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Research Article

Wolf–Caribou Dynamics Within the Central Canadian Arctic

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ABSTRACT The severity of recent declines of barren-ground caribou (*Rangifer tarandus groenlandicus*) across the central Canadian Arctic has led to harvest restrictions and concerns about population recovery. Wolves (*Canis lupus*) are the main predator of barren-ground caribou; however, the extent that wolves influence the decline and recovery of caribou herds is unknown. Such uncertainty confounds management responses (e.g., reducing harvest, predator control). We investigated wolf–caribou dynamics on the summer range of barren-ground caribou in the Northwest Territories and Nunavut, Canada (i.e., Bathurst caribou herd). Our primary objective was to test for a numerical response of wolves to changes in the abundance and spatial distribution of caribou. Caribou experienced a >90% decline in abundance over the study period (1996–2014). Using long-term data sets (1996–2012), we developed regression models to investigate relationships between abundance indices of wolves and range-use patterns of caribou. We monitored the movements of adult female wolves fitted with global positioning system (GPS) collars representing individual packs throughout the 2013 and 2014 denning periods. We also investigated pup recruitment, an index of population decline, at a time of low caribou abundance. Finally, we 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. As caribou abundance decreased, the late-summer distribution of the Bathurst herd contracted toward the calving ground. These movements correlated with low rates of wolf pup recruitment 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. In 2014, wolf density was estimated at <4 wolves/1,000 km^2. Our results suggest that these wolves exhibited a relatively strong numerical response to a single, declining prey base. Given the continued decline in the Bathurst caribou herd, the tundra wolf population on the Bathurst range has likely declined below our 2014 estimate. © 2016 The Wildlife Society.

KEY WORDS *Canis lupus*, Northwest Territories, numerical response, Nunavut, population dynamics, predator–prey relationships, *Rangifer tarandus groenlandicus*.

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) because alternate prey, such as moose (*Alces alces*) or muskoxen (*Ovibos moshatus*), occur at low densities in the central Arctic (Ecosystem Classification Group [ECG] 2012).

The barren-ground caribou herd in the Northwest Territories and Nunavut, Canada (i.e., Bathurst caribou herd), estimated at 350,000 (±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

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(±5,300 SE) animals in 2009, representing a 70% decline over 3 years (Adamczewski et al. 2009). Results from the latest reconnaissance survey in 2014 indicated that the Bathurst herd may have declined to 16,000 animals (Adamczewski et al. 2014). The factors influencing the decline of the Bathurst herd are not clear (Adamczewski et al. 2009, 2014; Boulanger et al. 2011). In the past, forage limitation and predation were the key mechanisms hypothesized to influence the population dynamics of large migratory caribou herds (Messier et al. 1988, Valkenburg 2001). Contemporary theories suggest that other factors (e.g., hunting pressure, anthropogenic development, insect harassment, disease, 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 may regulate the Bathurst caribou herd (Johnson et al. 2005, Boulanger and Gunn 2007, Boulanger et al. 2011, Barrier and Johnson 2012, Witter et al. 2012); however, direct links to long-term population-level fluctuations have not been made, leading to debate about the key influences and appropriate management responses.

The extent that tundra wolves influence caribou population dynamics in the Arctic is unknown (Thomas 1995, Valkenburg 2001, Boulanger et al. 2011). Theoretically, an estimate of overall predation rate from wolves can be calculated as the product of the functional and numerical response of the predator. 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). Some studies suggest that wolf predation can influence the abundance of large migratory populations of caribou but only during the decline phase of an assumed cyclical dynamic (Messier et al. 1988, Couturier et al. 1990). Wolves likely have a greater long-term influence when caribou densities are low (0.4 caribou/km^2) or when wolf densities are high (Messier et al. 1988, Thomas 1995, Bergerud 1996). For example, Bergerud (1996) generalized that wolf densities >6.5 wolves/1,000 km^2 may limit population growth for migratory caribou, although results varied among herds and were dependent on the availability of alternate prey such as moose, which could maintain wolf populations when caribou numbers declined.

The primary factors influencing wolf population dynamics on barren-ground caribou range are not clear. Although strong correlations between wolf density and ungulate biomass have been established in several wolf populations across North America (Keith 1983, Fuller 1989, Fuller et al. 2003, McRoberts and Mech 2014, Mech and Barber-Meyer 2015), recent studies suggest this relationship may not be linear (Cariappa et al. 2011, Cubaynes et al. 2014). For example, at low ungulate densities, a reduction in prey biomass can influence pup survival and population growth (Fuller et al. 2003, Gude et al. 2012, Stahler et al. 2013). However, when wolf densities are high, populations may be limited by social factors such as intraspecific strife or territorially that can influence adult survival and dispersal (Kreeger 2003, Mech and Boitani 2003, Creel and Rotella 2010, Cariappa et al. 2011, Cubaynes et al. 2014).

Heard and Calef (1986) and Heard and Williams (1992) suggested that tundra wolf populations responded 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 (Heard and Calef 1986, Messier et al. 1988, Couturier et al. 1990, Gunn et al. 2012, Klaczek et al. 2015). Each spring, 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). On the Bathurst caribou summer range, distances between den sites and the main distribution of caribou average between 250 km and 180 km during the calving and post-calving periods, respectively (Klaczek et al. 2015). When caribou are abundant, the herd returns earlier to the southern portions of the summer range and closer 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 results in the main distribution of the herd being farther from wolf dens for relatively longer periods of the summer (Heard and Williams 1992, Klaczek et al. 2015). Lower densities of caribou within the denning areas may force wolves to travel farther in search of prey to sustain their growing pups (Walton et al. 2001, Frame et al. 2004). Alternatively, ensuing prey shortages would likely lead to higher rates of pup mortality (Fuller et al. 2003). 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.

We investigated wolf–caribou dynamics on the summer range of the Bathurst caribou herd. Our primary objective was to test for a numerical response of wolves to changes in the abundance and spatial distribution of caribou. We hypothesized that wolves would demonstrate a numerical response to changing caribou densities. We predicted that during a period of low caribou density, pup recruitment would be limited and den occupancy and pup numbers would decline as caribou decreased in distribution and abundance.

STUDY AREA

We conducted our research within the summer range of the Bathurst caribou herd, an area encompassing approximately 71,000 km^2 in the Northwest Territories and Nunavut, Canada (Fig. 1). The region is influenced by a continental Arctic climate and experiences short cold summers and very cold and long winters (ECG 2012). The landscape comprises rolling uplands of Canadian Shield rock and lowlands that contain fens, bogs, and tundra lakes (ECG 2012). The area is used by the Bathurst caribou herd during spring migration

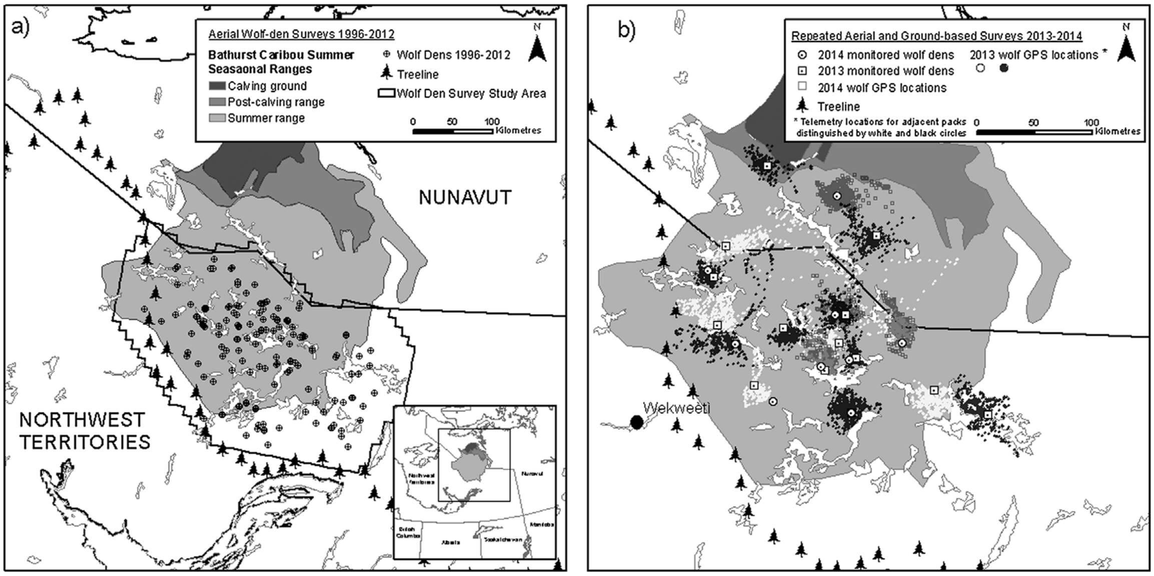

Figure 1. Location of the wolf study area on the summer range of the Bathurst barren-ground caribou herd Northwest Territories and Nunavut, Canada. Boundaries were delineated using movements of caribou monitored with satellite collars from 1996 to 2008. Wolf population monitoring consisted of (a) annual aerial surveys (1996–2012) that recorded active wolf dens ($n = 303$) in late May and early June (active dens were surveyed again in Aug to assess pup recruitment) and (b) repeated surveys of global positioning system (GPS)-collared adult female tundra wolves (circles, $n = 15$, 2013; squares, $n = 4$, 2014) representing individual packs during the 2013 and 2014 denning periods. We monitored 8 additional wolf packs without a GPS-collared adult female wolf in the 2013–2014 denning periods (2 and 6, respectively).

north to the calving ground and again during the mid- and late-summer, after the majority of the herd returns from their calving and post-calving ranges (Gunn et al. 2002, Klaczek et al. 2015). Wolves select den sites within close proximity to the early- and late-summer seasonal ranges of caribou (Klaczek et al. 2015). Spatially, these seasonal distributions represent reliable availability of caribou over the greatest portion of the denning period when wolves are restricted to areas near the den site caring for newborn pups (Heard and Williams 1992, Klaczek et al. 2015). The Bathurst herd typically remains along the treeline, within the southern portion of the study area, during the late-fall rutting period before returning to the taiga during winter (Gunn et al. 2002, 2013). Other ungulates in the study area include muskoxen, which are present in limited numbers and moose, which are considered scarce and only occur across the southern portion of the study area (ECG 2012). Other large carnivores that prey upon barren-ground caribou include grizzly bear (*Ursus arctos*) and wolverine (*Gulo gulo*; Mulders 2000, Gau et al. 2002, ECG 2012). The Bathurst caribou herd is highly valued for cultural and subsistence purposes by Aboriginal communities within the Northwest Territories and Nunavut, Canada. Mineral exploration and extraction are the predominant industrial land-use activities (Johnson et al. 2005). During the summer months, this area is only accessible by aircraft.

METHODS

Wolf Population Monitoring

We used a long-term data set of den occupancy and pup recruitment collected on the summer range of the Bathurst herd during a period of significant decline in caribou abundance. From 1996 to 2012, the Government of the Northwest Territories conducted annual aerial surveys of wolf dens during early spring (late May to early Jun) and late summer (mid to late Aug) to monitor den occupancy, pack size, and pup recruitment (Fig. 1). Active dens during 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.

We used repeated aerial- and ground-based surveys of wolves monitored with global positioning system (GPS) radio-collars to document changes in pup recruitment during a period of relatively low caribou abundance. From 21 to 24 June 2013, we captured 16 female wolves, 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 analysis. 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. The GPS collars were programmed to obtain a location every 1.5 hours (16 locations/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.

The treeless tundra and extended daylight hours provided an opportunity to count pups from the air or from a distance on the ground (Frame et al. 2008). However, aerial counts may be biased because of pups remaining in the den or under vegetation during surveys. We used a small fixed-wing aircraft on floats (Aviat Husky, Afton, WY, USA) or a helicopter to conduct aerial and ground-based surveys at wolf home sites in early and late summer (early Jul, mid-Aug, and early Sep 2013; Jul and late Aug 2014). We used the GPS-collar data to locate the dominant female wolf and we observed pack size and the number of pups for each monitored wolf pack. Those data allowed us to measure changes in pup survival over the summer and to generate a measure of fall recruitment.

To minimize disturbance while on the ground, we 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 behavioral response (e.g., wolf leaving the area). After 2 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 because pups typically came out of the den because they were likely curious and hungry.

Wolf Abundance Indices and the Spatial Distribution of Caribou

We examined the relationship between caribou migration patterns and the population dynamics of dependent wolf populations. We used location data from satellite- and GPS-collared adult female caribou collected over 17 years (1996–2012; $n = 135$ female caribou) to quantify patterns of range use (Fig. 2). From 1996 to 2008, Argos satellite collars were used exclusively and recorded locations from weekly to daily intervals. From 2008 to 2013, GPS and Argos collars were deployed, resulting in the collection of animal locations at daily and hourly intervals. We 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 (Klaczek et al. 2015) and summarized the mean distance across all caribou for each year of the study. Movement paths were generated from late-summer (19 Jul–22 Aug; Gunn et al. 2013) locations of collared adult female caribou in Bathurst herd. Although the distribution of the calving ground changed gradually over time (Gunn et al. 2002, 2013), we held the centroid constant (Adamczewski et al. 2009) to measure the relative changes in late-summer distribution of caribou at a broad spatiotemporal scale. We 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).

We used a linear regression and a negative binomial 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 (linear regression) and late summer den occupancy (count model) were documented during aerial surveys of wolf dens located on the herd's summer range over the period of caribou decline (1996–2012). We used these metrics as response variables that were regressed against the relative annual contraction in caribou distribution in late-summer (19 Jul–21 Aug) during the period of population decline. We conducted statistical analyses using Stata 12.1 (Statacorp,

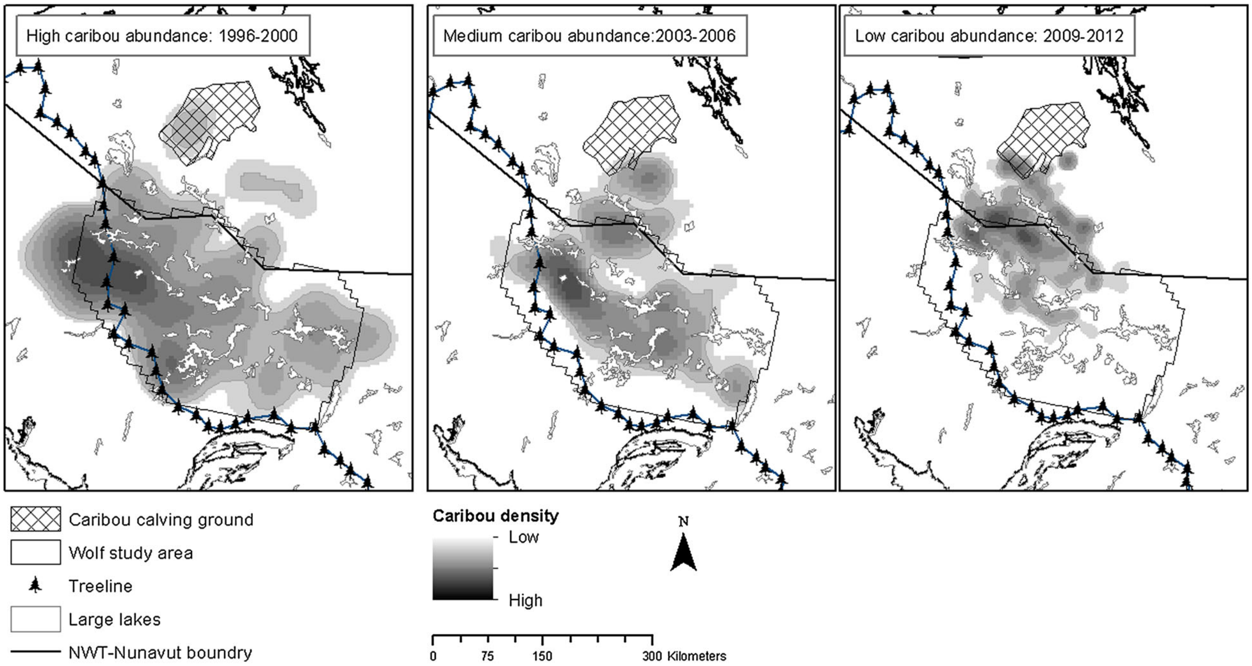

Figure 2. Late-summer (19 Jul–21 Aug) distribution of satellite-collared (Argos and global positioning system [GPS]) adult female caribou of the Bathurst herd at high, medium, and low abundance (population estimates: 349,000–300,000, 286,000–128,000, 32–35,000 caribou, respectively). Range use was calculated using a fixed-kernel density estimate with 90% isopleths and illustrates the density-dependent range contraction of the Bathurst caribou herd, Northwest Territories (NWT) and Nunavut, Canada.

College Station, TX, USA). We considered a P-value < 0.05 as statistically significant.

Wolf Population Dynamics

We developed a series of stochastic population models (VORTEX 9.99c; Lacy and Pollak 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. We constructed separate model scenarios using birth rates, recorded as late-summer pup counts, during 3 levels of caribou abundance: high 1996–2000 (349,000–300,000 animals), medium 2002–2006 (186,000–128,000 animals), and low 2009–2012 (32,000–35,000 animals). Parameter estimates were based on demographic data derived from aerial surveys collected over 16 years (1996–2012; Environment and Natural Resources [ENR] 2012); we used professional knowledge and published literature when other data were not available (Appendix A).

We derived recruitment from late August counts of pups and summarized recruitment by model period ($\bar{x}$ annual pups/pack). Reproductive success for wolves varies across spatio-temporal scales and may be influenced by a variety of environmental and demographic factors (Fuller et al. 2003). White (2000) defined this inherent stochasticity at the population level as process variation; we used this calculation to isolate the process variance ($V_w[R]$; White (2000)) for pup recruitment rates for each model scenario.

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

$$K = \frac{B_{\text{range}}}{P_{\text{territory}}} \times P_{\max} \qquad (1)$$

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

We estimated wolf density (wolves/1,000 km^2) for each year based on extrapolation using estimates of mean pack size ($\bar{P}_{\text{mean}}$) and mean den density ($\bar{D}_{\text{density}}$; active dens/1,000 km^2) recorded during aerial surveys (Ballard et al. 1987, 1997, Fuller and Snow 1988, Adams et al. 2008). For each model period, initial population size (N_{initial}) was based on mean wolf density estimates (Equation (2)). The initial population was distributed among age–sex classes according to a stable age distribution (Lacy and Pollak 2013):

$$N_{\text{initial}} = \bar{D}_{\text{density}} \times \bar{P}_{\text{mean}} \times B_{\text{range}} \qquad (2)$$

Population models were stage-structured, representing 3 age classes: pups (0–1 yr), yearlings and subadults (>1–2 yr), and adults (>2 yr; Kelly et al. 1999). Wolf survival likely varied among age classes (Fuller et al. 2003, Creel and Rotella 2010, Gude et al. 2012, Ausband et al. 2015); 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, Creel and Rotella 2010). Diseases (e.g., canine distemper, 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). Incentive programs are in place to increase the level of harvest of wolves on the Bathurst range (Wek'èezhìi Renewable Resources Board 2013, Adamczewski et al. 2014). For this population, however, harvest is likely low during summer because of poor fur condition (wolves are harvested mainly for pelts), in addition to the remoteness and inaccessibility of the area. Human-caused mortality is higher during winter as wolves move closer to communities and a winter ice road when they migrate with the caribou herd below treeline. Overall, the number of wolves harvested on the Bathurst range is thought to be low given the inherent difficulty in harvesting wolves in this remote area.

Recognizing this uncertainty, we used conservative estimates of wolf mortality based on rates reported by Fuller et al. (2003) for unexploited populations. Furthermore, we held that parameter constant across all model scenarios. We assumed that mortality rates for pups were higher and more variable than those of yearlings and subadults, and once wolves were >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).

As with mortality rates, we inferred other demographic parameters from the published literature, and held them constant across the 3 model scenarios (Appendix A). Wolves typically start breeding at approximately 2–3 years; however, the maximum breeding age was not clear. Older wolves (>4 or 5 years) may be replaced by younger breeders (Stahler et al. 2013), and as such, we 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 dynamics; sex ratio at birth was unknown and assumed at parity (Kelly et al. 1999).

The population model did not account for complex socio-behavioral processes such as age of dispersal, mate choice, or lone wolves not associated with a breeding pack. Although these factors can influence the persistence of wolf populations, rates can vary substantially because of a variety of environmental factors (Fuller et al. 2003, Adams et al. 2008). Few data were available to accurately describe these factors for wolves in the central Arctic.

We used the population model to project wolf population trajectories over 25 years, a period that allowed us to evaluate the influence of observed changes in pup recruitment on wolf population dynamics over a feasible management planning horizon. We ran simulations 10,000 times for each model scenario. We summarized changes in relative abundance (%) and used the geometric mean to summarize stochastic population growth (λ) across model scenarios. We iteratively decreased pup recruitment to assess the sensitivity of the model to uncertainty in this estimated parameter.

We generated population predictions for 3 time periods, represented as scenarios that corresponded to changes in abundance of the caribou herd in Bathurst (high, medium, and low abundance). We 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 caribou population decline (1996–2014). We used the initial population size for subsequent scenarios based on the final population that was predicted from the previous simulation (i.e., the final population size in scenario high was used as the initial population size in scenario medium and so forth). We compared the population estimates of wolves estimated by the model with those extrapolated from density estimates of wolves collected during aerial surveys (Appendix B).

RESULTS

Wolf Population Monitoring on the Bathurst Caribou Summer Range

In the late 1990s, pup counts collected during aerial surveys in August consistently averaged ≥ 3 pups/pack annually. 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 (Fig. 3; $n = 1–2$ 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 (Fig. 3). From 1996 to 2006, approximately half of the dens occupied during spring were still active in late summer ($\bar{x} = 53\% \pm 5$ SE). From 2007 to 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 ($\bar{x} = 2 \pm 0.4$).

Over the 2013 and 2014 denning periods, we monitored 27 wolf packs (17 and 10, respectively), 15 of which were monitored via a GPS-collared adult female (15 and 4 collared wolves in 2013 and 2014, respectively). We conducted over 204 aerial checks to track wolf packs and spent >111 hours observing wolf dens and rendezvous sites on the ground during 66 separate field visits. We assumed that the sample of observed wolves was unbiased and sufficient to document pup recruitment for the population.

In 2013, the mean number of pups/pack declined throughout the denning period from 2.9 (±0.31 SE) in July, 2.0 (±0.40) in August, and 1.7 (±0.37) in early September (Table 1). The mean number of wolves/pack was 5.1 (±0.5) and typically consisted of the breeding pair with 1 other adult or sub-adult and the pups. Six of the monitored packs relocated to nearby den or rendezvous sites during the study period. Only 3 packs remained at their respective whelping den throughout the denning period (early Sep); thus, litter loss accounted for 50% of observed den abandonment (Table 1).

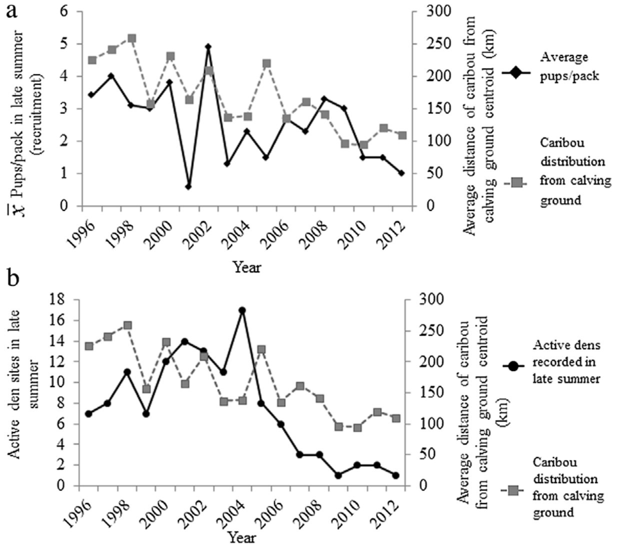

Figure 3. Temporal patterns for (a) wolf pup recruitment (black diamonds) and (b) late-summer den occupancy (black circles) recorded during aerial surveys in relation to the relative late-summer distribution of caribou from the calving ground (1996–2012; gray squares). For each year, the average Euclidean distance was measured from the centroid of the Bathurst calving ground (0 km) to caribou movement paths (19 Jul–22 Aug). This measure was used to calculate the relative distribution of satellite-collared adult female caribou in late summer.

In 2014, the mean number of pups/den declined throughout the denning period from 2.6 (±0.6) in early July to 1.8 (±0.7) in late August (Table 1). The mean number of wolves/pack was 4.8 (±0.9; Table 1). Pack structure was consistent with 2013 where the breeding pair was either alone or accompanied by 1 other adult or sub-adult wolf (usually female). 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, we censored these data from the recruitment estimate.

Wolf–Caribou Dynamics

The late-summer seasonal distribution of caribou contracted northward as the population declined in abundance (Fig. 2). From 1996 to 2000, the distances of collared caribou from the calving grounds averaged 223 km (±17.4 km SE) when population size of the herd was >300,000 animals. As the herd declined, however, 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) abundance periods, respectively (Fig. 3).

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 (Fig. 4). As the area of caribou range extended south during late summer, concurrent with a greater density of caribou, pup recruitment also increased (Fig. 4a; $F_{1,\,15} = 7.70$, $R^2 = 0.28$, $P = 0.014$). The negative binomial count model showed a similar relationship: rates of

Table 1. 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.

			Early[b] summer		Late[c] summer	
Year	**No. packs monitored[a] without and with GPS-collared adult female**	**Mean adults/pack (SE)**	**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 (0.80)	6	1.8 (0.69)	8
Pooled	27	2.6 (0.16)	2.8 (0.33)	19	1.8 (0.33)	25

[a] We present the number of packs with a global positioning system (GPS)-collared female in parentheses.

[b] Early July.

[c] Late August–early September.

den abandonment increased as the late-summer distribution of caribou contracted northwards towards the calving ground (Fig. 4b; $\chi_1^2 = 5.90$, $P = 0.015$).

Wolf Population Dynamics

With an average seasonal range of 961 km^2 (±137 km^2 SE, $n = 13$, 2013–2014), we estimated that approximately 74 wolf packs could occupy the 71,000-km^2 Bathurst summer range. We used an upper limit of 7 wolves/pack (Parker 1973), which provided an estimated carrying capacity of approximately 517 wolves or a density of 7.28 wolves/1,000 km^2 (Table 2). We extrapolated estimates of wolf density based on observed average pack size and den density recorded during aerial surveys (Table 2). When caribou abundance was high in the late 1990s, we estimated the wolf population at 497 individuals, slightly below the spatially derived estimate of K. The estimated wolf population declined to 295 and 177 individuals during medium and low periods of caribou abundance, respectively (Table 2).

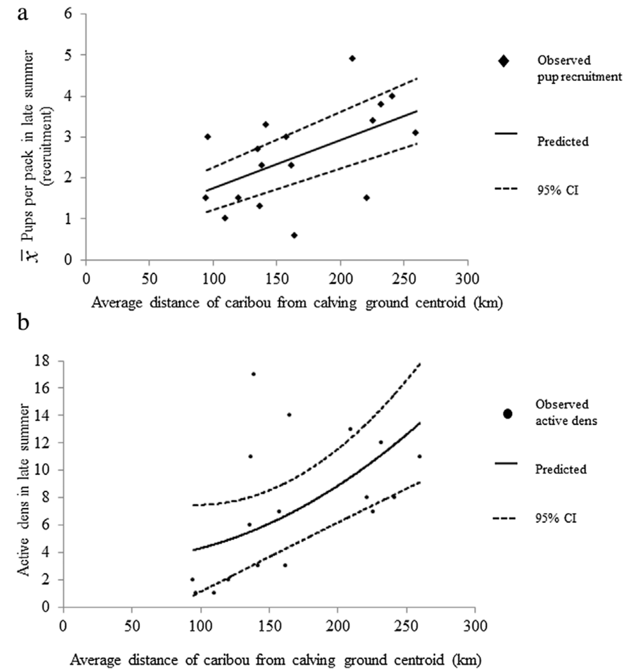

Figure 4. Spatial relationships between late-summer (a) wolf pup counts (black diamonds), and (b) den occupancy (black circles) and late-summer distribution of adult female caribou from the Bathurst herd Nunavut, Canada using a linear and negative binomial regression model, respectively. For each year, the average Euclidean distance was measured from the centroid of the Bathurst calving ground (0 km) to caribou movement paths (19 Jul–22 Aug). We used this measure to calculate the relative distribution of satellite-collared adult female caribou in late summer.

From 1996 to 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 ($\Delta \sim 5\%$; Fig. 5). From 2002 to 2006, pooled mean annual recruitment decreased to 2.54 pups/pack ($V_w[R] = 1.30$), resulting in population decline ($\lambda = 0.99$) and a 33% decrease in relative abundance of the wolf population over a 25-year period (Fig. 5). From 2009 to 2012, pooled mean annual recruitment decreased further to 1.75 pups/pack ($V_w[R] = 0.79$), the wolf population declined more rapidly ($\lambda = 0.94$), and we estimated a 95% decrease in relative abundance of the tundra wolf population after 25 years.

The stochastic population model represented wolf population dynamics over the period when the abundance of the Bathurst herd declined by >90% (1996–2014). We estimated initial wolf density at 7.0 wolves/1,000 km^2 in the mid-1990s and that density remained stable at 6.8 wolves/1,000 km^2 by 2002. From 2003 to 2008, modeled wolf density decreased slightly to 6.0 wolves/1,000 km^2 and more substantially to 3.7 wolves/1,000 km^2 by 2014 (Fig. 5). In comparison, results from extrapolation of aerial survey data suggested a density of 6.10 wolves/1,000 km^2 in 1996 and then 5.93, 3.57, and 2.71 wolves/1,000 km^2 in 2002, 2008, and 2012, respectively (Fig. 5). When holding other parameters constant, population trajectories increased when pup recruitment was >3.0 pups/den and decreased when recruitment was <2.5 pups/den (Appendix C).

DISCUSSION

We 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. Our results corroborate previous studies of wolves in North America (Keith 1983, Fuller 1989, Boertje and Stephenson 1992, McRoberts and Mech 2014, Mech and Barber-Meyer 2015) reporting that ungulate biomass strongly influences wolf population dynamics. Long-

Table 2. 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	High caribou 1996–2000	Medium caribou 2002–2006	Low caribou 2008–2012
Den density (dens/1,000 km^2; SE)	1.10 (0.06)	0.83 (0.10)	0.62 (0.05)
Average pack size (adults and sub-adults + pups; SE)	6.4 (0.2)	5.0 (0.7)	4.0 (1.0)
Wolf density (wolves/1,000 km^2)	7.0	4.2	2.5
Spatially derived carrying capacity (no. individuals)	517	517	517
Initial population size (no. 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)[a]			
Adults (>2 yr)	20 (5)	20 (5)	20 (5)
Subadults (1–2 yr)	25 (5)	25 (5)	25 (5)
Pups (<1 yr)	35 (10)	35 (10)	35 (10)

[a] Mortality rates estimated from literature (Fuller et al. 2003).

term aerial survey data revealed a reduction in pup recruitment and an increase in den abandonment as caribou abundance declined and the distribution of the Bathurst herd contracted northward. These results were consistent with repeated aerial and ground-based surveys during the 2013 and 2014 denning periods where we documented high rates of den abandonment and low pup recruitment for packs monitored with a GPS collar. Litter loss accounted for almost half of observed den abandonment and typically occurred in July, within or just following the period of spatial

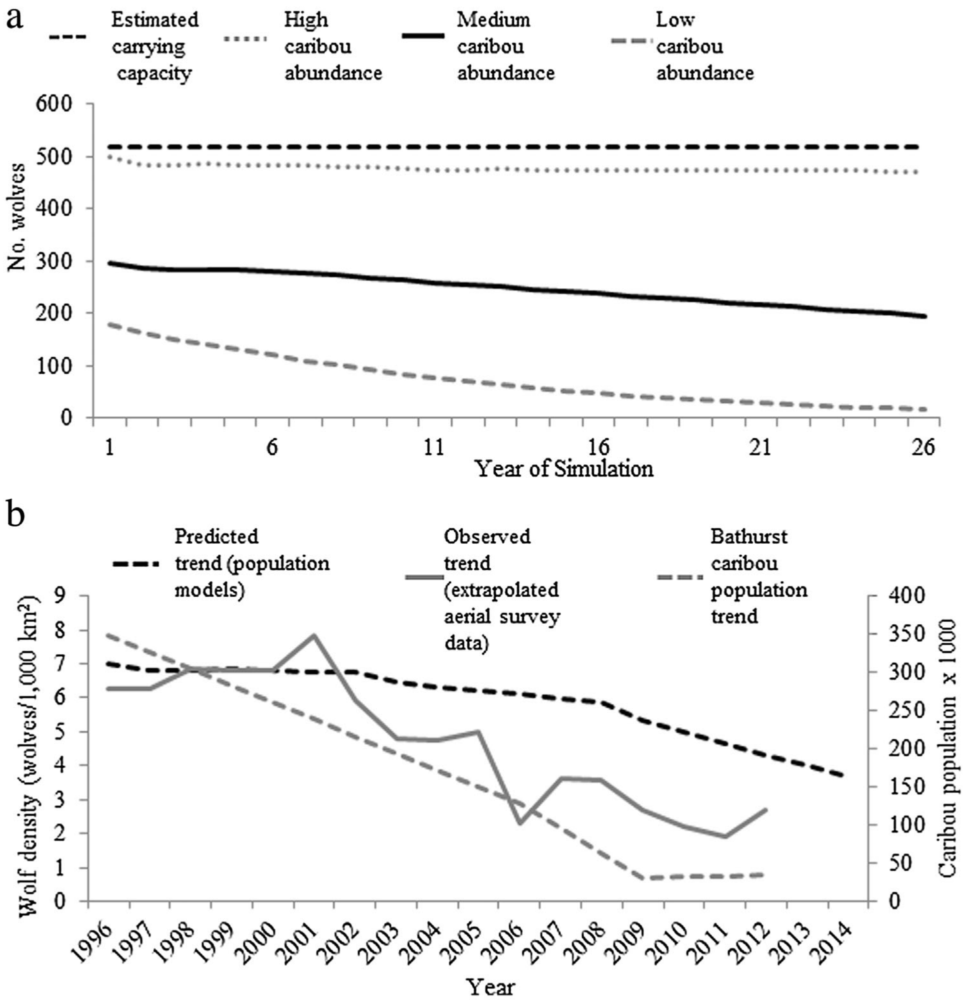

Figure 5. Estimated population trajectories (a) for tundra wolves in the Bathurst range, Northwest Territories and Nunavut, Canada using a stochastic population model. Model parameters were based on pup recruitment and wolf density estimates observed during 3 levels of caribou abundance. Estimated trends in wolf density (b) on the caribou summer range over the period of caribou decline 1996–2014. We derived wolf density estimates using pooled mean pup recruitment rates observed during periods of high, medium and low caribou abundance. 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.

separation between breeding wolves and the main distribution of caribou (Klaczek et al. 2015). 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. R. Klaczek, University of Northern British Columbia, unpublished data).

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 tundra wolf populations (Heard and Calef 1986, Heard and Williams 1992). In our study area, as the Bathurst herd declined, the seasonal ranges of caribou from post-calving through to fall rut contracted closer to the calving grounds. Wolves did not show a similar behavioral response by shifting den sites closer to the contracted ranges (Klaczek et al. 2015). 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 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 (Fig. 4).

Wolf Population Dynamics

Our population model, although simple, was based largely on empirical data collected during a long-term monitoring program of the tundra wolf population on the Bathurst range. We used measures of pack size and pup recruitment as the key parameters to describe wolf population dynamics over a 16-year period of caribou decline. Where data were not available, we 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, we 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 because we 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, Creel and Rotella 2010). Adult mortality across all models was held constant at 20%, yet we recorded a 25% mortality rate (4 of 16 wolves) in the GPS-collared adult female wolves from 2013. Furthermore, our models did not account for complex social behaviors (e.g., dispersal, mate choice, 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). We 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/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. We used 2 methods to estimate wolf density on the Bathurst range. Extrapolation of aerial survey data and stochastic population models provided crude but consistent approximations of wolf population trend and density. During the late 1990s, wolf populations remained stable and densities were consistent around 6.8 wolves/1,000 km^2. As the Bathurst herd declined during the 2000s, wolf density also decreased. Our population models projected a 48% decrease in wolf density over the study period. Density gradually decreased through the mid-2000s, above 6.0 wolves/1,000 km^2, and then a more substantive decrease after 2008, below 4.0 wolves/1,000 km^2 by 2014. Our extrapolation using aerial survey data suggested a 57% decline. Wolf density decreased more dramatically throughout the 2000s and by 2012 we estimated a wolf density of approximately 2.7 wolves/1,000 km^2. These results suggest a relatively strong numerical response by wolves to changing densities of caribou and complement findings by Keith (1983) and Fuller (1989), who report linear correlations between wolf density and prey abundance (Mech and Peterson 2003).

Estimates of wolf density on barren-ground caribou range vary considerably. Our estimates are similar to those reported on the Bathurst range by Kelsall (1968; >7 wolves/1,000 km^2 in the 1950s), H. D. Cluff (unpublished data; 6.6 wolves/1,000 km^2 in 2006), and Mattson et al. (5–10 wolves/1,000 km^2 in 2006). Our estimates are considerably lower than those of Kuyt (1969) and Parker (1973), who reported wolf densities of 57 and 49 wolves/1,000 km^2, respectively, 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 such observations lead to inaccurate estimates of density when extrapolated across the entire caribou range. In our study, we 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. R. Klaczek, unpublished data). The methods we 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).

Prey availability varies considerably for wolves by season, where changing environmental conditions influence the distribution, behavior, and body condition of ungulates. These aspects promote or hinder the ability of wolves to find and kill prey (Mech and Peterson 2003). In most areas of North America, the survival of wolf pups during summer is generally higher because of 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. Our 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. Although small mammals, migrating waterfowl, and even fish (H. D. Cluff, unpublished data) are consumed by denning wolves in our study area, caribou remain a vital food source (Kuyt 1972, Willams 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 we monitored (Klaczek 2015).

At broader scales, our results clearly illustrated the influence of caribou abundance and ultimately space-use patterns on wolf population dynamics. We 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 in the central Arctic are different than those documented in other study areas where alternative prey occur at relatively high densities and can sustain wolves in the absence of abundant caribou (Ballard et al. 1987, 1997; Kuzyk et al. 2006; Serrouya et al. 2011; Hervieux et al. 2014). For example, the home ranges of central Arctic wolves are amongst the largest in North America (Walton et al. 2001). In comparison, the home ranges of non-migratory wolves in Alaska are an order of magnitude smaller likely as a function of the greater diversity of large prey that includes caribou and moose (Ballard et al. 1987, 1997). Wolf densities in our study area are low, relative to Alaska and the southern boreal forest, because of limited prey in the denning areas and resulting high rates of pup mortality (Thomas 1995).

The severity of recent declines of barren-ground caribou 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 (Johnson et al. 2005, 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). The role of wolves in the population dynamics of migratory barren-ground caribou is not fully understood (Klein 1991, Bergerud 1996). Debate among 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). Although we did not measure cause-specific mortality for caribou or the role of predation in the decline and recovery of caribou populations, our results suggest that wolves on the Bathurst range have exhibited a relatively strong numerical response to a single, declining prey base. Thus, where some have argued that wolves cannot regulate populations of migratory caribou, our data suggest that declines in caribou can regulate dependent wolf populations (Messier et al. 1988). Population projections revealed that wolf densities have decreased from >6.5 wolves/1,000 km^2 in the late 1990s to 2014 levels ≤ 4 wolves/1,000 km^2. Corresponding to the continued decline in the Bathurst caribou herd (Adamczewski et al. 2014), the wolf population on the Bathurst range has likely decreased to below our 2014 estimates.

Estimates of wolf density in our study area are well below the 6.5 wolves/1,000 km^2 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 migratory George River caribou herd when wolf densities were estimated around 3–4 wolves/1,000 km^2. Although 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 the 2014 estimate of wolf density for the Bathurst range (Ballard et al. 1987, Boertje et al. 1996, Hayes and Harestad 2000, Hayes et al. 2003, Bergerud 2007).

MANAGEMENT IMPLICATIONS

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 herd recovery (Seip 1995, Thomas 1995, Paquet and Carbyn 2003). However, the data presented here suggest that reproduction of wolves in the central Arctic is regulated by the abundance of their primary prey, caribou. 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.

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APPENDIX A

Estimated parameters held constant in Vortex (9.99c; Lacy and Pollak 2013) simulation models used to model tundra wolf population dynamics on the summer range of the Bathurst caribou herd, Northwest Territories, Canada, 1996–2012. We assumed population age structure to be a stable age structure for adults, subadults, and pups.

Range: Bathurst	Parameter value	Reference
Age of first reproduction male	3	Kelly et al. (1999), Mahoney (2010)
Age of first reproduction female	2	Kelly et al. (1999), Mahoney (2010)
Recorded max. litter size (no. pups)	6	H. D. Cluff, personal communication (max. observed pups was 15 in a pack but possibly from 2 to 3 breeding females of the 9 adults present)
Reproduction life span (years)	8	H. D. Cluff, personal communication
Adult sex ratio	1:1	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

APPENDIX B

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. We extrapolated annual wolf density estimates using the pooled mean pack size for each pooled interval (1996–2000, 2003–2006, 2009–2012) multiplied by the mean dens/1,000 km^2 for each year in the survey.

Year	Average no. adults seen at dens >1 yr old	Average pups/den in Aug	SE pups/den	Active dens in Aug (*n*)	Dens/1,000 km^2
1996	2.8	3.4	0.26	7	0.98
1997	2.9	4.0	0.27	8	NA[a]
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

[a] Estimate not available.

APPENDIX C

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, Northwest Territories and Nunavut, Canada.