual packs during the 2013 and 2014 denning periods.

Repeated den surveys

Without the ability to track individual wolves, aerial surveys cannot distinguish between 1) total litter loss or 2) the relocation of pups to an alternative den. To help interpret these data, in 2013 and 2014 I conducted repeated aerial and ground-based surveys of wolves with GPS radio collars to document changes in pup recruitment and wolf movement. From 21-24 June 2013, wolves were captured by helicopter net-gunning and chemically immobilized with an intramuscular injection of Telazol[®]; a blood sample was taken from each wolf to test for disease. The breeding female in a pack was targeted for capture because of her role in pack dynamics and caring for pups throughout the denning period. GPS collars were programmed to obtain a location every 1.5 hours (16 locations per day) and were expected to function for 2.25 years (3 summers and 2 winters). All animal handling protocols were approved by the Northwest Territories Wildlife Care Committee in accordance with the Canadian Council on Animal Care Guidelines on the Care and Use of Wildlife.

Movement patterns from the collared female wolves revealed the locations of homesites (den and rendezvous sites), duration of use, and any relocations to another homesite. I used a small fixed-wing aircraft on floats (Aviat Husky) or a helicopter to conduct aerial and ground-based surveys at wolf homesites in early and late summer (early July, mid-August, and early September 2013; July and late August 2014); I recorded pack size and the number of pups for each monitored wolf pack.

The treeless tundra and extended daylight hours provide an opportunity to count pups from the air or from a distance on the ground (Frame et al. 2008). Counts may be biased due to pups remaining in the den or under vegetation during surveys. I addressed this

confounding behavior by conducting multiple ground or aerial surveys at known den sites, radio-tracking the dominant female wolf, or by visiting clusters of GPS locations that may have represented a relocated den or rendezvous site. To minimize disturbance while on the ground, we (myself and assistants) observed wolf dens with a spotting scope or binoculars at a distance of 400-800 m and remained concealed behind boulders or vegetation. We attempted to observe wolf dens downwind to avoid detection. When we were detected, our presence did not evoke an immediate or overt negative behavioural response (e.g., wolf leaving the area). After two hours of observations without any activity, we would howl at the den site to elicit a response. This worked best when the adults were away from the area, as pups typically came out of the den because they were curious and likely hungry.

Wolf Abundance Indices and the Spatial Distribution of Caribou

I used a linear regression and a count model to investigate correlations between wolf population data and density-dependent changes of range use by caribou within the denning areas of wolves. Mean pup recruitment and late summer den occupancy were documented during aerial surveys of wolf dens located on the Bathurst herd's summer range over the period of caribou decline (1996-2012). I used these metrics as response variables that were regressed against the relative contraction in caribou distribution in late-summer (19 July-21 August), a time when caribou typically are within closest proximity to the hunting areas of denning wolves (Chapter 2). I used a negative binomial count model after testing for over-dispersion (conditional variance exceeds the conditional mean) in the den occupancy data (Lindén and Mäntyniemi 2011, Cameron and Trivedi 2013). I used location data from satellite- and GPS-collared adult female caribou collected over a 17-year period (1996-2012; $n = 135$ female caribou) to quantify patterns of range use. From 1996-2008, Argos satellite collars were used exclusively and recorded locations from weekly to daily intervals. From

2008-2013, both GPS and Argos collars were deployed, resulting in the collection of animal locations at daily and hourly intervals.

I used a Geographic Information System (GIS) to measure the Euclidean (closest) distance from the centroid of the Bathurst calving ground to the movement path of each individual caribou in late summer (Chapter 2; 19 July-22 August) and summarized the mean distance across all caribou for each year of the study. Movement paths were delineated based on the late-summer (July 19-August 22; Gunn et al. 2013) locations of collared adult female caribou of the Bathurst herd. Although the distribution of the Bathurst caribou calving ground changed gradually over time (Gunn et al. 2002, 2013), I used Adamczewski et al.'s (2009) delineation and held the centroid constant to measure the relative changes in late-summer distribution of caribou at a broad spatiotemporal scale. I assumed that the distributional patterns of collared caribou were representative of the larger population relative to the scale of analysis; previous studies reported that collared individuals were predictive of caribou densities in the study area (Boulanger et al. 2004, Rescan Environmental Services 2006, Gunn et al. 2013). Statistical analyses were conducted using Stata 12.1 (Statacorp, College Station, Texas, USA). I considered a p value < 0.05 as statistically significant.

Wolf Population Dynamics

I developed a series of stochastic population models (VORTEX 9.99c; Lacy et al. 2013) to understand how pup recruitment might influence the numerical dynamics of wolf populations relative to changes in the abundance of the Bathurst caribou herd. I constructed separate model scenarios using birth rates, recorded as late-summer pup counts, during three levels of caribou abundance: 1) High 1996-2000 (349,000-300,000 animals), 2) Medium 2002-2006 (186,000-128,000 animals), and 3) Low 2009-2012 (32,000-35,000 animals). Parameter estimates were based on demographic data derived from aerial surveys collected

over 17 years (1996-2012; Environment and Natural Resources 2012); professional knowledge and published literature were used when data were not available (Appendix E).

Parameter estimates

Recruitment was derived from late August counts of pups and summarized by model period (mean annual pups/pack). Reproductive success for wolves varies across spatiotemporal scales and may be influenced by a variety of environment and demographic factors (Fuller et al. 2003). White (2000) defines this inherent stochasticity at the population level as process variation; I used this calculation to isolate the process variance ($V_w[R]$; see White 2000) for pup recruitment rates for each model scenario.

I calculated carrying capacity as the number of wolf territories across the summer range of the Bathurst herd (Morris and Doak 2002, Mahoney 2010). Average territory size (km^2) was calculated using 95% fixed-kernel density estimates (Worton 1989) on locations collected from GPS-collared breeding female wolves in 2013. Carrying capacity (K) was estimated as (Equation 1):

$$[1] \quad K = \frac{B_{range}}{\bar{P}_{territory}} \times P_{max}$$

The number of pack territories ($P_{territory}$) was extrapolated across the Bathurst summer range (B_{range} ; km^2) based on an upper limit of observed pack size (P_{max}) recorded during aerial surveys (D. Cluff, unpublished data) and in the literature (Parker 1973).

Wolf density (wolves/1000 km^2) was estimated for each year based on extrapolation using estimates of mean pack size ($\bar{P}_{mean}$) and mean den density ($\bar{D}_{density}$; active dens/1000 km^2) recorded during aerial surveys (Ballard et al. 1987, Fuller and Snow 1988, Ballard et al. 1997, Adams et al. 2008). For each model period, initial population ($N_{initial}$) size was based

on mean wolf density estimates using Equation 2. The initial population was distributed among age-sex classes according to a stable age distribution (Lacy et al. 2013).

$$[2] \quad N_{initial} = \bar{D}_{density} \times \bar{P}_{mean} \times B_{range}$$

Population models were stage-structured, representing three age classes: pups (0-1 yrs), yearlings/subadults (1-2 yrs), and adults (> 2 yrs) (Kelly et al. 1999). Wolf survival likely varied among age classes (Fuller et al. 2003); however, mortality rates and the degree of variation are difficult to estimate for tundra wolves. Generally, wolf populations are limited or regulated by several factors including ungulate biomass (Keith 1983, Fuller 1989, Boertje and Stephenson 1992), disease (Bailey et al. 1995, Fuller et al. 2003, Kreeger 2003), and human-caused mortality (Fuller 1989, Fuller et al. 2003). For this population, wolf harvest is likely low during summer due to poor fur condition (wolves are harvested mainly for pelts), in addition to the remoteness and inaccessibility of the area. Human-caused mortality is likely higher during winter as wolves move within closer proximity to communities and a winter ice road when they migrate with the Bathurst caribou herd below treeline. Incentive programs are in place to increase the level of harvest of wolves on the Bathurst range (Wek'èezhii Renewable Resources Board 2013, Adamczewski et al. 2014). Diseases such as canine distemper and canine parvovirus have been documented in adult wolves in the study area, although the influence of these diseases at the population level has not been established (Stasiak et al. 2014). With this uncertainty, I used conservative estimates of natural wolf mortality based on rates reported by Fuller et al. (2003) for unexploited populations and held parameter values constant across all models. I assumed that mortality rates for pups were higher and more variable than those of yearlings/subadults, and once wolves reached > 2 years of age, their probability of survival increased relative to the earlier age classes (Kelly et al. 1999, Chapron et al. 2003, Mahoney 2010).

Other demographic parameters were inferred from the published literature, but held constant across all models (Appendix E). As with most canids, wolves typically start breeding at approximately 2-3 years of age. The maximum breeding age was not clear. Older wolves (> 4 or 5 years) may be replaced by younger breeders (D. Cluff, pers comm), and as such, I assumed the maximum breeding age to be 8 years. Only 50% of males and females were available to breed each year to account for pack breeding dynamics; sex ratio at birth is unknown and was assumed at parity (Kelly et al. 1999). Population models did not account for complex socio-behavioural processes such as age of dispersal, mate choice, or lone wolves not associated with a breeding pack. While these factors can influence the persistence of wolf populations, rates can vary substantially both spatially and temporally due to a variety of environmental factors (Fuller et al. 2003). Few data were available to accurately describe these factors for wolves in the central Arctic.

I used the population models to project wolf population trajectories over 25 years, a period that allowed me to evaluate the influence of observed changes in pup recruitment on wolf population dynamics over a feasible management planning horizon. Simulations were run 10,000 times for each model scenario. I summarized changes in relative abundance (%) and used the geometric mean to summarize stochastic population growth (λ) across model simulations.

To provide insight into wolf population dynamics over the period of the decline of the Bathurst caribou herd, I ran model scenarios over 3 periods that corresponded to changes in abundance of the Bathurst caribou herd (High, Medium, and Low). I used recruitment rates calculated during the previous model scenarios, but ran these scenarios at slightly larger intervals (1996-2002; 2003-2008; 2009-2014) to represent wolf population dynamics and a crude estimate of wolf density over the period of Bathurst caribou population decline (1996-

2014). I used the initial population size for subsequent temporal models based on the final population that was predicted from the previous simulation (i.e., the final population size in scenario A was used as the initial population size in scenario B and so forth). I compared the population estimates from the population models with those extrapolated from density estimates of wolves collected during aerial surveys (Appendix F).

RESULTS

Wolf Population Monitoring on the Bathurst Summer Range

Aerial survey results 1996-2012

In the late 1990s, pup counts collected during aerial surveys in August consistently averaged ≥ 3 pups/pack annually. Pup recruitment declined from 2003-2012. During the early-mid 2000s, rates were more variable, but decreased compared to observations in the 1990s. By 2010, pup counts consistently averaged < 2 pups/pack, although high den abandonment resulted in small sample sizes (Figure 9; $n = 1-2$ active dens in late-summer; 2009-2012).

Similar to pup recruitment, the proportion of dens remaining active in late summer decreased over the study period (Figure 9). From 1996-2006, approximately half of the dens occupied during spring were still active in late summer ($\bar{X} = 53\% \pm 5$ SE). From 2007-2012, the rate of den abandonment increased considerably and only $9 \pm 2\%$ of the dens occupied in spring ($\bar{X} = 21 \pm 0.1$) were still active in late August ($\bar{X} = 2 \pm 0.4$).

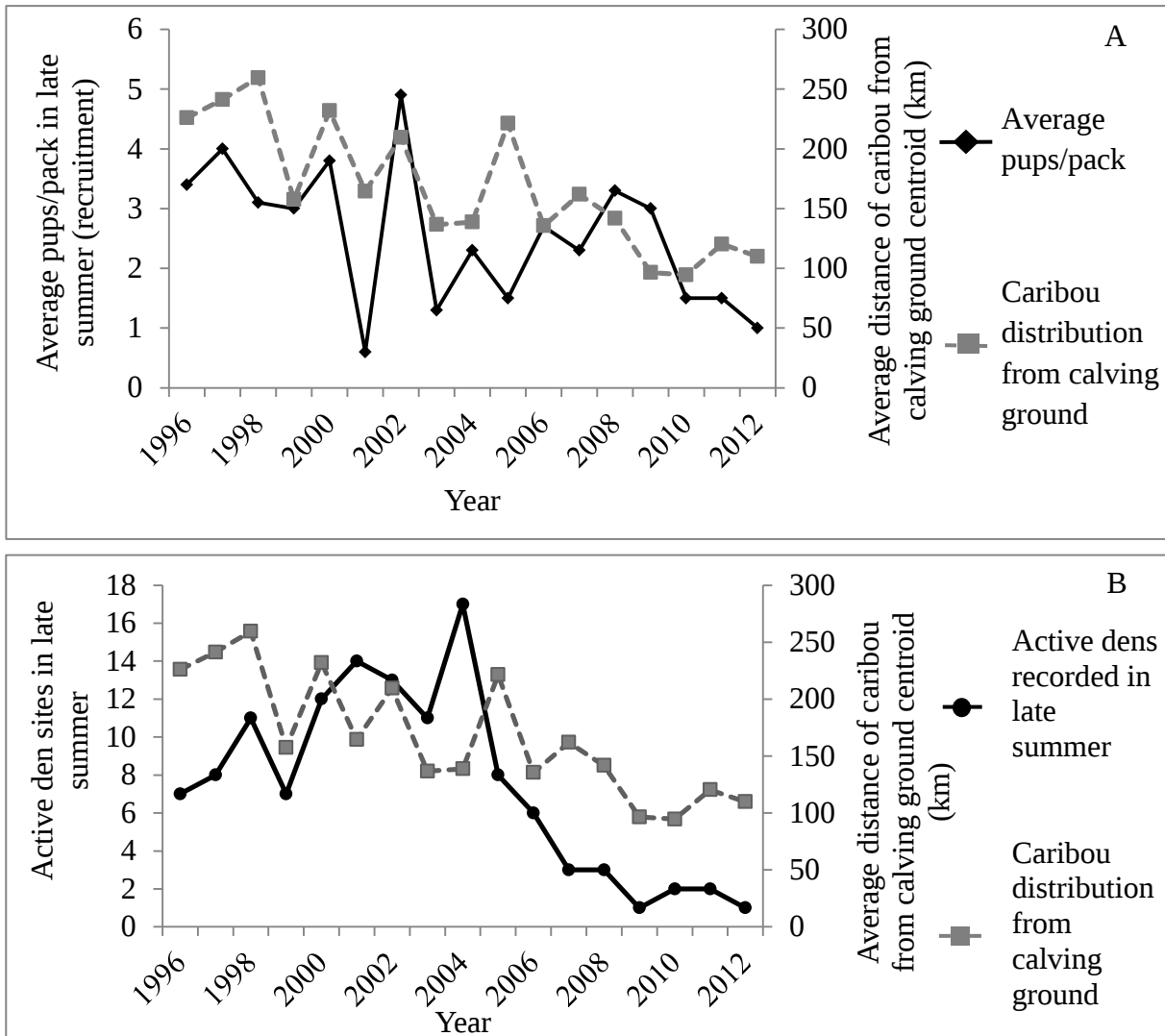


Figure 9. Temporal patterns for A) wolf pup recruitment and B) late-summer den occupancy recorded during aerial surveys in relation to the relative late-summer distribution of caribou from the calving ground (1996-2012). For each year, the average Euclidean distance was measured from the centroid of the Bathurst calving ground (0 km) to caribou movement paths (19 July-22August). This measure was used to calculate the relative distribution of satellite-collared adult female caribou in late summer.

Repeated Surveys during the 2013 and 2014 Denning Periods

From 21-24 June 2013, 16 female wolves were captured, each representing individual packs; 15 were breeding (lactating) females and 1 was a subadult (non-lactating) female. The subadult female dispersed out of the study area approximately 2 weeks after capture and was excluded from the analysis. Over the 2013 and 2014 denning periods, I monitored 27 wolf packs (17 and 10, respectively), 15 of which were monitored via a GPS-collared adult female

(16 and 4 collared wolves in 2013 and 2014, respectively). I conducted over 204 aerial checks to track wolf packs and spent > 111 hours observing wolf dens/rendezvous sites on the ground during 66 separate field visits.

During the 2013 denning period, all 15 GPS-collared adult females presented similar movement patterns in late June/early July, restricting their movements around their respective den sites, suggesting that pups were present. I obtained pup counts for 12 of the 15 monitored packs. Five of the GPS-monitored packs lost their pups by the end of July and 1 pack lost its pups by the end of August; thus only 9 packs with a GPS-collared female were observed with pups during my final survey in September (Table 4). I opportunistically observed 2 more packs during survey flights in August and September, and recorded pack size and composition. The mean number of pups/pack declined throughout the denning period from $2.9 (\pm 0.31 \text{ SE})$ in July, $2.0 (\pm 0.40)$ in August, and $1.7 (\pm 0.37)$ in early September (Table 4). The mean number of wolves per pack was $5.1 (\pm 0.5)$ and typically consisted of the breeding pair with one other adult or sub-adult and the pups. The largest pack consisted of 9 wolves (3 adults, 1 yearling, and 5 pups), although only 1 of the 5 pups in that pack survived through to September. Six of the monitored packs relocated to nearby den or rendezvous site during the study period. Only 3 packs remained at their respective whelping den throughout the denning period (early September); thus, litter loss accounted for 50% of observed den abandonment (Table 4).

After incurring wolf mortality and collar loss, I monitored 4 wolf packs via GPS collar during the summer of 2014. An additional 4 packs were located by revisiting previously used den sites from 2013, and 2 packs were located by checking den sites

occupied in previous years (prior to 2013). I conducted field surveys in early July and late August and obtained pup counts for 6 packs. Only 2 of the 4 GPS-collared females bred in 2014, and only 1 pack was observed with pups in late August. The mean number of pups/den declined throughout the denning period from 2.6 ($\pm$ 0.6) in early July to 1.8 ($\pm$ 0.7) in late August (Table 4). The mean number of wolves per pack was 4.8 ($\pm$ 0.9; Table 4). Pack structure was consistent with 2013 where the breeding pair was either alone or accompanied by one other adult or sub-adult wolf (usually female). The largest pack size was 10 wolves, with 6 adults and 4 pups. Similar to 2013, only 4 monitored packs remained at their whelping den throughout the denning period. Two wolf packs that had pups in July, abandoned their dens before the August surveys; these packs did not have a GPS-collared adult; as such, I censored these data from the recruitment estimate.

Table 4. Summary results from repeated wolf den surveys during the 2013 and 2014 denning periods on the summer range of the Bathurst caribou herd, Northwest Territories and Nunavut, Canada.

Year	# Packs Monitored (# Packs with GPS-collared adult female)	Mean Adults/Pack (SE)	Early ¹ Summer		Late ² Summer	
			Mean Pups/Pack (SE)	Packs (n)	Mean Pups/Pack (SE)	Packs (n)
2013	17 (15)	2.5 (0.12)	2.9 (0.31)	13	1.7 (0.37)	17
2014	10 (4)	2.8 (0.39)	2.5 (0.8)	6	1.8 (0.69)	8
Pooled	27	2.6 (0.16)	2.8 (0.33)	19	1.8 (0.33)	25

¹ early July

² late August-early September

Wolf-Caribou Dynamics

The seasonal distribution of caribou changed significantly over the course of the study. From 1996-2000, the distances of collared caribou from the Bathurst calving grounds averaged 223 km ($\pm$ 17.4 km SE) when population size of the herd was > 300,000 animals.

As the herd declined, however, the late-summer range contracted northwards towards the calving ground; the relative distances of satellite- and GPS-collared caribou averaged 158 km (± 21.1) and 105 km (± 6.0) from the calving ground during Medium (2002-2006) and Low (2009-2012) periods, respectively (Figure 9).

Both linear and the negative binomial regression models revealed significant relationships between pup recruitment and late summer den occupancy and the late-summer distribution of caribou (Figure 10). As the area of caribou range in late summer increased south from the calving grounds, concurrent with a greater density of caribou, pup recruitment also increased (Figure 10A; $F = 7.70$, $df = (1, 15)$, $R^2 = 0.28$, $p = 0.014$). The negative binomial count model showed a similar relationship: rates of den abandonment increased as the late-summer distribution of caribou contracted northwards towards the Bathurst calving ground (Figure 10B; $\chi^2 = 5.90$, $df = 1$, $p = 0.015$).

Wolf Population Dynamics

With an average seasonal range of 961 km² (± 137 km² SE, $n = 13$, 2013-2014), I estimated that approximately 74 wolf packs could occupy the 71,000 km² Bathurst summer range. I used an upper limit of 7 wolves per pack (Parker 1973), which provided an estimated carrying capacity of approximately 517 wolves or a density of 7.28 wolves/1000 km² (Table 5). I extrapolated estimates of wolf density based on observed average pack size and den density recorded during aerial surveys (Table 5). When caribou abundance was high in the late 1990s, I estimated the wolf population at 497 individuals, slightly below the spatially derived estimate of carrying capacity. The estimated wolf population declined to 295 and 177 individuals during Medium and Low periods of caribou abundance, respectively (Table 5).

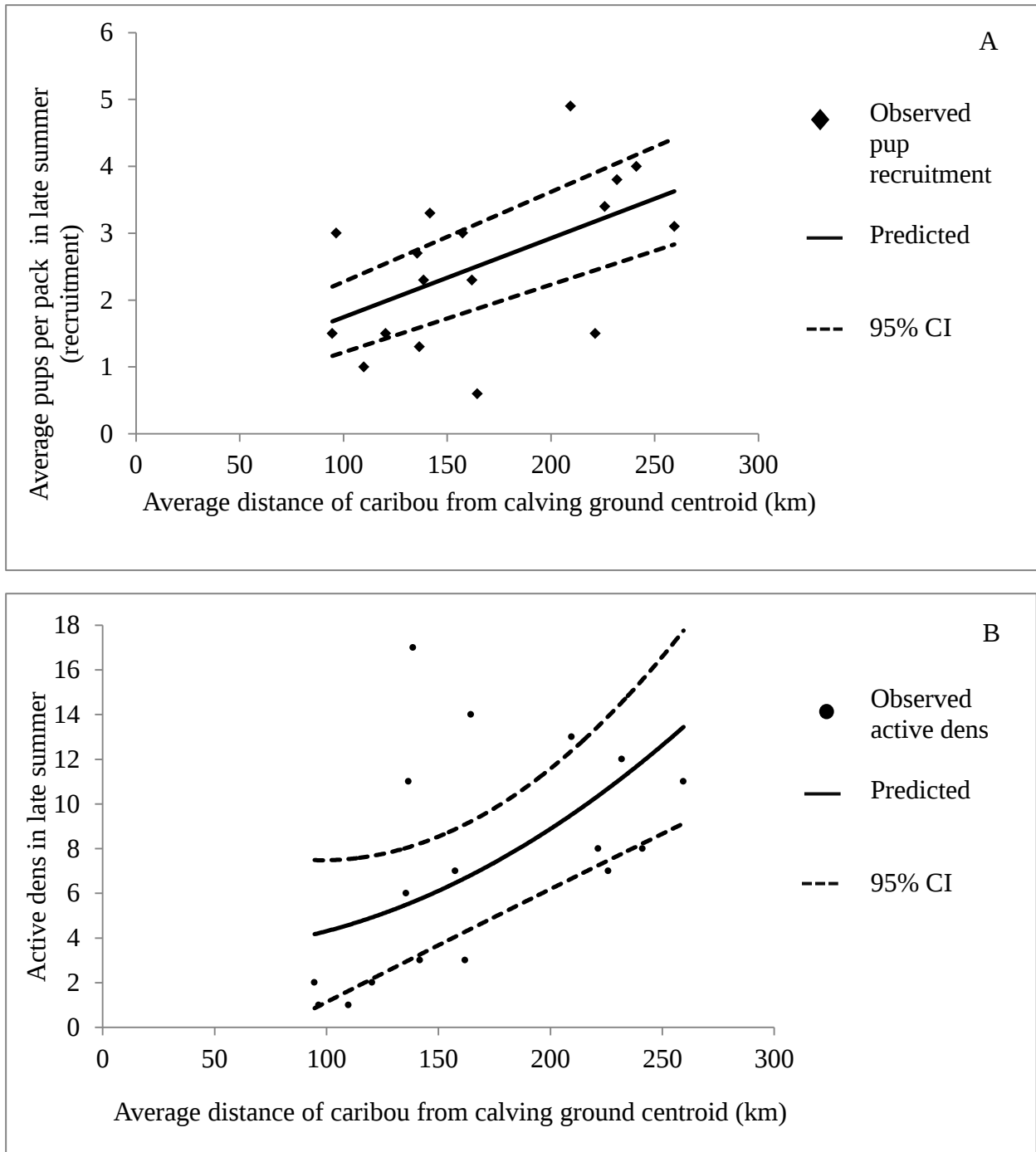


Figure 10. Spatial relationships between late-summer A) wolf pup counts, and B) den occupancy and late-summer distribution of adult female caribou from the Bathurst herd using a linear and negative binomial regression model, respectively. For each year, the average Euclidean distance was measured from the centroid of the Bathurst calving ground (0 km) to caribou movement paths (19 July-22 August). This measure was used to calculate the relative distribution of satellite-collared adult female caribou in late summer.

Table 5. Model scenarios and parameters used to assess the population dynamics of tundra wolves relative to changing caribou densities. Parameter estimates were based on observed wolf population data recorded during aerial surveys on the Bathurst caribou summer range, Northwest Territories, Canada, 1996-2012.

Model Parameters	A: High caribou 1996-2000	B: Medium Caribou 2002-2006	C: Low Caribou 2008-2012
Den density (dens/1000 km ² ; SE)	1.10 (0.06)	0.83 (0.10)	0.62 (0.05)
Average pack size (adults/sub-adults + pups; SE)	6.4 (0.2)	5.0 (0.7)	4.0 (1.0)
Wolf density (wolves/1000 km ²)	7.0	4.2	2.5
Spatially derived carrying capacity (# of individuals)	517	517	517
Initial population size (# of individuals)	497	295	177
Annual pooled mean pup recruitment (pups/pack) and process variance ($V_w[R]$)	3.46 (0.42)	2.54 (1.30)	1.75 (0.79)
Mortality (%) (SD) ¹	Adults (> 2 yrs)	Subadults (< 2 yrs)	Pups (< 1 yr)
	20 (5)	25 (5)	35 (10)

¹Mortality rates estimated from literature (Fuller et al. 2003).

From 1996-2000, pooled mean annual pup recruitment (R) was 3.46 pups/pack ($V_w[R] = 0.42$). Model simulation revealed a stable positive growth rate ($\lambda = 1.03$) and the relative abundance of the wolf population was similar after 25 years ($\Delta \sim 5\%$; Figure 11). From 2002-2006, pooled mean annual recruitment decreased to 2.54 pups/pack ($V_w[R] = 1.30$), resulting in negative population growth ($\lambda = 0.99$) and a 33% decrease in relative abundance of the wolf population over a 25-year period (Figure 11). From 2009-2012, pooled mean annual recruitment decreased further to 1.75 pups/pack ($V_w[R] = 0.79$), the

trajectory of the wolf population declined more rapidly ($\lambda = 0.94$), and I estimated a 95% decrease in relative abundance of the tundra wolf population after 25 years.

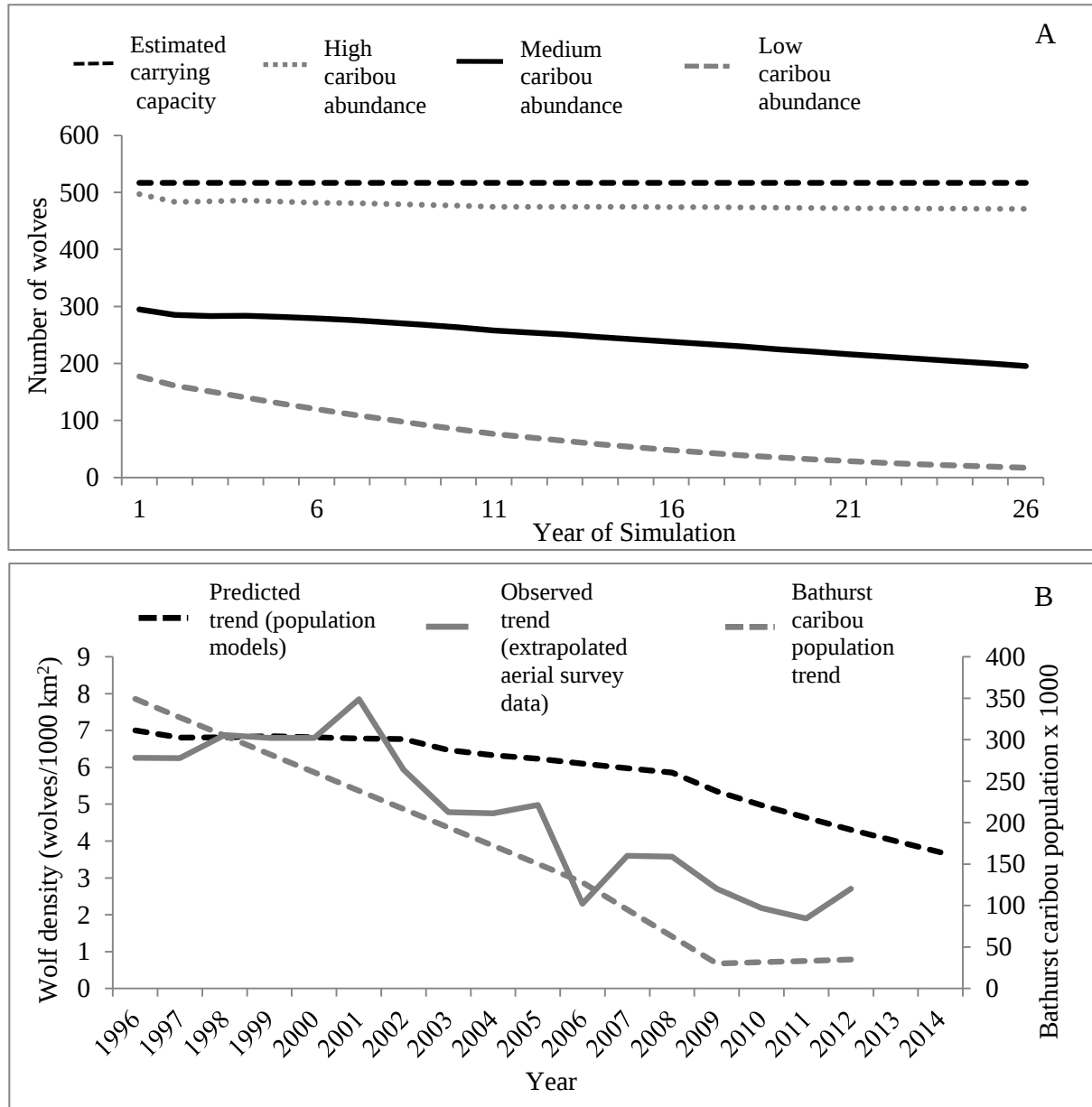


Figure 11. A) Estimated population trajectories for Bathurst wolves using a stochastic population model. Model parameters were based on pup recruitment and wolf density estimates observed during three levels of caribou abundance (Table 5). B) Estimated trends in wolf density on the Bathurst caribou summer range over the period of caribou decline 1996-2014. Wolf density estimates were derived using pooled mean pup recruitment rates observed during periods of High, Medium, and Low caribou abundance (Table 5). Observed trend was based on estimates of den density and average pack size recorded annually during aerial surveys. Population estimates for the Bathurst caribou herd were conducted in 1996, 2003, 2006, 2009, and 2012.

The stochastic population model represented wolf population dynamics over the period when the abundance of the Bathurst herd declined by > 90% (1996-2014). I estimated initial wolf density at 7.0 wolves/1000 km² in the mid-1990s and that density remained stable at 6.8 wolves/1000 km² by 2002. From 2003-2008, modelled wolf density decreased slightly to 6.0 wolves/1000 km² and more substantially to 3.7 wolves/1000 km² by 2014 (Figure 11). In comparison, results from extrapolation of aerial survey data suggested a density of 6.10 wolves/1000 km² in 1996 and then 5.93, 3.57, and 2.71 wolves/1000 km² in 2002, 2008, and 2012, respectively (Figure 11).

I iteratively decreased pup recruitment to assess the sensitivity of the population model to uncertainty in this estimated parameter. Population trajectories increased when pup recruitment was > 3.0 pups/den and decreased when recruitment was < 2.5 pups/den (Appendix G).

DISCUSSION

I investigated the co-varying population dynamics of wolves and barren-ground caribou using long-term data sets collected over a period when the Bathurst herd experienced a > 90% decline in abundance. My results corroborate previous studies of wolves in North America (Keith 1983, Fuller 1989, Boertje and Stephenson 1992, Fuller et al. 2003) reporting that ungulate biomass strongly influences wolf population dynamics. Repeated surveys of wolf packs over the 2013 and 2014 denning periods allowed me to reliably estimate pup recruitment and pack movement patterns during a period of low caribou abundance. In contrast, aerial surveys designed to count adults and pups (1996-2012) at den sites may underestimate pack size and annual recruitment because some adults may abandon the den

and/or not all pups could be visible from the air. However, estimates of pack size and recruitment rates were consistent between both survey methods.

I documented high rates of den abandonment and low pup recruitment for packs monitored with a GPS collar. Although pup productivity and survival varied among wolf packs, annual mean recruitment was < 2 pups/pack, suggesting that young-of-the-year were not replacing adults in the population. Litter loss accounted for almost half of observed den abandonment and typically occurred in July, within or just following the period of spatial separation between breeding wolves and the main distribution of caribou (Chapter 2). Pup mortality and occurrences of den abandonment decreased in August and most pups observed in September were also counted during a reconnaissance survey in early December of 2013 (M. Klaczek, unpublished data).

I was unable to determine specific causes of pup mortality, as carcasses were not recovered at den sites. However, the large distances between wolf dens and the majority of caribou during post-calving and early summer seasons (Chapter 2), the rate of litter loss that occurred during these periods, and the relatively few incidental sightings of caribou or other ungulate prey in the denning areas suggest that low prey availability was a regulating factor for this population. In addition to direct starvation among pups, a lack of nutrition could increase intraspecific strife, predation, and disease (Mech and Boitani 2003, Kreeger 2003). I did not observe any aggressive behaviour among wolves during surveys and recorded only a few occurrences ($n = 3$) of wolf-grizzly bear (*Ursus arctos*) interactions within the vicinity (1-2 km) of den sites. Adult wolves in my study have been exposed to canine parvovirus and canine distemper, but exposure of such diseases in the adult population has proven challenging to link to pup survival. Stasiak et al. (2014), for example, did not find any

correlation between the sero-prevalence rates in adult wolves and variation in rates of wolf pup recruitment or den abandonment. Nevertheless, food shortages could increase the effect of such diseases in the population and contribute to lower pup survival (Kreeger 2003).

The relocation of pups to a new den or rendezvous site accounted for half the observed den abandonment in 2013 and 2014. These findings do not necessarily suggest that homesite shifts have increased on the Bathurst range over the study period. In the late 1990s, when pup recruitment rates were relatively high, approximately half of the whelping dens were abandoned prior to the late-August pup count surveys. Also, pup relocation to a new den or rendezvous site has been documented for other populations of wolves (Joslin 1966, Chapman 1977, Mech and Boitani 2003, Packard 2003). The factors that influence the relocation of pups to different homesites are not well understood. Disturbance due to research activities is possible, but human actions causing packs to abandon den sites must be generally more intrusive (Chapman 1977, Frame et al. 2007), including the capture and handling of pups (Argue et al. 2008). Frame et al. (2007) tested a disturbance treatment in my study area where an observer approached the immediate vicinity of the den. They found that packs relocated after a second disturbance event. In my study, we were detected occasionally by adult wolves during ground-based surveys, but at a considerable distance from den sites (400-700 m) and these events were relatively short in duration (20-30 minutes after detection). In most cases, our presence did not appear to evoke an overt alarm response by adults or pups. Also, I did not detect a trend in den abandonment/pack relocation immediately following aerial or ground-based surveys. In 2013, the median date of ground visits to wolf packs that relocated pups was 7 July, while the median date of abandonment was 21 July. In 2014, the 1 pack that relocated pups did so prior to surveys in late June.

Indices of Wolf Abundance and the Spatial Distribution of Caribou

Some have hypothesized that density-dependent range expansion and contraction by caribou may drive the reproductive success of dependent wolf populations (Heard and Calef 1986, Heard and Williams 1992). In my study area, most wolves den within the southern portions of the Bathurst caribou summer range, where distances between den sites and the main distribution of caribou average between 250 and 180 km during the calving and post-calving periods, respectively (Chapter 2). The seasonal ranges of caribou from post-calving through to fall rut contracted closer to the calving grounds as the herd declined. Wolves did not show a similar behavioural response by shifting den sites closer to the contracted ranges (Chapter 2). As such, the period of spatial separation would have increased for breeding wolves as caribou numbers declined.

As the nutritional demands of the pups increase during the summer, so can the distances that wolves need to travel to secure food; low prey availability may result in food shortages leading to lower pup survival (Heard and William 1992, Frame et al. 2008). Results from the regression analysis revealed significant positive correlations between indices of wolf abundance and the late-summer distribution of caribou. Together, model results showed that density-dependent space-use patterns of Bathurst caribou had a regulating effect on this population of tundra wolves (Figure 10).

Wolf Population Dynamics

My population model, while simple, was based largely on empirical data collected during a long-term monitoring program of the tundra wolf population on the Bathurst range. I used measures of pack size and pup recruitment as the key parameters to describe wolf population dynamics over a 18-year period of caribou decline. Where data were not available, I inferred essential model parameters from the published literature, and held these

rates constant across model scenarios that represented changes in the abundance of caribou. In particular, I used liberal survival estimates (80% for adults) documented in unexploited wolf populations (Fuller et al. 2003). Thus, the population estimates for wolves are likely inflated, as I would assume that mortality rates would increase as the Bathurst caribou herd declined and competition for limited resources resulted in greater levels of intraspecific strife and starvation (Eberhardt 2002, Mech and Boitani 2003). Adult mortality across all models was held constant at 20%, yet I recorded a 25% mortality rate (4 of 16 wolves) in the GPS-collared adult female wolves from 2013. Furthermore, my models did not account for complex social behaviours such as dispersal, mate choice and lone wolves not associated with a pack. Other studies reported that wolf populations were typically composed of 10-15% lone wolves (Stephenson 1978, Fuller and Snow 1988, Fuller et al. 2003). I assumed that dispersal and the successful colonization of new wolf packs onto the Bathurst range was limited by competition for limited resources.

Fuller (1989) and Mech et al. (1998) noted that annual change in wolf populations was highly correlated with the average number of pups per pack from the previous fall. Results of the population model corroborate their findings and illustrate that even slight changes in pup recruitment can have significant effects on the density and ultimately the persistence of wolf populations. I used two methods to estimate wolf density on the Bathurst range. Extrapolation of aerial survey data and stochastic population models both provided crude approximations of wolf population trend and density, but also provided consistently similar results. During the late 1990s, wolf populations remained stable and densities were consistent around 6.8 wolves/1000 km². As the Bathurst herd declined during the 2000s, wolf density also decreased. My population models projected a 48% decrease in wolf density

over the study period. Density gradually decreased through the mid-2000s, above 6.0 wolves/1000 km², and then a more substantive decrease after 2008, below 4.0 wolves/1000 km² by 2014. My extrapolation using aerial survey data suggests a 57% decline. Wolf density decreased more dramatically throughout the 2000s and by 2012 I estimated a wolf density of approximately 2.7 wolves/1000 km². These results suggest a relatively strong numerical response by wolves to changing densities of caribou and compliment findings by Keith (1983) and Fuller (1989), who report linear correlations between wolf density and prey abundance (Mech and Peterson 2003).

Records of wolf density on barren-ground caribou range vary considerably in the literature. My estimates are similar to those reported on the Bathurst range by Kelsall (1968; > 7 wolves/1000 km² in the 1950s); Cluff (in prep; 6.6 wolves/1000 km² in 2006); and Mattson et al. (5-10 wolves/1000 km² in 2006). My estimates are considerably lower than those of Kuyt (1969) and Parker (1973), who reported wolf densities of 57 and 49 wolves/1000 km² on the winter ranges of the Bathurst, Beverly, and Qamanirjuaq herds during the 1960s and 1970s. Kuyt (1969) suggested that wolf densities during winter were locally or temporally concentrated around areas with high densities of caribou, and that such observations lead to inaccurate estimates of density when extrapolated across the entire caribou range. In my study, I tracked GPS-collared females during a winter reconnaissance flight in December 2013 and found that packs were observed in the same family groups as recorded during the summer denning period (n = 8 packs; M. Klaczek, unpublished data). The methods I used to estimate wolf densities on the Bathurst range are appropriate because of the minimal spatial overlap between packs during the summer denning period and the lack of a prey-based bias in distribution (Mech 1970, Hayes and Harestad 2000).

CONCLUSION

In most areas of North America, the survival of wolf pups during summer is high due to the seasonal increase in food abundance (Mech et al. 1998, Fuller et al 2003). This is not the case in the central Arctic, given the preponderance of caribou in the wolf diet and how caribou biomass decreases significantly during a period of spatial separation from many wolf denning areas. My results suggest that pup recruitment is low on the Bathurst range. These findings are consistent with those reported by Boertje and Stephenson (1992) and Frame et al. (2008), who suggest that ungulate biomass is the key driver influencing wolf reproductive success. While small mammals, migrating waterfowl, and even fish (D. Cluff, unpublished data) are consumed by denning wolves in my study area, caribou remain a vital food source (Kuyt 1972, Williams 1990) and there is no evidence to suggest that wolves have altered their diet in response to changing caribou densities. Results from a diet analysis of wolf scats collected from den sites on the Bathurst caribou range during 2013 suggested that caribou comprised approximately 71% of the diet of wolves that I monitored (Appendix H).

At broader scales, my results clearly illustrate the influence of caribou space-use patterns on wolf population dynamics. The temporal trends of decreasing pup recruitment and increasing den abandonment were apparent over the period of caribou decline. I also demonstrated that density-dependent range use by caribou correlated with the indices of wolf abundance. Together, these results suggest a mechanism for population regulation where the breeding success of the wolf population is limited by variation in the seasonal timing of migration patterns of caribou in addition to changes in abundance (Heard and Williams 1992, Heard et al. 1996, Frame et al. 2008).

The wolf-caribou dynamics I report in the central Arctic, as have other researchers (Kuyt 1969, Parker 1973, Heard and Calef 1986, Heard and Williams 1992, Walton et al. 2001, Musiani et al. 2007, Frame et al. 2008), are different than those documented in other study areas where alternative prey, specifically moose, occur at relatively high densities and can sustain wolves as caribou populations decline (Van Ballenberghe 1985, Bergerud and Elliot 1986, Ballard et al. 1987, 1997, Jenkins and Barten 2005, Kuzyk et al. 2006, Bergerud 2007, Serrouya et al. 2011, Hervieux et al. 2014). Wolves in the Arctic study area have amongst the largest home ranges in North America (Walton et al. 2001) being 10 times greater than those documented on barren-ground caribou range in parts of Alaska, where in most years wolves are non-migratory because moose occur in sufficient densities to provide an adequate alternate prey source (Ballard et al. 1987, 1997). Wolf densities in my study area remain low, relative to Alaska and the southern boreal forest, due to limited prey in the denning areas and resulting high rates of pup mortality (Thomas 1995).

CHAPTER 4: HUNTING STRATEGIES OF WOLVES DENNING ON BARREN-GROUND CARIBOU RANGE: LINKING MOVEMENT RESPONSES TO PUP SURVIVAL DURING LOW CARIBOU ABUNDANCE

ABSTRACT

Wolves that den on the tundra of the central Canadian Arctic prey primarily on barren-ground caribou. Prey may be scarce during a period when caribou migrate north to their calving and post-calving ranges, while most wolves remain farther south near their den sites. I investigated the hunting strategies of wolves over the summer denning period, when the collaborative effort of the pack focuses on finding a sufficient quantity of prey to sustain their growing pups. Barren-ground caribou of the Bathurst herd are the primary ungulate in the study area; numbers, however, were extremely low following a severe population decline. I hypothesized that wolves would respond functionally to a less abundant prey base by searching larger areas. These increased movements would correlate with litter loss if prey were unattainable. I used frequent and accurate location data collected from breeding female wolves monitored with GPS collars to document their hunting movements. I compared daily distances travelled from den sites to field data describing pup recruitment and used speed of movement and path sinuosity as indices of wolf hunting behaviour. Wolves denning farther from the Bathurst calving grounds made slower and more linear movements that were characteristic of searching patchy distributions of prey. Wolves that recruited pups remained relatively closer to their den, hunting in what I assumed were higher-quality habitats for locating caribou, whereas wolves that would lose their pups (total litter loss) made more linear movements searching farther from their den for more distant prey. My results suggest that caribou densities were low within the summer territories of some packs and these wolves could not respond functionally to prey shortages. On barren-ground caribou range, prey availability for wolves during early summer is critical for pup survival. Range contraction,

as a result of declining caribou numbers, may delay the return of caribou to the denning ranges, thus reducing wolf population growth.

INTRODUCTION

Home range for the gray wolf (*Canis lupus*) is broadly defined as the area needed to maintain its annual biological requirements, including seasonal feeding habitats, security, and denning, all of which influence the ability to successfully raise young (Paquet and Carbyn 2003). For many populations of wolves, the availability of ungulate prey is the primary factor that influences range size (Fuller et al. 2003, Paquet and Carbyn 2003). Such spatial dynamics can differ greatly among wolf populations, as is evident by their ability to occupy a wide range of habitats across their global distribution (Fuller et al. 2003). As an extreme example of adaptability to prey biomass, the movement and range occupancy patterns of tundra wolves reveal a distinct migratory behaviour that corresponds to the seasonal movements of barren-ground caribou (*Rangifer tarandus groenlandicus*; Kuyt 1972, Parker 1973, Walton et al. 2001, Hansen et al. 2013). These wolves spend winters following caribou within the taiga and move north onto the tundra for denning in spring (Walton et al. 2001, Hansen et al. 2013). Accordingly, tundra wolves have amongst the largest recorded home range among gray wolf populations (Walton et al. 2001, Musiani et al 2007).

Tundra wolves show strong fidelity to den sites, revisiting the same den or similar summer territory each year (Walton et al. 2001, M. Klaczek, unpublished data). Pups are born between late May and early June (Frame et al. 2008) and remain within close proximity of the den until mid-September when they are old enough to travel long distances with the pack. As such, adult wolves remain in close proximity to their pups throughout the denning period, leaving only occasionally to hunt for prey (Williams 1990, Walton et al. 2001, Frame et al. 2004).

For wolves denning on barren-ground caribou range, prey availability may be low in the vicinity of the den for a period each summer. Most caribou migrate to their calving and post-calving ranges near the Arctic coast, while wolves typically den farther south, closer to treeline. Scattered groups of caribou may remain close to the denning area throughout the summer (Banfield 1954, Parker 1973, Miller and Broughton 1974, Darby 1978 and 1979, Heard et al. 1996), and some breeding wolves may seek prey through long-distance movements away from their dens (Walton et al. 2001, Frame et al. 2004). These wolves typically can travel 40-50 km outside of their denning range in search of caribou located to the north (Walton et al. 2001, Frame et al. 2004). Such movements are unique when compared to most gray wolf populations, as extraterritorial movements are typically associated with dispersal in lower age classes and not among reproductive adults during the denning period (Fritts and Mech 1981, Messier 1985). On barren-ground caribou range, however, these movements suggest that prey are locally scarce within the summer territories of some packs, even when the abundance of caribou is relatively high across the broader distribution of the population (Walton et al. 2001; Frame et al. 2004, 2008).

Estimated at over 300,000 animals in the late 1990s, the Bathurst caribou herd has declined drastically over the past two decades. Estimates in 2014 indicate the population has decreased below 30,000 animals (Adamczewski et al. 2014), representing a > 90% decline in abundance. At large spatiotemporal scales, range use patterns of barren-ground caribou, including the extent of distribution, are density-dependent (Simmons et al. 1979, Bergerud et al. 1984, Heard and Calef 1986, Messier et al. 1988, Couturier et al. 1990, Gunn et al. 2012). Decreasing caribou densities result in caribou returning later to the denning area of tundra wolves (Chapter 2). Heard and Williams (1992) suggested that these co-occurring

distribution patterns result in a numerical response of wolf populations to caribou abundance because pup survival depends on caribou availability (Frame et al. 2008).

Adult wolves rely on body reserves to meet daily energetic requirements during times of prey scarcity (Peterson and Ciucci 2003), but pup survival is dependent on prey biomass. Long-distance hunting movements result in reduced nutrition for pups as adult wolves spend more time away from their den hunting and the feeding interval and digestion of prey increases, resulting in less food transferred to the pups. The reproductive success of wolves has been linked to the distribution of migratory caribou (Frame et al. 2008, Chapter 2). However, few data are available describing the behavioural response of migratory wolves to inter-annual decreases in the density of their prey and the subsequent implications of such movements on pup survival.

Contemporary methods of studying animal movement have allowed researchers to examine the ecological processes and life-history strategies of wide-ranging species in more detail than previously possible (Creel et al. 2005, Laundre 2010, DeCesare 2012, Hansen et al. 2013). In particular, the advent of global positioning system (GPS) technology has allowed for the collection of large quantities of frequent and accurate location data for individual animals. Step-lengths and turning angles along an animal's path can be analyzed and then assigned to a behavioural state (Fortin et al. 2005) which includes rest, excursions, and hunting (Moorcroft 2012).

I used measures of movement to investigate the behavioural responses of wolves to low caribou abundance during the denning period. I hypothesized that hunting patterns of wolves would be influenced by prey densities within their respective denning areas. I

compared the distances that breeding wolves travelled from their respective den or rendezvous sites during hunting forays to data describing pup survival. I expected long-distance movements to correlate with a higher likelihood of litter loss. I related the broad-scale distribution of caribou, increasing energetic demands of pups, and pup recruitment to indices of hunting behavior. Hunting behaviour is typically associated with shorter step lengths and high path sinuosity (Wiens et al. 1995, Williamson-Ehlers et al. 2014), while more linear movements (larger step lengths and low sinuosity) are associated with moving long distances in search of prey (Crist et al. 1992). I predicted that given low densities of caribou, wolves would demonstrate more linear movements and longer step lengths when pursuing more distant prey; these movements would correlate with litter loss if prey were unattainable.

METHODS

Study Area

I studied wolf-movement dynamics on the summer range of the Bathurst caribou herd in the Northwest Territories and Nunavut, Canada (Figure 12). The study area was defined by the locations of satellite-collared adult female caribou in the Bathurst herd from 1997-2005 (Gunn et al. 2002, Adamczewski et al. 2009). The area encompassed approximately 71,000 km² of Arctic tundra with the communities of Bathurst Inlet, Nunavut to the north and Wekweètì, Northwest Territories, to the west. During the summer, the area is only accessible by aircraft.

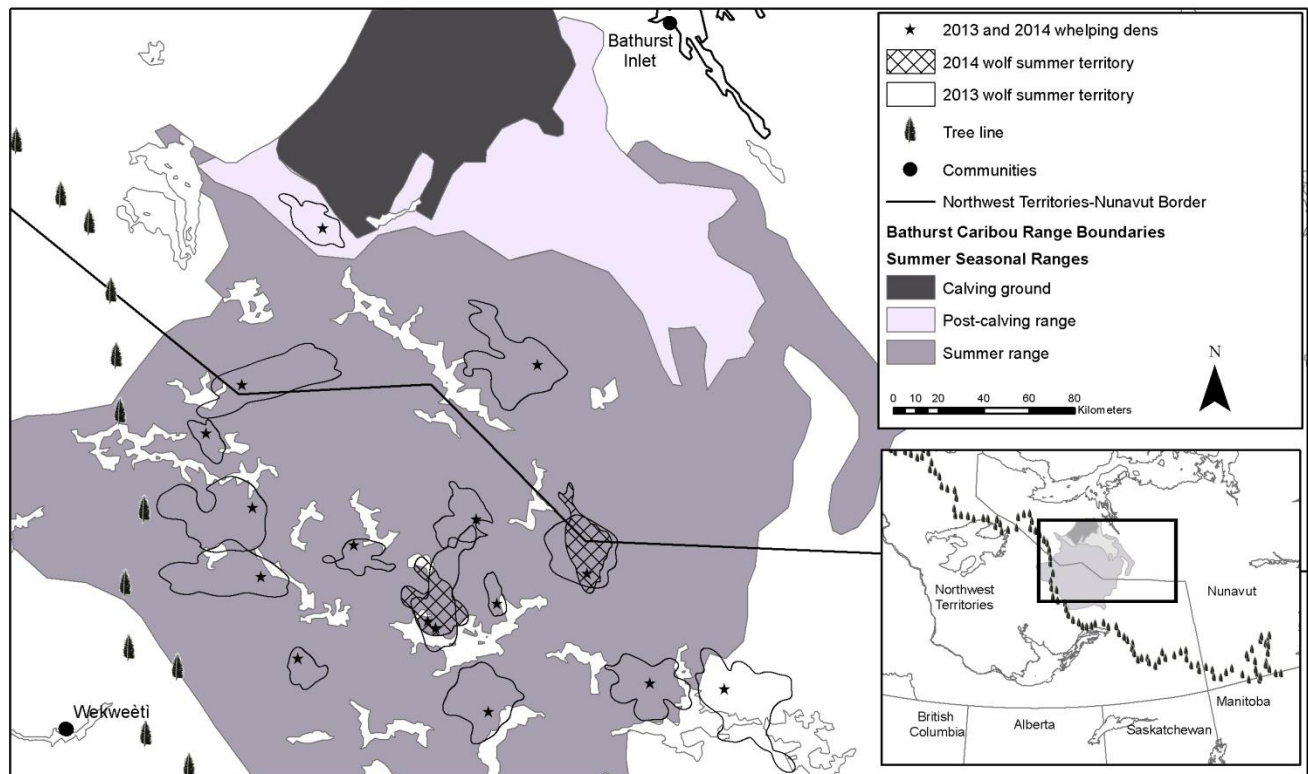


Figure 12. Study area located within the summer range of the Bathurst caribou herd in Northwest Territories and Nunavut, Canada. Wolf summer territories were delineated using a 95% fixed-kernel density estimate based on telemetry locations collected from GPS-collared breeding female wolves during the summers (June 25-August 31) of 2013 and 2014.

The study area is located within the southern Arctic ecoregion and characterized predominantly as tundra shield with low-growing black spruce (*Picea mariana*) within a taiga/tundra transition zone (i.e., treeline) in the south before yielding to open tundra to the northeast (Ecosystem Classification Group [ECG] 2012). The topography is comprised of rolling uplands of Canadian Shield rock and lowlands that contain fens, bogs, and numerous lakes. Barren-ground caribou of the Bathurst herd are the predominant ungulate within the study area (Gunn et al. 2002, 2013), and are the main prey source of tundra-denning wolves (Kuyt 1969, Williams 1990, Heard and Williams 1992, Walton et al. 2001, Frame et al. 2008). The northern portion of the study area is within close proximity of the calving and post-calving ranges, while the southern portion overlaps areas typically transited by caribou

during the spring and late-summer migration (Gunn et al. 2002, 2013; Adamczewski et al. 2009). Small groups of caribou, mainly adult males, typically remain in the southern portion of the study area throughout the denning period (Heard et al. 1996), although very few were observed during early summer field surveys in 2013 and 2014 (M. Klaczek, unpublished data). Other ungulates include muskoxen (*Ovibos moshatatus*) and moose (*Alces alces*), which are present in low numbers (Environment and Natural Resources [ENR] 2012).

Wolf Telemetry Data

In June 2013, 15 adult female tundra wolves, representing individual packs, were captured near their den and fitted with a GPS collar (Lotek Iridium M). The breeding female was targeted for capture because of her role in pack dynamics and caring for pups throughout the denning period (Fuller et al. 2003). Wolves were captured by helicopter net-gunning, physically restrained, and chemically immobilized by hand with an intramuscular injection of Telazol[®]. The GPS collars were programmed to obtain a location every 1.5 hours (16 locations per day) and were expected to function for 2.25 years (3 summers and 2 winters). All animal handling protocols were approved by the Northwest Territories Wildlife Care Committee in accordance with the Canadian Council on Animal Care Guidelines on the Care and Use of Wildlife.

Field Surveys

Movement patterns of GPS-collared adult female wolves revealed the locations of wolf homesites, duration of use, and relocation to another homesite. During the summers of 2013 and 2014, I used a small fixed-wing aircraft on floats (Aviat Husky) and a helicopter to conduct aerial- and ground-based surveys at wolf homesites. I recorded den occupancy and estimated recruitment by counting the number of pups of each monitored wolf pack during early and late summer.

Analyses

Wolf hunting distances from den sites

I used a Chi-square test to assess whether distances travelled away from the den during hunting forays were correlated with litter loss. During the summer, each monitored pack was assessed for the presence of pups. I categorized packs as having successfully recruited pups (1; > 1 pup alive during late-summer survey) or lost the litter of pups (0). I compared distances travelled by wolves of each category, recruited or did not recruit pups, for location data collected from 25 June, after wolves were initially collared, until 21 July, the median date associated with litter loss. I assumed that movements made by wolves away from the den were in search of prey, primarily barren-ground caribou (Walton et al. 2001, Mech and Boitani 2003, Frame et al. 2004). The number of GPS locations varied daily for each wolf due to missed fixes or transmission errors. I randomly sampled 8 of the 16 expected daily GPS-collar locations and measured the distance of the selected locations of each wolf from their respective den or rendezvous site identified during field surveys. Rarefaction ensured a common sampling effort and allowed for a standardized comparison of distance (Gotelli and Ellison 2013). I summarized the mean distance from den sites for each wolf by Julian day to provide a relative measure of the distances that wolves travelled during hunting forays.

Wolf hunting behaviours

I generated seasonal movement paths using locations from GPS-collared wolves collected over the denning period (25 June-31 August). For each wolf, I calculated movement rates and sinuosity using the total distance (km) of each path travelled by individual wolves during 24-hr (distance/day) and 7-day (distance/week) intervals. Sinuosity was calculated by dividing the total distance of each daily or weekly path by the net displacement (i.e., straight line distance between start and end locations of each path;

Williamson-Ehlers et al. 2014). Data were categorized according to the survival or loss of all pups. Within each category, I calculated the average movement rate and path sinuosity for each monitored wolf. Movement paths were censored from the dataset if the number of acquired locations was $\leq 50\%$ of the total number of expected GPS fixes at each daily or weekly interval (Williamson-Ehlers et al. 2014). Because my primary objective was the quantification of movements associated with hunting, I removed locations that were < 100 m from known wolf den and rendezvous sites; this distance was arbitrary, but likely removed the majority of paths associated directly with resting activities.

I used logistic regression to investigate factors that influenced the hunting strategies of wolves, as indicated by movement rate and path tortuosity. Model covariates included 1) the straight-line distance of each pack's whelping den to the calving grounds of Bathurst caribou herd (delineated by Adamczewski et al. 2009); 2) Julian day, an index representing the increasing energetic demands of growing pups over the denning period; and 3) pup survival, a binary variable indicating if pups were recruited or died during the summer (Table 6). Because I did not know the threshold between a long (1) and short (0) movement rate or sinuous (1) and less sinuous (0) paths, I used percentile thresholds calculated from the movement rate and sinuosity data to create a series of binary response variables. The percentile thresholds were increased incrementally by 5% between the 50th and 95th percentiles. Thus, for each metric and temporal scale (daily and weekly movement), I generated 10 logistic regression models and used the receiver operating characteristics (ROC) to determine the predictive accuracy of each model (Fielding and Bell 1997). Values ranging from 0.7-0.9 suggest the model has good predictive ability, whereas a value of 1.0 indicates a perfect predictor (Fielding and Bell 1997). Given the non-independence in wolf movement

locations and thus the possibility of inflating the type I error rate, I assigned individual wolves to separate clusters and used a robust variance estimator to control for autocorrelation within the dataset (Rogers 1993). I considered a $p < 0.05$ as significant in my statistical models; all analyses were conducted using Stata 12.1 (Statacorp, College Station, Texas, USA).

Table 6. Variables used to generate logistic regression models representing path movement rate and sinuosity of tundra wolves on the summer range of the Bathurst caribou herd, Northwest Territories and Nunavut, Canada.

Variable	Description
Pups	Binary value representing recruitment of pups in autumn; based on observation of pups in respective wolf pack in late summer ¹
Distance to calving ground	Straight-line distance from whelping den to the centroid of the calving grounds of the Bathurst caribou herd (based on Adamczewski et al. 2009 delineation)
Julian date	Julian day/week throughout the denning period (25 June-31 August); this temporal measure served as an index of energetic demands of growing pups during the denning period

¹ 01-05 September in 2013; 21-28 August in 2014

RESULTS

In 2013, I monitored 15 breeding adult female wolves with a GPS collar. Following wolf mortality and collar malfunction, I monitored 2 breeding females during the 2014 denning period. One adult wolf died in mid-July of 2013, likely due to starvation; intensive den surveys suggested that 7 of the 17 monitored packs lost their pups during the denning periods (Table 7). The median date of den abandonment due to litter loss was 21 July (Table 7). I recorded a total of 32 homesites (den or rendezvous site) used by the 17 monitored wolf packs over the denning period. The median date for relocation was 23 July. Pups that survived were relocated on average to 2.1 homesites (± 0.31 SE) over the denning period. On average, pups were moved 6.3 km (± 1.4 SE) to a new den or rendezvous site, although one pack moved their pups over 17 km to a new den in mid-July (Table 7). GPS collars

collected 90% of the attempted locations over the study period (96% and 94% acquisition rates for wolves that recruited (1) and lost pups (0), respectively).

Table 7. Spatial use of den sites and corresponding survival of pups for wolves monitored with GPS collars throughout the 2013 and 2014 denning periods on the Bathurst caribou summer range, Northwest Territories and Nunavut, Canada.

Year	Litter loss		Packs that relocated pups to new homesite							
	Median Date	Packs (n)	Median Date	Packs (n)	Distance between homesites (km)			Number of relocations		
					$\bar{X}$	min	max	$\bar{X}$	min	max
2013	21 July	6	23 Jul	9	6.3	0.4	17.5	2	1	4
2014	01 July	1	12 Jun	1	12.5	n/a	n/a	2	n/a	n/a

n/a = not applicable

Wolf hunting distances from den sites

I used 2,744 randomly selected GPS locations ($n = 8$ locations/wolf/day) to summarize the daily distances travelled by breeding wolves from their respective homesites during the early summer. I removed 84 locations that were below the 50% fix-rate threshold ($n = 15$ wolf-days or 3.4% of the available sample). Wolves that lost their pups travelled greater distances than wolves that recruited their pups ($\chi^2 = 13.1$, $p = 0.02$; Figure 13). During early-summer (25 June-21 July), wolves that eventually lost their pups travelled almost twice as far, on average, as wolves that were successful in recruiting pups ($\bar{X} = 13.8$ km, ± 1.56 SE; $\bar{X} = 7.28$ km, ± 0.70 ; respectively; Figure 13). The farthest straight-line distance from the den was 120 km, recorded for a wolf that would eventually lose her pups. For packs that recruited pups, the breeding females remained relatively closer to their respective den or rendezvous site (Figure 13); the farthest straight-line distance for this group of wolves was 60 km from the den. Distances increased gradually throughout the early denning period for wolves that recruited pups (Figure 13). Wolves that lost their pups still remained in their summer range (i.e., vicinity of their den) until late summer (Figure 13).

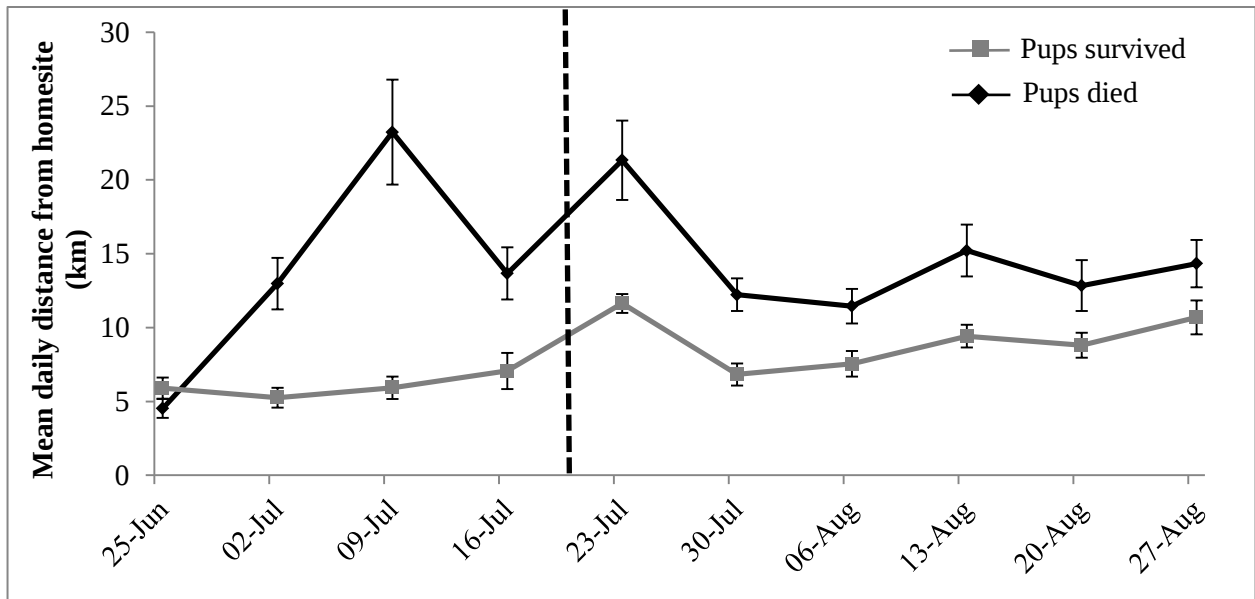


Figure 13. Mean ($\pm$ 95% CI) weekly distance from den or rendezvous sites at daily sampling periods for breeding adult female tundra wolves that recruited or lost their pups within the summer range of the Bathurst caribou herd, Northwest Territories and Nunavut, Canada, 2013-2014. The vertical dashed line indicates the median date (21 July) of litter loss (among those dens where it occurred; $n = 7$). Dates on x-axis indicate the start of the weekly interval.

Wolf hunting behaviours

I used 16,778 locations collected from GPS-collared adult female wolves to quantify the distance and sinuosity of daily and weekly movement paths. I removed 2,189 locations that were associated with a den or rendezvous site; an additional 719 and 761 locations were removed from daily and weekly paths respectively because collected locations were below the 50% fix-rate threshold. From the remaining locations I created 991 daily and 140 weekly movement paths. The mean number of movement steps for each path was 14.4 (2.75 SD, range: 8-16) and 96.0 (14.7 SD, range: 57-124) at both daily and weekly scales, respectively.

Overall, movement rates were similar when comparing wolves with and without pups. Slight variation did occur during early summer, in which wolves that recruited pups moved at relatively slower rates when compared to wolves that lost their pups. Over the summer the travelling distances for wolves with pups at the den averaged 23.0 km/day ($\pm$ 0.52 SE) while

wolves that would eventually lose their pups averaged 23.4 km/day (± 0.66 ; Figure 14). The maximum daily distance travelled was 102 km, where the female wolf returned to her den site; however, she lost her pups soon after and abandoned her den. Movement rates were similar between groups at the weekly scale (Figure 14). For females that recruited pups, weekly distances averaged 168 km/week (± 5.5) while wolves that lost pups averaged 173 km/week (± 6.5).

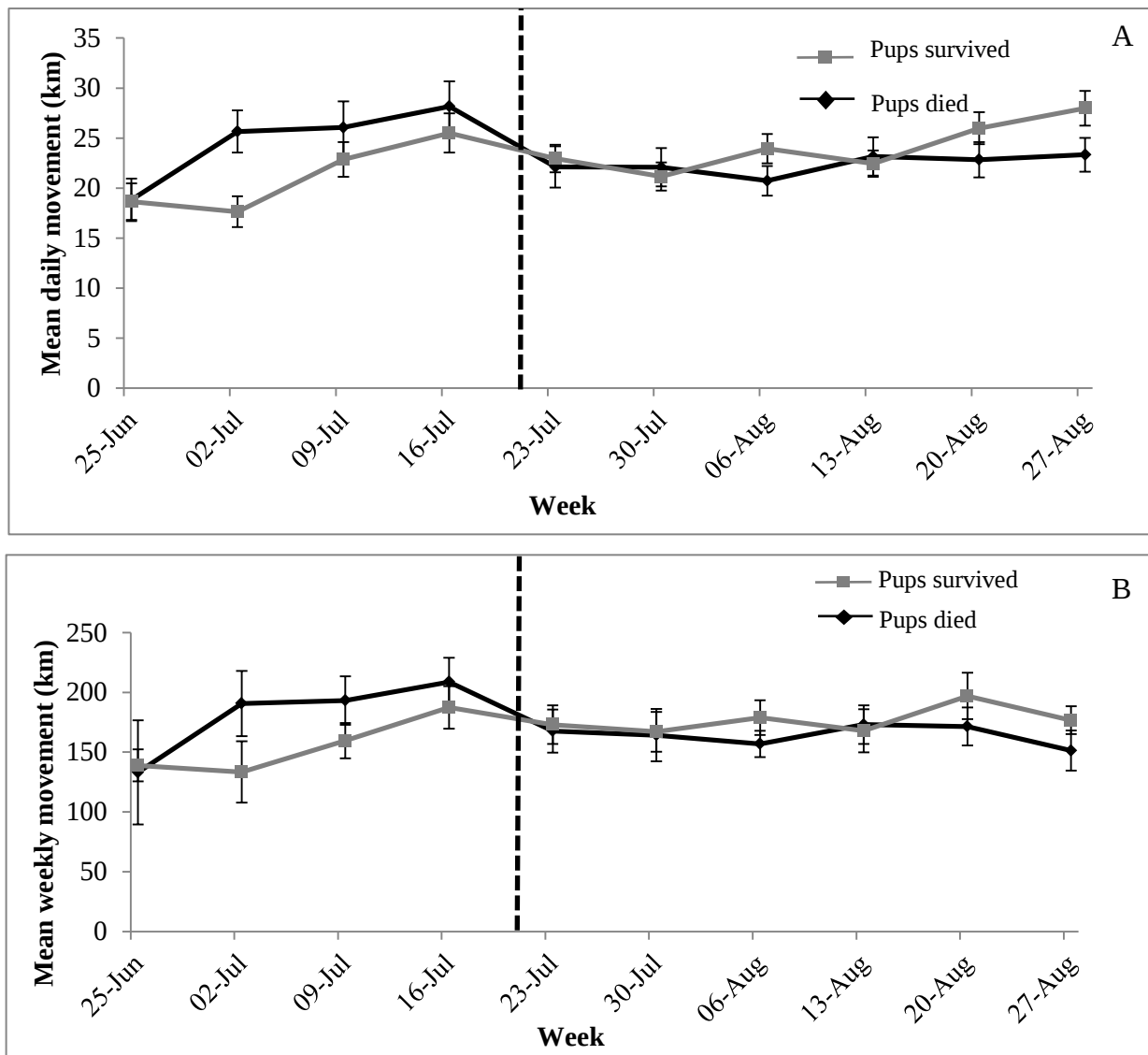


Figure 14. Mean ($\pm$ SE) weekly movement rates for daily (A) and weekly (B) sampling periods for breeding adult female tundra wolves that sustained or lost their pups within the summer range of the Bathurst caribou herd, Northwest Territories and Nunavut, Canada, 2013-2014. The vertical dashed line represents the median date (July 21) of litter loss for 7 active dens.

There was a poor fit to the logistic regression models differentiating movement rate at the daily time scale regardless of the breakpoint for defining fast and slow movements (AUC = 0.66 at the 95th percentile). Model covariates were not significant (Table 8), indicating that the hypothesized explanatory factors were not important for explaining wolf movement at the daily scale. Model fit improved when differentiating fast from slow movements at the weekly scale (AUC = 0.77 at the 90th percentile). None of the covariates, however, were significant predictors of wolf movement (Table 8). Although not statistically significant, both daily and weekly models revealed a consistent trend in which wolves moved at slower rates the farther their dens were located from the Bathurst calving ground ($p = 0.08$ daily and $p = 0.09$ weekly models respectively).

Path sinuosity varied between groups. Consistent with my prediction, wolves that lost their pups made more linear movements than wolves that successfully recruited pups. Daily sinuosity rates remained constant between groups until mid-July, when sinuosity decreased for packs that lost their pups (Figure 15). Logistic regression models revealed that pup recruitment was a significant predictor of wolf path sinuosity at the daily scale, although model fit was relatively poor (AUC = 0.65 at the 80th percentile; Table 8). Path sinuosity also decreased as the pups grew during the denning period, and wolves that denned farther from the calving grounds made more linear movements; the relationship, however, was not statistically significant. At the weekly scale, breeding females that eventually lost their pups made more linear movements earlier in the summer (Figure 15), consistent with the further distances travelled from their den. This logistic regression model had good predictive accuracy (AUC = 0.70 at the 95th percentile), but covariates were not statistically significant (Table 8).

Table 8. Statistical summary of logistic regression models used to delineate small- and large-scale movements at daily and weekly scales for adult female wolves denning on the summer range of the Bathurst caribou herd in the Northwest Territories and Nunavut, Canada, 2013-2014.

Model Theme	Best Model	Variables	β^2	95 % Confidence Intervals	
Daily Movement	95 percentile AUC ¹ = 0.66	Julian day	-0.01	-0.02	0.01
		Distance from calving ground	-0.01	-0.02	0.00
		Pups	-0.45	-1.26	0.36
Weekly Movement	90 percentile AUC = 0.77	Julian week	-0.12	-0.38	0.13
		Distance from calving ground	-0.02	-0.03	0.00
		Pups	-0.23	-1.72	1.26
Daily Sinuosity	80 percentile AUC = 0.66	Julian day	-0.02	-0.03	-0.01
		Distance from calving ground	< 0.01	-0.01	0.00
		Pups	0.79	0.05	1.52
Weekly Sinuosity	95 percentile AUC = 0.70	Julian week	0.03	-0.38	0.44
		Distance from calving ground	-0.01	-0.02	0.01
		Pups	1.48	-0.68	3.63

¹Area under the receiver operating characteristics curve

²Beta coefficients returned from logistic regression models

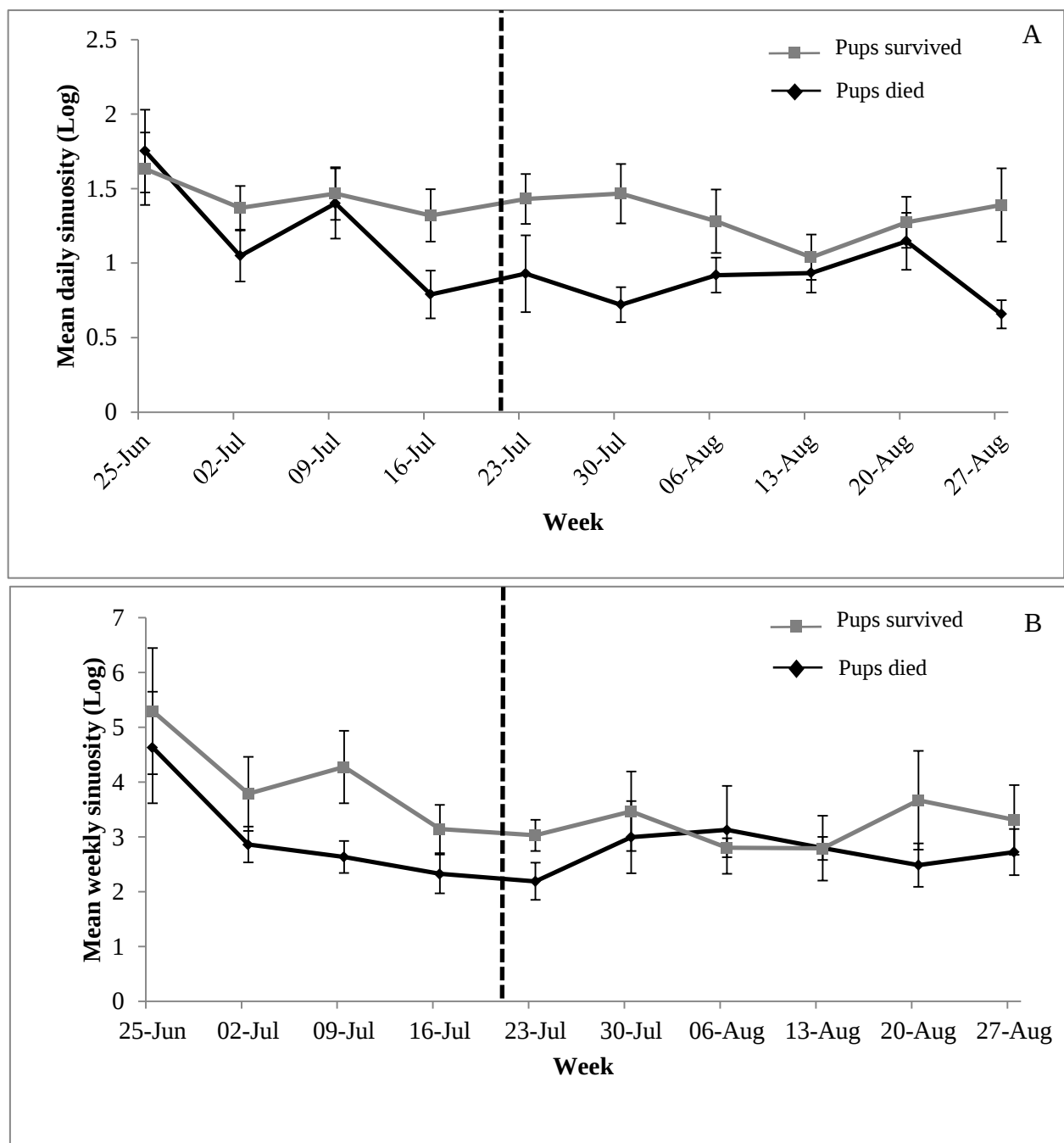


Figure 15. Mean ($\pm$ SE) weekly path sinuosity for daily (A) and weekly (B) sampling periods for breeding adult female tundra wolves that sustained or lost their pups within the summer range of the Bathurst caribou herd, Northwest Territories and Nunavut, Canada, 2013-2014. The vertical line represents the median date (21 July) of litter loss for 7 active dens.

DISCUSSION

I used frequent locations from GPS-collared female wolves combined with pup counts from their associated pack to assess the functional response of wolves to varying prey densities on the summer range of the Bathurst caribou herd. I expected the effects of habitat-induced GPS fix-rate bias (Johnson et al. 2002, Hebblewhite et al. 2007) to be minimal in an open-tundra environment. Although breeding wolves that remained in the den for longer periods would limit the number of available fixes collected by their GPS collars (Hebblewhite et al. 2007), this bias was small as the GPS collars performed well over the study period, collecting over 94% of possible locations.

Almost half of the monitored packs lost their pups during the denning period. GPS-collared wolves associated with these packs travelled farther from their den sites than those packs where pups were recruited by early fall. The availability of prey biomass is critical for pup survival (Fuller et al. 2003). At low caribou abundance, breeding female wolves were not able to respond functionally to lower prey densities within their summer territories. I can only speculate, however, on the exact mechanism that resulted in some packs moving greater distances to find caribou. There is likely a stochastic element related to prey availability and hunting success. Some packs, for example, may have access to muskoxen, moose, or small groups of caribou that are farther south of the larger herd aggregation. Nevertheless, variation in prey availability during the early summer, a period when caribou typically return to the hunting ranges of denning wolves during their southbound migration, influenced wolf movement.

Wolves are well equipped to travel far distances in search of prey (Walton et al. 2001, Peterson and Ciucci 2003, Frame et al. 2004), but they are also highly territorial, a

behavioural adaptation thought to be a response to competition for food resources (Mech and Boitani 2003). When caribou abundance is low, density-dependent range contraction may reduce their distribution which, in turn, limits the availability of prey for some wolf packs. Consequently, if caribou are temporally concentrated in one pack's territory, or a specific portion of the Bathurst summer range, prey may be unavailable for neighboring wolf packs. In my study, I suspect that variation in pup survival among the monitored packs was attributed to a clumped or distal distribution of caribou that provided hunting opportunities for some, but not all packs.

A variety of metrics have been used to characterize the behaviour of wolves at the population scale (Jedrzejewski et al. 2001, Whittington et al. 2004, Latham et al. 2011, Hansen et al. 2013, Williamson-Elhers et al. 2014). I used the rate of movement and path sinuosity to explore the behavior of reproductive female wolves associated with a litter of pups at the den. However, the resulting logistic regression models were not strong predictors of fast or sinuous movements. This may be a function of a mismatch in the scale of the dependent and predictor variables as well as the simplicity of the models I tested. Wolf behaviour is inherently complex with both physical and social factors influencing their patterns of movement (Mech and Boitani 2003, Packard 2003); I tested the effect of only three variables: distance to calving ground, time of year, and presence of pups throughout the summer. The hunting success of wolves depends on a variety of factors that I was not able to measure; for example, intraspecific interactions with neighbouring packs, experience of the dominant wolf, and the degree of prey vulnerability (Mech and Peterson 2003). These models were admittedly simple, likely only capturing a small portion of the environmental and social variation that explains the behavior and resulting movements of wolves. For

example, Whittington et al. (2004) and Williamson-Ehlers et al. (2014) reported a good fit between the observed movements of wolves and a broader set of factors that included anthropogenic landscape change, likely reflecting prey availability, and the presence of humans. Nevertheless, my models did provide some important insights into denning ecology of wolves as documented by the variation in their hunting behaviours.

Logistic regression models revealed that the rate of movement and path sinuosity decreased for wolves that denned farther from the Bathurst calving grounds. Although the results for the majority of the models were not statistically significant, I expect this relationship may be attributed to wolves searching for distant prey within the southern portion of the study area. During early summer, most caribou are distributed farther north within their calving and post-calving ranges. If caribou are within hunting distance, wolves may travel faster over larger areas in search of their migrating prey.

For wolves, tortuosity of movement paths may reflect the actual hunting behaviours such as stalking prey (Peterson and Ciucci 2003), or movements centered around a predation site (Whittington et al. 2004, Sand et al. 2005, Zimmermann et al. 2007, Webb et al. 2008, Merrill et al. 2010, McPhee et al. 2012). Path sinuosity was a more sensitive index of the behavior of wolves in my study. In general, movement paths were more linear for female wolves that lost their pups and more sinuous for wolves that recruited pups. Wolves that demonstrated more linear movements that were distant from the den also experienced a higher prevalence of litter loss. This indicates that wolves were not able to secure sufficient amounts of prey for their pups during the relatively longer hunting forays. Some component of the variation can likely be attributed to the timing of den abandonment that followed litter loss. For example, more linear movements even following den abandonment may be

consistent with a more nomadic hunting strategy, facilitated by the loss of pups (Mech 1995). Although weekly sinuosity rates were also consistent with distances travelled from the den during hunting forays (i.e., more linear for wolves travelling farther from the den), model covariates were not statistically significant; I expect this may be a function of a relatively smaller sample size.

CONCLUSION

Global positioning system locations collected at high frequencies offered a rare glimpse into the spatial ecology of wolves within remote areas of the central Arctic. Quantifying wolf movement at a fine spatiotemporal scale allowed me to investigate changes in hunting behaviors during the critical denning period, a time when the energetic demands of the pack are centered on caring for and feeding their pups (Mech and Boitani 2003). The extreme reduction in the density of the Bathurst caribou herd likely exacerbated the existing behavioural and population response of tundra wolves to patchy prey distribution during summer.

The hunting success of wolves depends on a variety of factors, most importantly the abundance and distribution of their prey (Mech and Peterson 2003). Ungulates, in general, have adapted a number of strategies to avoid predation in areas occupied by wolves (Mech and Peterson 2003). For caribou, movement is a key behavioural characteristic that provides refuge in the face of predation risk (Seip 1991, Thomas 1995). For example, woodland caribou space away from ungulates such as moose and deer (*Odocoileus spp*), which occur in higher densities and are the primary prey of wolves in boreal and mountain ecosystems (Seip 1991). On the tundra, barren-ground caribou migrate to their calving grounds, away from the

main concentration of wolves that den closer to treeline (Bergerud and Page 1987, Heard and Williams 1992, Adams and Dale 1998).

My data suggest that tundra wolves are most vulnerable to prey scarcity during the early denning period, when caribou are at the northern extent of their distribution and at greatest distance from occupied den sites. Such dynamics may force wolves to travel farther in search of prey to sustain growing pups. Thus, early July is a critical period for pup survival, where local variation in prey availability within the denning areas appears to be the difference between pup survival and mortality. This is demonstrated by the more linear movements travelled by wolves farther from their den sites in search of prey, which ultimately correlated to litter loss; a result that was not observed during movement studies when caribou abundance was considerably higher (Walton et al. 2001, Frame et al. 2004).

Wolves in my study responded functionally to varying prey densities within their territories by extending their movement in search of prey. The movement dynamics I documented suggest a regulatory mechanism, where the contraction in the distribution of caribou at low abundance lowers prey densities within denning areas of wolves to levels that affect pup recruitment. Such results provide further evidence of the numerical response of wolves to changing caribou densities at fine spatiotemporal scales.

CHAPTER 5: GENERAL CONCLUSIONS

SUMMARY

Some suggest that the spring migration of barren-ground caribou is primarily an anti-predator strategy where lower predation risk on their northern calving grounds is thought to outweigh the increased energetic costs associated with migration (Bergerud 1996, Heard et al. 1996, Mech and Peterson 2003, Bergerud et al. 2007). Here, large aggregations of caribou are effectively spaced away from most wolves, which occur in higher densities within their denning ranges near treeline (Heard and Williams 1992). In theory, Arctic caribou herds remain at low predator-prey ratios because most reproductive wolves do not follow caribou to their calving grounds and thus are food-limited at the population scale (Seip 1991, Heard and Williams 1992, Heard et al. 1996). In recent years, however, barren-ground caribou herds have declined across much of their circumpolar range (Vors and Boyce 2009). Although the direct cause of the decline is unknown (Adamczewski et al. 2009, Boulanger et al. 2011), wolves may have more influence on caribou population dynamics when herd abundance is low. Understanding the response(s) of wolves to severe caribou decline can provide important insights into the ecosystem dynamics of the central Arctic and help promote herd recovery through dynamic and effective management actions (Environment and Natural Resources 2011). In this thesis, I used long-term datasets to assess den site selection, project wolf population growth, and quantify hunting behaviours. My key objectives were to provide insight into the denning ecology of tundra wolves and investigate their responses, both behavioural and numerical, to a > 90% decrease in the abundance of the Bathurst caribou herd.

Previous research suggests that tundra wolves improve their reproductive fitness by denning closer to treeline (Banfield 1954, Kelsall 1968, Heard and Williams 1992) or along

major caribou migration routes (Clark 1971, Kuyt 1972, Frame et al. 2008). Such strategies maximize the accessibility of migrating caribou during the entire denning period, a time when reproductive wolves are tied to the vicinity of their den sites when caring for pups (Heard and Williams 1992). Using a long-term dataset (1996-2012) of active den locations, I developed a series of resource selection function (RSF) models to investigate the factors that influenced den site selection of wolves. I compared a temporal sequence of RSF models to evaluate whether wolf selection patterns changed over a period of caribou decline. These models revealed that both early and late-summer distributions of caribou were important predictors of den occurrence on the Bathurst summer range. As caribou declined, their summer ranges contracted closer to the calving grounds. My results suggest that wolves did not respond behaviourally by denning in closer proximity to the retreating caribou. As such, caribou were farther away from the denning areas of wolves for relatively longer periods of the summer.

Some have hypothesized that wolves would respond numerically to the density-dependent range-use patterns of caribou (Heard and Calef 1986, Heard and Williams 1992). In Chapter 3, I investigated the population dynamics of wolves denning on the summer range of the Bathurst caribou herd. Results from aerial surveys indicated that since 2007 most wolf dens active in spring were abandoned by late summer; this change in behaviour resulted in lower sample sizes to estimate annual pup survival rates, which have been < 2 pups/pack since 2010. During the 2013 and 2014 denning periods, I repeatedly tracked GPS-collared wolves, representing individual packs, to attain accurate measures of recruitment during low caribou abundance. My results provided empirical support of a numerical response of wolves to declining caribou densities. Regression models clearly illustrated the relationship

between caribou range contraction and wolf reproductive success. I estimated that wolf density declined by almost 50% over the study period (1996-2014). My findings were consistent with other studies that reported prey biomass as a key driver of wolf population dynamics (Keith 1983, Fuller 1989, Fuller et al. 2003, McRoberts and Mech 2014).

In Chapter 4, I conducted a fine-scale analysis of high-frequency location data to investigate wolf-hunting strategies during a period of low caribou abundance. Wolf-hunting success depends largely on the distribution and abundance of prey (Mech and Peterson 2003). On the Bathurst range, I assumed that hunting patterns would be influenced by the availability of caribou within their respective denning areas and hypothesized that long-distance movements, when prey were unattainable, would correlate with litter loss. I found that wolves that lost their pups moved relatively farther from their den sites in early summer, a period when most caribou typically return to the denning areas of wolves during their southbound migration. Wolf movement rates slowed and paths were linear as they denned farther from the Bathurst caribou calving grounds. I expected this result was attributed to a prey-searching behaviour in which wolves reduced their speed of movement while searching for distant prey. My results suggest that prey availability was low in the denning ranges of some packs, which correlated with litter loss. For wolves denning on barren-ground caribou range, prey availability during early summer is critical for pup survival.

Overall, the results from my thesis corroborate the findings of other researchers that linked the behaviour and ecology of tundra wolves to the abundance and distribution of barren-ground caribou (Kuyt 1969, Parker 1973, Heard and Calef 1986, Heard and Williams 1992, Walton et al. 2001, Musiani et al. 2007, Frame et al. 2008). My study provides empirical support of a wolf numerical response. By linking caribou space-use patterns to

wolf population dynamics, I identified a regulatory mechanism where variation in the seasonal migration patterns of caribou influenced pup recruitment and wolf population growth. The techniques and mechanisms used in my research apply to barren-ground caribou herds found across the central Arctic.

MONITORING WOLF DENS ON THE BATHURST SUMMER RANGE

Estimating population size and trend for wolves is challenging due to their broad distribution, low densities, and secretive behaviour (Fuller and Snow 1988, Becker 1991, Ballard et al. 1995, Patterson et al. 2004, Adamczewski et al. 2009). Estimates are even more difficult for tundra wolves because they follow migratory barren-ground caribou for most of the year, resulting in extremely large annual ranges (Walton et al. 2001). Consequently, repeated census or mark-recapture population estimates are not economically feasible. Since 1996, the Northwest Territories Department of Environment and Natural Resources has used aerial surveys to monitor wolf-den occupancy to gain an understanding of the population trend of wolves within the summer range of the Bathurst caribou herd (Adamczewski et al. 2009). The data set includes over 95 known individual den sites collected over a 17-year period. However, high rates of den abandonment have reduced the number of packs where pups were counted during late-summer recruitment surveys, potentially adding bias to survey results (D. Cluff, unpublished data). I monitored den occupancy and recruitment, at low caribou abundance, by conducting repeated surveys of wolf packs tracked by a GPS-collared adult female wolf. My findings were consistent with recruitment rates recorded during aerial survey results since 2010 and late-summer occupancy patterns since 2007. The continued and consistent monitoring of the tundra wolf population on the Bathurst range highlights the value of long-term monitoring programs.

These data provided essential insight into the behavioural and numerical responses of wolves over a period of decline for the Bathurst caribou herd.

MANAGEMENT IMPLICATIONS

The recent declines of many barren-ground caribou herds in the Northwest Territories have raised concerns among northern communities, wildlife professionals, and government. Faced with this challenge, some have promoted lowering wolf numbers by increasing harvest as one of the few feasible options available to facilitate herd recovery (Environment and Natural Resources 2011). For some caribou herds, wolf-control programs have been effective in lowering mortality, and caribou numbers have increased following a reduction in wolf density (Gasaway et al. 1983, Bergerud and Elliot 1986, Farnell and McDonald 1988, Hayes et al. 2003). However, for several programs in Alaska and Canada results have been unclear, mainly due to lack of monitoring and broad assumptions about complex predator-prey dynamics (National Research Council 1997). Removing wolves can reduce predation for ungulates, but the relationship is not linear. Thurber and Peterson (1993), for example, showed that a larger pack size kill fewer prey per wolf. In addition, predation rates may be influenced by the number of breeding pairs on the landscape and not necessarily the number of wolves in a population (Mech and Boitani 2003, Wielgus and Peebles 2014). Consequently, the removal of one or both breeding wolves may disrupt pack social dynamics, causing pack splitting within existing territories and result in an increase in local wolf density (Ballard and Stephenson 1982, Hayes et al. 2003, Brainerd et al. 2008, Wielgus and Peebles 2014). To be effective, a high proportion of wolves must be reduced over several years and over large areas in order to lower total reproduction and prevent rapid recolonization (Hayes et al. 2003, Mech and Peterson 2003, Hervieux et al. 2014). An effective predator control

program requires intensive management which is both controversial and expensive to implement (Cluff and Murray 1995, Haber 1996, Paquet and Carbyn 2003, Van Ballenberghe 2006, Brook et al. 2015).

The role of wolves in the population dynamics of migratory barren-ground caribou is not fully understood (Klein 1991, Bergerud 1996). Debate among both the public and biologists on whether wolves can regulate or limit caribou populations has been ongoing since the 1970s (Van Ballenberghe 1985, Bergerud and Ballard 1988, Messier et al. 1988, Valkenburg 2001, Bergerud 2007). In theory, the influence of wolf predation on caribou population dynamics is based on the number of wolves, kill rate, and the population size of caribou, which ultimately determine the resilience of the herd to withstand losses to predation (Seip 1995). At low caribou densities, the functional response of wolves can limit population growth (Bergerud and Elliot 1986, Dale et al. 1994, Hayes 1995); however, this may not apply to large migratory herds or simple predator-prey systems where wolves do not have alternative prey (Messier et al. 1988). Because their diet is almost exclusively caribou, the functional response of wolves on the Bathurst range is unlikely to change as caribou numbers decrease (Heard et al. 1996). Thus, the wolf numerical response, and the timing and scale of this dynamic, would be the primary driver in influencing wolf predation on the Bathurst caribou herd (Heard and Williams 1992, Heard et al. 1996). A lag in the numerical response of wolves, however, could result in a proportionally higher predation rate for caribou during the first years of population decline (Peterson and Page 1983, Theberge 1990, Messier 1991).

My results suggest that wolves on the Bathurst range have exhibited a relatively strong numerical response to a single, declining prey base. When caribou are at a low in their population cycle, range contraction limits the availability of prey in the denning areas for wolves, resulting in high rates of pup mortality. My population projections suggest that wolf

densities have decreased from > 6.5 wolves/1000 km² in the late 1990s to 2014 levels ≤ 4 wolves/1000 km². Estimates of wolf density in my study area are well below the 6.5 wolves/1000 km² threshold proposed by Bergerud and Elliot (1986) that may halt population growth of small populations of woodland caribou. Further, Bergerud (1996) reported an increasing population trajectory for the George River caribou herd in Ungava when wolf densities were estimated around 3-4 wolves/1000 km².

While ecosystem dynamics vary considerably across caribou herds, making direct comparisons a challenge, efforts to reduce wolves in other study areas have resulted in densities at or above my 2014 wolf density estimate for the Bathurst range (Gasaway et al. 1983, Ballard et al. 1987, Boertje et al. 1996, Hayes and Harestad 2000, Hayes et al. 2003, Bergerud 2007). In the past, trapping and hunting of tundra wolves depressed populations but did not eliminate them even with bounties (Kuyt 1972, Thomas 1995). However, skidoos and modernized hunting practices have the ability to severely limit tundra wolf populations (Thomas 1995), especially if wolves have already responded numerically to lower caribou densities. Nevertheless, small changes in survival of adult female caribou may strongly influence population trends (Eberhardt 2002, Boulanger et al. 2011) and wolf predation may interact with other regulatory factors to limit or lengthen caribou herd recovery (Seip 1995, Thomas 1995, Paquet and Carbyn 2003).

We require a further understanding of the implications of increased wolf harvest in the context of a much smaller caribou population if management agencies are to develop or adapt management plans that address the cumulative threats facing barren-ground caribou. In particular, wolf control, including the biological premise for such actions, should be thoroughly evaluated before it is implemented as a management strategy to decrease the

recovery time of the Bathurst caribou herd. Further research is needed to assist with management decisions focused on herd numbers and actions that might consider wolf removal programs.

RESEARCH NEEDS

In addition to survival and reproduction, high dispersal rates of wolves are influential in determining population growth rates (Fuller et al. 2003). In the central Arctic, dispersal rates of tundra wolves both within and among caribou range are not well understood. In my study, location data collected from GPS-collared wolves provided some evidence of movements between adjacent ranges as four of the sixteen monitored wolves migrated to the winter range of the adjacent Bluenose East caribou herd and one sub-adult female dispersed to the Beverly caribou range, soon after she was collared. I expected that immigration rates of wolves onto the Bathurst caribou range would be low due to increased competition for limited resources, but there is no evidence to support my assertion. Because of their high dispersal capability, wolf-removal efforts may be needed at broader scales across the central Arctic if such a management strategy is to be effective (Hervieux et al. 2014). Understanding these dynamics will be critical in determining the appropriate scope and scale of wolf-control measures.

Understanding how wolves influence caribou survival is critical for determining appropriate conservation and management actions. In particular, the survival of adult female caribou and calves strongly influences population trends (Eberhardt 2002). Wolf predation can be assessed as a limiting factor for the recovery of the herd by analyzing prey demographics and kill rate. When a wolf or wolf pack kills an animal, they typically stay at

that site longer than during most non-foraging movements; such activity results in a collection or cluster of locations with relatively short movement distances (Sand et al. 2005, Webb et al. 2008, Merrill et al. 2010, McPhee et al. 2012). Examining the geographic locations collected via GPS collars identifies clusters of activity that can indicate kill sites. Those patterns, confirmed and quantified over a seasonal period, provide an estimate of predation on caribou (Webb et al. 2008). To date, the functional response of wolves remains one of the key knowledge gaps in assessing the role of wolves in the population dynamics of caribou.

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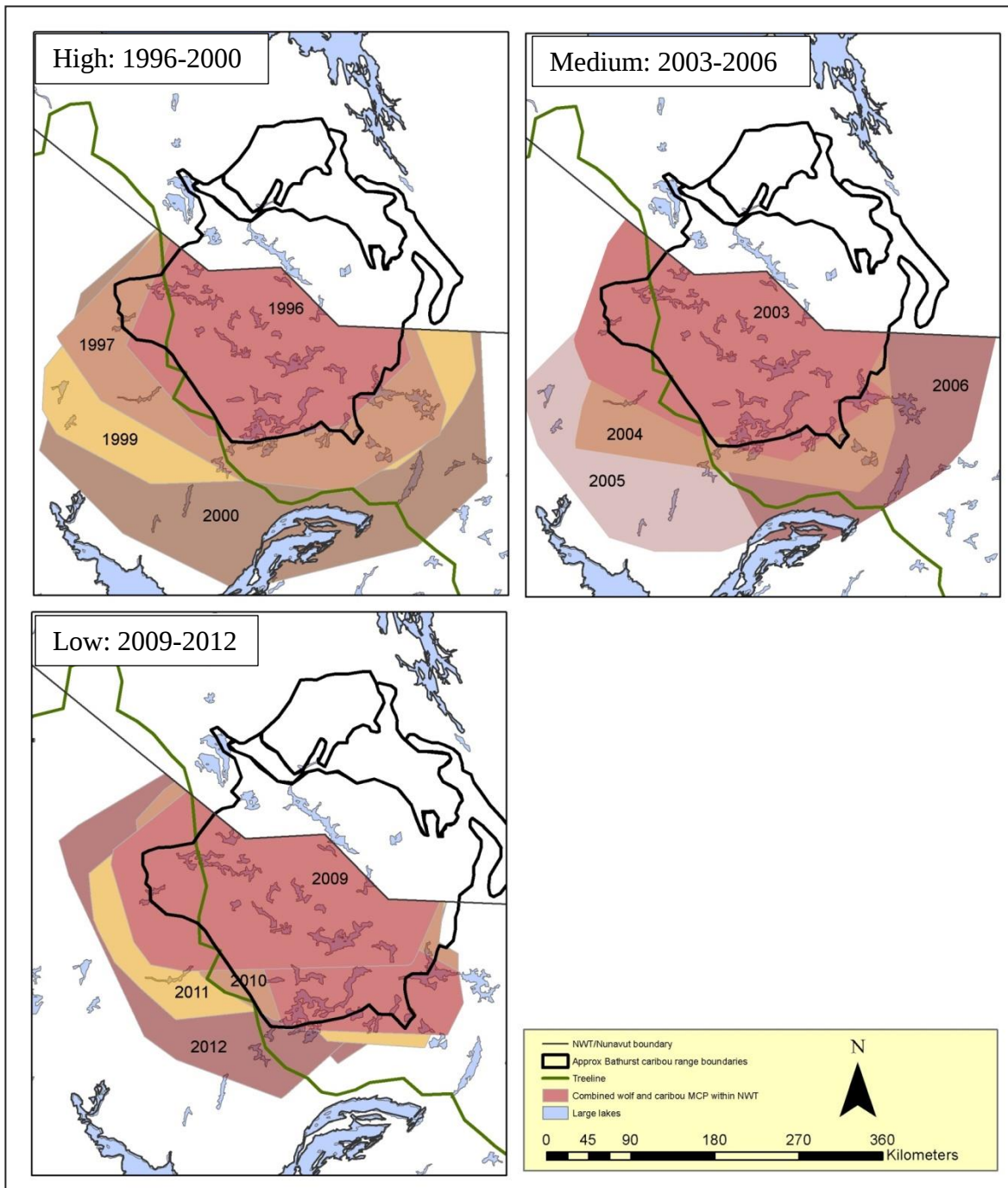
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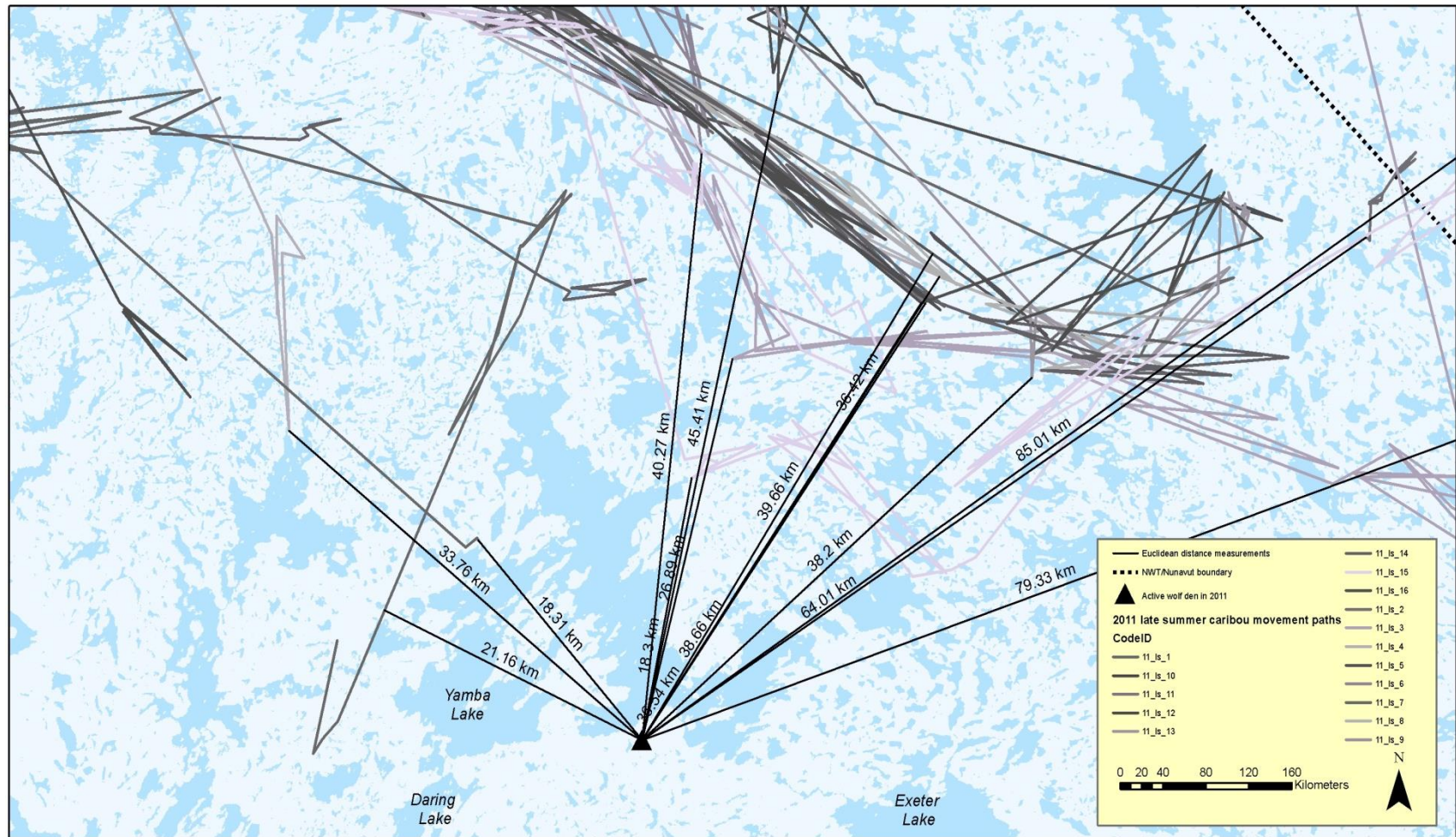
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APPENDIX A



Temporal patterns in the spatial extent of resource availability for denning wolves. For each year (1996-2012), a 95% minimum convex polygon (MCP) was calculated from the locations of satellite- and GPS-collared adult female caribou from 01 April to 30 September. These areas were merged with a 100% MCP around wolf dens within the study area for each year. This figure displays availability polygons for each model period (High, Medium, Low)

APPENDIX B



The late summer distribution of satellite-collared adult female caribou ($n = 16$) relative to an active wolf den in 2011. For each season, the distances from each den and random site were measured to the nearest edge of each individual caribou movement path. The median distance was used to summarize the relative distance of caribou from wolf dens on the Bathurst caribou summer range. This metric was used in RSF models to represent the seasonal variation in caribou distribution from wolf den sites through the study period (1996-2012).

APPENDIX C

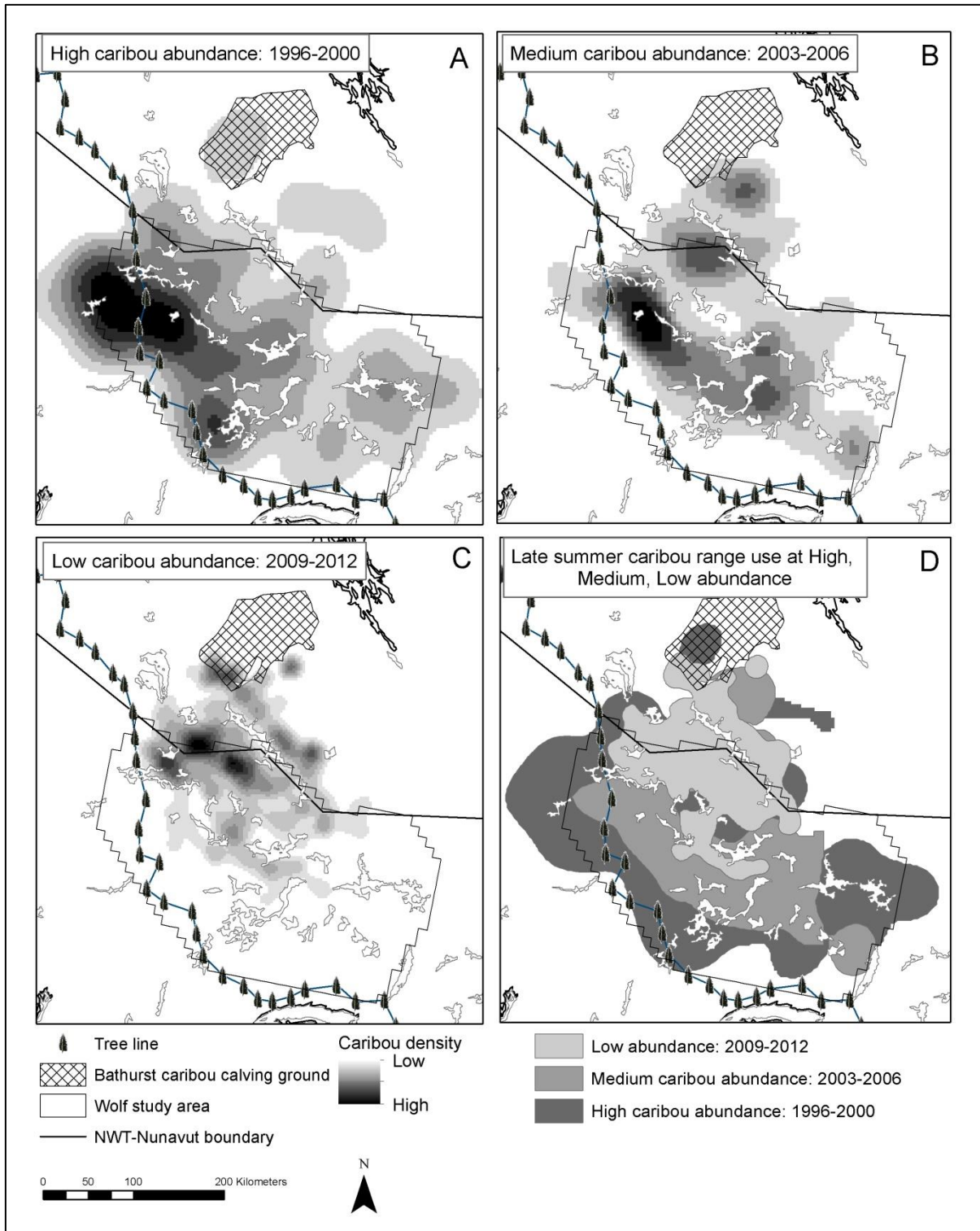
Model coefficients (β) and 95% confidence intervals from the most parsimonious resource selection function models used to investigate the mechanisms that influence den site selection and assess the behavioural response of wolves denning on the Bathurst caribou summer range over periods of varying caribou abundance (High, Medium, Low abundance)1996-2012 (excluding 1998).

Covariates	All: 1996-2012			High: 1996-2000			Medium: 2003-2006			Low: 2009-2012		
	β	95%CI		β	95%CI		β	95%CI		β	95%CI	
lowland tundra	<0.01	-0.02	0.02	0.01	-0.02	0.03	0.02	-0.06	0.10	-0.04	-0.08	<0.01
upland tundra	0.08	0.06	0.11	0.07	0.03	0.10	0.13	0.05	0.22	0.03	-0.01	0.07
shrub	0.01	-0.01	0.02	0.01	-0.03	0.06	0.03	-0.03	0.09	-0.03	-0.06	<0.01
wetlands	-0.01	-0.05	0.03	0.01	-0.05	0.07	0.05	-0.03	0.12	-0.09	-0.17	<0.01
esker	0.88	0.71	1.04	0.83	0.55	1.11	1.16	0.88	1.44	0.89	0.67	1.11
forest	-0.01	-0.04	0.02	0.02	-0.03	0.08	0.03	-0.03	0.09	-0.05	-0.11	0.01
water	<0.01	-0.02	0.02	-0.02	-0.06	0.01	0.04	-0.03	0.11	-0.02	-0.04	0.01
esker density	1.91	0.92	2.90	NI	NI	NI	NI	NI	NI	2.24	1.73	2.74
spring migration	<0.01	<0.01	0.01	0.01	<0.01	0.02	0.01	<0.01	0.02	<0.01	-0.01	0.02
calving	<0.01	-0.01	0.02	<0.01	-0.01	<0.01	<0.01	<0.01	0.01	0.01	<0.01	0.02
calving ² *	<0.01	<0.01	<0.01	NI	NI	NI	NI	NI	NI	NI	NI	NI
early summer	<0.01	<0.01	0.01	0.02	<0.01	0.03	0.02	-0.01	0.05	0.05	0.02	0.09
early summer ²	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01
late summer	<0.01	-0.01	<0.01	0.02	<0.01	0.05	<0.01	<0.01	<0.01	-0.06	-0.08	-0.03
late summer ²	NI	NI	NI	<0.01	<0.01	<0.01	NI	NI	NI	<0.01	<0.01	<0.01
fall migration	0.01	<0.01	0.02	-0.01	-0.01	<0.01	<0.01	-0.01	<0.01	-0.01	-0.03	<0.01
fall migration ²	<0.01	<0.01	<0.01	NI	NI	NI	NI	NI	NI	NI	NI	NI

NI: Not included; covariate excluded during modelling process

*Gaussian term for distance to seasonal caribou migration path

APPENDIX D



Late-summer (19 July -21 August) distribution of satellite-collared (Argos and GPS) adult female caribou of the Bathurst herd at A) High, B) Medium, and C) Low abundance (population estimates: 349,000-300,000; 286,000-128,000; 32,000-35,000 caribou, respectively). Range use was calculated using a fixed-kernel density estimate with 90% isopleths (map D) illustrating the density-dependent range contraction of the Bathurst caribou herd.

APPENDIX E

Estimated parameters held constant in Vortex (9.99c; Lacy et al. 2013) simulation models used to model tundra wolf (*Canis lupus*) population dynamics on the summer range of the Bathurst caribou herd.

Range: Bathurst	Parameter Value		Reference
Age of first reproduction	<u>Male</u>	<u>Female</u>	Kelly et al. 1999, Mahoney 2010
	3	2	
Recorded maximum litter size size (# pups)	6		D. Cluff, pers comm (maximum observed pups was 15 in a pack but possibly from 2-3 breeding females of the 9 adults present)
Reproduction life span (years)	8		D. Cluff, pers comm
Adult sex ratio	parity		No data: assumed
Proportion of adult females that breed each year	0.50		No data: assumed
Dispersal rate	Not included		No data
Age of dispersal	Not included		No data
Population sex and age structure			
Juvenile (< 1 yr)	Based on stable age structure		No data: assumed
Subadult (< 2 yr)			
Adult (> 2 yr)			

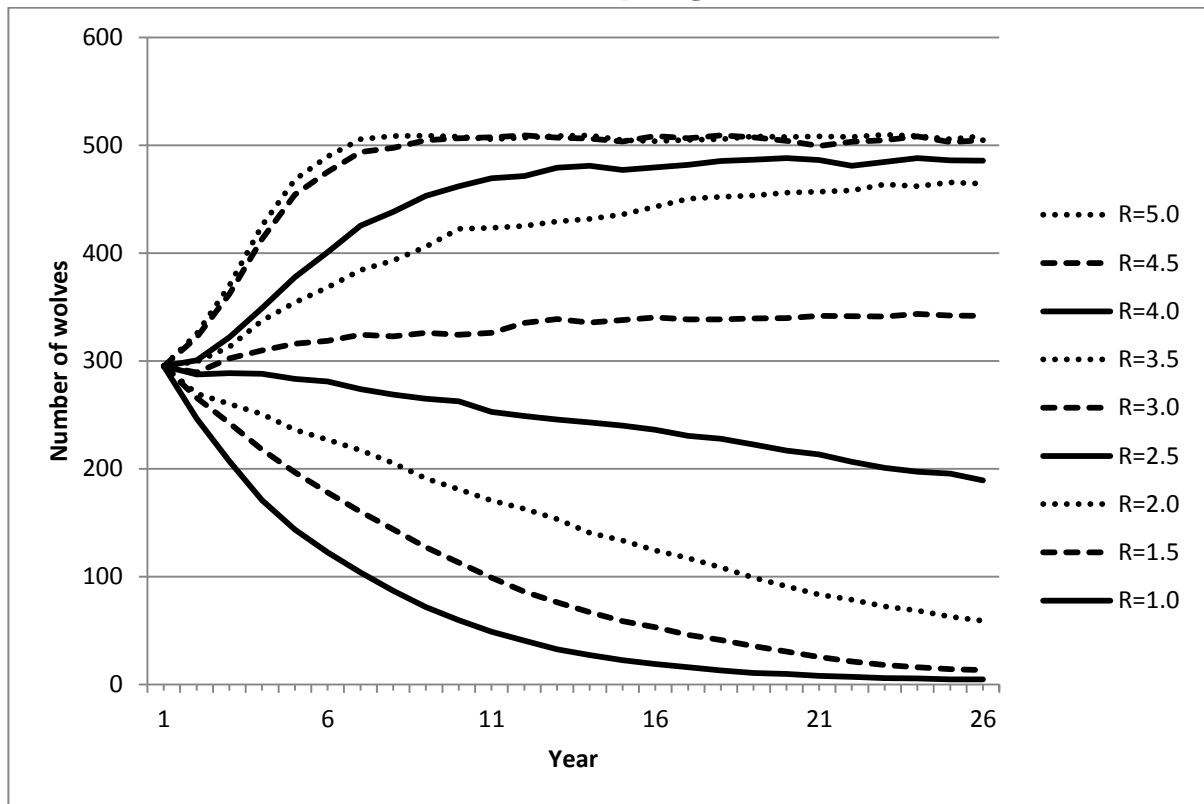
APPENDIX F

Annual aerial survey data collected at wolf dens on the summer range of the Bathurst caribou herd by the Government of the Northwest Territories, Department of Environment and Natural Resources. Annual wolf density estimates were extrapolated using the pooled mean pack size for each pooled interval (1996-2000, 2003-2006, 2009-2012) multiplied by the mean dens/1000 km² for each year in the survey.

Year	Average number of adults seen at dens > 1 yr old	Average pups/den August	SE pups/den	Active dens August (n)	Dens/1000km ²
1996	2.8	3.4	0.26	7	0.98
1997	2.9	4.0	0.27	8	NA*
1998	2.8	3.1	0.22	11	1.08
1999	3.3	3.0	0.37	7	NA
2000	2.7	3.8	0.34	12	NA
2001	2.7	0.6	0.10	14	1.23
2002	2.9	4.9	0.90	13	0.93
2003	2.8	1.3	0.15	11	0.97
2004	2.7	2.3	0.46	17	0.96
2005	2.3	1.5	0.71	8	1.01
2006	2.0	2.7	0.62	6	0.47
2007	2.1	2.3	0.66	3	0.73
2008	2.1	3.3	0.35	3	0.72
2009	2.2	3.0	0.00	1	0.71
2010	2.3	1.5	0.50	2	0.57
2011	2.2	1.5	0.50	2	0.50
2012	2.2	1.0	0.00	1	0.71

*NA= Not available; missing density estimates were summarized using the mean of adjacent years

APPENDIX G



Sensitivity analysis reflecting the influence of pup recruitment (R) rates on population predictions for tundra wolves denning on summer range of the Bathurst caribou herd.

APPENDIX H

Prey items isolated from wolf scats collected on the summer range of the Bathurst caribou herd, Northwest Territories and Nunavut, Canada, in 2013 (05 July-07 Sept). Prey items were determined by examining the medulla and cuticle patterns of hair found in scat (see Kennedy and Carbyn 1981).

Scat content			
Species	Number of Scats	Proportion	
Caribou	72	0.71	
Muskoxen	5	0.05	
Moose	1	0.01	
Arctic Hare	12	0.12	
Arctic Ground Squirrel	5	0.05	
Microtine	5	0.05	
Fish sp.	1	0.01	
Total Scats	101		

Prey Items in Scat			
	Number of Scats	Proportion	Total Caribou
1 Prey Type	66	0.76	52
2 Prey Types	20	0.23	19
3 Prey Types	0	na	na
4 Prey Types	1	0.01	1
Total Scats	87		72