


# Den site selection of wolves (*Canis lupus*) in response to declining caribou (*Rangifer tarandus groenlandicus*) density in the central Canadian Arctic

Michael R. Klaczek<sup>1</sup>  · Chris. J. Johnson<sup>2</sup> · H. Dean Cluff<sup>3</sup>

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**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. We investigated the factors that influenced den site selection for wolves on the summer range of the Bathurst caribou herd, Northwest Territories, Canada. We used a long-term data set (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. We 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 availability of caribou over the greatest portion of the denning period. As the caribou herd declined, the seasonal summer ranges contracted northward towards 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 behaviours reduce fitness and have implications for pup survival and population growth.

**Keywords** Resource selection function · *Canis lupus* · Behavioural response · *Rangifer tarandus groenlandicus*

✉ Michael R. Klaczek  
klaczekm@unbc.ca

Chris. J. Johnson  
johnsoch@unbc.ca

H. Dean Cluff  
dean\_cluff@gov.nt.ca

<sup>1</sup> Natural Resources and Environmental Studies Graduate Program, University of Northern British Columbia, 3333 University Way, Prince George, BC V2N 4Z9, Canada

<sup>2</sup> Ecosystem Science and Management Program, University of Northern British Columbia, 3333 University Way, Prince George, BC V2N 4Z9, Canada

<sup>3</sup> Department of Environment and Natural Resources, Government of the Northwest Territories, North Slave Region, Box 2668, Yellowknife, NT X1A 2P9, Canada

## Introduction

In most areas of North America, the grey 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 neighbouring 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 migrating caribou throughout most of the year and thus do not maintain annual territories (Walton et al. 2001; Hansen et al. 2013). In early spring, wolves migrate from their winter ranges 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). Prey availability may be low during the denning period (May through August) as 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 moshatatus*), is 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 tundra wolves select den sites where they can optimize the availability of caribou during the denning period; these areas include major migration routes (Clark 1971; Kuyt 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 ( $\pm 5300$  SE) in 2009 representing a 70 % decline over 3 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 in 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).

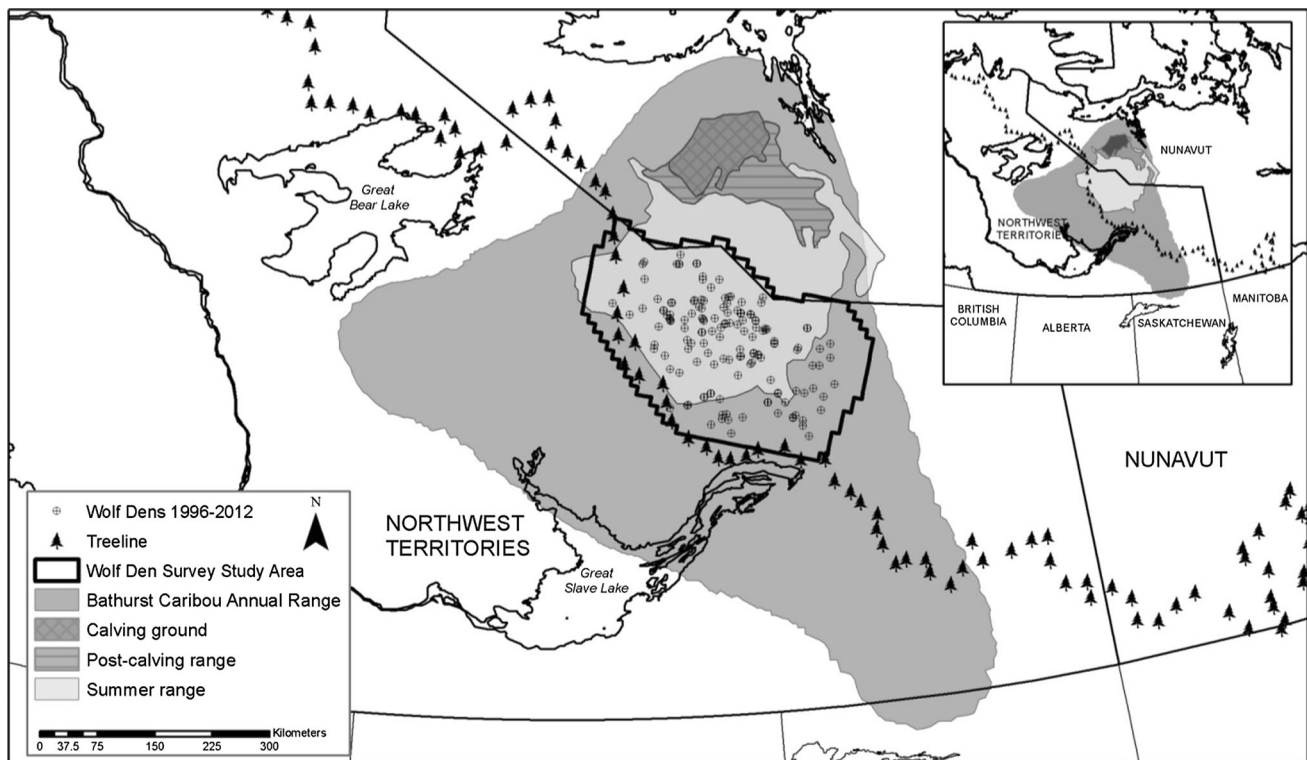
Heard and Calef (1986) and Heard and Williams (1992) hypothesized that wolf populations demonstrate a numerical response to caribou abundance, where density-dependent range expansion or contraction by caribou influences prey availability. For wolves limited to the area of caribou range adjacent to the den site, fewer prey results in higher pup mortality (Heard and Williams 1992; Walton et al. 2001; Frame et al. 2008) 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 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 spatio-temporal scales.

We investigated the mechanisms that influence the distribution of den sites for tundra wolves on the summer range of the Bathurst caribou herd relative to variation in prey availability over time. Specifically, we 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. We 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 behaviourally to declines in the availability of caribou over time.

## Materials and 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 (Fig. 1). Climate is characterized by short summers and very cold and long winters. The south-western portion of the study area encompasses Northern Canadian Shield Taiga (Ecosystem Classification Group [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 tree-line 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 north-east (Timoney et al. 1992).



**Fig. 1** 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 km<sup>2</sup>. 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 to 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 km<sup>2</sup> in the Northwest Territories

(Fig. 1). 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 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 to 2008, Argos satellite collars were used exclusively and recorded locations from weekly to daily intervals. From 2008 to 2012, 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 by season (Gunn et al. 2013).

### Resource selection functions

We 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

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

Variable	Description
<i>Land-cover types</i>	
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 <2 m, 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; include tree and shrub areas near and below treeline and are represented by sedge, moss, and low-shrub wetlands within the tundra
Eskers	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 <sup>2</sup> (8.54 km × 8.54 km) moving window across the study area
Seasonal caribou ranges <sup>a</sup>	Median straight-line distance from each den/random site to each seasonal caribou movement path

<sup>a</sup> 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)

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, we 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. We 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 (1996–2012, 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, we merged caribou polygons with a 100 % MCP around the locations of all active wolf dens recorded for each year.

We limited the northern extent of the analysis area to the political boundary of the Northwest Territories and Nunavut (Fig. 1) 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 (Fig. 1; Heard and Williams 1992; Walton et al. 2001; Frame et al. 2008). We quantified resource availability using five 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*

We identified land-cover types that were expected to explain the distribution of wolf dens at the landscape scale. We modified Northern Landcover/EOSD 30-m vegetation cover (Wulder et al. 2003; Olthof et al. 2009) into six classes representative of the broad cover types that occur in the study area (Table 1). We used CanVec Relief and Forms vector data (Natural Resources Canada 2007) to overlay the distribution of eskers across both boreal and

**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

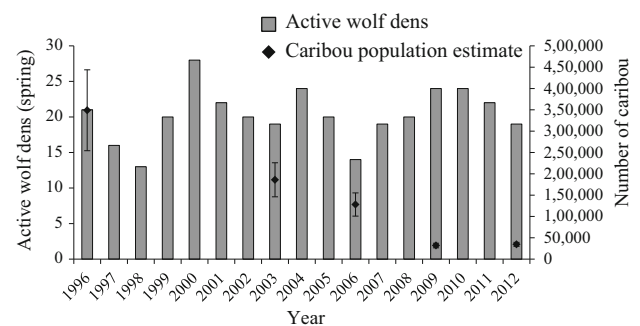
Model theme	Model parameters
Land cover	Percent cover of seven land-cover variables (Table 1) within 500-m radius of a den or random site
Land cover + esker density	Percent cover of seven land-cover variables within 500-m radius; number of esker pixels per 73-km <sup>2</sup> moving window
Land cover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

<sup>a</sup> Models were run with and without the squared (Gaussian) term to compare linear and nonlinear responses of wolves to caribou migration paths

tundra ecozones, resulting in a total of seven land-cover types. To model den site selection, we calculated the percent cover of each land-cover type within a 500-m radius of each den and random site. We 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-km<sup>2</sup> rectangular moving window to a binary image of esker habitat and calculating the density of pixels (ha/km<sup>2</sup>) across the study area (see Johnson et al. 2004, 2005).

#### Distance to seasonal caribou ranges

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). We 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 caring for newborn pups. We used the locations of satellite-collared (Argos and GPS) adult females from 1996 to 2012 to quantify the seasonal variation in the spatio-temporal distribution of caribou (Gunn et al. 2013; Table 1). We 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). We measured the straight-line distance from each den and random site to the closest edge of each caribou seasonal movement path. From each den, we then calculated the median distance from all seasonal paths and used this measure to represent the distance from each den to seasonal caribou areas, assumed from movement paths, typically used by caribou.



**Fig. 2** Total number of active wolf dens observed each spring (late May/early June) during aerial wolf den surveys on the summer range of the Bathurst herd in the Northwest Territories, Canada. Population estimates ( $\pm$ SE) for the Bathurst caribou herd based on calving ground aerial photo surveys

#### Model development and assessment

We 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 spatio-temporal variation in the availability of caribou (Table 2). First, we ran the set of candidate models using pooled den site data across all years (1996–2012; Fig. 2) to assess general factors that influence den selection by wolves. To assess the behavioural response of wolves to changing caribou densities, we 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 animals). A behavioural response would be inferred by a significant change in the value of coefficients between periods. We excluded 1998 from our analysis as only three caribou collars were functional over the majority of the denning period. To



**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

Model	<i>k</i>				$\Delta_i\text{AIC}$				$\text{AIC}w_i$			
	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 <sup>2*</sup>	14	13	14	15	<b>0.00</b>	<b>0.00</b>	2.04	10.06	0.62	0.56	0.22	<0.01
Full model**	15	14	15	16	1.41	0.52	<b>0.00</b>	<b>0.00</b>	0.30	0.43	0.63	0.99

The number of model parameters (*k*), differences in Akaike's information criterion scores ( $\Delta\text{AIC}$ ), 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

Bold numbers indicate the most parsimonious model

\* Gaussian term only included where appropriate

\*\* Full model = land cover + esker density + dist caribou + dist caribou<sup>2</sup>

identify variation in selection patterns as caribou declined, we excluded 2001–2002 and 2007–2008 from the response analysis (interval models).

We used a conditional (matched) logistic regression to model resource selection. Because merged caribou MCPs varied annually, we grouped the used and available data by year to represent annual changes in resource availability for wolves. We used a robust variance estimator to control for autocorrelation within the data set, as dens were used more than once during the study period (Rogers 1993). We 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). We used Akaike's information criterion (AIC) to select the most parsimonious model explaining selection of den sites (Anderson et al. 2000). The most parsimonious model had the lowest AIC score, explaining the greatest amount of variation in the observed data with the fewest parameters. We calculated  $\Delta\text{AIC}$  as the difference in AIC values between each model and the highest ranked model (Table 3). For further comparison, we calculated Akaike weights ( $\text{AIC}w_i$ ) for each model; this score represented the approximate probability that the selected model was the best among the proposed models (Anderson et al. 2000). We 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, we used  $\Delta\text{AIC}$  to determine whether a linear or a Gaussian term was appropriate. The nonlinear term was retained in RSF models if the additional quadratic parameter improved  $\Delta\text{AIC} \geq 2$  points.

Information theoretic approaches, such as AIC, provide relative measures of model fit. Thus, we used the receiver operating characteristic (ROC) to assess the predictive accuracy of each model. We conducted a onefold 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). We used 95 % confidence intervals to assess the strength of each predictor covariate. We conducted all analyses in Stata version 12.1 (StataCorp 2013).

### Descriptive analyses

Previous studies of wolves note that the spatial proximity of neighbouring packs should influence den site selection at the landscape scale (Paquet and Carbyn 2003). To help interpret RSF results, we measured the Euclidean distance between active wolf dens (interden distance; Ballard and Dau 1983) recorded on the Bathurst caribou range for each year. We 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). We 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. We 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

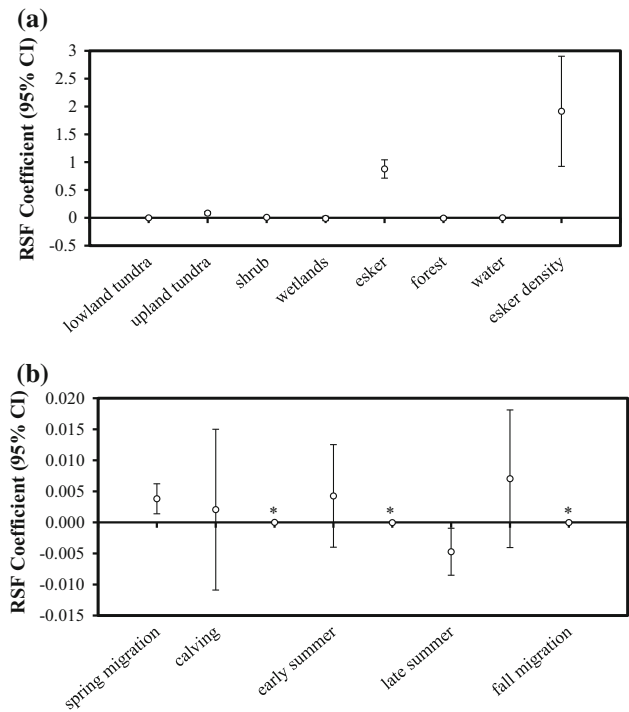
Surveys of wolf dens conducted by the Government of the Northwest Territories from 1996 to 2012 resulted in a total of 347 active den sites, of which 303 occurred within the study area (Fig. 2). On average, active den sites were reused 2.2 times (SD = 1.9) over the 17-year study period. We used locations from 135 Argos- and GPS-collared adult female caribou ( $\bar{X}$  = 14 collars/year; SD = 4.53, range = 5–23) to stratify seasonal migration routes from 1996 to 2012. The number of caribou fitted with collars over each abundance period averaged 9, 12, 17 collars per year for High, Medium, and Low periods, respectively (SD = 2.98, 4.6, 3.65; range = 7–16, 5–18, 11–23). We 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

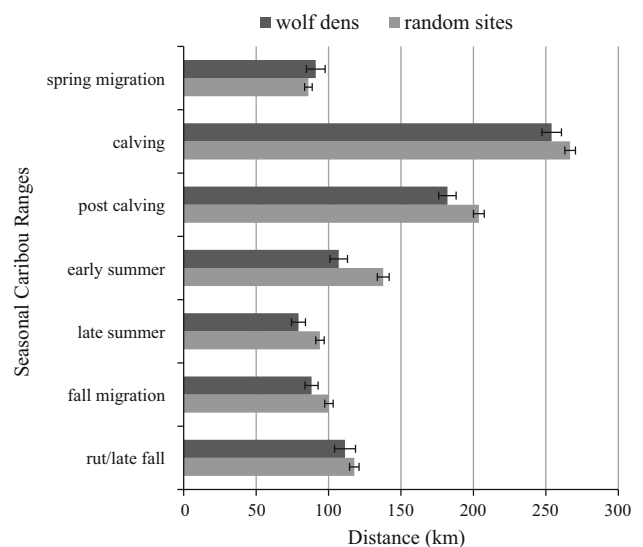
Across all years, the most parsimonious model for den site selection included covariates for land cover, distance to caribou migration routes, and esker density (Full Model; Table 3). The best model had good discriminatory ability (AUC =  $0.82 \pm 0.01$  SE). Within a 500-m radius of the den, wolves selected for esker and upland tundra features. The coefficient for esker was strongest; no other land-cover covariates besides these two influenced den site selection (Fig. 3a). Wolves selected areas with relatively high-density eskers (Fig. 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 (Fig. 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 (Fig. 4).

### Response of wolves to changes in caribou density

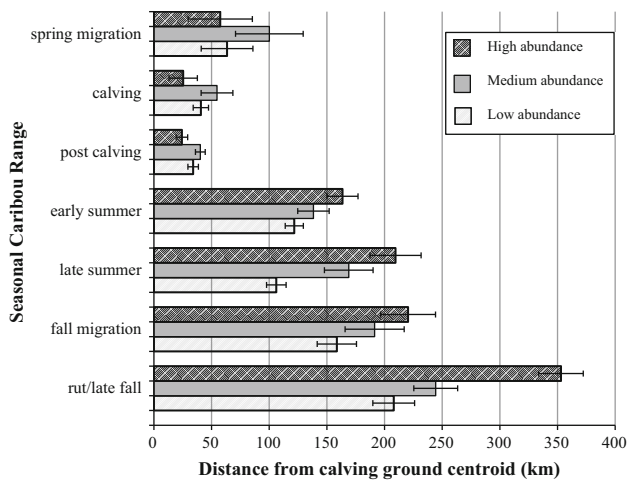
The summer range for caribou contracted significantly from the late 1990s when the herd was estimated at >300,000 animals to current estimates of 35,000 animals (ENR 2011). The 95 % caribou MCPs (based on locations 01 April to 30 September) to stratify annual availability decreased over time, from an average of 94,670 km<sup>2</sup> ( $\pm 20,466$  km<sup>2</sup> SE) during the High period, 79,465 km<sup>2</sup> ( $\pm 11,481$  km<sup>2</sup>) during the Medium period, to 59,185 km<sup>2</sup> ( $\pm 8,512$  km<sup>2</sup>) 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 towards the centroid of the calving



**Fig. 3** RSF 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 ranges on the Bathurst caribou summer range from 1996 to 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). Asterisk The Gaussian (squared) term was included for distance to seasonal migration path



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

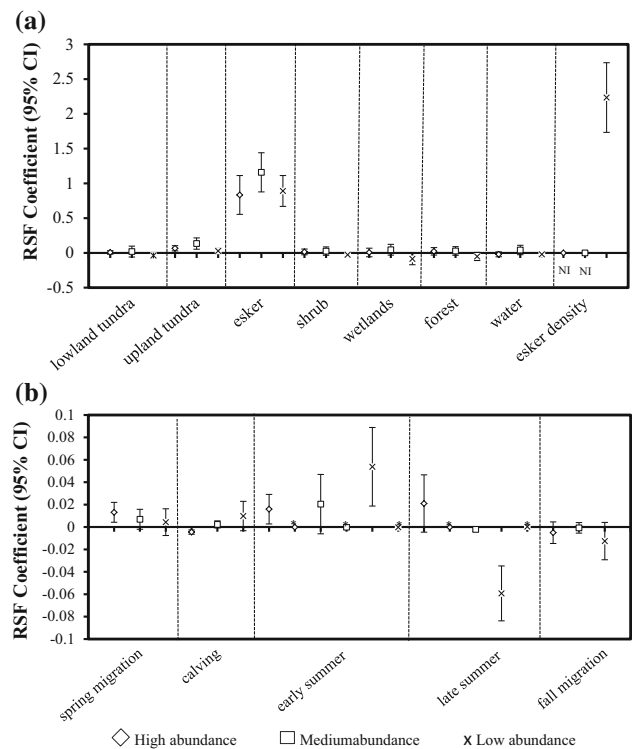


**Fig. 5** Relative change in the seasonal distribution of the Bathurst caribou herd ( $\pm 95\%$  CI) as represented by distance from calving ground. For each year, the Euclidean distance from the centroid of the Bathurst calving ground (constant) was measured to seasonal movement paths of Argos- and 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)

ground (Fig. 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  $21.7 (\pm 1.16)$  km to  $28.9 (\pm 1.88)$  km from High to Medium periods, respectively. Interden distance remained at  $28.32$  km ( $\pm 1.94$ ) during Low caribou years.

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 (Table 3). The second ranked model included an additional covariate for esker density and differed by  $<2$  AIC points (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 and the next most parsimonious model included the additional covariate for esker density (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 (Table 3) and the next most parsimonious model included only covariates for land cover and caribou migration route (Table 3). All models had relatively large ROC scores ( $AUC = 0.75 \pm 0.02$  SE,  $0.79 \pm 0.01$ ,  $0.75 \pm 0.02$ ; 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

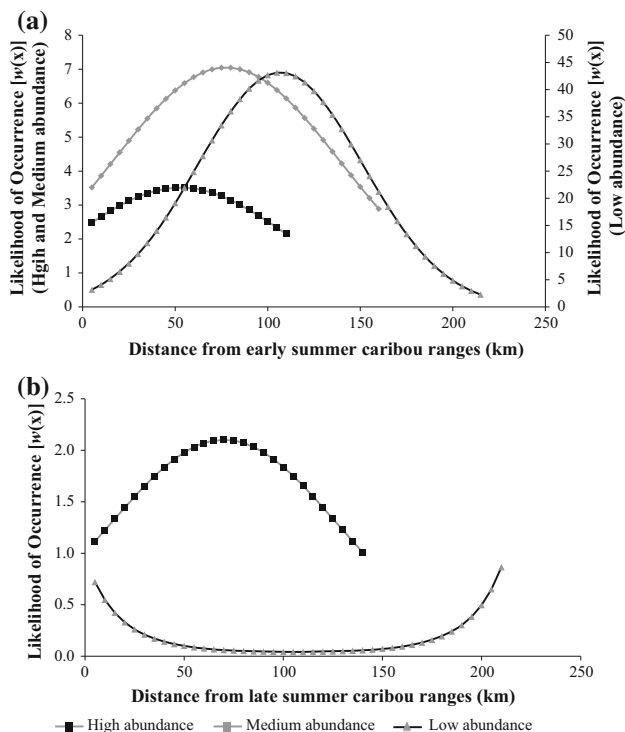


**Fig. 6** RSF coefficients and  $95\%$  confidence intervals from the best conditional fixed-effect logistic regression models used to investigate selection of wolf dens relative to **a** land-cover types and **b** the distribution of seasonal caribou ranges over three periods of abundance in the Bathurst 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. Asterisk The Gaussian (*squared*) term was included for distance to seasonal migration path

selected for eskers (Fig. 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 (Fig. 6a). Wolves selected for dens in areas of high esker density only when caribou abundance was low (Table 3; Fig. 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 seasonal ranges was nonlinear, with coefficients for the linear term being positive across all model periods, indicating the probability of occurrence increased to a distance and then decreased (Figs. 6b, 7a). Selection did not statistically differ between model periods; however, quadratic plots indicated that the peak probability of occurrence for a den increased with





**Fig. 7** Plots representing the strength of selection [ $w(x)$ ] for den sites of tundra wolves relative to seasonal caribou ranges 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 seasonal caribou ranges while all other model covariates were held at their mean values

distance from the early-summer seasonal ranges as the abundance of caribou declined (55, 80 and 105 km during High, Medium, and Low periods, respectively; Fig. 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 (Figs. 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 (Fig. 6b).

## Discussion

The application of resource selection functions to long-term and spatially extensive data of wolf den occupancy in the Arctic allowed us 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 may account for the consistent selection of eskers 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 our 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 our study area, dens were on average 190 m (SD = 201) from the nearest water source and random sites were only 30 m farther ( $\bar{X} = 220 \text{ m} \pm 168 \text{ m}$ ).

## Importance of seasonal caribou distribution for den selection

We 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).

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. Our 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. Klaczek, 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).

Our 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. 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 inherently increases the biomass of a more vulnerable prey base. Bathurst caribou were farthest 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 to 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 (Mech 1966; Peterson 1977; Musiani et al. 1998; Jedrzejewski et al. 2001). 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

We hypothesized that denning wolves would demonstrate a behavioural response to changing caribou densities on the Bathurst range. We 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. 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 movement paths from the calving ground, was reduced by half between periods of High and Low abundance. Relative to when caribou abundance was High, quadratic plots (Fig. 7) during Low caribou abundance indicated that late-summer probabilities of den occurrence decreased as distance increased from late-summer caribou seasonal ranges. 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 few 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.

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). We 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 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. We 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 grey 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 1983; 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. However, 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).

Our results suggest that as caribou numbers decreased, the main distribution of the Bathurst herd remained farther away from the denning areas of wolves for relatively longer periods of the summer. Although tundra wolves are well equipped to travel far distances in search of caribou (Walton et al. 2001; Frame et al. 2004), or rely more on other prey species such as muskoxen, flightless waterfowl, or Arctic ground squirrel (Williams 1990), such significant decreases in caribou biomass within their denning ranges inevitably led to prey shortages. In our study area, the lack of a behavioural response by wolves to significant changes in both the abundance and distribution of caribou resulted in lower fitness with implications for pup survival and population growth (Klaczek 2015). These dynamics support a regulatory mechanism whereby tundra wolf populations respond numerically to the density-dependent range use patterns of barren-ground caribou (Heard and Williams 1992; Klaczek 2015).

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