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Research Article

Demography of an Increasing Caribou Herd With Restricted Wolf Control

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ABSTRACT Understanding the limiting factors of a prey population is important before and during predator control programs, and optimal intensive management of an increasing prey population requires formal recognition of a sustainable population size. The migratory Fortymile caribou (*Rangifer tarandus*) herd in Alaska reached a low of approximately 6,000 caribou during 1973–1975. To regain peak numbers of approximately 50,000 caribou estimated in the 1960s, stakeholder groups gained approval for conservative harvest rates (1973–2013) and periods of restricted nonlethal (1998–2004) and lethal wolf (*Canis lupus*) control (2005–2013). We studied demography of the herd using radio-telemetry during 1990–2014, when herd size increased from about 22,000 to 52,000 caribou. Parturition rates in the early 1990s were among the highest reported, but parturition rates of primiparous females subsequently declined to a level indicating resource-limitation as caribou numbers approached and then exceeded 50,000. This and companion studies documented several other cautionary signals to an eventual decline, including declining October calf weights, early summer movement off the alpine and subalpine tundra to lower elevation spruce–moss taiga, relatively high caribou densities, a nearly 40-year history of increasing caribou numbers, and a return to previous peak numbers. We studied mortality of calves and older females during the 4 years before wolf control and the first 5 years of nonlethal wolf control. During those 9 years, annual mortality rates averaged 54% for calves and 9% for adult females. We detected no convincing support for decreased wolf predation during nonlethal control. We also detected no support for increased caribou survival during nonlethal or lethal wolf control. Based on counts of caribou during summer aggregations using a total search photocensus technique, rate of herd increase (λ_r) was negligible ($\lambda_r = 1.00$) during 1990–1995, highest during the 3 years immediately before nonlethal wolf control ($\lambda_r = 1.11$, 1995–1998), moderate during nonlethal wolf control ($\lambda_r = 1.07$, 1998–2003), and low during the period that included the first 5 years of lethal wolf control ($\lambda_r = 1.02$, 2003–2010). We combined observed cause of death with the 9 annual modeled starting populations (all newborn calves and adults) and estimated that wolves killed 10–15% of the populations annually, grizzly bears (*Ursus arctos*) killed 4–7%, other predators killed 2–4%, nonpredation factors killed 1–2%, and hunters killed $\leq$2%. Wolves killed 5–9% of the annual populations as calves and 5–6% as adults. In retrospect, nonlethal wolf control efforts were too localized to decrease wolf numbers (e.g., adjacent untreated wolf packs reached max. mean numbers). Lethal wolf control efforts had only seasonal and localized effects on wolf numbers. It is important that stakeholders focus on describing a preferred, sustainable herd size, or nutritional status and proceed toward managing this increasing herd in a sustainable manner because, when ungulates overshoot carrying capacity, the effects of high density, adverse weather, and increased predation can have synergistic negative effects on prey numbers and long-lasting negative effects on sustainable yields, contrary to the intended purpose of the wolf control programs. © 2017 The Wildlife Society.

KEY WORDS Alaska, caribou, demography, density dependent, mortality, parturition, predation, wolf control.

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Predation control programs are controversial and costly, yet demand for control programs is common when caribou (*Rangifer tarandus*) herds decline and users become disenfranchised (Boertje et al. 1995, Vors and Boyce 2009, Schneider et al. 2010, Festa-Bianchet et al. 2011, Hervieux et al. 2013). Range-wide, intensive, government-sponsored methods of wolf (*Canis lupus*) control have

resulted in well-documented increases in small caribou herds on ranges of $\leq$20,000 km^2 (Farnell and McDonald 1988, Boertje et al. 1996, Hayes et al. 2003). In contrast, relatively restricted predation control for small herds has typically resulted in negligible or strongly reduced levels of success at the population level (Valkenburg et al. 2004, Chisana Caribou Recovery Team 2010, Hervieux et al. 2014). In one exception, removing 28, 8, and 2 wolves near concentrated calving caribou during 3 calving seasons had clear success in increasing a previously declining herd of 600 caribou on the Alaska Peninsula (Riley 2011, Peterson 2013). Well-documented case histories are needed that evaluate the effects of predation control on the demography of large migratory ungulate populations.

Comprehensive studies of the prey population's limiting factors are recommended before and during predation control programs (National Research Council 1997, Boertje et al. 2010). Where prey numbers increase during predator control programs, a prey population's nutritional status or proximity to carrying capacity should be evaluated to avoid managing for prey abundances that inflict strong negative impacts on preferred habitat. From a practical standpoint, if nutritional status is declining as a result of population growth, incremental increases in prey numbers can be allocated to hunters to lessen the chance of density-driven population declines that disenfranchise users (Morellet et al. 2007, Boertje et al. 2009). Pursuant to Alaska legislation and regulations, the primary objective of predator control is to increase the sustainable yield of prey, not to produce an unsustainable number of prey (Boertje et al. 2009, 2010).

A central quest among ecologists is evaluation of the roles of reproductive and survival rates in regulating or limiting mammalian abundance (Gasaway et al. 1992, Brown et al. 1993, Mahoney and Schaefer 2002, Coulson et al. 2005). Past studies indicate that relatively constant adult survival and variable juvenile survival are typical of the population dynamics of large ungulates (Gaillard et al. 1998, Owen-Smith 2010). Combined wolf and bear (*Ursus* spp.) predation have strong negative effects on juvenile survival in some subarctic moose (*Alces alces*) and caribou populations, thereby maintaining these prey populations well below food-limited densities (Gasaway et al. 1992, Hayes et al. 2003).

Where this strong combined predation is less pervasive, prey population growth depends on the combined effects of density, and weather on individual nutritional status, which ultimately affects reproduction and survival (Clutton-Brock et al. 1985, Post and Stenseth 1999, Taillon et al. 2012). Boertje et al. (2012) concluded that caribou density, not weather, largely explained the changes in caribou nutritional status of the Fortymile population in Alaska, USA; weather variables explained little of the variability in Fortymile parturition rates, October calf:female ratios, and October calf weights during 1993–2010.

Gaillard et al. (2000) concluded that the sensitivity of young female parturition rates to density may be the critical component for evaluating nutritional effects on large herbivore population dynamics, regardless of the low relative effect of first births versus other births on population growth rates. For caribou, the parturition rate of 36-month-old caribou (i.e., the 3-year-old parturition rate) is considered a cumulative index of the 3 prior years' nutrition, because caribou that calve for the first time have reached an important herd-specific weight (Adams and Dale 1998, Boertje et al. 2012). In rare cases, where caribou were highly-nourished, many caribou gave birth at 2 years of age and regularly gave birth again at 3 years of age (Davis et al. 1991, Adams and Dale 1998, Bergerud et al. 2008).

As a response to the 1963–1973 decline in Fortymile herd size from approximately 50,000 caribou to 6,000, a series of different stakeholder planning groups gained approval for conservative harvests (1973–2013) and nonlethal (1998–2004) and lethal wolf control (2005–2013) because they envisioned a return of the herd to abandoned ranges in Interior Alaska, USA, and Yukon, Canada (Gronquist et al. 2005, Boertje et al. 2012). Alaska's governor is ultimately empowered to lead predator control programs for favored constituents. Biologists must be well-informed, respectful, and unbiased if they are to add credible substance to the value-driven policy-level decision-making process (Boertje et al. 2010, Smith 2011).

We had 2 primary objectives. First, we discussed factors and circumstances relevant to describing a sustainable population size or preferred nutritional status for the Fortymile caribou herd. We documented parturition rates (1990–2014) and herd size (1990–2010), and reviewed relevant literature. We expected to see density-dependent effects on caribou nutritional status most notably in the parturition rate of young females, so we updated comparisons among herds. Second, we reported on the effectiveness of consecutive, restricted, and experimental wolf control programs intended to increase the migratory Fortymile caribou herd. We documented calf recruitment (1990–2013) and causes and rates of calf mortality (1994–2003) and adult mortality (1991–2008). We also developed annual models (1994–2003) to investigate the roles of parturition rates and various causes of mortality on herd numbers before and during nonlethal wolf control. Specific objectives related to wolf control included estimating changes in wolf numbers within treatment areas and on the respective annual caribou ranges, plotting distribution of treated wolves in the study area, documenting fates of treated wolves, documenting percent overlap of movements of untreated wolves onto the caribou calving and core summer range, evaluating whether wolf control had detectable effects on caribou survival, recruitment, and numbers, and summarizing circumstantial support for and against the effect of wolf control on the caribou herd.

STUDY AREA

The study area encompassed 50,000 km^2 in east-central Alaska, USA, and west-central Yukon, Canada, centered around 64°N latitude and 143°W longitude (Fig. 1). We depicted the study area based on the outer boundaries of caribou locations during 16 years of radio-tracking (1992–2008; Boertje et al. 2012). Annual ranges of the Fortymile herd encompassed differing portions of the

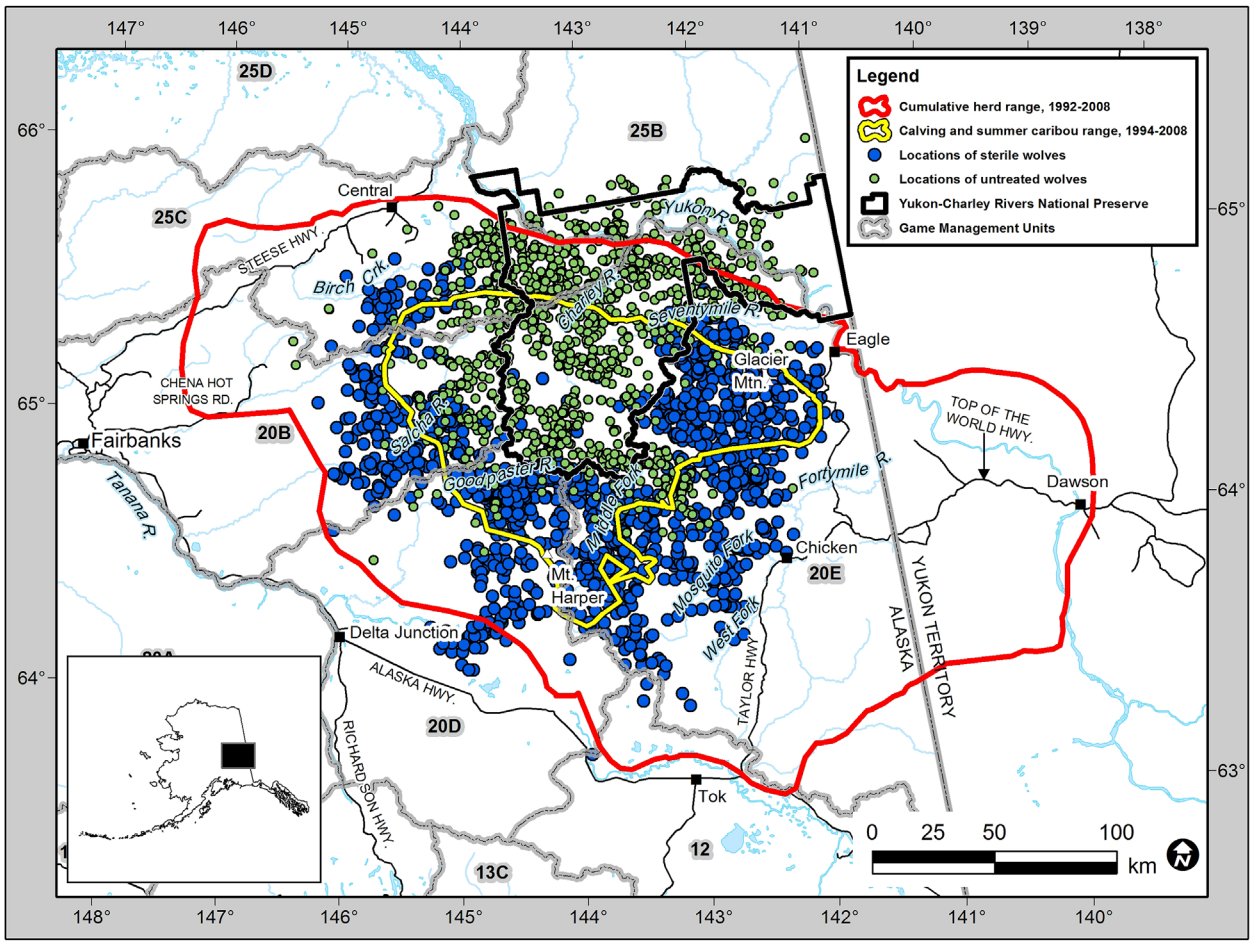

Figure 1. Cumulative range of the Fortymile caribou herd (1992–2008), calving and core summer range (1994–2008), and locations of sterile and untreated wolves (1998–2003), Interior Alaska, USA, and adjacent Yukon, Canada. The perimeter of the cumulative herd's range was the outer boundaries of caribou locations during 16 years of radio-tracking (Boertje et al. 2012). The perimeter of the calving (11–28 May) and core summer range (1 Jul–15 Aug) was the outer boundary of overlap during ≥8 of 15 years of summer telemetry studies and was closely aligned with the outer perimeter of the 1992–2008 calving and post-calving (28 May–30 Jun) ranges (Boertje et al. 2012). The 1,287 independent locations of 39 sterile wolves (radio-tracked an average of 3.3 yr) were from 15 original pack territories, where we translocated the nondominant wolves >160 km. The 1,315 independent locations of 46 untreated wolves were from 12 packs that denned in the Yukon-Charley Rivers National Preserve, Alaska (Burch 2011, this study).

study area (Boertje et al. 2012). The study area was sparsely populated containing 3 Alaska communities (Chicken, Eagle, and Central) with <100 year-round residents each, and 1 Yukon community (Dawson) with 1,300 residents. Crude airstrips provided primary access to the core study area, and 3 unpaved, seasonal highways, and adjoining off-road trails provided access to the eastern and western portions of the study area. The topography was largely rolling hills interspersed with subalpine and alpine areas (1,100–2,000 m) with 17% of the range above the approximate treeline (1,067 m; Boertje et al. 2012). The hills were largely covered with mature black spruce (*Picea mariana*) and white spruce (*P. glauca*) overstory with moss and lichen understory, and alder (*Alnus* spp.) at treeline. Subalpine shrub vegetation consisted primarily of dwarf birch (*Betula nana*) and willow (*Salix* spp.) interspersed with willow-lined drainages.

The climate was subarctic and continental. The average annual temperature in Eagle, Alaska was −4°C, and total annual precipitation averaged 31 cm (National Weather Service 2012). Leaves emerged on most shrubs during late May or early June, and leaf senescence occurred during the last 2 weeks of August.

Primary predators inhabiting the study area included wolves, grizzly bears (*Ursus arctos*), black bears (*U. americanus*), lynx (*Lynx canadensis*), wolverine (*Gulo gulo*), and golden eagles (*Aquila chrysaetos*). Prey included caribou, moose, Dall sheep, beaver (*Castor canadensis*), snowshoe hares (*Lepus americanus*), and hoary marmots (*Marmota caligata*). Common Alaska prey species largely absent from the study area included arctic ground squirrels (*Spermophilus parryii*) and salmon (*Oncorhynchus* spp.).

METHODS

Caribou Data Collection and Analysis

We radio-collared newborn calves during May 1994–2002 using techniques and collars described by Adams et al. (1995*b*) and Boertje and Gardner (2000*a*). Collars were expandable, which allowed for monitoring of calf survival to

12 months of age. We used R-22 helicopters (Robinson Helicopter Company, Torrance, CA, USA) to approach calves. We manually caught calves usually after a short chase (<50 m) with ≤2 minutes of disturbance for capture and handling. We weighed calves with a 12.5-kg spring scale with 100-g graduations (Model IN-025, Chatillon, NY, USA); we calibrated the scale at least daily. Most calves selected for collaring (62%) had radio-collared mothers, which we observed daily from about 11–28 May or until the day after radio-collaring newborns. We observed radio-collared adult females in the morning and collared newborns later the same day, so most calves were <36 hours old when collared. We estimated age of calves based largely on posture and degree of coordinated movements; we estimated a calf to be <2 days old (i.e., born day of capture or preceding day) when, during our pursuit, the calf's posture was slightly hunched and legs were not fully extended (Adams et al. 1995*b*). We conducted all aspects of this research in accordance with acceptable methods for field studies adopted by the American Society of Mammalogists (Animal Care and Use Committee 1998) and approved by the Alaska Department of Fish and Game (Protocol no. 04-006).

We previously described methods for darting and radio-collaring caribou ≥4 months of age (Boertje and Gardner 2000*a*). No calves previously fitted with radio-collars as newborns were darted. We deployed very high frequency (VHF) model 605-NH transmitters on CB-8 radio-collars (Telonics, Mesa, AZ, USA) on darted caribou. These collars usually transmitted for 8 years with a maximum of 10 years. We focused our radio-collaring efforts on 4-month-old caribou to maintain a sample of known-age adults. Replacing original collars was not financially feasible because efficient recapture was precluded by caribou being widely scattered and often in forested habitats during autumn capture operations.

To estimate herd parturition rates, we observed all radio-collared females from fixed-wing aircraft during ≥3 staggered flights that began about 11 May each year, 1992–2014. We deemed females parturient by the presence of a newborn calf, hard antlers, or a distended udder (Whitten 1995). To confirm non-pregnancy, we repeated observations ≥3 times (e.g., during the early, mid, and late calving seasons) because a few antlerless females developed udders and calved. In most years of daily 11–28 May flights (1992–2002), 1–3 collared females with distended udders or hard antlers were not seen with a calf, and we assumed these females gave birth after 28 May.

We tested for effects of age and previous pregnancy status on parturition in the current year using mixed logistic regression. To account for annual variability, we included a random effect for year. We used previous pregnancy status to assess the importance of reproductive pauses to current parturition, with significance tested via likelihood ratio tests (Zuur et al. 2009). Because of reduced sample sizes at older age classes and lack of senescence in the range of most observed ages, we treated age as a categorical explanatory variable, with groups for 2-, 3-, 4-, and ≥5-year-olds. We tested the significance of age using a conditional *F*-test (Zuur et al. 2009). To determine at what age individuals reached adult parturition rate, we included *post hoc* tests for differences between 3- or 4-year-old age classes compared to the ≥5-year-old age class using linear contrasts and adjusted for multiple comparisons using a Holm–Bonferroni correction (Holm 1979). We estimated a 5-year moving average of parturition rates weighted by annual sample sizes, for year t, as:

$$\hat{\bar{p}}_t = \frac{\sum_{i=t}^{t-4} n_i \hat{p}_i}{\sum_{i=t}^{t-4} n_i}$$

where $\hat{p}_i$ is the annual estimated parturition rate and n_i is the annual sample size (Boertje et al. 2012).

Each radio-collar had a mortality sensor that doubled the pulse rate (mortality mode) if the collar remained motionless for 1 hour (newborn calf collars) or 6 hours (other collars). To estimate mortality rates, we listened for mortality signals among all radio-collared caribou during each flight. We also visually checked for abandonment or perinatal mortality (i.e., mortality of newborns ≤2 days old) the first day after radio-collaring newborns. We radio-tracked caribou of all ages most frequently during the calf mortality studies (11 May 1994–10 May 2003), when we radio-tracked daily during 11–28 May, 10–13 times in June, weekly during July–September, and at least monthly during October–April. During periods when newborn calf collars were not deployed (1 Jan 1990–10 May 1994, 11 May 2003–31 Mar 2008), we radio-tracked at least twice each month in summer (May–Sep) and monthly during winter (Oct–Apr). After 1 April 2008, we radio-tracked only 4–6 times/year and only listened for radio-collars in portions of the herd's range. Thus, after 1 April 2008, we had insufficient data to compare mortality rates with prior periods.

When we heard a mortality signal during daily May fixed-wing flights (1994–2002), we immediately visually checked the mortality site for a predator. Subsequently, we investigated the site via helicopter, usually within 4 hours of detection. During all other periods, we investigated mortality sites via helicopter as soon as possible, usually within 1 day of detection. We necropsied carcass remains to assess cause of death. Hemorrhaging associated with puncture wounds, noncoagulated blood on collars, or blood on remnants of hide served as evidence of a violent death. In these cases scats, tracks, wounding patterns, other sign, and season of kill served to identify the predator involved (Adams et al. 1995*b*). Wolves often left the carcasses of young calves largely or entirely intact, so wolf kills could be identified by bite patterns. When wolves killed young calves, wolves often cached the carcass or portions of the carcass under snow, moss, or muskeg without obvious digging or scraping. Wolves occasionally carried and left the bloody or chewed collar some distance from any apparent kill site, which at times prevented us from finding the kill site. Bears often scraped up portions of the tundra mat and buried portions of the carcass or left crushed, cleaned bone fragments in a small

area with the collar. Based on observations of grizzly and black bears at May and June kill sites, grizzly bears left calf mandibles, skull caps, radio-collars, and smaller bones and fragments in a small area about 1 m^2, whereas black bears left larger portions more scattered. Eagles left tendons and ligaments attached to intact long bones. A collar completely soaked in blood indicated lynx predation, based on evidence of lynx predation in the snow at several sites. Wolverines cached the collar and portions of the carcass in rocks. In a few instances, intact collars had no blood or chewed fabric and could not be linked to a carcass, so we considered the collar prematurely shed over the head.

We evaluated mortality by hunters using caribou harvest reports collected from permit hunts. All harvest after 1992 was conducted under permit hunts, and 97% of permittees responded. In addition, we added estimates of illegal harvest from check station data and by including caribou reported as shot but not retrieved along roads and trails (Gross 2011). We considered Canadian harvest to be negligible, because Yukon and First Nation governments opted not to establish hunts.

We used 2 different approaches to estimate annual survival rates. For caribou older than calves, exact mortality dates were known with less certainty, but the risk of mortality was relatively constant throughout the year compared to that of newborns. Thus, we estimated annual survival rates using mixed logistic regression with a correction for number of unobserved days (included as a covariate in the model) to account for individuals radio-collared after the start of the year. We used an indicator variable to test for differences in mortality before (11 May 1994–10 May 1998) versus during nonlethal wolf control periods (11 May 1998–10 May 2003). To account for variability among years in this difference, we included year as a random effect on the model intercept. We assessed significance of the wolf control period using likelihood ratio tests. This approach assumes constant risk throughout the survey interval to adjust for censored individuals.

Although this assumption was appropriate for caribou older than calves, it was inappropriate for calf survival, because most of the mortality occurred within the first several weeks of life. Therefore, to estimate calf survival before and during nonlethal wolf control and test for differences, we used Cox proportional hazard modeling, with year as a frailty term to account for annual variation in survival rates (Hosmer et al. 2008). We included fixed covariates to evaluate the effect of sex and capture weight on calf mortality. Mortality dates were known with greater certainty for calves because most of the calf mortality occurred during May and June, the period of intensive radio-tracking. Because relocation surveys were less frequent in later months, we applied an Efron approximation for handling tied mortality dates (Efron 1977). Graphical assessment of log–log Kaplan–Meier curves indicated that the proportionality assumption underlying this regression was met.

To estimate herd composition, we classified caribou from a helicopter during late September or early October 1990–2013. Males, females, and calves were less segregated during this period than other periods of the year, although calves were often most abundant and males least abundant at the vanguard of migrating groups (Bergerud et al. 2008). We counted males >1 year old, females >1 year old, and calves using a mechanical tally counter during the 1-day survey each year. During these annual surveys, we counted 10–24% ($\bar{x} = 16\%$) of the prior June or July herd size from photocensuses (methods below). To locate groups of caribou for counting, a fixed-wing pilot relayed locations of all radio-collared caribou ($n = 64$–146 independent radios annually, $\bar{x} = 99$) to the helicopter crew. We attempted to correct for potential biases in sex-age classes in migrating groups and disproportionate counting among local areas of the migration by 1) counting caribou along the full extent of the migration each year using radio-collared female caribou to locate the migratory groups; 2) identifying and mapping 3–6 distinct areas, based on collar distribution; and 3) calculating a corrected ratio weighted by the proportion of radio-collared females in each area. The corrected ratio was the sum of the products of the individual area ratio × the proportion of radio-collars in the respective area.

We estimated numbers in the Fortymile caribou herd using counts of caribou between mid-June and mid-July using a radio search, total search, and aerial photo technique (i.e., photocensus; Valkenburg et al. 1985, Valkenburg and Davis 1989, Boertje and Gardner 2000*a*). Virtually all radio-collared caribou aggregated above treeline during hot, dry weather in June or early July. We monitored the location and extent of aggregations usually for several days prior to a photocensus. When caribou appropriately aggregated (>95% of the radio-collars associated with groups) above treeline, we divided the entire summer range among observers in 4–7 light aircraft during a 1-day photocensus. Pilots in these aircraft and a separate high-flying, radio-tracking plane communicated locations of caribou groups to the pilot of a de Havilland Beaver (de Havilland Aircraft of Canada, Toronto, Ontario, Canada) aircraft equipped with a large format (23 cm × 23 cm) Zeiss (Zeiss Ikon, Dresden, Germany) RMK-A aerial mapping camera. We used this camera to photograph all groups numbering ≥200 caribou, usually 10–25 groups during a census. We visually counted smaller groups or photographed these groups with 35-mm cameras; these smaller groups represented <5% of the total count. We counted caribou in photos using magnification (10×) under bright lights.

To calculate herd growth rates, we primarily used the counts from photocensuses and assumed no error. To derive annual growth rates (λ_r) for a period with >2 photocensuses, we regressed the ln of population sizes over the survey years to estimate the slope (m) of the line, and calculated $\lambda_r = e^m$ (Boertje et al. 1996).

We also used a demographic modeling approach to calculate a modeled growth rate (λ_m; Caswell 2001, Morris and Doak 2002) for the period 11 May 1994–10 May 2003. We parameterized a simple, female-only matrix population model using reduced versions of the mortality and parturition models described above. To match the photocensus, we used a birth pulse model with a post-calving census. We designed

the population model to match an 11 May–10 May mortality year with delayed reproduction until age 3. All calves entered the model immediately after calving, with an adjustment to the fecundity term of the model to account for overwinter adult mortality. We used predicted values from regression fits to parameterize a matrix for each year of the intensive study period (1994–2003). We estimated survival for each stage in the matrix (i.e., calves, yearlings, adults) using separate intercept-only models with random effects for year. As in our previous methods, we treated calf survival as time-to-event data (Cox proportional hazard modeling), whereas we fit the models for caribou older than calves using logistic regression. We calculated population growth rates for each annual matrix (λ_m) from the dominant eigenvalue of the matrix. We estimated standard errors for each λ_m by resampling the underlying parameter estimates assuming normally distributed error (on a logit scale) with variance terms from the variance-covariance matrix for the predicted values. For periods spanning multiple years, we estimated population growth by projecting the model starting from the most recent photocensus value.

By using a herd model with a birth pulse, we compared the proportions of calves in the 9 starting populations (all new calves and older caribou, May 1994–2002) with the proportions of annual deaths in the starting populations. Thus, annual birth and death rates had a common denominator. We used predicted calf survival from calving through 15 June to back-transform the census herd size to the predicted starting population in May of each year. For years in which photocensus data were unavailable, we used interpolated values from the adjacent years. We projected the age structure of the starting population from the annual matrix from the previous year. We averaged causes of death for radio-collared calves and older caribou for 2 time periods (before and during nonlethal wolf control) rather than use data from individual years. We conducted all analyses using the R statistical environment (version 3.1.0, R Development Core Team 2014), including the lme4 (Bates et al. 2014) and coxme (Therneau 2012) packages for specific regression functions.

Estimating Wolf Numbers and Reductions in Numbers

We estimated wolf and pack numbers within the herd's respective annual ranges before and during the most substantial years of nonlethal wolf control (1 Oct 1992–30 Sep 2000). We delineated annual ranges of the herd using locations of radio-collared female caribou (Boertje et al. 2012). We then mapped approximate wolf territories to assist in estimating wolf numbers. The basis for the annual mapping and estimates included wolf territories and wolf numbers from 16 to 20 packs containing $\geq$1 radio-collared member (Boertje and Gardner 1996, Adams et al. 2008). In addition, these surveys were facilitated by radio-collars in 4–12 packs that ranged in the Yukon–Charley Rivers National Preserve, Alaska and were largely radio-collared by the National Park Service (Fig. 1; Burch 2002, 2011). We located radio-collared wolves at least monthly. We gained additional survey information using standard track counts (Gasaway et al. 1992, Hayes et al. 2003, Gardner and Pamperin 2014) and information from local trappers and pilots (Boertje et al. 1996; Boertje and Gardner 2000*a, b*). We completed 2–3 wolf surveys/year in early and late winter within the herd's respective winter ranges.

After April 2000, we discontinued range-wide wolf surveys because of the impracticality of measuring wolf density on an expanding caribou range that increasingly overlapped Yukon, Canada, and because of the minimal effect of wolf control on range-wide wolf density. Instead we focused on enumerating wolves in 15 wolf pack territories where nonlethal treatment was allowed. The nonlethal wolf control program was restricted to reducing 15 packs with ranges overlapping a portion of the caribou calving and summer ranges. Treatment of wolves on the entire calving and summer ranges was disallowed because a portion was within the Yukon–Charley Rivers National Preserve (Fig. 1). Only packs that denned outside the preserve were allowed to be treated (Boertje and Gardner 1996).

Treatment of the 15 packs included sterilizing the dominant pair (Spence et al. 1999) and translocating all remaining wolves (Boertje and Gardner 2000*b*). We initially sterilized wolves in 7 packs during November 1997, and translocated the remaining wolves in those packs largely in April 1998. We similarly treated 7 additional packs in winter 1998–1999 and the final pack in winter 1999–2000. We maintained the number of wolves in the 15 pack territories as pairs an additional year (i.e., through Jun 2001) by translocating mostly singles or pairs of wolves that associated with the sterile wolves. We replaced radio-collars on sterile wolves a few years post-surgery to help evaluate fates of sterile wolves through June 2005. We translocated wolves when $\geq$9 months of age, and we released members of an individual pack together. We initially translocated wolves >160 km from the capture sites. After the first year of translocations, we noted 4 adult wolves returned from distances of about 160 km, so we subsequently moved all wolves >320 km, except some wolves 9–12 months of age that were moved >240 km (Boertje and Gardner 2000*b*). We detected no instances of wolves returning from these greater distances (Linnell et al. 1997).

We also investigated percent overlap of movements of untreated packs onto the caribou calving and core summer range. We assisted with monthly radio-tracking of untreated wolves that denned in the Yukon–Charley Rivers National Preserve (Burch 2002, 2011) and plotted independent locations ($n = 1{,}315$) of 46 untreated wolves from 12 packs (Fig. 1). We then described a 95% minimum convex polygon using locations of the untreated wolves, with 5% of the outer points eliminated. Finally, we calculated the percent overlap of this polygon with the caribou calving and summer range. The perimeter of the calving (11–28 May) and core summer range (1 Jul–15 Aug) was the outer boundary of overlap during $\geq$8 of 15 years of summer studies and was closely aligned with the outer perimeter of the 1992–2008 calving and post-calving (28 May–30 Jun) ranges (Fig. 1; Boertje et al. 2012).

Methods used to estimate wolf numbers during the lethal wolf control program (2005–2013; Gross 2012) were similar to those reported here for the initial study years (1992–2000), except wolf density was only practical to estimate in the respective treated areas, not on the entire herd's respective annual ranges. Lethal wolf control activities began in January 2005 on 17,100 km^2 of the southern portion of Game Management Unit 20E and northern Game Management Unit 12 and expanded beginning winter 2006–2007 onto 48,560 km^2 including about 80% of the herd's 50,000-km^2 range (Alaska Department of Fish and Game 2014; Fig. 1). Initially this program used only department-selected applicants from the public to kill wolves from the air using light aircraft. Beginning in late winter 2008–2009, Alaska Department of Fish and Game employees conducted additional control efforts on wolf packs within the calving and core summer range (12,030 km^2) by shooting wolves from helicopters.

Mandatory reporting provided information on Alaska wolf harvest, wolves taken in the lethal wolf control program, and additional information on pack sizes and distribution. In addition to permitted public aerial gunning, Alaska regulations allowed wolf hunting during 10 August–30 April and wolf trapping during 15 October–30 April on most of the herd's annual ranges.

RESULTS

We radio-collared 344 female calves 4 months old (14–20 annually) and 114 female caribou >1 year old (0–27 annually) during late September or early October 1990–2011. We also radio-collared 29 female calves approximately 11 months old in early May 2011–2012 to boost the eventual sample of 3-year-old females through 2014.

Caribou Parturition Rates

During 1993–2014, annual parturition rates of radio-collared caribou averaged 71% among 3-year-olds, 82% among 4-year-olds, and 86% among ≥5-year-olds (Table 1). Of 73, 2-year-olds observed between 1993 and 2002, only 4 (5%) were parturient, so we did not assess 2-year-old birth rates after 2002. These observed age-related differences were also supported by our model of caribou parturition rates ($D_3 = 269.04$, $P < 0.001$). Modeled parturition rates for 3-year-olds differed from 4-year-olds (with a multiple comparison adjustment: $Z = 3.01$, $P = 0.005$) and ≥5-year-olds ($Z = 4.94$, $P < 0.001$), whereas 4-year-old parturition rates were not different from older adults ($Z = 0.12$, $P = 0.61$).

During the study period, parturition rates among 3-year-old caribou showed substantial inter-annual variation ($\sigma^2_{yr} = 0.36$, $P < 0.001$; Fig. 2). The 5-year weighted moving averages among 3-year-olds ranged from 93% during the early portion of this study to 55% in 2012 (Table 1). These moving averages served as an indicator of herd nutritional status.

Delaying or pausing reproduction for a year did not increase parturition in the subsequent year. Among 4-year-olds without ($n = 34$) a birth the previous year, 85% were parturient; the same result of 85% occurred among 4-year-olds with a birth the previous year ($n = 106$). Also, among caribou ≥5 years of age without a birth the previous year ($n = 55$), 85% were parturient versus 89% for those with a birth the previous year ($n = 327$). All 3 surviving females that were parturient at age 2 also gave birth at age 3. For caribou ≥4 years of age, including previous reproductive status in the model had no effect on parturition in the current year ($\beta = 0.21$, SE = 0.32, $P = 0.514$).

Caribou Mortality

From 1994–2002, we annually radio-collared 52–78 newborn calves during mid- to late May to evaluate causes and rates of mortality. To estimate mortality from birth, the sample of 565 radio-collared calves included 9 calves that were dead or dying when we arrived to radio-collar calves of radio-collared females. The median calving dates during 1992–2003 were 19–23 May ($n = 24$–62 radio-collared females).

Calves ≤2 months of age were the most vulnerable to predation (Fig. 3). Of the 565 calves monitored, 24% died in May, 11% in June, and <5% in each of the months July–April (Table 2). To estimate the average annual mortality rate by cause, we attributed deaths to wolves (24%), grizzly bears (16%), golden eagles (5%), black bears (3%), wolverine (2%), lynx (1%), and nonpredation (3%; Table 3). The modeled annual mortality rate over all 9 years averaged 57% (SE = 5). Among calves estimated to be <2 days old at capture ($n = 498$), mortality risk during the first year of life declined with increasing newborn weight standardized by sex ($\beta_{weight} = -0.21$, SE = 0.07, $P = 0.003$). We found no evidence for sex-specific differences in mortality rates either to 4 months ($\beta_{sex} = 0.007$, SE = 0.13, $P = 0.96$) or 1 year of age ($\beta_{sex} = 0.003$, SE = 0.11, $P = 0.98$), and we documented a 50:50 sex ratio among newborn calves examined for sex (279 F, 276 M).

Surplus killing by wolves was evident; wolves left most young calf kills intact or partially consumed. Among 50 radio-collared newborn calves killed and left by wolves before 10 June and not attended by scavengers, 32% of the carcasses were intact, 22% were largely only eviscerated, 8% were 35–55% consumed, and 38% were >90% consumed. Wolves cached 7 (44%) of the 16 intact carcasses under snow, moss, or muskeg without obvious digging. The remaining carcasses were not cached.

We documented wolves making multiple kills of caribou during calving on 7 occasions during our 9-year study. During 24 May 1996, we observed from a plane a pair of radio-collared wolves hunting on the calving ground for 2 hours; the wolves killed 3 calves and an adult female giving birth and only consumed a small portion of 1 calf. Each kill site was approximately 200–400 m from the adjacent kill site. We saw multiple kills of calves at individual kill sites in 7 (12%) of 57 sites where wolves had killed young radio-collared calves during 11 May–10 June, 1994–2002. On 28 May 1994, we investigated a site where a radio-collared pack of 5 wolves had killed 16 calves (i.e., carcasses were warm, not cached, and virtually all were intact) in a 100-m radius; the 5

Table 1. Caribou parturition rates of known-age radio-collared females in the Fortymile herd, Alaska, USA, 1990–2014.

Year	Survey dates	3-yr-olds		5-year moving average of 3-yr-olds		4-yr-olds		≥5-yr-olds		≥3-yr-olds	
		%	n^a	%	n^a	%	n^a	%	n^a	%	n^a
1990	11–31 May									88	16
1991	11–31 May									91	11
1992	11–31 May									87	39
1993	11 May–3 Jun	44	9			100	1	73	37	68	47
1994	11 May–7 Jun	83	6			67	6	85	33	82	45
1995	11–19 May	71	7			67	3	90	31	85	41
1996	12–21 May	100	9			100	5	96	25	97	39
1997	10–20 May	100	6	78	37	88	8	81	32	85	46
1998	10–19 May	100	9	92	37	100	6	97	33	98	48
1999	11–19 May	83	12	91	43	100	9	85	47	87	68
2000	12–20 May	89	9	93	45	85	13	92	39	90	61
2001	13–21 May	70	10	87	46	86	7	93	40	88	57
2002	11–19 May	86	7	85	47	100	10	94	36	94	53
2003	12–23 May	82	11	82	49	14	7	74	35	68	53
2004	14–27 May	57	7	77	44	100	9	90	31	87	47
2005	12–22 May	33	6	68	41	100	7	81	26	77	39
2006	14–22 May	82	11	72	42	100	6	77	44	80	61
2007	11–27 May	83	6	71	41	100	10	89	45	90	61
2008	11–26 May	88	8	71	38	60	5	93	46	90	59
2009	12–24 May	33	9	65	40	71	7	78	40	70	56
2010	11–28 May	29	7	64	41	89	9	77	43	73	59
2011	14–27 May	67	3	58	33	71	7	87	47	88	72
2012	11–28 May	62	13	55	40	50	2	93	44	83	70
2013	14–27 May	83	18	60	50	92	13	90	49	89	80
2014	12–28 May	37	19	57	60	71	17	69	52	63	88
$\bar{x}$ and total		71	202	74	774	82	167	86	855	84	1,316

[a] Number of radio-collared females monitored during parturition surveys. We deemed females parturient by the presence of a newborn calf, hard antlers, or a distended udder (Whitten 1995).

wolves were feeding on a freshly killed adult female caribou 3 km distant. On 9 June 1994, 24 May 1996, 24 May 1999, and 25 May 2001, we found 2 recently killed calves 30–200 m apart. On 3 June 1999, we found an adult female and 2 calves recently killed by wolves in a 35-m radius. On 21 May 2000, we found an adult female and 2 calves killed by 2 wolves in a 200-m radius with fresh snow.

We documented perinatal deaths in 33 (9.3%) of 353 calves born to radio-collared females. Including an additional 2 years of data (1992–1993) when causes of death were not evaluated, 37 (9.7%) of 381 calves died when ≤2 days old. Predation was the chief cause of perinatal mortality. Predators caused 23 (70%) of 33 deaths among calves ≤2 days old and born to radio-collared females. We attributed 7 of the 23 deaths to grizzly bears, 6 to wolves, 5 to black bears, 4 to golden eagles, and 1 to a wolverine. Among the 10 perinatal deaths not caused by predators, we attributed 4 deaths to birth defects because the radio-collared females had distended udders and attended the calves. Also 3 calves were stillborn, 1 died from an accident, and 2 died from abandonment by radio-collared females without distended udders.

Wolves remained the dominant predator of caribou older than calves throughout our 1991–2008 study. Overall during 1 May 1991–1 April 2008, we determined causes of death among 97 radio-collared female caribou older than calves; we attributed deaths to wolves (76%), grizzly bears (12%), and factors other than predation and unrelated to humans (11%).

Herd Recruitment, Trend, and Modeling

Calf recruitment to October was similar throughout this study. Ratios averaged 33 calves:100 females before wolf control (1992–1997), compared with 32 calves:100 females during nonlethal wolf control (1998–2004) and 29:100 during lethal wolf control (2005–2013; Table 4).

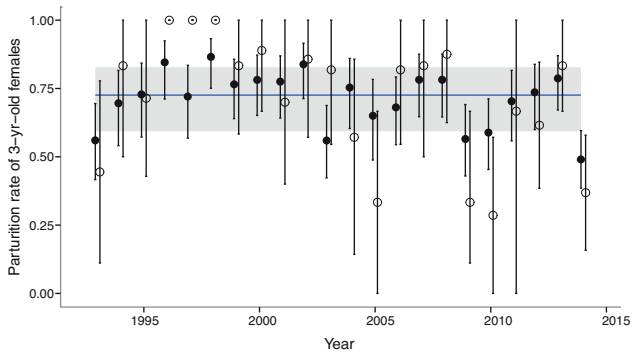

Figure 2. Observed parturition rates with 95% confidence intervals for 3-year-old female caribou (open circles) and corresponding annual predicted parturition rates with 95% prediction intervals (filled circles) compared to the 1993–2014 average rate (blue line) in the Fortymile caribou herd, Alaska, USA. We derived predicted parturition rates (±1 SD, shaded band representing expected annual variability) from an age-specific mixed logistic regression model with random intercepts for year. In 1996, 1997, and 1998, the observed parturition rates were 100%.

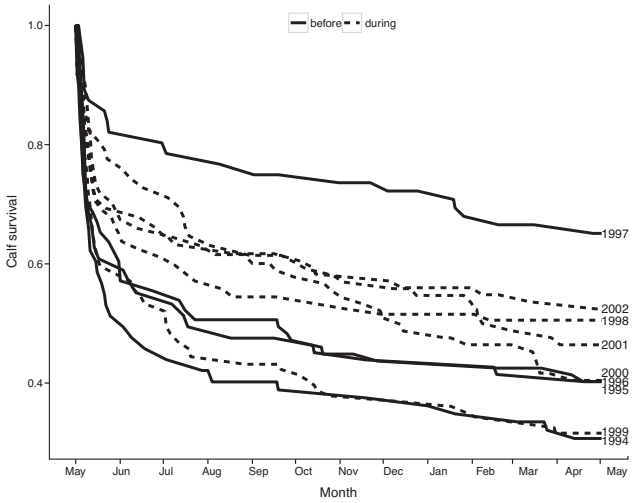

Figure 3. Annual survivorship curves among radio-collared calf caribou before (1994–1997 cohorts, solid lines) and during (1998–2002 cohorts, dotted lines) nonlethal wolf control in the Fortymile caribou herd, Alaska, USA.

Based on photocensus results (Table 4 and Fig. 4), the herd's rate of increase was negligible during 1990–1995 ($\lambda_r = 1.00$), highest during the 3 years immediately before nonlethal wolf control ($\lambda_r = 1.11$, 1995–1998), moderate during nonlethal wolf control ($\lambda_r = 1.07$, 1998–2003), and low during the period that included the first 5 years (2005–2010) of lethal wolf control ($\lambda_r = 1.02$, 2003–2010). In comparison, the female-only model indicated growth rates of 1.05 during the 3 years prior to wolf control (1995–1998) and 1.02 during nonlethal wolf control (1998–2003).

For the 9 annual models (11 May 1994–10 May 2003), the range of observed values for proportions of newborn calves (23–30%; Table 5) was similar to the range of observed values for proportions of annual modeled deaths (19–26%; Tables 5 and 6). Combining observed cause of death with the 9 annual models, we estimated that wolves killed 10–15% of the populations annually, grizzly bears killed 4–7%, other predators killed 2–4%, nonpredation factors killed 1–2%, and hunters killed $\leq$2%. Wolves annually killed 5–9% of the starting populations as calves (Table 5) and 5–6% as adults (Table 6).

Wolf Numbers, Fates, Distribution, and Densities

During the first 8 winters of study (1992–2000), the number of wolf packs preying on caribou ranged from 26 to 46 annually, depending largely on the extent of the annual caribou range (Table 7). During winter 1997–1998, when the first 7 packs were treated, the treated area covered about 8,600 km^2 or about 27% of the herd's annual range. By winter 1999–2000, when all 15 packs were first treated, the treated area covered about 18,500 km^2 (Fig. 1) or about 48% of the herd's annual range. The herd's annual range continued to increase with herd numbers and shifted each year (Table 7; Boertje et al. 2012).

In the 15 radio-collared wolf packs (range = 2–16 wolves/pack) selected for sterilization and translocation, we originally counted 129 wolves. During May 1998, after the first winter of treating 7 packs, wolf numbers were reduced 54% from the pre-control number. During the next 6 springs (1999–2004), wolf numbers in the 15 packs were reduced 68%, 79%, 81%, 72%, 60%, and 57%, respectively, from the pre-control number. Thus, spring wolf numbers were reduced an average of 67% from pre-control autumn numbers during 7 years. Wolf numbers were recovering slightly beginning spring 2002 but remained at reduced levels through spring 2004 because surviving sterile wolves maintained territories. In January 2005 lethal wolf control began, which further reduced these wolf numbers.

During the 4 winters of nonlethal control, 1997–1998 through 2000–2001, we sterilized 13, 14, 6, and 6 wolves. We successfully returned all 39 sterile wolves to their respective territories, and radio-located these wolves at least monthly. We plotted 1,287 independent locations of the sterile wolves (Fig. 1). To our knowledge, no sterile wolves emigrated from the study area. We observed sterile wolves an average of 3.3 years before death or loss of contact; 16 (41%) of the 39 sterile wolves lived $\geq$4–7 years post-surgery in pack sizes of 2–3 wolves. We evaluated causes of death among 25 sterile wolves with active radio-collars; 13 (52%) were killed by trappers, 10 (40%) were killed by wolves, 1 (4%) died from a uterine infection, and 1 (4%) fell from a cliff.

Also during the 4 winters of nonlethal control, we translocated 32, 42, 32, and 23 wolves. Most translocated wolves were only ear-tagged, but we radio-collared 35

Table 2. Timing of mortality of 565 caribou calves radio-collared as newborns in the Fortymile herd, Alaska, USA, 11 May 1994–10 May 2003. Nonlethal wolf control reduced wolf numbers on portions of the calving and core summer range during springs 1998–2002.

		% of all radio-collared calves dying by period							
Year	No. calves radio-collared	May	Jun	Jul	Aug	Sep	Oct	Nov–May	Annual mortality
1994–1995	52	35	17	2	4	0	2	8	67
1995–1996	52	35	10	2	4	2	2	4	58
1996–1997	60	28	13	5	2	0	5	8	62
1997–1998	55	13	5	4	2	2	0	11	36
1998–1999	72	25	8	6	1	3	0	1	44
1999–2000	78	28	17	8	3	1	5	6	68
2000–2001	67	15	16	1	4	1	3	18	60
2001–2002	63	14	10	5	8	2	3	8	49
2002–2003	66	27	5	6	0	2	3	3	45
$\bar{x}$	62.8	24.4	11.2	4.3	3.1	1.4	2.6	7.4	54.3

Table 3. Annual causes of mortality (%) among 565 caribou calves radio-collared as newborns in the Fortymile herd, Alaska, USA, 11 May 1994–10 May 2003. Nonlethal wolf control reduced wolf numbers on portions of the calving and core summer range during springs 1998–2002.

		% annual radio-collared calf mortality by cause of death							
Year	No. calves radio-collared	Wolf	Grizzly bear	Golden eagle	Black bear	Wolverine	Lynx	Nonpredation[a]	Annual mortality
1994–1995	52	25	21	6	2	2	0	12	67
1995–1996	52	25	15	6	8	2	0	2	58
1996–1997	60	30	18	8	0	2	0	3	62
1997–1998	55	24	11	0	0	2	0	0	36
1998–1999	72	14	14	6	8	1	0	1	44
1999–2000	78	28	27	1	6	3	1	1	68
2000–2001	67	31	15	3	0	0	6	4	60
2001–2002	63	17	16	10	2	0	3	2	49
2002–2003	66	20	11	6	2	2	2	5	45
$\bar{x}$	62.8	23.8	16.4	5.1	3.1	1.6	1.3	3.3	54.3

[a] Among the 18 deaths from nonpredation, 7 died from accidents (4 broke legs, 2 fell into rock pits, and 1 was trapped and suspended in a small forked tree), 4 may have died from birth defects because the attending adult females had distended udders, 2 were abandoned by adult females without apparent udders, 3 were stillborn, 1 drowned, and 1 eventually died from an infection through the umbilicus.

translocated wolves ≥11 months of age to evaluate causes of death. We radio-tracked approximately monthly for 12 months; 23 (66%) died the first year after translocation. Twelve (52%) of these 23 were killed by trappers, 4 (17%) were shot, 4 (17%) died of unknown causes, 2 (9%) were killed by moose, and 1 (4%) collided with a car. We translocated 17 of these radio-collared wolves in or near Unit 12 south of Tok (Fig. 1) and 18 to the Kenai Peninsula, Alaska; both areas had relatively high trapping pressure compared to other relocation areas.

Despite our success in actively reducing wolf numbers in 15 selected packs during winters 1998–2001, autumn wolf density on the herd's respective annual ranges remained stable or increased during 1992–2000 (6–8 wolves/1,000 km^2; Table 7). The percentage of wolves removed by harvest and translocation from the annual ranges of the

Table 4. Modeled mortality rates of radio-collared calves (i.e., newborns and older calves combined) and older females for 12 months, estimated caribou numbers from photocensuses, herd growth rates, and herd composition and relevant sample sizes of females ≥1 year old in the Fortymile herd, Alaska, USA, 1990–2013.

	Mortality rates of calves			Mortality rates of F ≥ 12 months old					Herd trend from model				
Year	%	95% CI	n[a]	%	95% CI	n[a]	Estimated herd size	Herd trend (λ)[b]	(λ_m)	SE	No. radios in herd	Oct calves:100 F ≥ 1 yr old	No. F ≥ 1 yr old (n)
1990						17	22,766	1.07			16	29	1,002
1991				9.6	9.4–9.8	53						16	931
1992				9.3	9.0–9.5	63	21,884	0.98			64	30	1,417
1993				9.1	8.9–9.3	65						29	2,095
1994	65.2	50.1–80.3	52	9.4	9.2–9.6	55	22,104	1.01			91	27	1,710
1995	58.9	43.6–74.2	52	9.2	9.0–9.4	55	22,558	1.02	1.01	0.018	85	32	1,879
1996	59.1	43.8–74.4	60	9.4	9.2–9.6	56	23,458	1.04	1.03	0.018	97	36	2,601
1997	39.3	25.7–52.8	55	9.0	8.8–9.2	70	25,910	1.10	1.03	0.018	113	41	3,313
1998	50.0	37.6–62.3	72	9.0	8.8–9.2	74	31,029	1.20	1.08	0.015	146	38	2,433
1999	66.9	54.8–79.1	78	9.5	9.3–9.7	90	33,110	1.07	1.05	0.014	130	37	2,347
2000	58.2	45.7–70.7	67	9.3	9.1–9.5	81	34,640	1.05	1.00	0.016	111	27	3,780
2001	54.5	41.9–67.2	63	8.8	8.6–8.9	75			1.02	0.014		38	3,658
2002	51.0	38.4–63.5	66	9.6	9.4–9.8	76			1.04	0.014		39	3,347
2003				9.6	9.4–9.8	69	43,375	1.08	1.02	0.012	97	17	3,777
2004				9.7	9.5–9.9	68						28	2,445
2005				9.3	9.1–9.5	78						18	1,391
2006				8.9	8.7–9.1	79						34	2,839
2007				9.1	8.9–9.3	79						37	3,031
2008												33	2,164
2009							46,510	1.01			71	34	2,036
2010							51,675	1.11			79	32	4,146
2011												25	2,369
2012												22	2,996
2013												28	2,374

[a] n = Maximum number of caribou at risk during 12-month period.
[b] We calculated λ between the most immediate previous and current photocensus using the difference between the ln-transformed population size estimates: $\lambda = e^{(\ln(Nt2) - \ln(Nt1)) / (t2-t1)}$.

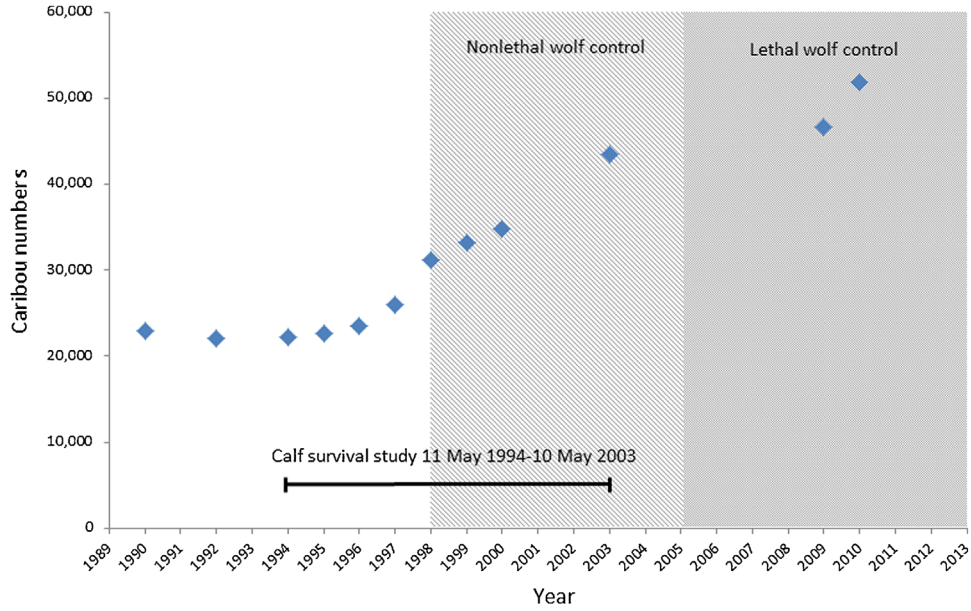

Figure 4. Growth of the Fortymile caribou herd based on photocensuses, 1990–2010, and timelines of wolf control and the study of calf survival (newborns to 12 months of age) using radio-telemetry, Alaska, USA.

Fortymile herd was 39% during the first winter of nonlethal control (1997–1998) and 27–28% during the following 2 winters (1998–2000; Table 7).

Given that we reduced wolf numbers on only a portion of the calving and core summer range, we estimated the extent of untreated wolves on the entire calving and core summer range. During 11 May–15 August, untreated wolves that denned in the Yukon–Charley Rivers National Preserve occupied an area that overlapped 44% of the caribou calving and core summer range ($n = 321$ locations; Fig. 1). The Yukon–Charley Rivers National Preserve contained 32% of the calving and core summer range (Fig. 1). The calving and core summer range contained portions of the herd at least through 30 November each year. On a year-round basis, the untreated wolves occupied an area that overlapped 78% of the caribou calving and core summer range ($n = 1{,}315$ locations; Fig. 1).

Both at the beginning of lethal wolf control efforts (Jan 2005) and at the end of this study (Nov 2013), we estimated early winter wolf density at 7–8 wolves/1,000 km^2 in Alaska's portion of the herd's range (about 40,000 km^2; Fig. 1). During the first 2 winters of lethal wolf control, wolf removal was 37% and 27% in Game Management Unit 20E (28,000 km^2; Fig. 1), with much lower removal in the remainder of the herd's range. In contrast, during winters 2006–2013, wolf control occurred in a 40,000-km^2 expanded control area, covering 80% of the herd's 50,000 km^2 multi-annual range, where overwinter reductions in wolf numbers

Table 5. Annual empirical modeling outputs for starting numbers and calf production and mortality in the Fortymile caribou herd, Alaska, USA, 1994–1995 through 2002–2003. Annual data are from 11 May through 10 May The number of caribou in the year's starting population is the number immediately pre-calving plus all calves born that year before any calf mortality.

				Calf mortality by cause									
		Calf production		Wolves		Grizzly bears		Other predators		Nonpredation		All factors	
Year	No. caribou in starting population	No. calves in starting population	% calves in starting population	No. killed	% of total	No. killed	% of total	No. killed	% of total	No. killed	% of total	No. killed	% of total
1994–1995	24,614	6,894	28	2,117	9	1,339	5	742	3	297	1	4,495	18
1995–1996	24,876	7,571	30	2,100	8	1,329	5	736	3	294	1	4,459	18
1996–1997	26,013	7,057	27	1,964	8	1,243	5	688	3	275	1	4,170	16
1997–1998	27,436	8,222	30	1,521	6	962	4	533	2	213	1	3,228	12
1998–1999	33,420	8,910	27	1,843	6	1,429	4	1,006	3	214	1	4,452	13
1999–2000	36,730	10,471	29	2,901	8	2,250	6	1,584	4	336	1	7,008	19
2000–2001	38,028	11,025	29	2,656	7	2,059	5	1,450	4	308	1	6,415	17
2001–2002	40,898	11,892	29	2,686	7	2,082	5	1,466	4	311	1	6,487	16
2002–2003	43,759	10,201	23	2,152	5	1,669	4	1,175	3	250	1	5,199	12
$\bar{x}$			28		7		5		3		1		16

Table 6. Annual empirical modeling outputs for mortality of caribou older than calves in the Fortymile caribou herd, Alaska, USA, 1994–1995 through 2002–2003. Annual data are from 11 May through 10 May. The number of caribou in the year's starting population is the number immediately pre-calving plus all calves born that year before any calf mortality.

		Mortality of caribou older than calves by cause									
		Wolves		Grizzly bears		Nonpredation		Harvest[a]		All factors	
Year	No. caribou in starting population	No. killed	% of total	No. killed	% of total	No. killed	% of total	No. killed	% of total	No. killed	% of total
1994–1995	24,614	1,475	6	47	<1	138	1	328	1	1,987	8
1995–1996	24,876	1,413	6	45	<1	132	1	225	1	1,814	7
1996–1997	26,013	1,585	6	50	<1	148	1	150	1	1,932	7
1997–1998	27,436	1,539	6	49	<1	144	1	151	1	1,882	7
1998–1999	33,420	1,644	5	317	1	252	1	155	<1	2,368	7
1999–2000	36,730	1,860	5	358	1	285	1	155	<1	2,658	7
2000–2001	38,028	1,861	5	358	1	285	1	150	<1	2,654	7
2001–2002	40,898	1,886	5	363	1	289	1	708	2	3,246	8
2002–2003	43,759	2,399	5	462	1	368	1	887	2	4,115	9
$\bar{x}$			5		1		1		1		7

[a] Harvest was composed largely of male caribou during this study (90–97% M during 1994–2000 and 70–78% during 2001–2002; Boertje et al. 2012).

averaged 45%. We observed individual overwinter reductions in wolf numbers in the expanded control area of 32%, 25%, 62%, 54%, 44%, 52%, and 43% from pre-control autumn 2004 numbers. Again, there was much lower removal in the remaining 20% of the herd's range, primarily the portion in Yukon, Canada. Our best estimates of reductions among all wolves in packs that overlapped the calving and core summer range indicated that spring wolf numbers were reduced by 69%, 71%, 62%, and 84% from November 2004 levels during springs 2009, 2010, 2012, and 2013.

Influence of Nonlethal Wolf Control on Caribou Mortality

We found no differences in calf caribou mortality to 1 year of age before versus during nonlethal wolf control based on either mortality rate (no. deaths/no. calves: $\beta_{control} = -0.06$, SE $= 0.30$, $P = 0.84$; Fig. 3 and Table 4), the wolf-based mortality rate (no. wolf kills/no. calves: $\beta_{control} = -0.08$, SE $= 0.20$, $P = 0.67$), or the proportion of mortalities caused by wolves (no. wolf kills/no. deaths: $\beta_{control} = -0.08$, SE $= 0.16$, $P = 0.64$). Because nonlethal wolf control was focused on a portion of the calving and core summer range (Fig. 1), we also compared the wolf-based mortality rate from birth through June before and during nonlethal wolf control. During calving through June, wolves killed 16.5% of radio-collared calves before wolf control versus 12.9% during nonlethal wolf control ($\beta_{control} = -0.27$, SE $= 0.25$, $P = 0.29$). We also found no differences in calf mortality after removing the 1997 cohort; high survival of the 1997 cohort immediately before wolf control could be construed as highly influential on the ability to detect a difference in calf mortality rates before and during wolf control (Fig. 3).

Table 7. Estimated autumn wolf numbers, density, and harvest in the respective annual ranges of the Fortymile caribou herd, Alaska, USA, before and during the most intensive years of low-intensity nonlethal wolf control, 11 May 1992–10 May 2000. We reduced 7 packs to 2 sterile wolves each in April 1998, and reduced another 7 packs to 2 sterile wolves each in winter 1998–1999. Fifteen packs were reduced to 2 sterile wolves each during winter 1999–2000.

Year	Area of annual caribou range ($\times$1,000 km^2)	No. wolf packs preying on the herd	Estimated autumn wolf numbers in annual caribou range[a]	Wolf density on annual caribou range per 1,000 km^2	Wolf harvest and translocations in and adjacent to respective range	Estimated wolves harvested and translocated (%)
1992–1993	29.1	32	187	6.4	54	29
1993–1994	23.1	26	156	6.8	49	31
1994–1995	30.4	35	186	6.1	40	22
1995–1996	27.7	33	220	7.1[a]	126[b]	57[b]
1996–1997	35.0	37	239	6.8	68[b]	28[b]
1997–1998	30.7	37	233	7.6	90[c]	39
1998–1999	24.0	29	172	7.2	46[d]	27
1999–2000	38.4	46	297	7.7	83[e]	28

[a] To account for single wolves, we added 10% to the number of wolves estimated to be in the annual range. Autumn wolf numbers were from the respective annual ranges of the Fortymile herd. We included only 50% of the wolves in the border packs, except in 1995–1996 when large numbers of wolves were harvested along the border. Wolves in 1995–1996 ranged in about 31,000 km^2. Number of border packs ranged from 5 to 9 annually.
[b] A private Caribou Calf Protection Program provided a monetary incentive to increase harvest during winters 1995–1997.
[c] Harvest totaled 59 and we translocated 31 wolves.
[d] Harvest totaled 7 and we translocated 39 wolves.
[e] Harvest totaled 50 and we translocated 33 wolves.

Among female caribou older than calves, we also found no evidence of reduced mortality during nonlethal wolf control. Annual mortality rates of yearling and adult females averaged 8.4% before nonlethal wolf control versus 9.3% during nonlethal control ($\beta_{control} = 0.11$, SE = 0.29, $P = 0.69$; Table 4). Of the known deaths during these time periods, wolves caused 86.1% of deaths ($n = 36$) before compared with 71.4% ($n = 35$) during nonlethal wolf control ($\beta_{control} = -0.76$, SE = 0.62, $P = 0.22$).

DISCUSSION

Factors and Considerations Relevant to Describing a Sustainable Herd Size

We documented a decline in parturition rates of young females that indicated density-dependent nutritional restriction, and the potential for the increasing Fortymile herd to soon reach an unsustainable population size (Boertje et al. 2012). To thoroughly evaluate density-dependent factors to guard against overabundance, we would monitor a set of indicators that indexed habitat quality, herbivore abundance, and herbivore nutritional status, as described for optimal intensive management of roe deer (*Capreolus capreolus*; Morellet et al. 2007) and moose (Boertje et al. 2007, 2009). However, evaluating density dependence in caribou is more complex.

First, indexing habitat quality for management of roe deer and moose is relatively easy because woody tissue is measured over a fixed area. In contrast, caribou rarely consume woody tissue and prefer a more diverse non-woody diet (Boertje 1984), and herd movements often change over time (Bergerud et al. 2008, Boertje et al. 2012). Because density-dependent effects on caribou nutritional status are most noteworthy via effects on juvenile growth rate (Taillon et al. 2012), changes in the diversity and quality of the spring and summer diets are particularly important as caribou numbers increase to elevated densities (Boertje 1990, Crête and Huot 1993, Bergerud et al. 2008). Manseau et al. (1996) described degradation of the calving and summer habitat of a barren-ground herd coincident with a large increase in caribou numbers and diminished birth rates.

Second, surveying caribou abundance is difficult because of changing weather, habitats, and movement patterns. Despite annual attempts to photocensus the Fortymile herd, effective photocensuses became increasingly sporadic during this study, given either cool weather conditions in June that inhibited caribou aggregations, or in dry summers, increased large-scale wildfires with smoke that interfered with aerial operations. As of 2016, we had not completed a photocensus for 6 years. To manage for a sustainable population size without population estimates, stakeholders could agree to manage the herd based on nutrition-related, density-dependent indices (e.g., calf weights or parturition rates of 3-year-old females; Boertje et al. 2007, 2009).

Fortunately, caribou investigators have often measured female reproductive success, particularly among the youngest age classes (Table 8), which is an established index to herbivore nutritional status (Langvatn et al. 1996, Adams and Dale 1998, Gaillard et al. 2000, Morellet et al. 2007, Boertje et al. 2009). When parturition rates of 3-year-old caribou fell below 55%, independent measures of condition indicated that caribou were experiencing reduced nutritional status (Adams and Dale 1998, Valkenburg et al. 2003). More specifically, Boertje et al. (2012) reviewed all available data and proposed a cautionary signal to density-dependent nutritional limitation using a 5-year moving weighted average of parturition rates of 3-year-old females. We provided an updated summary of the comparative data (Table 8). A decline below 55% in this moving average signaled initiation of lengthy periods of important nutrition limitation in all 3 prior case histories where data were available: the Delta herd (1991–1997), Nelchina herd (2001–2008), and Mulchatna herd (2005–2011). Boertje et al. (2012) also showed that rates of increase in herd size were positively related to average parturition rates of 3-year-olds ($n = 12$ multiple years of consistent trend in 8 unmanipulated herds). Furthermore, rates of increase were consistently negative when average parturition rates of 3-year-olds were <40% and consistently positive when average parturition rates of 3-year-olds were >65%. No data were available to investigate trend with average parturition rates between 40% and 65%.

During the early years of this study, 1993–2001, the average annual parturition rate among 3-year-olds (82%) in the Fortymile herd was similar to the average (83%) in the Denali herd, which was the most productive herd monitored in this manner to date (Table 8; Adams and Dale 1998). Parturition rates among 2-year-old caribou (5%) in the Fortymile herd were only measured prior to 2003 and indicated moderate nutritional status compared to 4 herds described as well-nourished (Bergerud et al. 2008). Using data prior to 2009, the Fortymile herd's average parturition rate among 3-year-olds (78%) ranked fourth highest among 8 herds (Table 8). Parturition rates of 3-year-olds declined substantially during 2009 (30%) and 2010 (29%), and remained low for 2 additional springs (2011 = 67% and 2012 = 62%) causing the 5-year moving weighted average to decline to a low of 55% by 2012, indicating a decline in nutritional status (Table 8; Boertje et al. 2012). Little of the variability in parturition rates of caribou in the Fortymile herd could be explained by weather variables, and parturition rates in 2 other Interior Alaska herds (i.e., Denali and Nelchina) exhibited little change during 2009–2012 (Table 8; Boertje et al. 2012).

Other signs indicating reduced nutritional status of caribou in the Fortymile herd included declining October calf weights and early summer movement off the alpine and subalpine tundra to lower elevation spruce-moss taiga (Boertje et al. 2012). Increased, early use of spruce-moss taiga may well be associated with less desirable summer diets (Boertje 1984, 1990) and increased insect harassment (Boertje 1985*a*, *b*). Early movements off overused summer range have been noted during peak numbers and declines in barren-ground herds in eastern Canada (Messier et al. 1988, Mahoney and Schaefer 2002, Bergerud et al. 2008). Elevated caribou densities

Table 8. Percentage of radio-collared caribou 36 months of age observed parturient during respective calving seasons in 9 herds[a], Alaska, USA, 1981–2014. We provided annual percentages and sample sizes and 5-year weighted moving averages. When a herd's data stream lapsed for a year, we provided 4-year weighted moving averages. All caribou were radio-collared as calves. Sources included Boertje et al. (2012) and Harper and McCarthy (2015).

	Denali			Chisana			Porcupine			Fortymile			Central Arctic			Delta			Mulchatna			Nelchina		
Year	%	*n*	5-yr $\bar{x}$[b]	%	*n*	5-yr $\bar{x}$[b]	%	*n*	5-yr $\bar{x}$[b]	%	*n*	5-yr $\bar{x}$[b]	%	*n*	5-yr $\bar{x}$[b]	%	*n*	5-yr $\bar{x}$[b]	%	*n*	5-yr $\bar{x}$[b]	%	*n*	5-yr $\bar{x}$[b]
1981																77	13							
1982																100	2							
1983																100	7							
1984																89	9							
1985																90	10	87.9						
1986																89	9	91.9						
1987	67	3															0	91.5[c]						
1988	100	2														100	1	89.7[c]						
1989	91	11														60	5	84.0[c]						
1990	64	11														60	10	72.0[c]						
1991	86	14	80.7													29	7	52.3[c]						
1992	100	9	85.3													0	1	50.1						
1993	25	8	75.6							44	9					0	5	39.4						
1994	85	13	74.8							83	6					22	9	31.3						
1995	100	4	79.4							71	7		0	4		64	11	33.5						
1996	92	12	80.6							100	9			0		100	5	45.2						
1997	88	8	78.1							100	6	78.1	0	1		50	10	47.6				50	6	
1998	86	7	89.0							100	9	91.8	100	2		90	10	62.3				45	11	
1999	100	3	91.5							83	12	90.5	100	7	64.3[d]	86	7	74.6				25	12	
2000	100	4	91.5							89	9	93.3	80	10	85.0[d]	66	12	74.9				0	8	
2001	75	4	88.7							70	10	86.9	77	13	81.8	25	8	63.7	75	4		17	6	27.8
2002	100	4	91.0							86	7	85.1	77	12	82.4	50	6	65.0	57	7		64	11	33.4
2003	100	1	93.8	71	7					82	11	81.7		0	81.5[d]	63	8	58.5	25	8		30	10	29.9
2004	100	6	94.7	100	2					57	7	77.4	88	8	79.7[d]	83	6	57.4	0	2		55	11	37.2
2005	83	6	90.4	89	9		60	10		33	6	68.3	86	7	80.8[d]	85	13	63.6	40	5	42.3	38	8	43.8
2006	100	5	95.4	79	19		100	1		82	11	71.5	71	7	80.2[d]	75	4	73.2		0	36.3[e]	100	2	50.3
2007	100	12	96.6	87	15	82.8	100	4		83	6	70.7	100	4	84.7[d]	50	6	73.2	0	5	20.0[e]	50	4	46.0
2008	90	10	94.8	89	19	85.9	83	6		88	8	71.1		0	84.7[d]				40	10	27.3[e]	100	4	58.9
2009	100	11	95.4				100	7	82.1	33	9	65.0	60	5	78.2[d]				83	6	42.2[e]		0	61.3[f]
2010	80	10	93.8				14	7	71.8	29	7	63.5	60	5	71.3[d]				69	13	52.8[e]	60	10	70.0[f]
2011	100	8	94.1					0		67	3	57.7	50	4	66.7[d]				67	3	53.9	0	2	60.0[f]
2012	100	10	93.9					0		62	13	55.3	71	7	61.8[d]				75	15	66.4	25	8	50.0[f]
2013	100	10	95.9				67	3		83	18	60.0	75	4	63.9				86	14	77.0	39	23	39.5[f]
2014	82	11	91.9					0		37	19	56.8		0					100	8	79.8	0	4	36.1
$\bar{x}$	89			86			75			71			68			66			55			41		

[a] Data on the Northern Alaska Peninsula herd were gathered only during 1989 and 1999 ($\bar{x} = 33\%$, $n = 18$).
[b] Column headers labeled 5-yr $\bar{x}$ contain 5-year weighted moving averages, except as indicated below.
[c] Delta herd 4-year weighted moving averages are provided during 1987–1991, as $n = 0$ in 1987.
[d] Central Arctic herd 4-year weighted moving averages are provided during 1999, 2000, and 2003–2012, as $n = 0$ in 1996, 2003, and 2008.
[e] Mulchatna herd 4-year weighted moving averages are provided during 2006–2010, as $n = 0$ in 2006.
[f] Nelchina herd 4-year weighted moving averages are provided during 2009–2013, as $n = 0$ in 2009.

especially during calving were also likely causing nutritional stress (Bergerud et al. 2008, Boertje et al. 2012). The Fortymile herd's historical abandonment and changing use of calving grounds were likely indicators of past nutritional stress (Valkenburg and Davis 1986). As of 2016, the herd had not reestablished use of the abandoned calving and summer range north of the Steese Highway (Fig. 1) that was used prior to the herd's substantial decline during the 1960s and early 1970s. We speculate that the herd may either expand onto abandoned ranges and remain at similar or increasing levels for some time, or remain on and near the current range and be near peak herd size (Boertje et al. 2012). In either scenario, eventual declines in numbers may well be related to density-dependent nutritional status during density-independent adverse weather events (Valkenburg et al. 1994, 1996, 2016; Adams et al. 2005; Bergerud et al. 2008).

In describing a sustainable herd size, stakeholders should be aware of additional potential predictors of herd decline, including the herd's elevated density, uniquely long period of herd growth, and the return to former peak numbers (Valkenburg et al. 1994, 1996). The recent density of the Fortymile herd (0.88 caribou/km^2; Boertje et al. 2012) was higher than densities in 27 of Alaska's 31 herds ($\leq$0.5 caribou/km^2; Valkenburg et al. 1996). Higher caribou densities across North America were observed only among insular or manipulated herds, or arctic herds where alternate prey were rare on the calving areas and wolves experienced endemic rabies (Bergerud 1980, Ballard et al. 1997, Bergerud et al. 2008). Also, the 1920s peak in caribou numbers in Interior Alaska was linked to a scarcity of wolves and disease epidemics that killed canids (Murie 1944, Boertje et al. 2012). Density of the Fortymile herd was similar to the Delta

herd's peak density in 1989 (0.89/km^2), when adverse weather and reduced nutritional status initiated a strong and prolonged decline in numbers and density (Boertje et al. 1996, Valkenburg et al. 2016). Hayes et al. (2003) concluded that, even with conservative harvest rates and optimal habitat, densities of 0.03–0.24 caribou/km^2 would likely be the norm in most areas of Yukon and Alaska given largely unmanipulated levels of predation. The Fortymile herd is an apparent exception.

Not considering many small herds that appeared regulated by predation, Valkenburg et al. (1996) concluded that size of caribou herds was likely to be a function of the number of caribou during the previous population low and the number of years of favorable nutrition and weather in the interim. We concur. Boertje et al. (2012) documented growth of the Fortymile herd for 37 years (1973–2010 photocensuses). We found no evidence of other herds increasing for such a long period.

The current return to former peak numbers in the 1960s should also be a consideration among those describing a sustainable herd size. Valkenburg et al. (1994) attributed the 1960s Fortymile decline from peak numbers, of approximately 50,000 caribou, to adverse weather events in combination with elevated wolf numbers; these factors have not reoccurred (Boertje et al. 2012, this study). Also the latter portion of this decline was attributed to excessive harvest, which reportedly accelerated the decline from 10,000 to 6,000 caribou. We expect harvest rates to remain near the conservative levels reported here, unless stakeholders recommend elevating harvest rates to manage increasing herd numbers for a relatively stable herd size. The current population objective for the Fortymile herd is to sustain 50,000–100,000 caribou. To our knowledge, the Nelchina herd is the only caribou herd that has been intentionally harvested at sufficiently high rates to retain herd size well below former peak size (Valkenburg 1998; Valkenburg et al. 2003, 2016; Boertje et al. 2012). The Nelchina herd declined from peak size twice before managers opted to intentionally elevate harvest to manage for relatively stable herd size. Despite relatively stable herd size, the Nelchina herd expanded its range into adjacent herd ranges, including the southeastern portion of the Fortymile herd range (Davis and Valkenburg 1991; Valkenburg et al. 1996, 2003; Boertje et al. 2012). As such, stakeholders need to acknowledge that managing the Fortymile herd for a set sustainable size or nutritional state will not necessarily restrict herd movements.

Describing adverse weather events adequate to decrease caribou nutritional status and numbers also needs to be part of describing a sustainable herd size, so declines in caribou nutritional status can be appropriately related to adverse weather when possible and not simply density-dependent resource limitation. The primary adverse weather event during this study coincided with the low parturition rates in 1993 (e.g., 44% among F 3 years of age and 68% among F $\geq$ 3 years of age; Table 1). This adverse weather event was shared by herds across North America and was linked to the short, cold summer of 1992 because of the eruption of Mount Pinatubo in the Philippines in June 1991 (Adams et al. 2005, Bergerud et al. 2008:298–299; Boertje et al. 2012). Isolated reproductive pauses, such as those that occurred in 1993, were presumably related to adverse weather and individual traits. Pauses should not be considered a mechanism that simply ensured a subsequently higher birth rate (Davis et al. 1991, Valkenburg et al. 2016, this paper). We found that pausing reproduction for a year or more provided no benefit to an individual's overall parturition rates.

Comparing results among calf mortality studies may also help stakeholders describe a sustainable herd nutritional state. Among the 4 calf mortality studies published to date, the difference in the abandonment rate is perhaps most noteworthy. The low abandonment rate by females in the Fortymile herd (0.6% of 353 calves) was similar to that observed during calf mortality studies in the smaller and more southerly Denali and Delta herds (Adams et al. 1995*b*, Valkenburg et al. 2004). In contrast, in the larger and more northerly barren-ground Porcupine herd, 13% of 210 newborn calves were abandoned by females after newborn calves were radio-collared on the herd's arctic, coastal calving ground (Whitten et al. 1992). The high abandonment rate reported among caribou in the Porcupine herd is likely related to elevated nutritional stress at calving (i.e., after enduring longer, more severe winters combined with more erratic Arctic resource limitation; Espmark 1980, Whitten 1996). Although we did not see significant levels of abandonment in the Fortymile herd, newborn weights were highly related to mortality risk, indicating the importance of monitoring newborn weights.

Selecting appropriate harvest rates is a key part of managing for sustainable herd numbers. Reductions in harvest of largely male caribou from 1% to 2% of the herd during 1990–1995 to <1% during 1996–2000 had little influence on herd growth between 1995 and 2000 (Table 6). The reduction in harvest was initiated to improve social acceptance of the controversial plan to reduce wolf numbers (Boertje and Gardner 1996). Harvests had already been intentionally held low since 1973 (1–3%) to encourage herd growth, and, after 2000, harvest continued to be restricted to $\leq$2% of the herd (Boertje et al. 2012). Male:female ratios for caribou older than calves in the Fortymile herd ($\bar{x}$ = 45 M:100 F, range = 36–59, 1994–2010; Boertje et al. 2012) were not reduced by male selective harvest compared with ratios from the only Interior Alaska herd with negligible harvest ($\bar{x}$ = 35 M:100 F, range = 29–42 in the Denali herd, 1994–2010; Adams 2011, Valkenburg et al. 2016). Bergerud and Elliott (1986) suggested that populations with high recruitment would have a more balanced sex ratio because young males typically have higher survival compared with older males. Our balanced sex ratio among radio-collared newborns through 1 year of age indicate that the skewed male:female ratio largely resulted from survival differences among older males and females. Bergerud et al. (2008) reviewed data from several studies and concluded that a nearly equal sex ratio occurred at birth, and differential high natural mortality of males occurred at

6–10 months and >7 years of age, with the least differential mortality at 3–7 years of age.

Because of fundamentally different ecology among most caribou herds (Valkenburg et al. 2016), describing a sustainable herd size will require detailed knowledge of the relevant, and perhaps unique, ecology. The 3 general ecotypes previously described for caribou herds may, in many cases, be inadequate to help describe sustainable numbers. For example, the Fortymile herd is categorized within the ill-defined Alaska ecotype, described as having substantial variation among herds, but no well-defined strategy for avoiding predation, unlike the woodland, and barren-ground ecotypes (Davis and Valkenburg 1991, Adams et al. 1995*a*, Valkenburg et al. 2016). The Alaska ecotype reportedly benefits from calving on a concentrated calving ground (Adams et al. 1995*a*), and virtually all Fortymile parturient caribou concentrated on a calving ground each year, usually at or above treeline (Boertje et al. 2012). Most of the adjacent Yukon's small herds were described as mountain variations of the woodland ecotype, distinguished by a relatively nonmigratory behavior and spacing out during calving to reduce predation, rather than calving in a concentrated manner (Bergerud et al. 1984; Bergerud and Page 1987; Farnell et al. 1996, 1998). In contrast, the barren-ground ecotype is distinguished by lengthy migrations to high-density calving areas with limited overlap with other ungulates, and thus, spacing away from predators (Bergerud and Page 1987) and with competition for high-quality summer forage potentially becoming regulatory (Mahoney and Schaefer 2002, Bergerud et al. 2008). The barren-ground Porcupine herd is a possible exception, because erratic Arctic resource limitation appeared to be a major factor limiting numbers (Whitten 1996).

Evaluation of the Wolf Control Programs

Wolf predation is a major factor limiting caribou in Interior Alaska and southern Yukon (Davis and Valkenburg 1991, Adams et al. 1995*a*, Hayes et al. 2003). Three well-documented studies exist where wolf populations were strongly suppressed and caribou harvests were largely eliminated across the entire herds' ranges, and response in caribou numbers was measured. Specifically, average spring wolf numbers were reduced 69–77% from pre-control autumn numbers for 5–7 winters followed by substantial increases in the Delta herd in central Alaska (16%/yr; Gasaway et al. 1983, Boertje et al. 1996), the Finlayson herd in east-central Yukon, Canada (18%/yr; Farnell and McDonald 1988, Larsen and Ward 1995, Farnell 2009), and the Aishihik herd in southwestern Yukon (15%/yr; Hayes et al. 2003). In these 3 programs, autumn wolf numbers were reduced an average of 55–59% from pre-control autumn numbers. All 3 herds were stable or declining prior to wolf control, with caribou harvest largely eliminated. In the Aishihik experiment, the wolf control program was partially nonlethal (i.e., sterile dominant wolves were retained in the pack territories; Hayes et al. 2003), similar to our nonlethal program.

These 3 herds inhabited smaller, more manageable ranges (17,000–20,000 km^2) compared with the Fortymile herd range (50,000 km^2), and each herd numbered only 700–2,800 caribou prior to wolf control. All 4 herds were similar in that wolf predation was a predominant cause of caribou mortality prior to wolf control, and wolves in all herds had the same alternate large prey (moose and Dall sheep [*Ovis dalli*]; Gasaway et al. 1992; Boertje and Gardner 2000*a, b*; Hayes et al. 2003). However, wolves likely had less effect on population dynamics of the Fortymile herd, given that the herd grew from 6,000 to 22,000 caribou ($\lambda_r = 1.08$, 1973–1990) without significant wolf control (Valkenburg et al. 1994). Compared to the 3 smaller herds, the Fortymile herd was also unique in having greater seasonal and year-round caribou densities, longer and less predictable caribou migration paths, and a larger proportion (83%) of habitat below treeline in the herd's annual range (Boertje et al. 2012).

Wolf populations can sustain average winter reductions of 29–77% (Adams et al. 2008, Murray et al. 2010, Gude et al. 2012). The average winter wolf reductions of <35% from pre-control autumn numbers over the Fortymile herd's range were inadequate to cause wolf densities to decline below 6–8 wolves/1,000 km^2 during most autumns in pre-control and control years. In comparison, Hayes et al. (2003) documented a wolf control program in southwest Yukon for the Aishihik caribou herd (1993–1997) where a pre-control February wolf density of 8.9 wolves/1,000 km^2 was reduced 69–83% from the pre-control density during the next 6 springs. The 6 spring wolf densities averaged 2.1 wolves/1,000 km^2 and the 5 interim winter densities averaged 3.2 wolves/1,000 km^2 prior to the respective winter's wolf removal. The Aishihik herd responded with a λ of 1.15 versus 0.98 before wolf control. In contrast, we reported λ_r of 1.07 and 1.02 during nonlethal and lethal wolf treatment periods versus 1.11 during the 3 years before wolf control.

Clearly, wolf predation was lower in this study compared to pre-control wolf predation in the 3 studies where wolf control effectively increased caribou numbers ≥15% annually (Gasaway et al. 1983, Farnell and McDonald 1988, Hayes et al. 2003). For example, caribou numbers in the Fortymile herd increased the 3 years before wolf control, and we estimated wolves killed only 10–15% of the annual starting populations of calf and older caribou before and during wolf control. Predicting how a greater degree of wolf control may influence caribou numbers in the Fortymile herd is problematic given potential complicating factors including the seasonal rate of wolf recovery, compensatory causes of caribou mortality, adverse weather, and density-dependent nutritional restriction.

The Fortymile herd grew regardless of the largely untreated levels of predation with 6–8 wolves/1,000 km^2, which included surplus killing of caribou on the calving grounds. Miller et al. (1985) described surplus killing of calf caribou after studying wolf predation strategies in the presence of large numbers of vulnerable calves. Our results were largely consistent with a published North American model that predicts caribou numbers increase with an average of <6.5

wolves/1,000 km^2 (Bergerud et al. 2008:79). However, Adams et al. (1995*a*) concluded that interactions between wolves and the Alaska caribou ecotype could not be fully described through range-wide wolf:prey ratios alone and neonatal losses to wolves were not related to wolf density. Factors that were masked or ignored at the gross numerical level included the distribution of wolves, the efficacy of wolf-evasion strategies, deaths from other factors, and effects of snow on calving dispersion and caribou condition, particularly birthweights.

Several factors reduced the effectiveness of the control programs for wolves that preyed on caribou in the Fortymile herd. First, the nonlethal program treated too few packs. Second, the effectiveness of lethal aerial wolf control was strongly reduced by unfavorable snow conditions for tracking wolves during winters 2006–2007, 2007–2008, and 2009–2010. Third, all packs using the calving and core summer range could not be controlled during either control program given protection related to the Yukon–Charley Rivers National Preserve. Fourth, as caribou numbers in the herd increased and range use expanded to new areas (Boertje et al. 2012), additional wolf packs unaffected by control programs preyed on caribou. Finally, during the nonlethal program, treating 15 wolf packs by leaving 2 sterile wolves/pack to defend territories appeared to help boost wolf numbers in adjacent untreated packs. For example, adjacent untreated wolf packs reached maximum mean numbers of 8.3–9.1 wolves/pack during early winters 1999–2004, coincidental to the 5 early winters after treating 14–15 packs (Burch 2011: figure 14). These adjacent packs were monitored and untreated during early winters 1993–2005, resided immediately adjacent to the sterilized wolves, and 6–7 of these packs with 40–61 wolves used a majority of the caribou calving and summer range (Fig. 1). We inferred that adjacent untreated packs increased as a result of less competition from the sterile wolf pairs, continued low harvest rates of wolves, and increasing caribou numbers.

Several previous authors, in advocating for nonlethal control and cooperative management planning, prematurely assumed that the nonlethal wolf control program contributed to the coincidental recovery of the Fortymile herd (Hayes et al. 2003, Gronquist et al. 2005, Farnell 2009). Other advocates of the nonlethal wolf control program may point to treated versus untreated comparisons as evidence that wolf control was effective at increasing Fortymile herd numbers (National Research Council 1997, Boertje et al. 2010). For example, λ_r in the treated Fortymile herd exceeded λ_r in 4 adjacent untreated herds, which inhabited the north slopes of the Alaska Range and numbered several hundred to several thousand caribou each (Adams 2011, Bentzen 2011, DuBois and Parker McNeill 2011, Seaton 2011). Only the Fortymile herd increased ($\lambda_r = 1.07$, 1998–2003); adjacent herds were either stable (Denali herd, $\lambda_r = 1.01$; Macomb herd, $\lambda_r = 0.99$) or declining (Delta herd, $\lambda_r = 0.92$; Chisana herd, $\lambda_r = 0.89$ for 1998–2002). Harvest rates in these adjacent herds were similar to the low rates in the Fortymile herd, except in the Denali herd, which was largely protected from hunting. However, each herd had a unique ecology, demography, and density-dependent and density-independent factors affecting abundance (Valkenburg et al. 2016).

We recognize the deficiencies in using treated versus untreated comparisons to test hypotheses on the scale of large-mammal systems (Sinclair 1991). Indeed, the circumstantial support provided above for the possible treatment effect of nonlethal wolf control was weak and misleading, because the Fortymile herd's rate of increase was also highest before nonlethal wolf control. During 1990–1995, the Fortymile herd was the only stable herd ($\lambda_r = 1.00$); all 4 adjacent herds declined substantially ($\lambda_r = 0.82$–0.93; Gardner 2001, Valkenburg et al. 2004). The adjacent herds experienced extreme weather during 1990–1995, which decreased reproduction and survival to various degrees with long-term negative consequences (Adams et al. 1995*a,* 2005; Boertje et al. 1996, 2012; Valkenburg et al. 1996, 2016). In contrast, the relatively dry, continental weather patterns in the range of the Fortymile herd presumably helped buffer against the sharp declines experienced by adjacent herds in and near the Alaska Range (Boertje et al. 2012). Given the lack of direct evidence that nonlethal wolf control increased caribou survival, we inferred that more favorable weather and inherently lower predation were likely causative factors in the improved rates of increase in the Fortymile herd relative to rates in the adjacent smaller, more sedentary herds.

The increase in year-round density of caribou in the Fortymile herd from upper, typical levels for Interior Alaska (0.40–0.53 caribou/km^2, 1980–1996) to an unusually high level for Interior Alaska (0.88 caribou/km^2, 2003–2008) also provided circumstantial evidence that predation was effectively reduced by wolf control (Boertje et al. 2012). The only other cases where Interior Alaska herds of caribou reached such high densities in recent times occurred in the Nelchina and Delta herds (Davis and Valkenburg 1991, Valkenburg et al. 1996), where substantial reductions in wolf numbers were documented (Ballard et al. 1987, Boertje et al. 1996). However, given the lack of direct evidence that wolf control increased caribou survival or recruitment, any effect of wolf control on herd numbers was likely negligible.

We concluded that too few wolves were affected by nonlethal and lethal control over the herd's summer and annual ranges to elicit a measurable response in the herd. We documented that wolves were the primary predator before and during nonlethal wolf control. We verified that nonlethal wolf control using translocation and fertility control can reduce local wolf numbers substantially, and that the effects of such a control program on individual packs can endure for $\geq$3 years following cessation of wolf sterilization and translocation. We inferred that a nonlethal wolf control program, restricted to affecting 15 wolf packs, would be more suited to annual caribou ranges of $\leq$20,000 km^2 (Hayes et al. 2003, Clout and Russell 2007).

MANAGEMENT IMPLICATIONS

Where a high-density, increasing caribou herd is intensively managed via predator control for elevated sustained yield and

is accessible to adequate numbers of hunters, managers need to be prepared to substantially increase harvest to curtail herd growth as the herd approaches carrying capacity. The importance of linking increasing herbivore numbers with declining herbivore nutritional status should not be underestimated. For this purpose, we recommend continued monitoring of trends in the reproductive rates of young female caribou, October calf weights, and birthweights (inversely related to mortality rates). These data will be essential if managers are to convince stakeholders and policymakers that increased harvest is timely and prudent. When ungulates overshoot carrying capacity, the effects of high density, adverse weather, and increased predation can have synergistic negative effects on prey numbers and long-lasting negative effects on sustainable yields, contrary to the intended purpose of wolf control programs.

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